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Fishery Bulletin

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(Continued on back cover)

Seattle, Washington

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Fishery Bulletin

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Notes

AWARD
AWARD

Best NMFS publications for 1981

The Publications Advisory Committee of the National Marine Fisheries Service has announced the best publications authored by the NMFS scientists and published in the *Fishery Bulletin* and the *Marine Fisheries Review* for 1981. Only effective and interpretive articles which significantly contribute to the understanding and knowledge of NMFS mission-related studies are eligible, and the following papers have met this requirement.

For the *Fishery Bulletin*, the paper "The spawning energetics of female northern anchovy, *Engraulis mordax*" by J. Roe Hunter and Roderick Leong was awarded as the best publication, appearing in the *Fishery Bulletin* 79(2): 215-230. Hunter and Leong are both fishery biologists with the Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, La Jolla, Calif.

For the *Marine Fisheries Review*, the paper "Low temperature preservation of seafoods: A review" by Louis J. Ronsivalli and Daniel W. Baker II was awarded the best publication, appearing in the *Marine Fisheries Review* 43(4):1-15. Ronsivalli, now retired, was the former Director of the Northeast Fisheries Center Gloucester Laboratory, NMFS, NOAA, Gloucester, Mass.; Baker is a mechanical engineering technician with the same laboratory.

CHANGES IN SIZE OF THREE DOLPHIN (*STENELLA* SPP.) POPULATIONS IN THE EASTERN TROPICAL PACIFIC

TIM D. SMITH[1]

ABSTRACT

Dolphins from three populations, one of *Stenella attenuata* and two of *S. longirostris*, have been killed incidentally in the yellowfin tuna purse seine fishery in the eastern tropical Pacific, two populations since about 1959 and the other since about 1969. Size changes in these populations are estimated from numbers killed each year, population size estimates in 1979, and net recruitment rates. Ranges of values for some parameters are considered, accounting for some uncertainties. Assuming central values of the ranges of maximum net recruitment rate (3%) and the population level giving maximum net productivity (65%), one *S. longirostris* population, the eastern spinner dolphin, is near 20% of pre-exploitation levels; the *S. attenuata* population, the northern offshore spotted dolphin, is between 35 and 50%; and the second *S. longirostris* population, the whitebelly spinner dolphin, is between 58 and 72% of pre-exploitation levels.

Purse seine fishing for tuna in the eastern tropical Pacific often involves dolphins found in association with yellowfin tuna. Tuna fishermen pursue and capture the dolphin-yellowfin tuna complex, releasing the dolphins from the net while retaining the tuna (Green et al. 1971). Mortality of dolphins occurs incidental to this fishing process.

Purse seine fishermen were using dolphin schools to catch tuna by 1959; there is anecdotal information suggesting limited use as early as the 1940's (anonymous reviewer). Starting in the mid-1960's the Bureau of Commercial Fisheries, predecessor of the National Marine Fisheries Service (NMFS), conducted limited research to document the situation and to collect data on numbers and kinds of dolphins killed. This research expanded in the 1970's, especially after passage of the Marine Mammal Protection Act (MMPA) of the United States in 1972, and continues. Substantial research efforts were mounted to assess the status of the dolphin stocks and to develop procedures for reducing incidental mortality and injury.

Two assessments of the condition of dolphin populations involved in the yellowfin tuna purse seine fishery have been completed in recent years.[2,3] I describe the results of the latest assessment of the three populations most affected by the fishery; calculation of population sizes from 1959 through 1978 is emphasized, based on estimates of the population size in 1979, on annual numbers killed from 1959 through 1978, and on net recruitment rates. These results, based on data available through the end of 1980, do not necessarily represent NMFS policy, which involves additional considerations. A third assessment of these populations is scheduled for 1984 and will include information since 1980.

POPULATION MODEL

Methods developed in 1976 (footnote 2) for estimating pre-exploitation abundance are based on a simple recursive relationship

$$N_{t+1} = N_t - K_t + R_t\,(N_t - \tfrac{1}{2}\,K_t),$$

where t denotes the year; N, the abundance; K, the number of animals killed; and R, the net recruitment rate. This model assumes that the population size in the next year is simply the present population size, minus the present incidental kill, plus the net number of individuals recruited to the population during the year. This latter quantity is taken to be the net recruitment

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[2]Southwest Fisheries Center La Jolla Laboratory. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-76-29, 53 p.

[3]Smith, T. D. (editor). 1979. Report of the workshop on status of porpoise stocks, La Jolla, Calif., 27-31 August 1979. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-70-41, 120 p.

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rate (birth rate less natural death rate) multiplied by the number of animals actually reproducing in a given year. The number of reproducing animals is approximated by assuming that one-half the animals killed in a year reproduce before dying. Solving this relationship for N_t, one obtains

$$N_t = \frac{N_{t+1} + \frac{1}{2}K_t}{1 + R_t} + \frac{1}{2}K_t. \quad (1)$$

Repeatedly applying this equation to estimate the population size for any number of years (s) prior to the year (c) for which an independent estimate of population size (N_c) is available yields in general

$$N_s = \frac{N_c}{\prod_{i=1}^{s}\left(1 + R_i\right)} + \sum_{j=1}^{s} \frac{K_j\left(1 + \frac{1}{2}R_j\right)}{\prod_{i=j}^{s}\left(1 + R_i\right)}. \quad (2)$$

The 1979 workshop (footnote 3) extended this procedure by calculating the recruitment rate R_i, i years prior to the present, using the density-dependent relationship (Allen 1981)

$$R_i = R_m\left\{1 - \left(\frac{N_i}{N_p}\right)^z\right\}. \quad (3)$$

N_p is the estimated population size at the beginning of the first year of exploitation, p years earlier; R_m, the maximum net recruitment rate; Z, the density-dependent exponent; and N_i and N_p, estimated from Equation (2). Because N_p in Equation (3) is not known until the series in Equation (2) has been calculated, an iterative procedure is required to solve the equations for historical population size. Equations (1) and (3) together form a special case of the generalized production model of Pella and Tomlinson (1969).

In Equation (3) the net recruitment rate is maximum (R_m) when the population size approaches zero, decreasing to zero as the population size approaches N_p. Z determines the population size at which the rate of change of the population is maximum, the maximum net productivity level (*MNPL*). The values of Z correspond to the *MNPL* approximately as (Polacheck 1982)

$$MNPL = \frac{N_p}{\left(1 + Z\right)^{1/Z}}. \quad (4)$$

If $Z = 1$, then the *MNPL* is one-half the equilibrium population size; if Z is >1, then *MNPL* is greater than one-half the equilibrium size. The fraction of the maximum reproductive rate, R_m, realized at a given population size, increases as the value of Z increases.

Statistical properties of the estimate of N_p and the ratio N_c/N_p are examined in detail in Smith and Polacheck (1979), wherein methods are developed for calculating the variances. Tests of sensitivity of the estimates of N_p to the values N_c, K_t, and R_m show that the estimates are most sensitive to the value of present abundance and least sensitive to the net recruitment rate. Examination via simulation of the shape of the sampling distribution shows that if N has a symmetrical sampling distribution, then so does the estimate N_p.

Several estimates of each parameter required by the model are available in working documents and technical memoranda prepared by the staff of the Southwest Fisheries Center. I rely on the most current estimates, primarily minor revisions of those used by the 1979 workshop, with reference to papers describing earlier estimates as needed to document methods.

POPULATIONS

Populations affected most by the yellowfin tuna purse seine fishery are of the genus *Stenella*, and are found in the area from just south of the Equator to an approximate lat. 20°N and west from the Mexican and Central American coasts to an approximate long. 150°W. Two populations of spotted dolphins, *S. attenuata*, and three populations of spinner dolphins, *S. longirostris*, are found in this region.

The two spotted dolphin populations are referred to as "offshore" and "coastal" forms. The coastal spotted dolphin population occurs nearshore and around islands, while the offshore spotted dolphin ranges from nearshore to an approximate long. 150°W. The two forms overlap in range near the coast.

Perrin (1975) distinguished these two forms of *S. attenuata* morphologically. He noted that 1) the larger coastal form occurs seaward to 50 km while the offshore form occurs as nearshore as 20 km, and 2) the coastal form was involved in only 7 of 1,373 purse seine sets on dolphins observed between 1971 and 1974. Additional data collected since then, including reexamination of specimens collected during sets in the years 1971-74,

indicate that through 1978, a total of 22 sets have been observed on coastal spotted dolphins, out of a total 9,672 observed overall (about 0.2%).

The yellowfin tuna purse seine fishery was concentrated nearshore in the early 1960's, and many sets were made in the area probably occupied by both coastal and offshore spotted dolphins. Direct observations in the 1960's distinguishing these forms of the spotted dolphin are not available. Based on observations made in the 1970's where these forms were distinguished, however, it appears that the coastal form has never been significantly involved in this fishery. Since 1978, sighting data collected by scientific observers aboard tuna vessels have been edited, using consistent criteria of school size, body size, and coloration for distinguishing coastal and offshore spotted dolphins. In 1979, for example, within about 50 km of the coast there were 46 sightings of coastal spotted schools, 160 sightings of offshore spotted schools, and 25 sightings of spotted dolphin schools which could not be distinguished to form with the available data. These three school types were subsequently set on in 2, 73, and 6 instances, respectively. Even assuming that all schools not identified to form were coastal spotted dolphins, the proportion of sighted coastal spotted dolphin schools subsequently set on is much smaller than that of the offshore form (0.11 vs. 0.46, $P<0.001$). This differential selection exists even though the catch of yellowfin tuna in sets on coastal spotted dolphins has been approximately twice that on offshore spotted dolphins. If coastal spotted dolphins were a significant part of this fishery, one would expect their involvement in sets to be proportional to the rate at which they are encountered.

In addition, 18 of the 22 sets on coastal spotted dolphins occurred in 1973, and, except for one set, these were made by two vessels in the Gulf of Nicoya, a small area off the Costa Rican coast. Based on this information, I have assumed that the coastal spotted dolphin has been involved only rarely in this fishery.

Two spinner dolphin populations, referred to as the "eastern" and "whitebelly" forms, are involved in the yellowfin tuna purse seine fishery. A third form, termed the Costa Rican spinner, occurs near the coast from Mexico to Panama, but is not involved in the fishery. The eastern and whitebelly forms overlap broadly in range, with the whitebelly spinner dolphin generally occurring more seaward. The eastern form has been involved with this fishery since 1959, whereas the whitebelly spinner dolphin population apparently became increasingly involved as the fishery expanded seaward in the 1960's.

The whitebelly spinner and the offshore spotted forms have Southern Hemisphere populations (Perrin et al. 1979). These populations have been involved only recently with the yellowfin tuna purse seine fishery, as it has expanded southward, and are only lightly exploited. Data on reproductive condition of these southern populations are used as estimates of reproductive rates for unexploited or equilibrium populations.

1979 POPULATION SIZE ESTIMATES

Holt and Powers (1982) gave estimates of abundance based on aerial and research-vessel sighting surveys and data from scientific observers aboard fishing vessels. Estimates of the size, N_i, of the ith population in their survey area are based on the equation

$$N_i = P_t \; S_t \; D \; P_i \; A, \tag{5}$$

where P_t denotes the proportion of dolphin schools containing dolphin of the genera *Stenella*, *Delphinus*, and *Lagenodelphis*; S_t, the mean size of these schools; D, the estimated density of all dolphin schools sighted; P_i, the fraction of schools containing dolphins of the ith population; and A, the area inhabited. This equation is applied to 1) a nearshore stratum, surveyed using both an airplane and research vessels, and 2) an offshore stratum, surveyed only by research vessels. The nearshore stratum extends seaward from the coastline about 800 km, and from lat. 22°N to 12°S. The offshore stratum extends from the outer edge of the nearshore stratum to the boundary of the dolphin range.

Approximate areas of the maximum historical range of the three dolphin populations are used for the area inhabited, A in Equation (5). These are estimates of the area enclosed by a smooth curve which includes most locations where dolphins of different species have been reported by both fishing vessels and research vessels, as described in Holt and Powers (1982).

While occasional sightings of dolphin schools have been reported outside these areas, the areas are overestimated in that "...at any point in time it is likely that each of the various dolphin species

only occupies a portion of its historical range."[4] Overlap between coastal and offshore forms of spotted dolphin is not reflected in the population estimates given by Holt and Powers (1982). Due to the large differences in areas inhabited, however, adjustments to account for the unknown degree of overlap would increase the offshore spotted dolphin population estimate by 3% at most, which is insignificant for the general results being presented here.

The density estimate for the nearshore area is obtained from line transect theory applied to aerial survey sighting data. This follows earlier applications (Smith 1981), but with several improvements. For instance, the aircraft we used had superior downward visibility; right-angle distance from the aircraft trackline to the sighted dolphin schools was determined directly, either by electronic navigation equipment or visually for shorter distances, rather than being calculated from visual estimates of range and bearing; and the originally used negative-exponential sighting model was replaced with the superior Fourier series model (Burnham et al. 1980). The density estimate for the offshore area, which could not be surveyed by air, is obtained by comparing relative dolphin school sighting rates from research vessel surveys in nearshore and offshore areas with absolute density estimates from the nearshore area. The resulting density estimate of all dolphin schools of >15 animals in the nearshore area is about 3.6 schools/1,000 km^2, while the density estimate in the offshore area is about one-half that value.

The school size estimate is about 200 animals, based on visual estimates of the size of schools seen during the aerial survey. The accuracy of these visual estimates has been confirmed by counts of individual dolphins from aerial photographs, and the accuracy of the counts from these photographs has been confirmed by counts of dolphins released from a purse seine (Allen et al. 1980). This estimated school size also includes an adjustment for the tendency of larger schools to be more readily visible at greater distances from the aircraft, and hence to be overrepresented in the sample.

Allen et al. (1980) also demonstrated that accurate school size estimates could be made from ships. Although not used by Holt and Powers (1982), the mean school size estimated from research vessel sighting data was about 180, not significantly different from the value derived from aerial data described above. In contrast, the mean school size estimated from tuna vessel sighting data collected by scientific technicians was about 580, significantly higher ($P<0.001$) than the other two values. This difference implies either nonrandomness of the sample of dolphin schools encountered by the tuna vessels, or biases in the estimation techniques used by the technicians.

P_i for each of the 22 populations involved in the yellowfin tuna purse seine fishery can be estimated from data collected aboard either tuna vessels or research vessels. Fishing vessels encounter significantly more schools composed primarily of spotted and spinner dolphins than do research vessels. The reason for this difference is not known, but it is possible that fishing vessels encounter spotted and spinner dolpin schools more frequently than would be expected under random search because they are searching for tuna, which occur with these two schools more frequently than with other species of dolphins. Studies of the searching process of tuna fishing vessels are being conducted which should help resolve this question. Because the proportions P_i are different for unknown reasons, Holt and Powers (1982) gave several sets of estimates of total abundance, depending on the estimates of P_i from different combinations of the research vessel and tuna vessel data. Two sets of estimates are considered here (Table 1), one using research vessel data alone and the other using combined tuna vessel and research vessel data.

Aerial survey procedures used in the present population-size estimates are still being refined. For instance, a field study was completed in mid-

TABLE 1.—Population size estimates (thousands) at the beginning of 1979 for three populations of dolphins in the eastern tropical Pacific, using estimates of the species mix from research vessel data alone, and from combined tuna vessel data and research vessel data, with standard deviations in parentheses (Holt and Powers 1982).

Population	Research vessel data only	Fishing and research vessel data
Offshore spotted	1,682.0 (471.8)	2,775.0 (761.4)
Eastern spinner	292.7 (71.0)	292.9 (64.4)
Whitebelly spinner	216.0 (67.4)	380.4 (134.9)

[4]Hammond, P. S. (editor). 1981. Report of the Workshop on Tuna-Dolphin Interactions, Managua, Nicaragua, April 1981, p. 5. IATTC Spec. Rep. 4, Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093.

1980 to determine the effect of sea state and sun position on the visibility of dolphin schools directly on the trackline. Data from this experiment, which have not yet been completely analyzed, will be of use in the design of future surveys and in the evaluation of earlier surveys.

INCIDENTAL KILL ESTIMATES

Incidental kill (K_t) of dolphins in year t is estimated by multiplying the mean kill of dolphins per set in year t (KPS_t) by the total number of net sets involving dolphins made by the tuna fleet in year t ($NSETS_t$), as

$$K_t = KPS_t \; NSETS_t. \tag{6}$$

These estimates are obtained for each year with the data stratified by vessel fish-carrying capacity, amount of tuna caught in the net set, and geographic location of the set, following the general approach described by Lo et al. (1982).

Kill rate information is available from a limited set of tuna fishing trips in the 1960's and from a more extensive set in the 1970's collected by scientific observers placed aboard a large proportion of the U.S. fishing vessels. To illustrate the data, some mean kill rates, stratified by amount of tuna caught, are shown in Table 2. Higher kill rates are apparent in successful (>¼ ton tuna caught) than in unsuccessful (<¼ ton tuna caught) sets, as are marked declines in kill rates over time. Numbers of dolphin sets and fishing trips on which observations of numbers of dolphins killed were made are shown in Table 3.

Observations of the numbers of dolphins killed in the 1960's were made by both the crew and the scientists. Although few observations were made, there is no consistent difference between kill rates reported by both types of observers (59 and 52, respectively); this suggests the presence of a noncrew-member observer had no significant effect on the kill rate of dolphins in the 1960's.

All data on kill rates of dolphins for the period 1971-78 were collected by noncrew-member scientists, precluding a direct comparison of kill rates between fishing trips with (observed) and without (unobserved) scientific observers for this period. Croom,[5] however, reported dolphin kill rates on a fishing trip in 1979 with no scientific observer on board; his kill rates were about 4 times higher than the average rate in 1979 for scientist-observed trips and were approximately 20 times higher than on previous and succeeding observed fishing trips by the same vessel and captain. This difference in mean kill rates was due to the significantly lower proportion of sets with few dolphins killed on Croom's trip than on the scientist-observed trips. For instance, the proportion of sets with zero dolphins killed was 0.23 on Croom's trip with 0.76 for observed trips.

Although limited information is available, it appears that kill rates on some unobserved vessels were higher in the late 1970's, and that this could result in the observed kill rates being lower than the actual rates. If there has been an "observer effect," it most likely occurred in the late 1970's, because regulations were adopted in the United States in 1976 requiring the use of certain dolphin-release procedures, and because scientific observers were then used to collect regulation compliance information. If kill estimates for the last few years were revised with this in mind, it would only slightly affect the calculations presented here, since the large number of animals killed through 1975 tends to dominate in Equation (2). However, such revisions to the kill estimates could markedly change our perception of the current rate of change of these populations.

In addition to the known direct kill of dolphins in the fishery, research has been conducted to estimate both the number of dolphins injured and released alive from the purse seines, and the possible number of dolphins which, while not exhibiting injuries, die or suffer reduced viability from stress of capture and handling in the purse seining operation. Observations of the number of injured dolphins have been made aboard tuna vessels since 1975; estimates of the number in-

TABLE 2.—Observed mean kill of dolphins per net set (KPS) by U.S. tuna purse seiners 1964-78, for successful and unsuccessful net sets, with sample sizes (N), from NMFS records.

	Successful sets (>¼ t tuna)		Unsuccessful sets (<¼ t tuna)	
Year	KPS	N	KPS	N
1964-72	55.7	343	7.9	25
1973	22.6	576	0.6	130
1974	15.7	753	2.4	261
1975	18.9	778	2.5	169
1976	16.1	627	5.7	126
1977	3.4	2,706	0.9	495
1978	4.2	1,434	3.9	249

[5]Croom, M. M. 1980. The tuna-porpoise problem: Management aspects of a fishery. M.S. Internship Rep., Marine Resour. Manage. Program, Oreg. State Univ., Corvallis, 41 p.

jured fluctuate around 4.8% of the number killed directly, ranging from 3 to 7%. The problem of stress-induced mortality or debility was explored in a workshop of experts on large mammal physiology and pathology, and research plans to approach this problem were developed.[6] Subsequently one aspect of this problem was examined with dolphin specimens collected aboard tuna vessels.[7] Reproductive tracts were examined for evidence of spontaneous abortion, and muscle tissue for myopathy; no evidence of either was found. No estimates of the magnitude of such effects have been made, and currently no research is underway to investigate stress-induced mortality. As a conservative measure, given our limited knowledge, I assume in the estimates of total dolphin mortality given here that all of the injured dolphins subsequently die of their injuries. Thus estimates of total kill of dolphins are the sum of the estimated numbers killed directly and the numbers injured.

Numbers of net sets made by the tuna purse seine fleet have been recorded by the Inter-American Tropical Tuna Commission (IATTC) from logbooks kept by the fishermen (Table 3). In the logbooks the type of each net set may be recorded, along with tuna catch, location, and other information. The three major types of sets are 1) those known to involve dolphins, 2) those known not to involve dolphins, and 3) those for which the data indicate neither the presence nor absence of dolphins. Types of sets not involving dolphins include "floating object sets" (e.g., a rope, board, log, etc.), a "school fish set" (i.e., a net set on tuna sighted at or near the surface), and a "porpoise set." The logbook data are incomplete, however, because some members of the fleet do not report and because, in some cases, only limited information was recorded by the fishermen. The logbook coverage rate, however, is high.

The data in columns *D*, *N*, and *U* in Table 3 have only recently become available, and analyses are proceeding to use this information directly to estimate the total number of sets made on dolphins. Preliminary results for the total numbers of sets for each year[8] are similar to those given in column *E* of Table 3, but the results are not yet available in the stratified form needed to estimate numbers killed, described below. Earlier estimates of the total number of sets made on dolphins (column *U* of Table 3) were obtained indirectly for the years prior to 1970, based on the catches of tuna, and include an adjustment for nonreported sets.

TABLE 3.—Number of tuna purse seine sets, 1959-78, (*D*) known to have been made on dolphins in the eastern tropical Pacific, (*N*) known not to have been made on dolphins, and (*U*) unknown if made on dolphins (IATTC text footnote 8), with (*E*) estimates of the total number of sets made on dolphins (Smith text footnote 3). Also shown are the numbers of observed fishing trips and purse seine sets on porpoise from NMFS records.

Year	Sets made				Sets observed	Trips observed
	D	*N*	*U*	*E*		
1959	132	759	2,985	1,037	0	0
1960	1,644	1,256	7,390	5,696	0	0
1961	3,617	3,825	8,694	8,247	0	0
1962	2,886	8,830	4,337	4,060	0	0
1963	3,290	9,266	6,322	4,687	0	0
1964	5,933	7,681	4,745	8,090	67	2
1965	6,172	7,176	5,631	7,981	0	0
1966	5,443	7,001	5,247	7,250	28	1
1967	3,510	10,018	3,594	4,478	0	0
1968	3,833	8,988	1,642	4,271	15	1
1969	7,664	6,552	2,055	8,678	0	0
1970	7,912	9,692	1,664	8,552	0	0
1971	4,816	10,728	3,404	5,039	78	5
1972	8,193	4,682	3,514	9,036	272	12
1973	8,686	9,463	3,672	9,998	752	22
1974	7,955	11,669	4,835	8,539	1,120	36
1975	8,172	13,396	4,902	8,951	1,049	31
1976	7,481	17,789	5,184	7,910	1,295	45
1977	7,485	15,005	7,643	9,757	3,335	94
1978	5,174	21,527	5,639	5,910	1,771	102

For the Period 1959-72

Estimating the annual rate of dolphin kill during the period 1959-72 is difficult because observations were few, especially in the early part of the period; consequently, extrapolation of information on kill rates is necessary. One effect on rate of kill is the development and improvement of the "backdown" dolphin-release procedure (Coe and Sousa 1972; Barham et al. 1977), by which the vessel moves in reverse during a short portion of the purse seine retrieval, thereby pulling the net out from under the dolphins. Barham et al. (1977) reported that the "backdown" dolphin-release procedure was developed aboard one vessel in 1959 and 1960, and transferred to a second vessel in 1961. Subsequently, the use of the procedure expanded rapidly within the fleet, although

[6]Stuntz, W. E., and T. B. Shay. 1979. Report on capture stress workshop, La Jolla, California, May 1979. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-28, 24 p.

[7]Cowan, D., and W. Walker. 1979. Disease factors in *Stenella attenuata* and *Stenella longirostris* taken in the eastern tropical Pacific yellowfin tuna purse seine fishery. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-32, 21 p.

[8]Inter-American Tropical Tuna Commission. 1981. Tuna-dolphin investigations. Background paper 6, prepared for the 39th meeting of the IATTC, Paris, October 1981. Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093, 17 p.

full use was not evident even by 1964. Comparing kill rates with and without "backdown" is complicated however, because the effectiveness of the release procedure has increased over time.

No information is available on kill rates from non-U.S. vessels during 1959-72, but the non-U.S. fleet was small. There is little reason to suspect that these kill rates were different, because fishermen of both fleets were still learning how to use purse seine gear for catching tuna in association with dolphins and how to release the caught dolphins.

The available kill rate data for this period were stratified, for use in Equation (6), by amount of tuna caught, size of the vessel, and frequency of use of the "backdown" procedure. The data were pooled across the years 1964-72 and extrapolated back to the years 1959-63 when no kill rate data were collected. These stratified kill rates were multiplied by the number of sets made on dolphins in each stratum to estimate the total number of dolphins, of all populations, killed directly in this fishery.

Estimating proportions of the total kill of dolphins from each population for this period is difficult because the yellowfin tuna purse seining was expanding westward and because data on the species of dolphins observed killed are available only for 1971 and 1972. Prior to 1969 this fishery operated shoreward of the range of the whitebelly spinner dolphin, primarily within the range of the eastern spinner and offshore spotted dolphins. The total kill estimates are prorated to population for the years 1959-72, based on observed proportions in the 1971-72 data of 70, 23, and 3% for offshore spotted, eastern spinner, and whitebelly spinner dolphins, respectively. The other 4% consisted of several species, primarily common dolphins, *Delphinus delphis*, which are not considered in this study. Although the tuna purse seine fishery was expanding seaward throughout the 1960's toward the range of the whitebelly spinner dolphin, a major seaward shift occurred in 1969. Lacking detailed data, I assume this year to be the first significant involvement of the whitebelly population.

Some additional data on the species of dolphins involved in each set has recently become available from the IATTC, suggesting a declining proportion of sets involving spinner dolphins and an increasing proportion involving spotted dolphins throughout the 1960's. Preliminary examination of these data indicates that the overall proportions of sets involving each species are not greatly different from the 1971-72 observer data. Direct use of these new data will involve making a number of assumptions about species-specific kill rates.

Using the above proportions based on the 1971-72 data and increasing the estimates of total number killed by 4.8% to account for those dolphins possibly dying of injuries, I estimated the total numbers of dolphins killed, by population (Table 4). These are revisions of estimates used by the 1979 workshop (footnote 3).

TABLE 4.—Estimates of numbers (in thousands) of dolphins killed by all fleets in the eastern tropical Pacific, 1959-78, for three populations of dolphins (Smith text footnote 3).

Year	Offshore spotted	Eastern spinner	Whitebelly spinner
1959	71	27	0
1960	357	133	0
1961	402	150	0
1962	167	62	0
1963	183	69	0
1964	306	115	0
1965	337	126	0
1966	306	115	0
1967	206	77	0
1968	178	67	0
1969	365	122	15
1970	355	118	14
1971	176	59	7
1972	288	96	12
1973	131	32	33
1974	95	26	47
1975	105	45	34
1976	47	9	20
1977	22	5	5
1978	19	2	4

For the Period 1973-80

Substantially more data exist on kill rates for the period 1973-78 than for the period 1959-72. The 1973-78 data are more reliable because they were collected by NMFS employees trained specifically for obtaining kill information. Starting in 1974 fishing trips were randomly selected for observation to obtain a representative sample. Greater cooperation by the fishing fleet resulted in an increasing proportion of selected trips actually observed from 1974 to 1976. However, it was not until 1976 that fishing trips begun after July were sampled. In the early 1970's fishing tended to occur farther offshore later in the year; because kill rates are generally higher in the offshore areas, the failure to collect data from late-season trips probably resulted in an underestimate of actual dolphin kill rates in those years. This problem is partially accounted for by stratifying the data by area. The species composi-

tion of the kill was also recorded, allowing direct estimates of total kill of dolphins, from Equation (6), for each population.

The number of dolphins killed per set from 1973 to 1976 for successful and unsuccessful sets was about 18 and 3, respectively, a decrease from the 1964-72 levels of 56 and 8. The number killed in successful and unsuccessful sets in 1977 and 1978 was again lower, about 4 and 2, respectively (Table 2). These decreases occurred as U.S. regulations were developed and eventually implemented, and as methods for more effective use of backdown and other dolphin-release procedures were developed and used. The decreases in kill rates were apparently due, at least in part, to wider adoption of procedures for dolphin release.

The non-U.S. tuna purse seine fleet increased markedly during this period. First observations of the kill rate for this fleet were in 1979, which showed that the rate was very similar to that of the U.S. fleet (Allen and Goldsmith 1981). Given this similarity in 1979, it is reasonable to assume that during the earlier part of the 1970's the non-U.S. kill rate declined, as did the U.S. kill rate (Table 2), as dolphin-release technology developed by the U.S. fleet became known. If such a decline in the non-U.S. kill rate occurred, however, it would probably have been somewhat slower than that for the U.S. fleet, because of lack of legal pressure to reduce the incidental kill and time lags in technology transfer. Following the procedure developed by the 1979 workshop (footnote 3), I estimated the non-U.S. kill by assuming 1) the same kill rate in 1971-72 for the non-U.S. fleet as that observed aboard U.S. vessels in those years; 2) the same kill rate in 1973 for the non-U.S. fleet as that of the U.S. fleet in 1975; and 3) a linear convergence of the two rates toward the 1979 U.S. rate. Estimates of numbers of dolphins killed by non-U.S. vessels obtained under these assumptions are used here. However, additional study is needed, especially since the recorded kill rate for the non-U.S. fleet in 1980 was somewhat higher than that for the U.S. fleet (Allen and Goldsmith 1982).

These kill rates, stratified by vessel size, amount of tuna caught, and area fished, are used in Equation (6), along with the estimated number of sets on dolphins, to estimate total direct kill by population for each year. These estimates are then increased by 4.8% to account for dolphins assumed to die of their injuries (Table 4). The results in Table 4 are slight revisions of the estimates used by the 1979 workshop (footnote 3).

NET RECRUITMENT RATE ESTIMATES

Maximum net recruitment rate (R_m) is required to estimate historical abundance. This is calculated as the difference between gross production of calves and the natural mortality rate, assuming that natural mortality does not change, when a population is reduced substantially below its equilibrium level.

Gross Reproductive Rates

Gross recruitment rates can be estimated as the product of the female fraction of the population, the mature female fraction, and the annual pregnancy rates. Estimates of these parameters are given in Table 5, based on samples of dolphins collected by scientific observers aboard tuna vessels from 1973 to 1978. Two methods were used to estimate the annual pregnancy rate: The first method (I) is the observed proportion of pregnant females in the population divided by the gestation period; the second method (II) is similar, but uses additional information on frequency of nursing calves in the samples from each net set (Perrin et al. 1977a, b, c).

There are known sampling biases in these data for spotted dolphin because of the fishing process, partly accounted for by using data for spotted dolphin recruitment rates from only those sets where more than 40 dolphins were killed. In addition, the observed fraction of the mature, pregnant female dolphins has varied among years, with a general decline in offshore spotted dolphin and a large degree of variability in eastern spinner dolphin.

Age-specific effects are not accounted for in the analyses so far, however, particularly the

TABLE 5.—Proportion of sampled dolphins (female and mature) of three populations and estimates of annual pregnancy rate (P) and gross reproductive rate (G), using two methods.[1] See text for details.

			Annual production			
	Proportion		Method I		Method II	
Population	Female	Mature	P	G	P	G
Offshore spotted	0.56	0.56	0.38	0.119	0.32	0.100
Eastern spinner	0.51	0.43	0.34	0.075	0.45	0.099
Whitebelly spinner	0.51	0.52	0.36	0.096	0.33	0.088

[1]Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rates of gross annual production in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-1978. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-80-02, 51 p.

lower pregnancy rate that probably occurs in older animals. New methods are being developed for age determination, and an effort is being made to apply these methods to age the samples of dolphins. With accurate data on age of animals, a more detailed examination of sampling biases will be undertaken.

Natural Mortality Rates

No direct estimates of natural mortality rates exist for the eastern Pacific dolphin populations, as might be obtained from tagging data or from a sampled age structure. Ohsumi (1979) presented a statistical relationship between natural mortality rate and body length for cetaceans, from which can be derived an annual, natural mortality rate of around 0.14 for the eastern Pacific dolphin populations. However, this estimate is obtained by extrapolating the relationship outside the range of his data, and consequently is unreliable.

Another method of estimating natural mortality rate is from information on gross reproductive rate for a population in equilibrium with its environment, assuming natural mortality does not change with population size. This approach was used in the 1976 workshop (footnote 2). An estimate of gross reproductive rate of 0.09 (Kasuya et al. 1974) for a population off Japan, thought to be lightly exploited, was used as the natural mortality rate estimate for the eastern tropical Pacific populations. It now appears that the population off Japan had, in fact, been exploited to a greater degree than was thought, and that there is segregation of prepubertal dolphins into separate schools (footnote 3, p. 41). The assumption, consequently, of a natural mortality rate of 0.09 is probably not valid.

In the 1979 workshop (footnote 3), estimates of the gross reproductive rate of lightly exploited Southern Hemisphere populations of spotted and spinner dolphins in the eastern tropical Pacific were used as estimates of natural mortality rates. These rates were 0.098 and 0.067 for spotted and spinner dolphins, respectively.

Net Rates

Net recruitment rates for the offshore spotted, eastern spinner, and whitebelly spinner dolphin populations can be estimated as the differences between the gross reproductive rate estimates, listed in Table 5, and the corresponding natural mortality rate estimates given above. Using method I estimates of pregnancy rates, one obtains estimated net reproductive rates of 0.021, 0.008, and 0.029 for these three populations, respectively. Using method II estimates of pregnancy rates, one obtains estimates of 0.002, 0.032, and 0.021, respectively. These highly variable estimates are unsatisfactory, because they are based on data with known sample biases, and they differ among populations in unexpected ways. In particular, it is not expected that the net reproductive rate of the whitebelly spinner dolphin, which has been relatively less exploited, should be higher than that of the more heavily exploited eastern spinner dolphin population.

Due to these uncertainties, specific point estimates were not obtained by the 1979 workshop participants. Rather, a range of values from 0.0 to 0.04 were considered equally likely, given the available information. The lower value of 0.0 was selected by the 1979 workshop to reflect uncertainties about unexpected changes in some reproductive rates, and the small magnitude of the estimates of net reproductive rates. This range compares with the estimates from the 1976 workshop of 0.02-0.06, with a midpoint estimate of 0.04. Although higher rates of increase of cetacean populations have been reported, contrary to the conclusions in the 1979 workshop report, there are no reliable estimates of rates of increase for dolphin populations which can be used with confidence. Pending better information, the range of estimates considered in the two workshops will be used here, recognizing that higher rates may be possible.

Rate Dependent on Population Size

The evidence on which to base an estimate of the value of Z in Equation (3) for dolphin populations is limited. Fowler (1981) argued that for large, long-lived mammals, Z is greater than unity. He based this conclusion on a review of empirical data, primarily from terrestrial populations, and on an analysis of the demographic constraints which come with long life and extended parental care. McCullough (footnote 3, p. 8) gave preliminary estimates of maximum net productivity level ($MNPL$), and hence Z, for four large terrestrial mammal populations. His estimates agree with Fowler's conclusions that Z is greater than unity, and that later reproducing animals would have higher values of Z.

The 1976 workshop (footnote 2) concluded that the available information implies $MNPL$ is within the range of 50-70% of the equilibrium population size, corresponding to values of Z from 1 to 5.1. The 1979 workshop recognized that "There had been a shift of scientific opinion in recent years [since 1976] towards accepting the idea that relative net productivity in mammals, especially large, K-selected species, is a non-linear function of population size," (footnote 3, p. 7) and concluded that $MNPL$ for these dolphin populations is probably in the range of 65-80% of the equilibrium population size (Z from 3.5 to 11.5). I consider the values for $MNPL$ of 50-80% (Z from 1 to 11.5) of equilibrium population size in order to explore the sensitivity of the calculations to this uncertainty.

HISTORICAL TRENDS IN ABUNDANCE

Estimates of population sizes prior to 1979 from Equations (2) and (3) for each population are shown in Table 6. Values are given using 1) two different estimates of present (1979) abundance (from combined research vessel and fishing vessel data, and from research vessel data alone), and 2) the parameters $MNPL = 65\%$ and $R_m = 0.03$. For this range of parameter values, the offshore spotted dolphin population in 1959 was between about 4,800,000 and 5,600,000 animals. The eastern spinner dolphin population in 1959 numbered about 1,500,000, while the white-

TABLE 6.—Estimates of population size (in thousands) of offshore spotted, eastern spinner, and whitebelly spinner dolphins from 1979 back to 1959, using Equations (2) and (3) and parameters $MNPL = 65\%$ and $R_m = 0.03$. 1979 estimates are based on species proportions from (FR) combined research vessel and fishing vessel data and (R) research vessel data alone.

	Offshore spotted		Eastern spinner	Whitebelly spinner	
Year	FR	R	$FR = R$	FR	R
1979	2,775	1,682	293	380	216
1978	2,719	1,653	287	376	215
1977	2,668	1,628	283	373	214
1976	2,673	1,629	284	386	229
1975	2,675	1,686	320	434	258
1974	2,679	1,732	336	456	301
1973	2,754	1,824	358	486	331
1972	2,967	2,046	443	494	340
1971	3,064	2,164	488	499	345
1970	3,340	2,457	591	512	358
1969	3,264	2,756	695	527	373
1968	3,720	2,865	742	527	373
1967	3,844	3,001	799	527	373
1966	4,071	3,239	893	527	373
1965	4,335	3,520	998	527	373
1964	4,574	3,754	1,092	527	373
1963	4,695	3,879	1,141	527	373
1962	4,803	3,991	1,185	527	373
1961	5,169	4,358	1,323	527	373
1960	5,519	4,708	1,454	527	373
1959	5,590	4,779	1,481	527	373

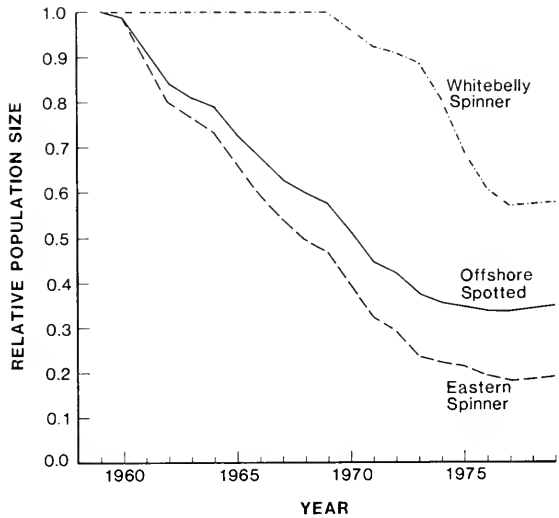

FIGURE 1.—Relative population sizes of whitebelly spinner, offshore spotted, and eastern spinner dolphins, 1959-79, using population estimates based on species proportions from combined research and fishing vessel data, and assuming $R_m = 0.03$ and $MNPL = 65\%$ of equilibrium abundance. Population sizes are relative to estimated population sizes in 1959.

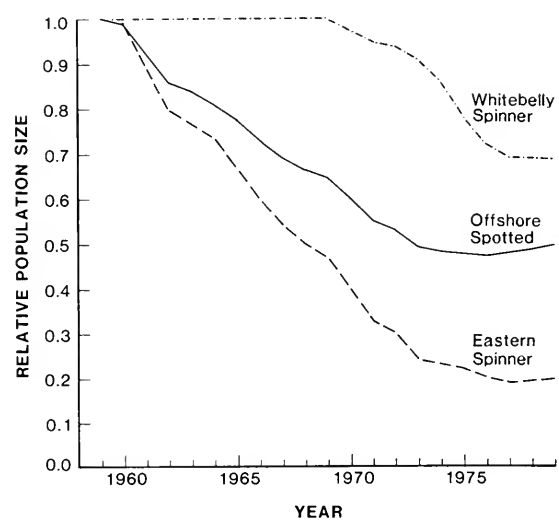

FIGURE 2.—Relative population sizes of whitebelly spinner, offshore spotted, and eastern spinner dolphins, 1959-79, using population estimates based on species proportions from research vessel data alone, and assuming $R_m = 0.03$ and $MNPL = 65\%$ of equilibrium abundance. Population sizes are relative to estimated sizes in 1959.

belly spinner dolphin population in 1969 numbered between 400,000 and 500,000. The offshore spotted and eastern spinner dolphin populations declined rapidly in the 1960's and early 1970's in the face of kills which were, for example, on the order of 7-12% of the 1965 population sizes. The whitebelly spinner dolphin population declined most rapidly in 1974 when the kill was between 11 and 16% of its population size.

These estimates of absolute population sizes are shown in Figures 1 and 2 relative to the equilibrium population size (N_t/N_p), so that the trend in abundance of these populations can be examined. For all of the parameter values considered, these dolphin populations have declined substantially relative to their pre-exploitation sizes.

The ratio of 1979 to pre-exploitation population sizes for different values of R_m and $MNPL$ (and hence Z) shows the sensitivity of the calculations to changes in parameter estimates (Table 7; Figs. 3, 4). The value of $MNPL$ when R_m is zero is not meaningful, as the estimate of pre-exploitation population size (Equation (2)) collapses to the sum of the present population size estimate and the total numbers killed over all years. This is reflected in Figures 3 and 4 in the convergence of the lines when R_m is zero.

TABLE 7.—Estimates of 1979 relative population sizes of offshore spotted, eastern spinner, and whitebelly spinner dolphin populations, using two estimates which differ in species proportions from (FR) combined fishing and research vessel data and from (R) research vessel data alone, for ranges of maximum net recruitment rate (R_m) and maximum net productivity level ($MNPL$).

R_m	$MNPL$ (%)	Offshore spotted		Eastern spinner	Whitebelly spinner	
		FR	R	$FR = R$	FR	R
0.00	—	0.40	0.29	0.17	0.66	0.53
0.03	50	0.45	0.32	0.18	0.69	0.55
	65	0.50	0.35	0.20	0.72	0.58
	80	0.53	0.37	0.21	0.77	0.61
0.06	50	0.49	0.35	0.20	0.71	0.57
	65	0.60	0.42	0.23	0.78	0.63
	80	0.68	0.47	0.25	0.86	0.69

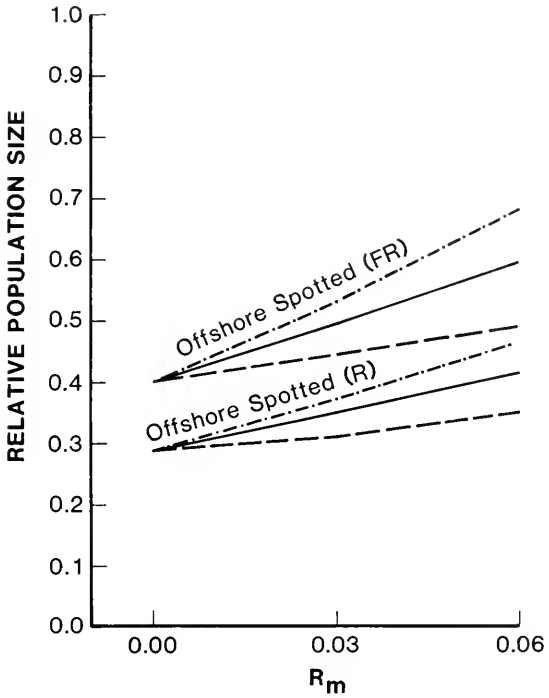

FIGURE 3.—Population size of offshore spotted dolphins in 1979 relative to 1959 (N_{79}/N_{59}) as a function of maximum recruitment rate ($R_m = 0, 3, 6\%$) using two current population estimates which differ in species proportions from (FR) combined fishing and research vessel data and from (R) research vessel data alone. $MNPL$ values of 50% (dashed lines), 65% (solid lines), and 80% (dot-dashed lines) are shown.

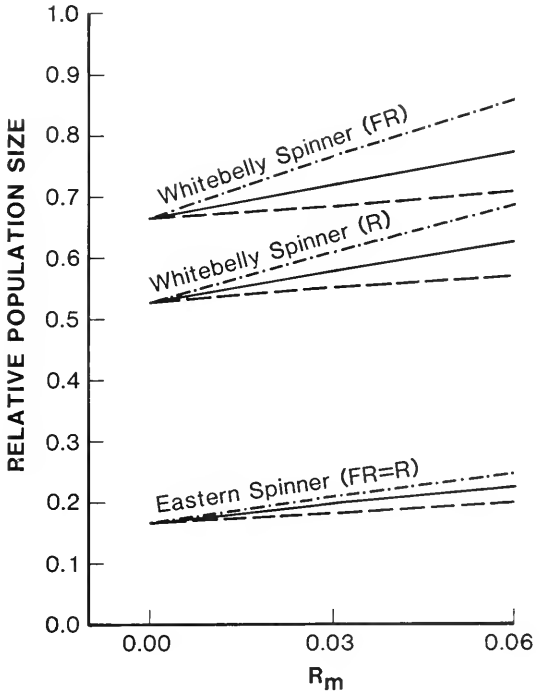

FIGURE 4.—Population sizes of eastern spinner and whitebelly spinner dolphins in 1979 relative to 1959 (N_{79}/N_{59}) as a function of maximum recruitment rate ($R_m = 0, 3, 6\%$) using two current population estimates which differ in species proportions from (FR) combined fishing and research vessel data and from (R) research vessel data alone. $MNPL$ values of 50% (dashed lines), 65% (solid lines), and 80% (dot-dashed lines) are shown.

DISCUSSION AND CONCLUSIONS

The three populations of dolphins involved with the yellowfin tuna purse seine fleet in the eastern tropical Pacific have declined since 1959 and the decline was not arrested until recently (Figs. 1, 2). Assuming the historical kill level, and the central values for R_m and $MNPL$, the whitebelly spinner dolphin population has declined to between 58 and 72% of its pre-exploitation levels; the offshore spotted dolphin population has declined to between 35 and 50% of its pre-exploitation size; and the eastern spinner dolphin population has declined to around 20% of its pre-exploitation size.

Examination of Figures 3 and 4 shows that the numerical values of the estimates of relative abundance in 1979 for offshore spotted dolphin and whitebelly spinner dolphin are relatively more sensitive to changes in the maximum net recruitment rate and the maximum net productivity level parameters than are the estimates for the eastern spinner dolphin. Also, the sensitivity of these calculations to the maximum net productivity level increases markedly as the value of the maximum net recruitment level increases. The sensitivity (in percent change) in the ratio of present to pre-exploitation abundance, however, is largest for the offshore spotted dolphin and least for the whitebelly spinner dolphin. This is due in part to the shorter time span over which the whitebelly spinner dolphin has been exploited, and in part to the lower $\frac{N_t}{N_p}$ ratio for the eastern spinner dolphin ratio, which makes smaller differences result in a larger percentage.

Although there are a number of uncertainties about specific parameter estimates used in these calculations, the general declines in abundance change relatively little over the ranges of parameter estimates explored. For example, rather rapid declines in the 1960's, followed by decreasing rates of decline in the 1970's, are evident for all parameter values considered. Specific aspects of these declines in abundance, however, depend to a greater degree on the actual parameter values. For example, the estimated changes in population sizes from 1975 to 1978 vary with the specific values of maximum net recruitment rate, while the estimated changes in population sizes in the 1960's are relatively insensitive to this parameter.

In order to improve our estimates of reproductive and mortality rates, a complete review of vital rates for these dolphin populations and for cetaceans in general should be carried out. Several approaches to this problem have been identified, including a detailed review of the eastern tropical Pacific dolphin data and of the existing data for other cetacean populations. Given the gaps in our knowledge of cetacean reproductive processes, analyses of alternate mathematical models of such processes will be fruitful.

Although improvements in estimates of abundance and kill levels are needed, these areas are generally much better understood than the recruitment process. Population-size estimation techniques are still being improved upon; current emphasis is on testing the assumptions needed in applying line transect theory to aerial sighting survey data and in estimating dolphin school size. Future work will emphasize improved shipboard sighting methodology for possible application of line transect theory.

Marked improvements in the estimates of numbers of dolphins killed are not anticipated; key areas needing additional information are the kill rates both in the non-U.S. fleet and on unobserved fishing trips. Neither of these areas is readily amenable to study, although further analysis of the kill rates on unobserved trips may provide some basis for exploring this uncertainty. The possible levels of indirect mortality or debility due to the stress of chase and capture are also of concern. Because of the large numbers of dolphins captured and released each year, even very low rates of indirect mortality could have a significant effect on the population.

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This assessment of the status of the dolphin populations is built on data collected by many individuals. The collection of these data has been made possible in large measure by the cooperation of the U.S. tuna fishing fleet. In addition, many individuals have contributed to the analysis of the data, including National Marine Fisheries Service staff and numerous scientists from various organizations. It is not possible to acknowledge the contributions of specific individuals to information presented here because of the large numbers of people who have been involved, but without their efforts the present analysis would not be possible. I also wish to acknowledge the very helpful reviews of an earlier draft of this paper by Douglas Chapman, John Gulland, Linda Jones, and Jeff Breiwick.

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FOOD HABITS OF YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA* (STORER), FROM OFF THE NORTHEASTERN UNITED STATES

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ABSTRACT

Stomachs of 1,021 yellowtail flounder caught in 1973-76 contained primarily polychaetes (43%) and crustaceans (18%) as a percentage weight of total contents. The most important prey were *Spiophanes bombyx* (9.68%) and *Unciola* sp. (13.65%). Predator size had little effect on diet composition whereas geographic distribution did. *Spiophanes bombyx* was three times more important as prey on Georges Bank than in southern New England, and amphipods were more important in southern New England than on Georges Bank. From the middle Atlantic to southern New England to Georges Bank the total weight of stomach contents increased from 0.12% to 0.14% to 0.21% of the fishes' body weight. Year-to-year differences were inconsistent; however, fish stomachs from spring cruises contained more food, 0.20%, than those from autumn cruises, 0.14% body weight. During a composite 24-hour day, peak stomach content weight occurred in the afternoon to early evening. Polychaetes accounted for less of the stomach contents at night while amphipods increased in importance during the night. Sex of the fish had no effect on diet composition although the stomachs of females were fuller than males, 0.15% vs. 0.11% body weight. Neither diet composition nor the percentage of empty stomachs were related to gonadal maturity stages, but stomachs from spawning fish contained the least amount of prey, 0.06%, while resting-stage fish contained the most, 0.24% body weight. Over a 12°C temperature range there was little change in diet composition, but between 3° and 8°C a greater percentage of stomachs contained prey and a larger quantity of prey than between 9° and 15°C. Over a 220 m depth range the stomach content weight increased with depth for smaller fish (<15 cm), while the percentage of empty stomachs increased for larger fish (>21 cm). Diet composition showed the greatest effect of depth with *S. bombyx* dominating the diet in the 74-110 m depth zone (26.6% of the stomach content weight) and *Crangon septemspinosa*, also being dominant in a single depth zone, comprising 39.6% of the diet at 147-183 m.

The yellowtail flounder, *Limanda ferruginea* (Storer), is a right-handed, thin-bodied flounder that occurs along the eastern seaboard of North America from Labrador to Chesapeake Bay (Bigelow and Schroeder 1953; Royce et al. 1959). It has contributed significantly to the total flatfish catch, primarily from southern New England and Georges Bank, since about 1935 (Royce et al. 1959; Sissenwine et al. 1978[2]). Biological information has been summarized by Bigelow and Schroeder (1953) and updated by Lux and Livingston (in press). These summaries qualitatively describe the diet as consisting of small crustaceans, worms, and molluscs. Quantitative work on the diet is limited. Inshore yellowtail flounder have been examined by Libey and Cole (1979) off Cape Ann in Massachusetts while Efanov and Vinogradov (1973) surveyed the offshore feeding pattern of yellowtail flounder in southern New England and on Georges Bank. Langton (1979[3]), Grosslein et al. (1980), and Langton and Bowman (1981) described the diet of fish from the middle Atlantic to western Nova Scotia, and Pitt (1976) conducted a study on the Grand Banks. These papers generally agree that crustaceans, particularly amphipods, and polychaetes are major prey items. However, the absolute quantities of prey in the stomachs differ, being influenced by both biological and abiotic factors. Only one of the studies lists the stomach contents by predator size (Pitt 1976) and none of the studies evaluate comprehensively all factors influencing the diet

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[2]Sissenwine, M. P., B. E. Brown, and M. M. McBride. 1978. Yellowtail flounder (*Limanda ferruginea*): Status of the stocks, January 1978. Northeast Fisheries Center Woods Hole Laboratory Reference No. 78-02, 27 p.

[3]Langton, R. W. 1979. Food of yellowtail flounder, *Limanda ferruginea* (Storer). International Council for Exploration of the Sea. C.M. 1979/G:54, 10 p.

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of this predator. The purpose of the present paper is to describe the stomach contents of yellowtail flounder and quantitatively evaluate factors influencing the quantity and composition of the animal's stomach contents.

METHODS

Yellowtail flounder stomachs were collected on eight bottom trawl survey cruises conducted from 1973 through 1976. The dates of the cruises are as follows: 16 March-15 May 1973; 26 September-20 November 1973; 12 March-4 May 1974; 20 September-14 November 1974; 4 March-12 May 1975; 15 October-18 November 1975; 4 March-8 May 1976; 20 October-23 November 1976. Fish collections were made from the RV *Albatross IV* or RV *Delaware II*, using a #36 Yankee otter trawl for autumn surveys and a #41 Yankee otter trawl for spring surveys. A scheme of stratified random sampling was carried out in the continental shelf waters between Nova Scotia and Cape Hatteras, N.C. For survey purposes this region has been divided into five geographic areas, which are further subdivided into depth strata as depicted in Clark and Brown (1977) and described by Grosslein (1969[4]).

Yellowtail flounder were selected from the catch in, primarily, two of the five geographic areas, i.e., southern New England and Georges Bank which include the three major fishing grounds and major yellowtail flounder stocks in U.S. waters (Lux 1963). Stomachs were labelled according to vessel, cruise, station, length, sex, and sexual maturity and were preserved individually in a gauze wrapping in 10% Formalin[5]. The sampling strategy was designed to collect fish, more or less at random, from the population without bias towards a specific length, except as described below. We attempted to collect 50 fish per geographic area per cruise for fish both above and below 12 cm TL (total length). Twelve centimeters in length approximates the length of 1- to 2-yr-old fish, and these smaller fish were preserved intact after the body cavity was cut open to insure fixation of the contents.

In the laboratory, individual stomachs were opened, and the contents emptied onto a fine mesh screen and rinsed with seawater. The various items were sorted and identified to the lowest possible taxa. Each distinct group was blotted dry and immediately weighed. In the text and tables these weights have been expressed as a percentage of the total weight of stomach contents. In the text these percentages are often given in brackets after the mention of taxa to quantify their relative importance.

Twelve percent of the fish collected fell into the three smallest size classes (Table 1) with a mean length of 7.6 cm. Fish >15 cm TL were equally distributed around the 31-35 cm size class with 70% ($n = 715$) of all fish examined falling between 26 and 40 cm TL. The average length of all fish comprising this peak is 32.8 cm. For some analyses two size-related groupings of fish, representative of this bimodal distribution, have been differentiated while in other cases the data are presented by 5 cm length classes or expressed as a percentage of the fishes' body weight according to the length/weight equation in Wilk et al. (1978). [$W = aL^b$ where $a = 0.4514^{-5}$, $b = 3.1257$, and L is in millimeters.]

RESULTS

Food

Of the 1,021 stomachs examined, 684 contained prey which weighed in total 422 g. The overall mean fish length and standard deviation was 29.4±10.5 cm. The prey were allocated into 148 different categories, which included all taxonomic levels of identification and such miscellaneous categories as sand and unidentifiable animal remains. The most important major taxonomic groupings were polychaetes and crustaceans (Table 1).

Polychaetes accounted for 43% of the stomach contents. The families Spionidae (13.27%), Lumbrinereidae (1.90%), Sabellidae (1.42%), and Nephtyidae (1.19%) were all of some importance. *Spiophanes bombyx* was the major prey, making up 9.68% of the weight of the total stomach contents. Other polychaetes (17.24%) and polychaete tubes (7.94%) accounted for the remainder of the prey in this taxon.

Crustaceans (18.0%) were second in importance, the amphipods (13.65%) being the major prey group. *Unciola* sp. (4.41%), *Leptocheirus pinguis* (2.25%), and *Byblis serrata* (1.72%) were important amphipod prey. Other gammarids (1.92%), ampeliscids (1.56%), and corophiids (0.3%) made up most of the remaining amphipod

[4]Grosslein, M. E. 1969. Groundfish survey methods. Northeast Fisheries Center Woods Hole Laboratory Reference No. 69-2, 34 p.

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

TABLE 1.—Principal items in stomachs of yellowtail flounder, *Limanda ferruginea*, by 5 cm length classes. Data are expressed as a percentage of the total weight of stomach contents (+ indicates present but <0.01%).

Stomach contents	Fish length intervals in centimeters										
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55
Anthozoa						1.09	0.69	4.24	8.10	3.69	9.71
Other Cnidaria								0.01			
Spiophanes bombyx		11.74			5.82	0.93	10.28	11.97	11.99	11.06	
Spionidae					0.60	1.77	2.71	4.91	9.80		
Sabellidae					2.02	0.97	3.34	0.88	0.16		
Annelida tubes						1.01	4.46	12.12	9.16	14.35	
Lumbrinereidae					0.54	3.05	3.49	1.05	0.11	2.22	
Nephtyidae				+	0.54	0.28	2.80	0.92	0.23	0.39	
Other polychaetes		10.82	11.91	13.64	29.19	23.35	21.83	14.51	16.46	12.26	0.33
Byblis serrata		1.73		2.02	0.59	1.24	1.24	2.35	2.50	2.34	0.03
Other Ampeliscidae		14.71	0.79	1.81	0.71	2.45	2.25	1.40	0.54	0.92	
Unciola sp	+	2.22	3.64	15.28	12.86	12.03	5.36	3.44	0.26	0.60	
Other Corophiidae		4.02	3.31	0.93	0.33	1.34	0.32	0.07		0.01	
Gammaridae	+	3.77	4.96	1.47	1.61	4.21	2.14	1.35	2.79	0.12	
Leptocheirus pinguis	+			8.51	4.77	3.81	1.92	3.11	1.96		
Other Amphipoda		6.24	0.93	1.43	1.27	2.55	1.03	1.53	0.18	3.87	
Crangon septemspinosa	41.38	9.09	11.98		3.25	7.14	2.53	0.71	0.01		
Dichelopandalus leptocerus			31.83			0.64	1.96	0.66	0.09		
Other crustaceans	58.62	19.16	4.37	19.28	6.94	2.32	1.96	0.72	10.65	0.16	
Animal remains	+	15.39	7.28	28.42	24.46	19.30	16.09	15.47		36.79	0.59
Sand		0.93	0.60	1.81	10.19	8.22	10.22	17.34	23.02	10.30	88.45
Other groups	+	0.19	18.40	5.39	0.31	2.28	3.38	1.25	1.99	0.93	0.88
Number examined	39	77	21	23	63	187	337	191	60	18	2
Number empty	22	25	6	9	16	63	108	62	20	4	0
Mean weight per stomach (g)	0.0001	0.021	0.072	0.103	0.230	0.242	0.375	0.563	0.950	2.445	9.652
Mean length (cm)	4.0	8.3	12.0	18.1	23.4	28.3	32.7	37.7	42.3	47.5	51.0

prey. Only two other crustaceans were of significance in the yellowtail flounder's diet, namely, the shrimps *Crangon septemspinosa* (1.89%) and *Dichelopandalus leptocerus* (0.94%).

All other taxonomically distinct groups contributed only 4.96% of the weight of stomach contents. Unidentifiable animal remains (17.18%) and sand (16.92%) accounted for the remainder of the total weight of stomach contents.

Size-Related Feeding Habits

Amphipods were the most important prey for the smaller yellowtail flounder although stomachs from every size class of fish contained amphipods (Table 1). Polychaetes comprise a greater percentage of the stomach contents of the larger fish but, like amphipods, they occur in stomachs from most every size class. The occurrence of anthozoans in the larger size fish (>26 cm) might reflect a tendency for larger yellowtail flounder to be selecting "wormlike" prey.

Geographic Comparison

Composition of the diet of yellowtail flounder in southern New England and on Georges Bank was similar, with polychaetes and amphipods accounting for 50 to 70% of the total weight of stomach contents in both areas (Table 2). Polychaetes were the major prey in both regions with

TABLE 2.—Principal items in stomachs of yellowtail flounder, *Limanda ferruginea*, by geographic area in the northwest Atlantic. Data are presented as a percentage of the total weight of stomach contents (+ indicates present but <0.01%).

Stomach contents	Middle Atlantic	Southern New England	Georges Bank
Anthozoa		1.93	3.52
Other Cnidaria		0.01	
Spiophanes bombyx		4.35	13.18
Spionidae		4.41	3.12
Sabellidae		3.30	0.25
Annelida tubes	5.47	7.53	8.24
Lumbrinereidae	+	2.57	1.50
Nephtyidae		2.66	0.28
Other polychaetes	9.80	22.74	13.89
Byblis serrata	8.15	2.18	1.34
Other Ampeliscidae	1.55	2.44	1.01
Unciola sp.	1.50	7.01	2.81
Other Corophiidae	5.36	0.36	0.19
Gammaridae	0.77	2.25	1.72
Leptocheirus pinguis	4.38	3.25	1.58
Other Amphipoda	0.54	1.38	1.58
Crangon septemspinosa		2.16	1.75
Dichelopandalus leptocerus		1.90	0.35
Other crustaceans		1.82	1.34
Animal remains	41.57	15.53	17.85
Sand	20.09	7.75	22.65
Other groups	0.83	2.46	1.86
No. fish examined	16	502	502
No. empty stomachs	4	163	169
Mean weight per stomach ±SD (g)	0.242±0.324	0.323±0.578	0.512±1.452
Mean length ±SD (cm)	28.2±8.2	29.2±9.2	29.7±11.7

Spiophanes bombyx being the most important species identified. On Georges Bank *S. bombyx* was three times more important as prey than in

southern New England. The other major difference between areas was in the quantity of other polychaetes, but a large percentage of this group was unidentified remains (12.93% in southern New England and 11.61% on Georges Bank). The diversity of polychaete prey was very similar in the two areas; 27 families of polychaetes in the stomach contents of fish from southern New England and 24 different families on Georges Bank. Eleven different genera of polychaetes were identified in each area. Six of these were common to both regions, but only *Spiophanes* contributed >1% to the total stomach contents weight.

Amphipods made up almost twice the percentage of the weight of stomach contents in southern New England than on Georges Bank (18.87% vs. 10.23%). The same species were important in both areas (Table 2). There was, however, a slightly greater reliance on *Unciola* sp. and *Leptocheirus pinguis* in southern New England than on Georges Bank. The diversity of amphipod prey was greater on Georges Bank, 16 genera as opposed to 11 genera, although yellowtail flounder from the two areas preyed on 9 of the same genera.

Crustaceans such as *C. septemspinosa* and *D. leptocerus* played a minor role in the diet of yellowtail flounder as did all other arthropod groups except the amphipods. The only other category of stomach contents that differed substantially between areas was the quantity of sand in the stomachs. This might be related to the heavy predation on *S. bombyx* on Georges Bank, since this polychaete is reported to prefer a fine sand substrate (Light 1978).

The percentage of empty stomachs was virtually the same in southern New England and on Georges Bank, but was less in the Middle Atlantic (Table 2). The mean weight per stomach increased from the Middle Atlantic to Georges Bank and the mean fish length also increased from south to north (Table 2). This size difference did not counterbalance the increase in stomach content weight. The mean weight of stomach contents ranged from 0.12% in the Middle Atlantic to 0.14% in southern New England and 0.21% body weight on Georges Bank.

Yearly, Seasonal, and Diurnal Variation

Data were collected over a 4-yr period in both the spring and autumn and throughout the day-night cycle. It is, therefore, possible to examine the influence of the time of capture on the composition of the diet as well as on changes in the absolute quantity of prey in the stomachs.

On a year-to-year basis, polychaete worms were always the most important prey, between 36 and 44% of the diet, followed by amphipod crustaceans, 10 to 33% of the diet. Within these two taxa the actual percentage composition of the various groups fluctuated, but no systematic changes in diet were discernible. Within the Polychaeta, for example, *S. bombyx* made up between 2 and 12% of the diet from 1973 to 1974 and ranged from 9 to 11% between 1975 and 1976, respectively. At the family level, Spionidae, the range increased from 2 to 16% for the first 2 yr and 9 to 18% for the latter 2 yr. When spionids were most important, there was also a very large percentage of sand in the stomachs, 20 and 27% for 1974 and 1976, respectively, which probably relates to predation on these particular polychaetes. Among the amphipods, *Unciola* sp. showed the greatest fluctuation, ranging from 16% of the diet in 1973 to 1% in 1975 but increasing to just under 5% in 1976.

The mean weight of prey showed an increase from 1973 to 1976, but when this was corrected for fish size, there was no pattern evident in these changes. The slightly larger mean fish lengths occurring in 1975 and 1976 counterbalanced the increase in the mean weight of stomach contents. The percentage of empty stomachs also showed no consistent yearly change, fluctuating around the overall mean value of 33%.

Species composition of the diet showed no drastic shift between spring and autumn. Polychaetes were more important in the spring (49%) than in the autumn (35%), and the same was true for amphipods, 19% vs. 13%. Both of the changes may, however, simply reflect the higher percentages of unidentified animal remains and sand in the fish stomachs collected in the autumn.

In all years, except 1976, stomachs collected on spring cruises contained a greater mean weight of prey than stomachs from fish collected in the autumn. Although the mean length of fish in the spring was only slightly larger (30.0 cm vs. 28.8 cm). The 4-yr mean weight of prey in the stomachs was 0.505 g (0.20% body weight) for the spring and 0.298 g (0.14% body weight) in the autumn. The percentage of empty stomachs was also lower in the spring than the autumn; 22.7% of the 574 stomachs examined from spring cruises versus 46.3% of 447 stomachs examined from autumn cruises.

An examination of the data for a composite 24-h day revealed a diurnal feeding pattern.

Although there was a certain degree of hour-to-hour variability, a peak in the weight of stomach contents occurred during the afternoon-early evening period (Fig. 1). In Figure 1 the day has been divided into four periods—dawn (0300-0800 h), day (0900-1400 h), dusk (1500-2000 h), and night (2100-0200 h)—which accounts for seasonally variable day length in the dawn and dusk period. Despite a seasonal change in day length, the composition of the diet also changed over a 24-h period. Polychaetes were less important prey during the night than during any of the other three time periods. They dropped from values ranging from 41-47% to 24% as a percentage of the weight of stomach contents. Conversely, crustaceans, amphipods in particular, were more important at night (values ranging from 15 to 23% vs. 34%). Unidentifiable animal remains also accounted for their smallest percentage of the diet (13.0%) in the dusk period when the fish stomachs were fullest. The greatest percentage of empty yellowtail flounder stomachs was found during the night (46%) and the smallest (19%) during the day with intermediate levels occurring at dawn (34%) and dusk (26%).

To evaluate whether the diurnal feeding pattern shown in Figure 1 is statistically significant, an analysis of variance, including time of day and seasonal factors, was conducted. The results of this analysis are given in Table 3 for transformed data using an inverse hyperbolic sine transformation ($Y' = \sin h^{-1}(\sqrt{Y})$) to account for the extreme skewness of the data (i.e., a large number of empty and almost empty stomachs) (see Bartlett 1947). Both time of day and season are significant factors in determining the weight of stomach contents for yellowtail flounder. This analysis confirms that there are statistically significant differences in stomach content weight over a 24-h period. These results are, however, influenced by the level of interaction between time of day and season, such that it is not clear which of these two factors is the most important

TABLE 3.—Analysis of variance of the weight of stomach contents for yellowtail flounder, expressed as percent body weight, for time of day and season. See text for details.

Source	df	Sum of squares	F
Time of day	3	0.03376	14.59*
Season	1	0.02464	31.93*
Interaction	3	0.00894	3.86*
Error	1,011	0.78005	

*Significant, $P = 0.05$.

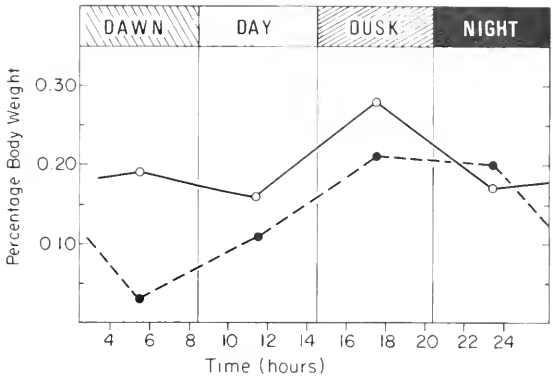

FIGURE 1.—Weight of stomach contents, as a percentage of the body weight, for yellowtail flounder collected during the spring (open circles) and autumn (solid circles) over a composite 24-h day from 1973 through 1976. Data points are 6-h weighted averages for the periods identified in the figure as dawn, day, dusk, and night.

in determining the shape of the curve for the weight of stomach contents over the composite 24-h period. Further study specifically evaluating the effects of time and season on stomach content weight is warranted.

Determining what influence size might have on the feeding periodicity of yellowtail flounder is difficult because of the small number of samples when the data are distributed among both size classes and time. To distinguish between mature and immature fish the data were divided into two size classes, 0-15 cm and 21-49 cm fish, which accounts for the bimodal distribution of fish collected for stomach content analysis (see section on Methods). For the 1-15 cm fish the sample sizes were small and unevenly distributed, and no conclusions can be made as to feeding periodicity. However, 66% of these smaller fish were caught at night and an additional 24% were caught during the dawn period. In contrast, the 21-49 cm fish were taken both day and night in much more equal proportions. Only 30% of the catch was taken at night and 20% was caught during the daytime period. The feeding periodicity of these larger fish is adequately represented by the data in Figure 1. There was a gradual increase in the mean weight of stomach contents from dawn to a peak in the dusk period. The major influence of the smaller, 1-15 cm, fish is that they have relatively more in their stomachs which increases the overall mean in the night period when the numbers of juveniles caught was at a maximum.

Sexual and Maturity Stage Influences

Of 1,021 fish examined for stomach content analysis, 376 were males, 466 females, and 179 were not sexed. Females were slightly larger than males, mean length of 34.4±6.3 vs. 31.8±5.1 cm, respectively, and contained a larger mean quantity of prey in their stomachs, 0.57±1.37 g (0.15% body weight) vs. 0.32±0.76 g (0.11% body weight). Females also had a lower percentage of empty stomachs, 29% vs. 36%, than males. The 179 fish that were not sexed were small and presumably immature with a mean length of 11.7±8.9 cm and mean weight of stomach contents of 0.203±0.83 g.

When the sex of a fish was determined, the maturity stage of the gonads was evaluated subjectively. A percentage of the fish examined were not classified as to their state of sexual maturity and another group, those <15 cm, was routinely classified as immature. The remainder of the fish were classified as either resting, developing, ripe and/or spawning, or spent. Although the average size of individuals in these last four categories was quite similar, there was a substantial difference in the mean weight per stomach. Spawning fish had the least amount of prey in their stomachs, mean = 0.21 g (0.06% body weight), while developing-stage fish contained the most, mean = 0.58 g (0.16% body weight) although on a percentage body-weight basis resting-stage fish contained a larger quantity of prey in their stomachs than developing-stage fish (0.24% vs. 0.16%). The percentage of empty stomachs and the actual composition of the diet showed no pattern to the fluctuation in values which was related to the maturity stage of the gonads.

Physical Factors

Temperature, over the 12°C range in which yellowtail flounders were caught, had no apparent effect on diet composition. In contrast, although the data are variable, the stomach content weights appeared to vary with temperature. The weight was higher at the lower temperatures, with one exception. In the range from 3° to 8°C the stomach content weight ranged from 0.13 to 0.26% body weight. Between 9° and 15°C the range was greater, 0.05 to 0.65%. However, exclusion of the 13°C value of 0.65% reduced the high point of the range to 0.14%. The percentage of empty stomachs was also related to temperature. Between 3° and 8°C the percentage of empty stomachs averaged 23%, while between 9° and 15°C it averaged 37%. The ranges for these averages were 14-27% and 19-79%, respectively. The value of 79% occurred at the 15°C point, and this may be the result of temperature inhibition of feeding even though 24 fish were collected at this water temperature. Perhaps a more typical range estimate is 19 to 55% with the 55% empty stomachs being recorded at 12°C from a sample size of 118 fish.

To evaluate the relationship between temperature and fish size, the yellowtail flounder data were divided into two size groups, fish between 1 and 15 cm and 21 through 49 cm. For the small size class, fish were collected at temperatures between 4° and 15°C. More fish were collected in the 4° through 7°C temperature range (no samples from 8°C) than the 9° through 15°C range, 80 vs. 51, respectively. Fish from this lower range were also, on the average, larger (9.3 cm vs. 5.3 cm TL) and had a greater quantity of prey in their stomachs, 0.51% vs. 0.35% body weight. Fish in the 21-49 cm size group were also collected in slightly larger numbers, 426 vs. 373, in the lower temperature range. They were slightly larger fish, mean length of 33.6 cm vs. 32.5 cm and the mean weight of stomach contents was greater, 0.15% vs. 0.08% body weight, respectively.

Yellowtail flounder were caught in depths ranging from shallow water to 220 m. To evaluate the influence of depth on the stomach content data the data were divided into 37 m depth intervals. The majority of fish (68%) was taken from waters 38 to 73 m deep with an additional 23% of the fish taken from the next depth category, 74-110 m. The average size of fish and the percentage of empty stomachs fluctuated haphazardly over the depth class groupings. The relation between fish size and depth was further investigated by dividing the data into two size class groupings, 1-15 cm and 21-49 cm. A total of 147 fish fell into the smaller size range and, as with the grouped data, most fish (92%) were caught between 38 and 110 m although the maximum depth from which the smaller fish were taken was only 146 m. There was no obvious relationship between depth and size for these small fish or even for depth and the percentage of empty stomachs. The stomach content weight did, however, increase with depth from 0.28% at 38-73 m, to 1.29% body weight at 111-146 m. For fish in the 21-49 cm group, the major difference from the smaller fish is that the percentage of

empty stomachs showed an increase from 18 to 56% over depth ranges 0-37 m to 111-146 m. At the deepest depth, 147-220 m, the sample sizes were too small (<8 fish) to evaluate this factor. The stomach content weight values were highest at the shallowest depth, 0.28% body weight, but did not systematically decrease with depth.

Certain prey were more prevalent in the stomachs of the yellowtail flounder at different depths. The polychaete *S. bombyx* accounted for 26.6% of the diet of fish in the 74-110 m range and only 9.3 and 2.9% of the stomach content weights for fish in the next lowest and highest depth range, respectively. *Spiophanes* did not occur in stomachs of yellowtail flounder collected outside 38 and 146 m. *Crangon septemspinosa* also predominated in only one depth group, 39.6% of the diet at 147-183 m, although it did occur in stomachs at all depths <147 m. There was no pattern to the occurrence of other prey species in stomachs of yellowtail flounder which could be related to depth.

DISCUSSION

Predator size was of little importance to the diet composition of yellowtail flounder when considering the entire study area. For all sizes of fish, polychaete worms and amphipod crustaceans were the primary prey, although amphipods were somewhat more important for small fish and polychaetes more important for larger fish. Pitt (1976) also observed relatively few changes in diet composition for different-sized yellowtail flounder on the Grand Bank. Size does, however, have an obvious influence on the absolute amount of food in the stomachs with an increase in mean weight of stomach contents increasing with fish size (Table 1).

Predator size also had an observable effect on several other factors which were reflected by differences in the stomach contents. Perhaps the most interesting size (diet?)-related observation is that the majority (66%) of the smaller fish, <15 cm long, were caught at night while the larger fish (21 to 49 cm) were caught both day and night in much more equal proportions. Since the fish were taken at random from the catch, this is likely to be indicative of a behavioral difference between the small and large yellowtail flounder. This same catch pattern has been observed before. Beamish (1966) found a significantly larger catch of small yellowtail flounder (<22.5 cm) at night than during the day, while studying vertical migration by demersal fishes. This difference in catch was not found for the larger fish. Beamish (1966) attributed his results to visual conditions where small yellowtail flounder could escape through the net more easily during the day than at night. Larval yellowtail flounder, however, show strong diel movements and rise towards the surface at night (Smith et al. 1978). It may be that the juvenile yellowtail flounder continue to demonstrate some nocturnal activity, with a resultant increase in vulnerability to the trawl, and this behavior pattern decreases slowly with an increase in fish size. In any event, the larval fish do not appear to be migrating solely for the purpose of feeding (Smith et al. 1978), and the data presented here are inconclusive about any feeding periodicity for these smaller yellowtail flounder. A complete understanding of the factors controlling this size-related difference in catchability, and any relationship that this has to feeding, will have to await further study.

Data on feeding periodicity may be interpreted to suggest that yellowtail flounder are daytime feeders with a peak in food consumption in the afternoon-early evening hours (Fig. 1). However, it is quite likely that the fish are feeding throughout the day, and the stomach contents accumulate at a faster rate than they are digested, resulting in the dusk period stomach content weight maximum followed by the peak in the percentage of empty stomachs at night. In European waters the yellowtail flounder's congener, *Limanda limanda*, has been observed to feed during the day (Arntz 1971). This daytime feeding pattern is consistent throughout the year with the only difference being that there is more food in the stomachs during the spring than in the autumn (compare with Figure 1). Changes in diet composition were also observed which may support the argument that yellowtail flounders are daytime feeders. Polychaetes are less and amphipods more important as prey at night. This shift may simply be the result of a differential digestion rate for these two prey types. The soft-bodied polychaetes would presumably digest more quickly than the crustacean body parts. Studies on digestion and prey selection are needed to understand fully these observed changes in stomach content weight.

Seasonal effects on diet include the difference in the absolute amount of food in stomachs between spring and fall (Fig. 1) and differences related to the reproductive cycle. Yellowtail flounder spawn from March to July with the peak

usually occurring in mid-May (Lux and Livingston in press). Prior to spawning the gonad goes through various stages of development which were evaluated in relation to the fishes' diet. Spawning fish were found to contain the least amount of prey in the stomachs, which is consistent with Libey and Cole's (1979) observations on feeding intensity related to spawning, and fish with resting-stage and developing gonads contained the greatest quantity of prey. These later two stages were usually observed in late autumn or on spring survey cruises and are reflected in the larger values of the mean weight of stomach contents in the spring. In contrast to the yellowtail flounder's congener, *L. limanda*, there were no seasonal or reproductive stage influences on the actual composition of the diet (Arntz 1971).

The major difference in diet over the geographic range of this study was the change in the mean weight of stomach contents from the Middle Atlantic through southern New England onto Georges Bank. There was, for example, a 75% increase (0.12 to 0.21% body weight) in the relative mean weight of stomach contents from the Middle Atlantic to Georges Bank. This same pattern was observed by Efanov and Vinogradov (1973), who noted that yellowtail flounder feed more intensively on Georges Bank than in southern New England.

In summary, the yellowtail flounder is a benthic predator occurring, for the most part, in depths of 38 to 110 m and at temperatures ranging from 3° to 15°C. All size classes and both sexes of yellowtail flounder prey heavily on polychaetes and amphipods throughout the year and over their entire geographic range. Yellowtail flounder feed more intensively in the spring, prior to spawning, than in the fall. They also feed more intensively on Georges Bank than in other geographic areas and are daytime feeders with a peak in the stomach content weight occurring in the late afternoon to early evening.

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Numerous people helped in the collection and stomach content analysis described herein. In particular, I want to thank Edward Brown-Leger, Ray Bowman, Jacqueline Murray, and Barbara North for their assistance and persistence in overcoming the problem in establishing and maintaining an extensive data collection system; Clem Walton for reviewing the paper; and Pat Hoyt for typing the manuscript.

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DEVELOPMENT AND DISTRIBUTION OF THE YOUNG OF NORTHERN SMOOTHTONGUE, *LEUROGLOSSUS SCHMIDTI* (BATHYLAGIDAE), IN THE NORTHEAST PACIFIC, WITH COMMENTS ON THE SYSTEMATICS OF THE GENUS *LEUROGLOSSUS* GILBERT

JEAN R. DUNN[1]

ABSTRACT

Development of the northern smoothtongue, *Leuroglossus schmidti*, is described from yolk-sac larva through pelagic juvenile based on plankton-caught specimens from the northeast Pacific Ocean and eastern Bering Sea.

Larvae of *L. schmidti* may be readily distinguished from those of other bathylagid smelts in the northeast Pacific Ocean and eastern Bering Sea by a combination of myomere counts (47-52), possession of short-stalked eyes, and pigment patterns. Pigment patterns in preflexion larvae about 5-13 mm SL (standard length) consist primarily of two lateral bands, at about 33-40% and 60-64% SL, and dorsal and ventral pigment on the notochord tip. With growth, these bands diffuse into scattered stellate melanophores on the lateral body wall, one on the gut near the anus, and the other on the caudal peduncle. Transformation from larva to juvenile takes place at about 31-35 mm SL, and juveniles acquire dark melanistic pigment characteristic of bathylagid fishes.

Although some bones ossify in relatively small larvae of *L. schmidti*, a number of structures do not calcify until transformation. The general sequence of ossification is cleithrum, dentary and vomerine teeth, pharyngeal teeth, other bones associated with the feeding apparatus, most other cranial bones, caudal fin and, at or near transformation, axial skeleton, median and paired fins, gill rakers, and secondary caudal fin rays.

Larvae of *L. schmidti* are at times the dominant bathylagid taken in plankton samples from the northeast Pacific Ocean and eastern Bering Sea, accounting for up to 5% of the fish larvae collected. Although neither the southern nor northern limits of the spawning range of this species are known, adult *L. schmidti* range from at least southern British Columbia to the central Bering Sea and westward to the Okhotsk Sea.

Based on this study and work of previous authors, *L. schmidti* is considered specifically distinct from *L. stilbius*, and *L. schmidti*, not *L. callorhini*, is considered the correct name. *Leuroglossus* lacks an orbitosphenoid which is present in *Bathylagus*; hence the genus *Leuroglossus* Gilbert is considered to be distinct from *Bathylagus* Günther.

The northern smoothtongue, *Leuroglossus schmidti* Rass, family Bathylagidae, ranges from about southern British Columbia to the Bering and Okhotsk Seas (Borodulina 1968; Peden 1981). Its known congeners are *L. stilbius stilbius* Gilbert, which reportedly ranges from British Columbia to the Gulf of California (Borodulina 1968; Ahlstrom 1969; Peden 1981), and *L. stilbius urotranus* Bussing, which apparently ranges from the eastern tropical Pacific (Ahlstrom 1969) to the Peru Trench (Bussing 1965; Borodulina 1968).

Larvae of *L. schmidti* are at times the dominant bathylagid taken in samples collected from the northeast Pacific Ocean and the eastern Bering Sea, accounting for up to about 5% of the fish larvae collected (Waldron and Vinter[2]; Kendall et al.[3]). The larvae usually are taken over the continental slope (Waldron and Vinter footnote 2; Kendall et al. footnote 3) but also occur in coastal waters (Mattson and Wing 1978). Distributional data for larvae and juveniles in the Bering Sea were reported by Waldron [1981], for Kodiak

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[2]Waldron, K. D., and B. M. Vinter. 1978. Ichthyoplankton of the eastern Bering Sea. Unpubl. manuscr., 88 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[3]Kendall, A. W., Jr., J. R. Dunn, R. J. Wolotira, Jr., J. H. Bowerman, Jr., D. B. Dey, A. C. Matarese, and J. E. Munk. 1980. Zooplankton, including ichthyoplankton and decapod larvae, of the Kodiak Shelf. Unpubl. manuscr., 393 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

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Island by Kendall et al. (footnote 3), and for the eastern Gulf of Alaska by Naplin et al.[4]

Presented here is the first published description of the development of *Leuroglossus schmidti*. Ahlstrom (1965) presented illustrations of 5.4, 15.7, and 28.5 mm SL (standard length) specimens of *L. stilbius stilbius*; subsequently he[5] presented illustrations of, but did not publish, a size series (8.4, 20.5, and 31.5 mm SL) of *L. schmidti*. Ahlstrom (1969) also described the eggs of *L. schmidti*, *L. s. stilbius*, and *L. s. urotranus* and presented supporting arguments for recognizing *L. schmidti* as a distinct species. Differences of opinion exist over the correct name of *L. schmidti* (Ahlstrom 1965, 1969; Borodulina 1968), its specific status (Hart 1973; Peden 1981), and the validity of the genus *Leuroglossus* Gilbert (Cohen 1956, 1964; Ahlstrom 1968, 1969; Borodulina 1969). I also attempt here to resolve the nomenclature of *L. schmidti*, to confirm the validity of the genus *Leuroglossus* Gilbert, and to describe the known distribution of eggs and larvae of this species in the northeast Pacific Ocean and eastern Bering Sea.

Relatively little is known about the biology of the northern smoothtongue. Adult *L. schmidti* have been taken at the sea surface as well as at depths to 700 m, and larval and juvenile specimens have been found in the stomachs of several species of fish (Hart 1973).

METHODS

Specimens

Larvae and juveniles of *Leuroglossus schmidti* were obtained from plankton samples collected by the Northwest and Alaska Fisheries Center (NWAFC) in the eastern Bering Sea in 1971 and 1976-79 and from the Gulf of Alaska in 1971, 1972, and 1977-79. Several hundred specimens were examined in the course of this study. Additional juvenile specimens were obtained from the collections in the College of Fisheries, University of Washington (UW). Radiographs of *L. schmidti* were made from juvenile specimens in collections at NWAFC; additional radiographs were obtained from the College of Fisheries, UW.

Comparative material consisting of larvae and juveniles of *Bathylagus pacificus*, *B. ochotensis*, *B. milleri*, and *L. stilbius stilbius* was obtained from collections at the NWAFC and College of Fisheries, UW. Radiographs and cleared and stained specimens of *B. ochotensis*, *B. nigrigenys*, *B. milleri*, *B. wesethi*, *B. bericodes*, *B. longirostris*, and *L. stilbius stilbius* were examined from collections at the Southwest Fisheries Center (SWFC), NMFS, La Jolla, Calif.

Measurements

The following measurements were made on 152 unstained larvae and juveniles, 4.9-55.0 mm SL, using an ocular micrometer in a stereomicroscope.

Standard length = snout tip to notochord tip until notochord is fully flexed and the posterior margin of the forming hypural bones is vertical, then to posterior margin of hypurals.

Snout to anus = horizontal distance along midline of body from tip of snout to vertical through posterior edge of the anus.

Head length (HL) = horizontal distance from tip of snout to posterior margin of cleithrum until no longer visible, then to posteriormost margin of opercle.

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

Interorbital width = width of fleshy tissue dorsal to the eyes.

Eye width = horizontal distance through midline of pigmented eye.

Eye height = vertical distance through center of pigmented eye.

Body depth at pectoral fin base = vertical distance across body at pectoral fin base.

Body depth at anus = vertical distance across body at anus.

Snout to origin of dorsal fin = horizontal distance along midline of body from tip of snout to vertical from origin of dorsal fin.

Snout to origin of anal fin = horizontal distance along midline of body from tip of snout to vertical from origin of anal fin.

Snout to origin of pelvic fin = horizontal distance from tip of snout to vertical through origin of pelvic fin.

[4]Naplin, N. A., J. R. Dunn, and K. Niggol. 1973. Fish eggs, larvae, and juveniles collected from the northeast Pacific Ocean, October-November, 1971. Unpubl. manuscr., 83 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[5]E. H. Ahlstrom (deceased), Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, class notes taken by the author in August 1971.

Caudal peduncle depth = minimum vertical distance across caudal peduncle in juvenile specimens.

Caudal peduncle length = medial horizontal distance from vertical through base of terminal anal fin ray to posterior margin of hypural bones in juvenile specimens.

Osteology

To determine the onset and sequence of ossification, counts of meristic structures were made on 102 *L. schmidti* larvae and juveniles (5.9-51.6 mm) cleared and stained with Alizarin Red and Alcian Blue (Dingerkus and Uhler 1977). Structures were considered ossified even if only slightly stained with Alizarin Red. Variation may occur in the ability of specimens to accept alizarin stain because of the variable lengths of time they have been preserved (Dunn 1983). Only general trends in sequences of ossification are, therefore, discussed in this paper.

Counts were made of dorsal, anal, pectoral, pelvic, and caudal fin rays (principal and secondary); neural and haemal spines; abdominal and caudal centra; hypural, epural, and uroneural bones; branchiostegal rays; upper and lower gill rakers; and teeth on the left dentary and palatine as well as all teeth on the vomer and glossohyal.

The sequence of ossification of bones of the cranium, axial skeleton, pectoral and pelvic girdles, and median and paired fins and their supporting bones was traced on the same specimens used for counts of meristic structures. The size of the specimen was noted when individual bones commenced ossification and when bones were consistently ossified. Nomenclature of bones followed Norden (1961) and Borodulina (1969).

Illustrations were made with the aid of a camera lucida. Specimens had been preserved in 3-5% Formalin[6] buffered either with sodium borate or sodium acetate. Illustrations of caudal fin development were made from cleared and stained specimens.

IDENTIFICATION OF *LEUROGLOSSUS SCHMIDTI*

A series of larval and juvenile specimens from plankton samples was linked together by pigment pattern and myomere counts. Adipose fins were present in transformed specimens, indicating they were salmoniform or myctophiform fishes; dorsal and anal fins in postflexion larvae formed in the finfold and attached to the body by "streamers" (Ahlstrom 1969; Moser [1981]), indicating the series was argentinoid. Only two branchiostegal rays were formed in postflexion and juvenile specimens, indicating they were bathylagid fishes. Positive identification was based on knowledge of all bathylagid larvae known to occur in the area (Ahlstrom 1965, 1972, footnote 5) and the following meristic characters (Ahlstrom 1969, footnote 5; Borodulina 1968; Peden 1981; this study):

Dorsal fin rays	= 10-11
Anal fin rays	= 11-14
Pectoral fin rays	= 8-9
Pelvic fin rays	= 8-9
Abdominal vertebrae	= 26-29
Total vertebrae	= 47-52
Branchiostegal rays	= 2
Gill rakers	= 8-9+17-19 = 26-27

Larvae of *L. schmidti* can be readily distinguished from larvae of the other bathylagid and argentinid species occurring in the northeast Pacific Ocean and eastern Bering Sea, based on myomere counts, pigment patterns, and noting whether the eyes are attached to long or short stalks. *Leuroglossus schmidti* larvae, with eyes on short stalks, may be distinguished from their more southerly occurring congener *L. stilbius stilbius* by their larger myomere number (47-52 vs. 38-42) and differences in pigment patterns. Yolk-sac larvae of the two species have similar pigment patterns and can best be separated by myomere counts. Preflexion larvae of *L. schmidti* have two lateral bands of pigment on the trunk whereas preflexion larvae of *L. s. stilbius* have two patches, one near the terminus of the gut and one on the ventral body wall near myomere 16 (Ahlstrom 1965, 1972). Postflexion larvae of *L. schmidti* have several (3-8) lateral melanophores on the body whereas those of *L. s. stilbius* have one or none as shown by Ahlstrom (1965, 1972). *Bathylagus milleri* larvae also lack stalked eyes, have 50-54 myomeres, and, in small larvae (<9 mm), have pigment limited to the ventral body wall and gut near their terminus and on the caudal peduncle; with growth the pigment migrates dorsally, increases to three or four patches, and, in postflexion larvae, is concentrated primarily on the dorsal and ventral body margin and lat-

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

erally on the caudal peduncle and pectoral fin areas (footnote 5). *Bathylagus ochotensis* larvae have eyes borne on moderately long stalks, lateral body melanophores which increase in number during ontogeny, as shown by Ahlstrom (1972), and possess 46-48 myomeres. *Bathylagus pacificus* larvae have eyes carried on long stalks, possess 44-48 myomeres, and initially (at about 4 mm) only two lateral pigment bands—one near the gut terminus and one near the notochord tip. An additional lateral band of melanophores develops at about 45-50% SL (approximately covering myomeres 14-17) in larvae 5-12 mm long. In larvae larger than about 13 mm, the lateral pigment increases to 3-5 patches over the lower body wall and gut (pers. obs.).

Because of the fragile nature of the eye stalks in bathylagid larvae, specimens frequently have their eyes missing or damaged by the collecting gear. If the eyes of the specimen are missing, then at certain sizes (about 5-13 mm), *L. schmidti* could be confused with *B. pacificus*. In addition to a lower myomere count, *B. pacificus* larvae in this size range have lateral body melanophores at about 40-48% and 64-69% SL, whereas *L. schmidti* have such pigment patches located at about 33-40% and 60-64% SL. Also, the pigment on the notochord tip in *B. pacificus* is longer and covers the lateral wall of the notochord, whereas such pigment in *L. schmidti* is limited to the dorsal and ventral portions of the notochord tip.

Larvae of *L. schmidti* in the northeastern Pacific Ocean may be readily distinguished from more southerly cooccurring argentinid larvae in that the latter are characteristically much more intensely pigmented at nearly all sizes as depicted by Schmidt (1906, 1918), Sanzo (1931-33), and Russell (1976).

DEVELOPMENT OF *LEUROGLOSSUS SCHMIDTI*

(Figures 1, 2, 3)

Pigmentation

Although pigmentation in *L. schmidti* varies among similar size specimens and changes in quantity and location with ontogeny, basic trends persist that provide characters useful in identifying the larvae. Descriptions of pigment patterns are based primarily on 57 larvae (4.9-35.0 mm SL) and on 9 transformed juveniles (31.3-55.0 mm SL) preserved <3 yr, in which fading of pigment therefore was minimal.

Head Region

Pigment in the head region is limited primarily to the eyes, jaw, and opercle, develops gradually, and is sparse until transformation. In small larvae (about 5.0-6.5 mm), the head and eyes are unpigmented. The eyes are pigmented in 7 mm larvae, and pigment is sometimes present on the tip of the lower jaw. A pigment spot is present on the posterior portion of the opercle in some larvae as small as 16 mm; this pigment is not consistently present until the larvae reach about 30 mm. At this size, and until transformation (about 31-35 mm), the number and size of the opercle melanophores may vary from one or two large melanophores to three or four small pigment spots; the tip of the lower jaw is sometimes pigmented. After transformation, the head becomes heavily pigmented and the opercle acquires dark melanistic pigment.

Preanal Region

In larvae from about 5.0 to 6.5 mm, gut pigment is limited to a single patch of pigment in the middle portion of the gut. By 7 mm, pigment consists of two lateral bands at about 37-40% SL and 60-64% SL. In larvae 11-12 mm, the anterior and posterior pigment bands have begun to spread laterally to form stellate melanophores. As the larvae grow (about 16-24 mm), one or two pigment spots are sometimes present on the ventral gut below the larval pectoral fins; lateral body pigment usually consists of two to eight stellate melanophores or diagonal streaks of pigment. Pigment near the anus consists of a series of three to six melanophores. In larvae 24-34 mm in length, gut pigment continues to be limited to one or two pigment spots below the larval pectoral fins and a few (3-6) melanophores near the anal tube. Lateral body pigment consists of generally three (range 3-5) stellate melanophores. The pigment spots in the gut region persist in various sizes and numbers until transformation, when the juvenile acquires characteristic dark melanistic pigment over the entire region.

Postanal Region

Preflexion larvae (about 5.0-13.0 mm) lack postanal pigment except on the dorsal and ven-

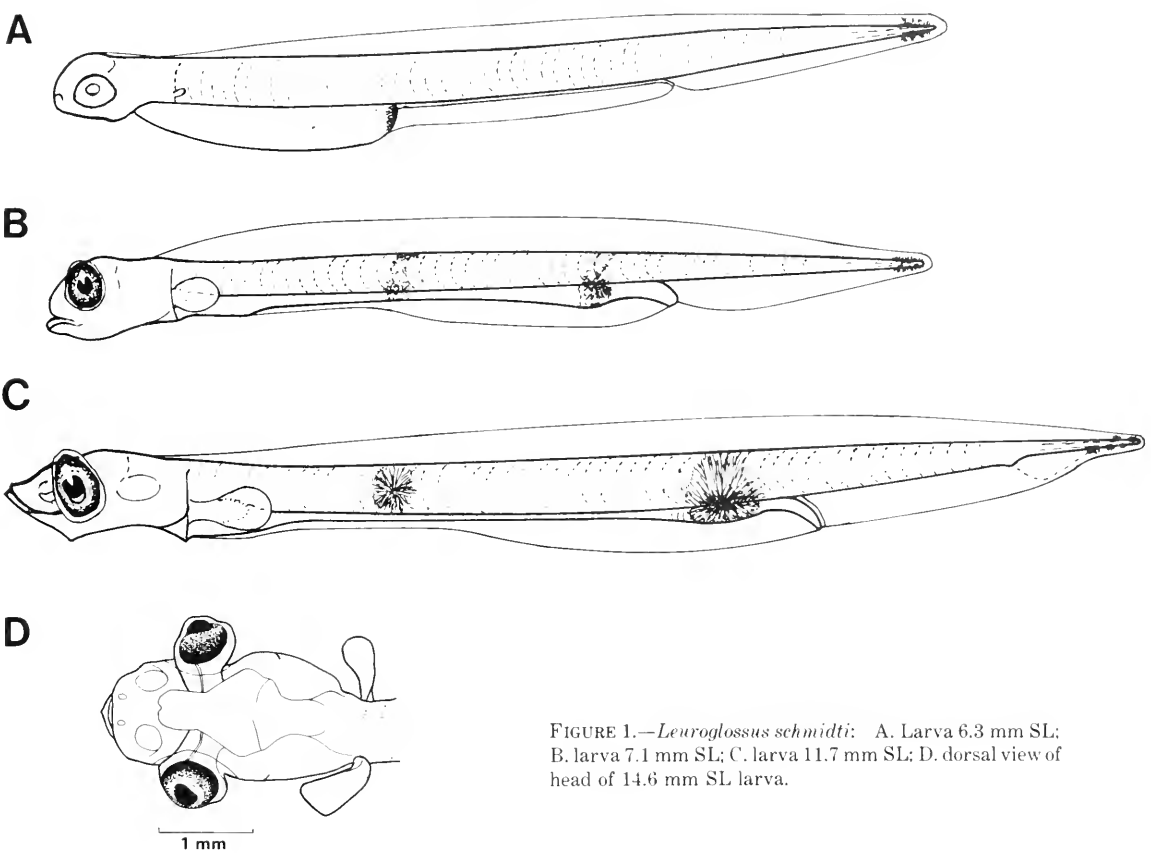


FIGURE 1.—*Leuroglossus schmidti*: A. Larva 6.3 mm SL; B. larva 7.1 mm SL; C. larva 11.7 mm SL; D. dorsal view of head of 14.6 mm SL larva.

tral terminus of the notochord. Dorsal pigment tends to disappear before the pigment on the ventral surface, and notochord pigment is usually lacking in larvae longer than 13 mm. Flexion larvae (13-18 mm) either lack pigment in the postanal region or have a single melanophore in the caudal peduncle region. Postflexion larvae 18-21 mm have zero to two melanophores on the caudal peduncle; larvae from about 22 mm until transformation usually have two lateral melanophores, one on the caudal peduncle and one near the base of the caudal fin rays. After transformation, the juveniles become heavily pigmented with the postanal region covered with small melanophores.

Morphology

(Tables 1, 2)

Larvae of *L. schmidti* are slender, their greatest body depth (about 7-10% SL) occurring at the pectoral fin base. The gut is relatively long, about 75% SL. Notochord flexion begins at about 13 mm and is completed by 18 mm, although the notochord extends posteriad of the hypural bones until transformation (about 31-35 mm). Larvae have a distinctive protruding lower jaw, noticeable at about 7 mm, which becomes more pointed with ontogeny (Figs. 1-3). Eyes are borne on stalks, most noticeable in late flexion larvae (Fig. 1D).

The snout to anus length ranges from about 72% SL in preflexion larvae to nearly 78% SL in postflexion larvae; it is about 74% SL in transformed juveniles. Head length increases as a proportion of standard length from nearly 16% in preflexion larvae to about 29% in transformed juveniles. The eyes are narrow and oblong in larvae. Eye height as a percentage of head length decreases from 39% in preflexion larvae to about 25% in postflexion larvae. Eye width declines as a percentage of head length from nearly 30% in preflexion larvae to about 20% in postflexion larvae.

Interorbital width remains relatively constant,

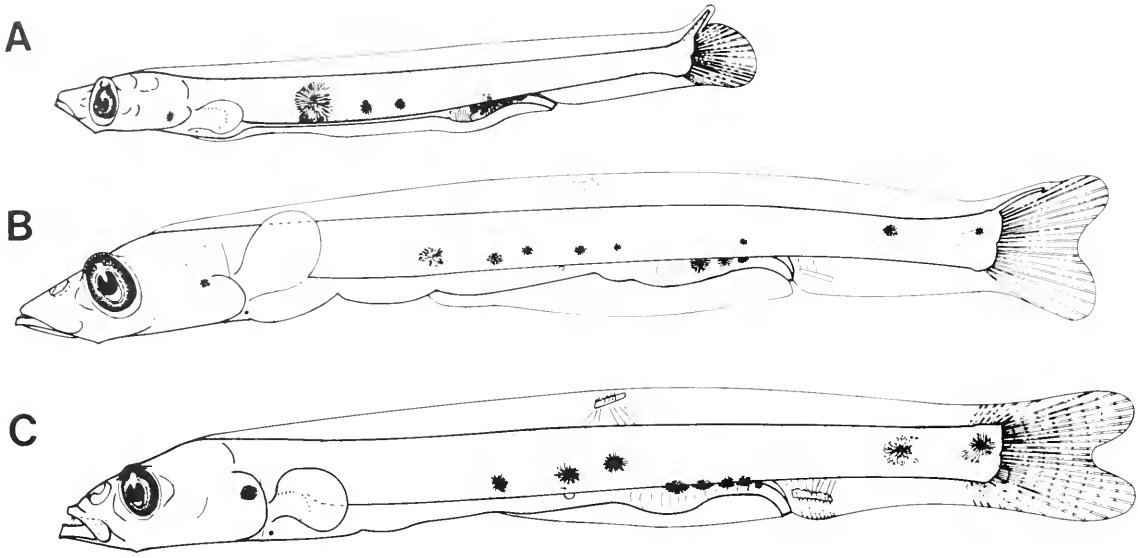


FIGURE 2.—*Leuroglossus schmidti* larvae: A. 16.1 mm SL; B. 24.1 mm SL; C. 33.5 mm SL.

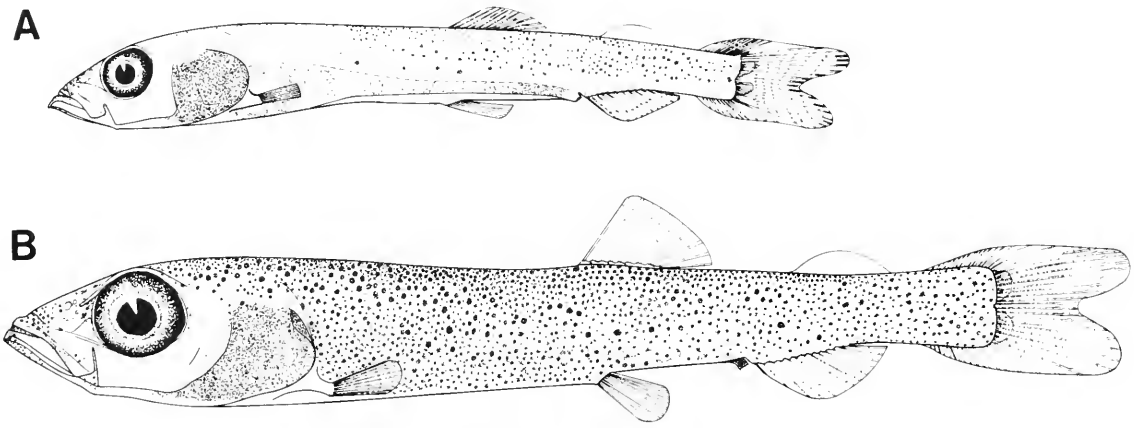


FIGURE 3.—*Leuroglossus schmidti* juveniles: A. 33.1 mm SL; B. 47.8 mm SL.

about 26-30% HL, in larvae but decreases to 22% HL in juveniles. Snout length as a proportion of head length increases from about 24% in preflexion larvae to nearly 32% in postflexion larvae, but declines to about 27% in transformed juveniles. Body depth at the pectoral fin base increases as a percentage of standard length during ontogeny, from about 7% in preflexion larvae to about 14% in transformed juveniles. Body depth at anus also increases during development; in preflexion larvae it is about 5% SL and reaches nearly 9% SL in transformed juveniles.

Larval pectorals are the first fins to form (Fig. 1); pelvic fin buds begin to form in larvae 22-24 mm (Fig. 2B). In postflexion larvae, dorsal and anal fins form in the finfold (Fig. 2B, C) and attach to the body by "streamers" (Ahlstrom 1969) or "hyaline strands" (Moser [1981]).

Considerable morphological changes occur during transformation. The eye stalks disappear and the eyes become round (Fig. 3). Eye height in transformed specimens is nearly 28% and eye width about 29% of head length. The dorsal and anal fins move to attach to the body surface (Fig.

TABLE 1.—Measurements (mm) of plankton-caught larvae and juveniles of *Leuroglossus schmidti*. Specimens between dashed lines are undergoing notochord flexion; specimens between solid lines are juveniles. Numbers in parentheses after measurements indicate sample size for that measurement if different from total sample size.

Length interval (mm)	Sample size (*N*)	Mean length (mm)	Snout to anus length	Snout length	Head length	Inter-orbital width	Eye width	Eye height	Depth at pectoral fin base	Depth at anus	Snout to dorsal fin length	Snout to anal fin length	Snout to pelvic fin length	Caudal peduncle depth	Caudal peduncle length
4.0-4.9	1	4.9	3.4	0.14	0.36	0.20	0.22	0.19	0.31	0.22					
5.0-5.9	1	5.4	4.1	0.26	0.69	0.19	— (0)	— (0)	0.33	0.25					
6.0-6.9	6	6.57	4.62	0.16(3)	0.78	0.23(2)	0.28(2)	0.37(2)	0.49	0.33					
7.0-7.9	11	7.56	5.43	0.15(5)	1.24	0.34(5)	0.32(5)	0.48(5)	0.51	0.32					
8.0-8.9	7	8.31	5.94	0.33(5)	1.34	0.33(5)	0.36(5)	0.52(5)	0.54	0.36					
9.0-9.9	6	9.47	6.72	0.39(3)	1.49	0.38(3)	0.36(3)	0.49(3)	0.57	0.44					
10.0-10.9	10	10.50	7.67	0.46(5)	1.80	0.53(5)	0.47(5)	0.58(5)	0.74	0.49					
11.0-11.9	3	11.30	8.23	0.64(1)	1.95	0.50(1)	0.48(1)	0.56(1)	0.74	0.48					
12.0-12.9	2	12.35	8.70	0.58(1)	2.17	0.65(1)	0.49(1)	0.54(1)	0.91	0.64					
13.0-13.9	3	13.57	10.33	0.55	2.51	0.45	0.51	0.73	1.10	0.63					
14.0-14.9	5	14.42	10.92	0.68	2.71	0.80	0.58	0.75	1.14	0.70					
15.0-15.9	5	15.58	11.84	0.74	2.99	0.76	0.60	0.77	1.31	0.77					
16.0-16.9	5	16.50	12.90	0.88	3.19	0.94	0.59	0.75	1.39	0.85					
17.0-17.9	5	17.46	12.80	0.95	3.34	0.88	0.69	0.86	1.46	0.88					
18.0-18.9	5	18.20	14.08	1.23	3.74	0.99	0.77	0.97	1.63	1.04					
19.0-19.9	5	19.66	15.40	1.28	4.05	1.10	0.82	1.02	1.74	1.04					
20.0-20.9	5	20.36	15.92	1.51	4.10	1.15	0.77	1.05	1.81	1.08		16.2(1)			
21.0-21.9	5	21.20	16.38	1.33(4)	4.32	1.21(4)	0.73	1.17	1.91	1.19		17.1(1)			
22.0-22.9	5	22.48	17.62	1.43	5.00	1.34	1.11	1.18	2.22	1.32		17.90(3)	12.4(1)		
23.0-23.9	5	23.42	17.62	1.60	4.98	1.47	1.03	1.33	2.20	1.35		17.97(3)			
24.0-24.9	5	24.26	20.86	1.85	5.55	1.45	1.19	1.48	2.30	1.36	13.6(1)	18.82(4)	13.0(1)		
25.0-25.9	6	25.35	21.66	1.83	5.84	1.46	1.29	1.53	2.65	1.52	14.38(4)	20.03	13.85(4)		
26.0-26.9	5	26.42	21.70	1.96	6.08	1.42	1.17	1.46	2.60	1.60	15.03(4)	21.18	14.33(3)		
27.0-27.9	5	27.38	22.82	2.07	6.65	1.64	1.44	1.59	2.91	1.66	15.32	21.88(4)	14.46		
28.0-28.9	5	28.36	24.02	2.13	6.54	1.55(4)	1.33	1.57	2.86	1.70	15.54	22.06	15.26		
29.0-29.9	5	29.14	24.25	2.12	7.04	2.04	1.35	1.66	3.16	1.83	16.88	23.18	16.30(4)		
30.0-30.9	5	30.46	25.17	2.25	7.25	1.66	1.58	1.63	3.38	2.02	17.46	24.26	17.04		
31.0-31.9	1	31.2	25.0	2.3	7.5	2.5	1.4	1.8	3.8	2.0	17.9	25.4	17.5		
32.0-32.9	3	32.43	25.17	2.22	7.56	2.50	1.43	1.69	3.45	2.16	18.43	25.60	17.63		
33.0-33.9	1	33.5	25.9	2.2	7.8	2.2	1.5	1.8	3.6	2.2	18.8	26.2	18.4		
34.0-34.9	1	34.0	26.4	2.4	7.8	2.6	1.5	1.8	4.0	2.3	19.8	26.8	17.6		
[1]35.0-35.9	1	35.0	25.9	2.4	10.0	1.3	2.9	2.6	4.6	2.8	19.3	25.7	19.6		
31.0-31.9	1	31.3	23.5	2.5	8.8	2.6	2.5	2.2	4.2	2.4	18.0	24.1	17.4	1.9	5.1
33.0-33.9	2	33.35	24.95	2.48	9.46	1.58	2.50	2.31	4.51	2.78	19.20	25.70	19.15	2.12	4.91
34.0-34.9	1	34.1	25.3	2.7	10.3	1.6	3.0	2.7	4.9	2.9	19.4	25.9	19.5	2.2	5.0
36.0-36.9	1	36.1	26.2	2.8	10.4	1.9	3.0	2.9	4.3	2.9	20.5	26.8	20.4	2.4	5.8
37.0-37.9	1	37.0	27.6	3.1	11.1	2.4	3.4	3.3	5.4	3.3	22.0	28.5	22.0	2.5	5.6
47.0-47.9	1	47.8	35.4	3.9	14.3	3.9	4.5	4.1	6.7	4.3	27.3	36.6	27.6	3.3	6.9
51.0-51.9	1	51.5	38.6	4.6	15.4	4.2	4.8	4.8	8.3	4.8	30.2	40.0	30.5	3.4	7.4
55.0-55.9	1	55.0	39.2	4.7	16.2	4.2	5.0	5.0	9.2	5.8	31.8	40.5	31.0	4.4	7.8

[1]Transforming specimen.

3) and rays develop. Rays develop in the pectoral and pelvic fins. Distinctive "muscle bands," which overlap the base of the caudal fin rays develop in transforming and juvenile specimens (Figs. 2C, 3). The adipose fin develops after transformation (Fig. 3).

TABLE 2.—Body proportions of larvae and juveniles of *Leuroglossus schmidti*. Values given are percentages: mean, standard deviation, and range (in parentheses).

Item	Preflexion larvae		Flexion larvae		Postflexion larvae		Transformed juveniles	
	Number measured	Values	Number measured	Values	Number measured	Values	Number measured	Values
SL range	47	(4.9-12.7)	23	(13.3-17.8)	73	(18.1-35.0)		(31.3-55.0)
Snout to anus length/SL	46	71.8±2.8 (63.5-80.0)	23	75.9±3.4 (66.7-80.7)	73	77.7±1.6 (74.0-80.8)	9	74.0±1.6 (71.3-76.7)
Head length/SL	47	15.7±3.0 (7.0-20.0)	23	19.0±1.6 (16.6-22.8)	73	22.5±2.1 (17.3-28.4)	9	29.2±1.0 (27.5-30.3)
Eye height/HL	23	39.0±13.6 (25.6-78.4)	23	26.2±3.1 (21.6-32.4)	73	24.9±2.6 (17.8-30.6)	9	27.6±2.8 (24.1-31.3)
Eye width/HL	23	29.9±11.9 (22.5-62.8)	23	20.2±2.6 (14.7-24.2)	73	20.4±3.1 (11.3-32.9)	9	29.2±2.0 (25.9-31.5)
Interorbital width/HL	24	29.8±10.3 (18.7-55.6)	23	26.4±6.1 (15.8-38.3)	71	26.6±4.8 (12.9-35.4)	9	22.0±5.4 (15.3-29.4)
Snout length/HL	25	23.8±8.8 (11.1-38.9)	23	26.0±4.1 (14.5-32.4)	72	31.6±3.6 (23.9-46.3)	9	27.4±1.4 (25.7-29.7)
Depth at pectoral fin/SL	47	6.8±1.0 (4.3-9.2)	23	8.3±0.7 (6.9-9.4)	73	10.0±1.1 (8.2-13.1)	9	14.2±1.5 (11.8-16.7)
Depth at anus/SL	46	4.6±0.5 (3.4-5.6)	23	4.9±0.5 (4.2-6.4)	73	6.0±0.7 (4.4-8.0)	9	8.8±0.9 (7.6-10.6)
Snout to dorsal fin length/SL	—	—	—	—	36	56.7±1.5 (53.1-59.3)	9	57.7±0.9 (56.8-59.5)
Snout to anal fin length/SL	—	—	—	—	49	79.0±1.8 (73.4-82.4)	9	76.3±1.6 (73.6-78.6)
Snout to pelvic fin length/SL	—	—	—	—	35	54.6±1.9 (50.6-59.5)	9	57.4±1.4 (55.6-59.5)
Caudal peduncle depth/SL	—	—	—	—	—	—	9	6.7±0.6 (5.9-8.0)
Caudal peduncle length/SL	—	—	—	—	—	—	9	15.0±1.0 (13.3-16.2)

Osteology

(Tables 3, 4; Figure 4)

Although a few structures ossify in relatively small *L. schmidti* larvae, a number of skeletal elements do not calcify until the larvae transform into juveniles. Other portions of the skeleton do not completely ossify until well into the juvenile stage. The general sequence of ossification is as follows: cleithrum; dentary and vomerine teeth; pharyngeal teeth; parasphenoid, dentary, maxillary, vomer, premaxillary; most other bones of the cranium; certain elements of the caudal fin and, at or near transformation, axial skeleton; dorsal, anal, and paired fins; and gill rakers and secondary caudal fin rays.

Teeth

Teeth on the dentary and vomer begin to form in 8 mm larvae (Table 3), increasing in number as the larvae grow and doubling in number at transformation. Dentary teeth appear to increase in number with growth in transformed juveniles, but vomerine teeth remain relatively constant in number. In specimens about 12 mm long, one pharyngeal tooth develops on each plate (Table 4); after transformation the teeth then increase to three. Borodulina (1969) also reported three teeth on the pharyngeal plate in adult *L. schmidti*. Teeth on the glossohyal and palatine develop in larvae 16-18 mm long (Table 3). Glossohyal teeth disappear during transformation and are absent in juveniles and adults: hence, the common name "smoothtongue" for *L. schmidti*. A single palatine tooth is present during the larval stage; the number of palatine teeth increases after transformation (Table 3).

Skull

The dentary, maxillary, parasphenoid, and operculum begin to ossify in 14-15 mm larvae (Table 3). In larvae 18-21 mm long, the premaxillary, pre-, sub-, and interopercle bones, vomer, symplectic, branchiostegal rays, and urohyal begin ossifying in some larvae (Tables 3, 4). These structures, however, are not consistently calcified until larvae reach about 28 mm long (32 mm for the urohyal).

Certain bones of the olfactory, orbital, otic, and oromandibular regions and much of the hyoid arch begin to ossify in some larvae 24-26 mm

TABLE 3.—Development of meristic and other structures in *Leuroglossus schmidti* larvae and juveniles. Mean data are given for specimens in the specified length range. Specimens between dashed lines are undergoing notochord flexion; those between solid lines are juveniles.

SL (mm)	Sample size	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays	Principal caudal rays		Secondary caudal rays		Neural spines	Haemal spines	Centra		
						Upper	Lower	Upper	Lower			Abdom	Caudal	Total
5.9-7.9	12													
8.0-8.9	6													
9.0-9.9	5													
10.0-10.9	1													
11.0-11.9	1													
12.0-12.9	2													
13.0-13.9	1													
14.0-14.9	1													
15.0-15.9	3													
16.0-16.9	1													
17.0-17.9	3													
18.0-18.9	6					2.2	2.0							
19.0-19.9	3													
20.0-20.9	4					4.3	4.5	0.3	0.3					
21.0-21.9	1					10.0	9.0	2.0	2.0					
22.0-22.9	5					2.0	1.8	0.4	0.4					
23.0-23.9	5					4.0	3.6	1.0	1.2		0.4			
24.0-24.9	4					5.0	4.5	1.0	1.3		0.3			
25.0-25.9	5					8.0	7.2	1.2	1.8		0.2			
26.0-26.9	6					6.7	6.0	0.3	0.3					
27.0-27.9	3					6.7	6.0	0.7	1.0		0.7			
28.0-28.9	4					7.5	6.8	3.0	3.0		0.8			
29.0-29.9	4					10.0	9.0	3.0	3.3	0.5	0.8		0.3	0.3
30.0-30.9	4					10.0	9.0	3.3	4.8	0.8	2.0		0.3	[1]12.8
31.0-31.9	2					10.0	9.0	3.0	4.0		0.5		0.5	0.5
32.0-32.9	1					10.0	9.0	2.0	1.0					
33.0-33.9	1					10.0	9.0	5.0	5.0	2.0	2.0		1.0	1.0
34.0-34.9	1					10.0	9.0	4.0	5.0		1.0		1.0	1.0
31.0-31.9	1	10.0	13.0	9.0	8.0	10.0	9.0	13.0	14.0	49.0	23.0	27.0	23.0	50.0
33.0-33.9	1	10.0	13.0	7.0	9.0	10.0	9.0	13.0	12.0	51.0	24.0	28.0	24.0	52.0
35.0-35.9	2	10.0	12.5	7.5	9.0	10.0	9.0	14.0	13.5	49.5	23.5	27.0	23.5	50.5
37.0-37.9	1	10.0	11.0	9.0	9.0	10.0	9.0	15.0	15.0	49.0	24.0	27.0	24.0	51.0
44.0-44.9	1	10.0	11.0	6.0	9.0	10.0	9.0	15.0	13.0	49.0	23.0	27.0	23.0	50.0
51.0-51.9	1	10.0	12.0	9.0	9.0	10.0	9.0	15.0	15.0	50.0	24.0	27.0	24.0	51.0

SL (mm)	Sample size	Hypurals	Epurals	Uroneurals	Branchiostegal rays	Gill rakers			Teeth			
						Upper	Lower	Total	Dentary	Glossohyal	Vomer	Palatine
5.9-7.9												
8.0-8.9	6								0.7		0.7	
9.0-9.9	5								0.4		0.4	
10.0-10.9	1											
11.0-11.9	1								2.0		1.0	
12.0-12.9	2											
13.0-13.9	1								2.0		1.0	
14.0-14.9	1								3.0		1.0	
15.0-15.9	3				0.3				2.0		0.7	
16.0-16.9	1								5.0	2.0	3.0	
17.0-17.9	3								3.7	1.7	1.3	0.3
18.0-18.9	6				0.7				4.0	1.3	2.5	0.2
19.0-19.9	3				0.7				4.3	1.3	2.0	0.7
20.0-20.9	4	1.8		0.5	1.0				10.0	2.5	3.0	0.8
21.0-21.9	1	7.0		2.0	2.0				10.0	3.0	3.0	2.0
22.0-22.9	5	1.4		0.4	0.4				9.0	3.0	3.0	1.0
23.0-23.9	5	2.8		1.0	1.2				10.4	2.8	3.0	1.0
24.0-24.9	4	3.0		1.3	2.0				10.8	2.3	3.0	1.0
25.0-25.9	5	1.2		1.6	1.2				11.8	2.4	3.0	1.0
26.0-26.9	6			1.3	1.7				12.0	2.3	3.0	1.0
27.0-27.9	3	2.3		1.3	1.3				11.0	3.0	3.0	1.0
28.0-28.9	4	5.3		1.5	2.0				13.0	2.8	3.0	1.0
29.0-29.9	4	4.8		2.0	2.0				11.8	2.8	3.0	1.0
30.0-30.9	4	5.0		2.0	2.0	1.0	2.8	3.8	14.0	3.0	3.0	1.0
31.0-31.9	2	6.0		2.0	2.0				13.0	2.5	3.0	1.0
32.0-32.9	1			2.0	2.0				14.0	3.0	3.0	1.0
33.0-33.9	1	7.0		2.0	2.0				12.0	3.0	3.0	1.0
34.0-34.9	1	7.0		2.0	2.0				11.0	3.0	3.0	1.0
31.0-31.9	1	7.0		2.0	2.0	7.0	15.0	22.0	24.0	2.0	6.0	3.0
33.0-33.9	1	7.0		2.0	2.0	7.0	14.0	21.0	28.0		9.0	4.0
35.0-35.9	2	7.0		2.0	2.0	7.0	14.5	21.5	27.5		6.5	4.0
37.0-37.9	1	7.0	1.0	2.0	2.0	7.0	14.0	21.0	34.0		8.0	7.0
44.0-44.9	1	7.0		2.0	2.0	7.0	17.0	24.0	32.0		10.0	4.0
51.0-51.9	1	7.0	1.0	2.0	2.0	9.0	17.0	26.0	46.0		9.0	5.0

[1]Haemal spines not fully differentiated on one specimen with 50 centra ossifying. It was therefore not possible to determine the number of precaudal vertebrae in that specimen.

TABLE 4.—Sequence of ossification in larvae and juveniles of *Leuroglossus schmidti*. The initial ossification of an element is indicated by X. A dashed line indicates that an element is ossified in some, but not all, specimens; a solid line indicates the element is consistently ossified. A question mark indicates the length at which ossification commences is unknown.

Element	Standard length (mm)																															
	7.0–7.9	8.0–8.9	9.0–9.9	10.0–10.9	11.0–11.9	12.0–12.9	13.0–13.9	14.0–14.9	15.0–15.9	16.0–16.9	17.0–17.9	18.0–18.9	19.0–19.9	20.0–20.9	21.0–21.9	22.0–22.9	23.0–23.9	24.0–24.9	25.0–25.9	26.0–26.9	27.0–27.9	28.0–28.9	29.0–29.9	30.0–30.9	31.0–31.9	32.0–32.9	33.0–33.9	34.0–34.9	31.0–31.9	33.0–33.9	35.0–35.9	37.0–37.9	44.0–44.9	51.0–51.9
Olfactory region																																
Supraethmoid																					x											
Infraethmoid																					x											
Vomer												x																				
Nasal																		x														
Antorbital																							x									
Prefrontal																																
Orbital region																																
Pterosphenoid																																
Suborbital																			x													
Postorbital																																
Supraorbital 1																					x											
Supraorbital 2																					x											
Preorbital																																
Parietal																																
Frontal																x																
Dermosphenotic																																
Otic region																																
Sphenotic																																
Pterotic																x																
Prootic																						x										
Epiotic																							x									
Exoccipital																			x													
Neurocranium																																
Parasphenoid																																
Opisthotic								x												x												
Extrascapular																							x									
Basioccipital																				x												
Supraoccipital																							x									
Frontal															x																	
Oromandibular region																																
Premaxillary													x																			
Maxillary									x																							
Palatine																		x														
Ectopterygoid																					x											
Quadrate																	x															
Mesopterygoid																x																
Anular								x																								
Angular																	x															
Retroarticular																		x														
Coronomeckelum																													x			
Hyoid arch																																
Hyomandibular																x																
Symplectic														x																		
Interhyal																												x				?
Ceratohyal																	x															
Hypohyal																x																
Urohyal														x																		
Basihyal																	x															
Epihyal																	x															
Glossohyal															x																	
Opercular series																																
Preoperculum												x																				
Operculum									x																							
Suboperculum												x																				
Interoperculum												x																				
Branchial arches																																
Pharyngeal teeth						x																										?
Hypobranchials																												x				?
Ceratobranchials																												x				?
Epibranchials																												x				?
Pharyngobranchials																												x				?
Appendicular skeleton																																
Cleithrum	x																															
Posttemporal												x																				
Supracleithrum									x																							
Scapula																																?
Proximal radials (pectoral)																																?
Basipterygium																												x				?
Coracoid																													x			?

TABLE 4.—*Continued.*

Element	Standard length (mm)																											
	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149	150–159	160–169	170–179	180–189	190–199	200–209	210–219	220–229	230–239	240–249	250–259	260–269	270–279	280–289	290–299	300–309	310–319	320–329	330–339	340–349	'310–319	'330–339	'350–359	'370–379	'440–449	'510–519
Axial skeleton																																		
Proximal radials (dorsal fin)																														x				?
Medial and distal radials (dorsal fin)																																		?
Proximal radials (anal fin)																														x				?
Medial and distal radials (anal fin)																																		?
Predorsal bones																																x		?
Ribs																													x	—	—	—	—	?
Epineural ribs																													x	—	—	—	—	?
Epipleural ribs																													x	—	—	—	—	?

long (Table 4). However, most of these bones are not consistently ossified until the specimens reach transformation.

In larvae 26-31 mm long, most cranial structures begin to ossify, although a number of bones are not consistently ossified until the larvae transform (Table 4). Most structures in the oromandibular region and opercle series are consistently ossified in 30 mm larvae. Conversely, most elements of the olfactory, orbital, and otic regions as well as most bones of the neurocranium and hyoid arch are not consistently ossified until the larvae transform. Some bones (nasal, antorbital, prefrontal, epiotic, extrascapular, supraoccipital, and ectopterygoid) become consistently ossified after transformation; others (interhyal and all of the branchial arches), however, are not consistently ossified even in the largest transformed juveniles examined (51.6 mm).

Axial Skeleton

The haemal spine on preural centrum 1 (PU_1) commences ossification in some larvae 23-24 mm long [I follow Ahlstrom and Moser (1976) in considering the centrum adjacent to the anterior ural centrum as preural centrum 1; this would be PU_2 of Monod (1968)]. The neural spine on PU_1 is partially ossified in some larvae 29-30 mm long. Neural and haemal spines apparently ossify rapidly during transformation; all are fully ossified in transformed juveniles. The sequence in which neural and haemal spines ossify could not be determined.

The first vertebra to ossify is the first ural centrum (U_1), which is ossified in some larvae 29-30 mm long. Centra, like neural and haemal spines, ossify rapidly as the larvae transform. Generally, either only the first ural centrum accepts alizarin stain or all the vertebrae are ossified. In one specimen 30.6 mm long, however, 50 centra are partially ossified. In this specimen, centra 6-41 are completely encircled with red, whereas centra 1-5 and 42-50 are ossified only at the ventral surface. This pattern of ossification suggests that the preural centra initially ossify near the center of the vertebral column and ossification proceeds both anteriorly and posteriorly.

Other structures of the axial skeleton ossify during or after transformation (Table 4). Proximal radials of the dorsal and anal fins begin ossifying after transformation; medial and distal radials are not ossified in any samples examined. Ribs, on centra 2 to 27-28, are ossified on all trans-

formed specimens as are epineural (centra 1-35) and epipleural (centra 17-34) ribs. Predorsal bones (18 in specimens examined) are partially ossified only in one 37.1 mm transformed juvenile, but not in a 51.6 mm specimen.

Appendicular Skeleton

The cleithrum is the first bone to commence ossification (at about 7 mm) in larvae of *L. schmidti* (Table 4), but it is not consistently calcified in larvae <24 mm. The supracleithrum and posttemporal are ossifying in some specimens as small as 15 and 18 mm, respectively. The coracoid is ossified in only one transformed specimen; the scapula and proximal radials of the pectoral fin are not ossified in any transformed specimens. The basipterygium of the pelvic fin is ossified in transformed specimens.

Fins

The caudal fin is the first fin to commence development in *L. schmidti* (Table 3), but secondary rays are not completely formed until after transformation. The caudal complex consists of seven preural and two ural centra (the latter fuses into a single urostyle during ontogeny), two pairs of uroneurals, one epural, and seven hypural bones (Table 3; Fig. 4). There are 10 superior and 9 inferior principal caudal rays. The numbers vary, but generally 15 dorsal and 15 ventral secondary caudal rays are supported by cartilaginous plates, lying between the neural and haemal spines of the caudal complex.

The anlage of the caudal fin is evident in 6.4 mm larvae (Fig. 4a). In 11.5 mm larvae, four cartilaginous hypural bones and the posteriormost haemal spine are evident (Fig. 4b). In a 15.3 mm larvae, three haemal spines and five hypural bones are present in cartilage. The hypural bones support 4+2 unossified principal caudal rays (Fig. 4c). In larvae 18-19 mm long, seven unossified hypural bones are present; they support 10+9 principal caudal rays, variable numbers of which are beginning to ossify (Table 3). The anterior uroneural is discernible but unossified (Fig. 4d). Development of the caudal fin proceeds rapidly in larvae >20 mm. In a 23.1 mm specimen (Fig. 4e) all seven hypural bones, 10+9 principal rays, and 2+2 secondary rays are ossifying. Both pairs of uroneurals are ossified. A single unossified epural and a number of unossified neural and haemal spines can be observed. The

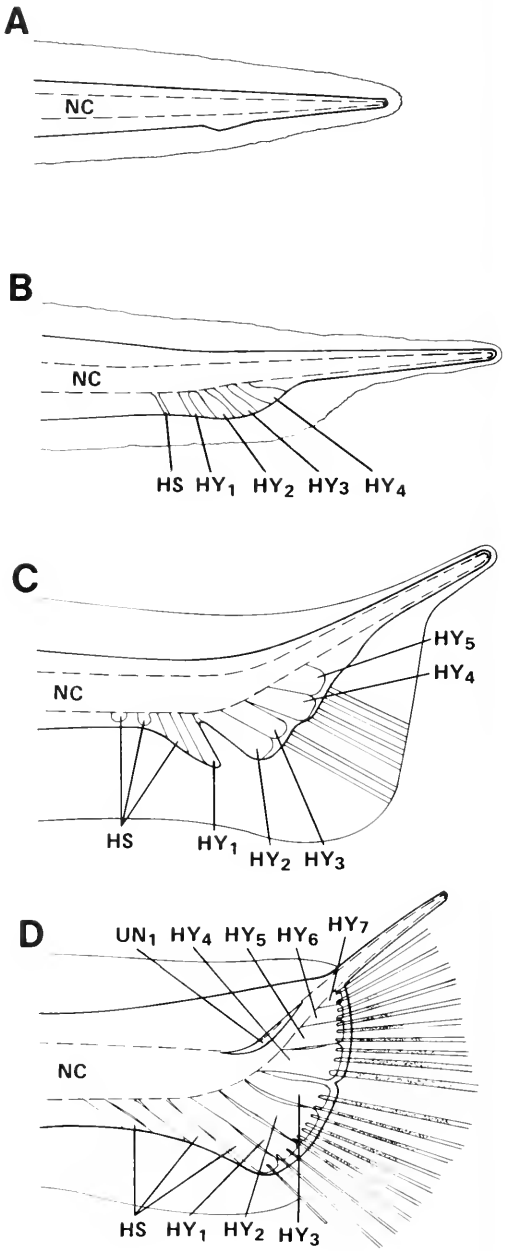
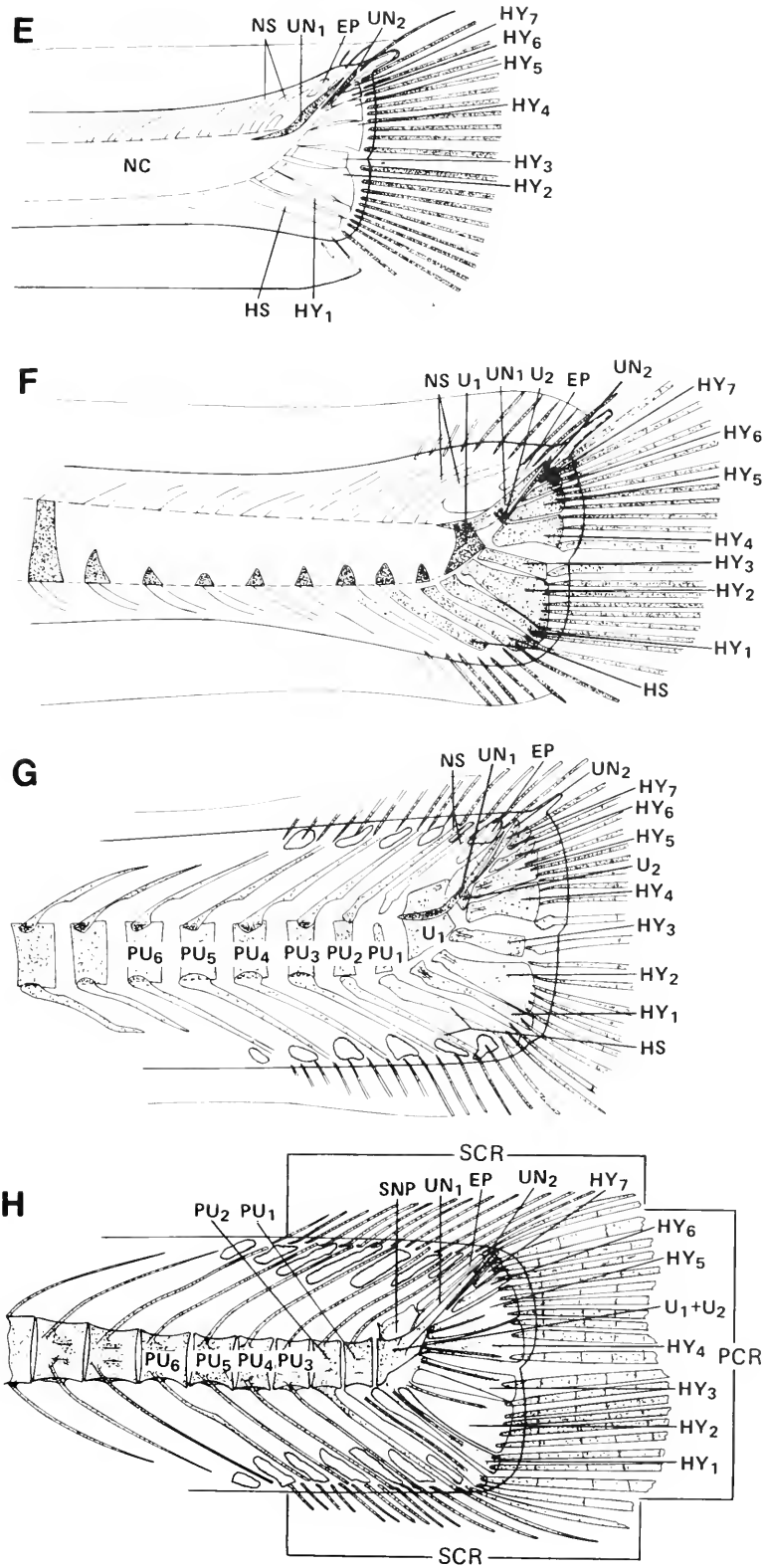


FIGURE 4.—Development of the caudal fin of *Leuroglossus schmidti*: A, 6.4 mm SL; B, 11.5 mm SL; C, 15.3 mm SL; D, 18.4 mm SL; E, 23.1 mm SL; F, 30.6 mm SL; G, 35.1 mm SL; H, 51.6 mm SL. Ossified elements are stippled. NC = notochord; HY = hypurals; EP = epural; HS = haemal spine; UN = uroneural; NS = neural spine; U = ural centra; PU = preural centra; SNP = specialized neural process; PCR = principal caudal rays; SCR = secondary caudal rays.


E
NS UN1 EP UN2
HY7
HY6
HY5
HY4
HY3
HY2
NC
HS HY1
F
NS U1 UN1 U2 EP UN2
HY7
HY6
HY5
HY4
HY3
HY2
HY1
HS
G
NS UN1 EP UN2
HY7
HY6
HY5
U2
HY4
HY3
HY2
HY1
HS
U1
PU6 PU5 PU4 PU3 PU2 PU1
H
SCR
SNP UN1 EP UN2 HY7
PU2 PU1
HY6
HY5
U1+U2
HY4
HY3
HY2
HY1
PCR
PU6 PU5 PU4 PU3
SCR

adult complement of 10+9 principal caudal rays is consistently ossified in 29-30 mm larvae, but secondary caudal rays are not completely developed until after transformation. In a 30.6 mm specimen (Fig. 4f), ural centra 1 and 2 are ossifying as are two neural spines associated with preural centra 1 and 2 and haemal spines associated with preural centra 1-4. The bases of preural centra 1-8 are beginning to ossify.

In a 35.1 mm transformed juvenile, all centra of the caudal complex, preural and ural, are ossified as is the specialized neural process (Hollister 1936) dorsad to U_1 (Fig. 4g). Ural centra 1 and 2 are still separate. Neural and haemal spines and principal and secondary caudal rays are fully ossified. The hypural bones are separate and autogenous in this specimen. A 51.6 mm juvenile has ural centra 1 and 2 fused into a single urostyle (Fig. 4h). The single epural is beginning to ossify and hypural bones 1-3 are fused together at their bases and ankylosed to the urostyle. Hypural bones 4-7 are still autogenous in this specimen. In this specimen, the 10 superior principal caudal rays are distributed as follows: hypural 7, one ray; hypural 6, two rays; hypural 5, four rays; hypural 4, three rays. The inferior nine principal rays included one ray on hypural 3, five rays on hypural 2, two rays on hypural 1, and one ray on the posteriormost haemal spine. During the development of the caudal fin, the ventralmost principal caudal ray is associated with hypural 1; it apparently is displaced to articulate with the ultimate haemal spine in some, but not all, juvenile specimens.

Dorsal and anal fin rays ossify rapidly during transformation as do pectoral and pelvic fin rays (Table 3). It was not possible to follow the sequence of ossification of individual rays in these fins. The adult complement of dorsal, anal, and pelvic fin rays is present on the smallest transformed specimen. The adult complement of eight to nine pectoral rays, however, is not present in all transformed specimens examined. Scales are not present in a 55.0 mm juvenile, but they are reported to be deciduous (Hart 1973), and hence, may have been lost during capture.

COMMENTS ON THE VALIDITY OF THE GENUS *LEUROGLOSSUS* GILBERT AND THE SPECIFIC STATUS AND NAME OF *L. SCHMIDTI*

The results of this study offer support for the validity of the genus *Leuroglossus* Gilbert which has been questioned. Gilbert (1890) erected the genus *Leuroglossus* in the family Argentinidae for specimens from the Gulf of California that he described as *Leuroglossus stilbius*. Chapman (1943) reviewed *Leuroglossus* Gilbert, removed it from Argentinidae, and placed it in Bathylagidae. Cohen (1964) synonymized *Leuroglossus* Gilbert with *Bathylagus* Günther. Borodulina (1968) stated *Leuroglossus* lacked an orbitosphenoid bone, although Cohen (1964) said it was present in *Leuroglossus* and used its presence as a generic character for *Bathylagus*. Borodulina (1969) later described the osteology of *L. schmidti* and compared it with *B. pacificus* (based on Chapman 1943). She stated that *Leuroglossus*, in contrast to *Bathylagus*, lacked an orbitosphenoid, possessed teeth on the palatine, had three denticles on the last pharyngobranchial, and possessed antorbitals. Ahlstrom (1969) described differences in the movements of oil globules between *Bathylagus* and *Leuroglossus* eggs which, with the lack of an orbitosphenoid in *Leuroglossus* (as reported by Borodulina 1968), he felt, lent additional support to the validity of *Leuroglossus* as a genus distinct from *Bathylagus*.

My samples of *Leuroglossus* lacked an orbitosphenoid, whereas those cleared and stained specimens I examined of *Bathylagus* did possess an orbitosphenoid. Specimens of *B. pacificus*, *B. ochotensis*, and *B. milleri* I examined lacked teeth on the pharyngobranchials, whereas *Leuroglossus* possesssed three teeth on the fourth pharyngobranchial.

Based in part on the lack of an orbitosphenoid in *Leuroglossus*, the presence of one in *Bathylagus* and the differences in the movements of oil globules in the eggs of these two genera, as reported by Ahlstrom (1969), I follow Borodulina (1969) and Ahlstrom (1969) in considering the two genera distinct. The number of valid genera in the Bathylagidae and analysis of their relationships, however, await further study of the entire family.

This study provides additional evidence to recognize *L. schmidti* as a species distinct from *L. stilbius*. Rass (1955) described a northern subspecies, *L. stilbius schmidti*, from the Kurile-Kamchatka Trench, based on morphometric measurements which differed from measurements described by Gilbert (1890). Cohen (1956) synonymized *L. s. schmidti* with *L. stilbius*, asserting that the proportions used by Rass to describe *L. s. schmidti* were size dependent. Borodulina (1968) pointed out that *L. stilbius* had

39-42 vertebrae, whereas *L. schmidti* possessed 49-51 vertebrae. Borodulina (1968) considered *L. schmidti* to be a subspecies of *L. stilbius*, although she suggested that *L. schmidti* might subsequently be recognized as a separate species, a suggestion that she did not pursue because of insufficient material. She also considered *L. urotranus* (Bussing 1965), described from the Peru-Chile Trench, to be another subspecies of *L. stilbius*. Ahlstrom (1968) noted the differences in vertebral counts in *L. stilbius* and *L. schmidti*. Subsequently Ahlstrom (1969) pointed out the differences in egg size, pattern in migration of oil globules during embryonic development, larval pigment, and body proportions between *L. stilbius* and *L. schmidti* which, along with differences in vertebral counts, he felt, enabled recognition of *L. schmidti* as a distinct species.

Peden (1981) examined vertebral numbers in *Leuroglossus* from samples collected from Mexico to the Aleutian Islands and westward to Japan. He noted that samples of *Leuroglossus* from British Columbia waters had an average of 8.5 more vertebrae than those samples collected off Oregon. He therefore recognized *L. schmidti* as distinct from *L. stilbius stilbius*. As presently known, the geographical ranges of the two species do not overlap, as discussed below. Based on the differences in vertebral counts in the two nominal species reported by Borodulina (1968, 1969) and Peden (1981), the evidence presented by Ahlstrom (1968, 1969), and the results of this study, I consider *L. schmidti* specifically distinct from *L. stilbius*.

The valid name of the northern smoothtongue is considered here to be *L. schmidti*, rather than *Therobromus callorhini* or *Leuroglossus callorhini*. *Therobromus callorhini* was described by Lucas (in Jordan and Gilbert 1899) from bones extracted from fur seal stomachs collected in the Bering Sea. He noted that the specimens had 26 precaudal and 23 caudal vertebrae and placed the species in Osmeridae. Chapman (1941) showed that *T. callorhini* was not an osmerid and later (Chapman 1943) he suggested that *T. callorhini* (emended to *callorhinus*) was most likely identical with either *Bathylagus pacificus* or *B. alascanus* (= *B. milleri*). Cohen (1964) synonymized *Therobromus* Lucas with *Bathylagus* Günther. Ahlstrom (1968, 1969) suggested that the correct name of *L. schmidti* was *Leuroglossus callorhini*, but did not formally propose such a synonomy.

If the two names do refer to the same species, then *L. schmidti* is a junior synonym of *T. callorhini*. The type material of *Therobromus callorhini* Lucas apparently no longer exists (according to D. M. Cohen[7]). However, as the name *T. callorhini* has apparently not been used as a senior synonym in more than 50 yr (Chapman 1943), *T. callorhini* constitutes a *nomen oblitum* according to the International Code of Zoological Nomenclature (Stoll et al. 1964). Hence, I consider the valid name of the northern smoothtongue to be *Leuroglossus schmidti*.

OCCURRENCE OF EGGS AND LARVAE OF *LEUROGLOSSUS SCHMIDTI*

(Figure 5)

Eggs and larvae of *L. schmidti* are broadly distributed in near-coastal waters from about southern Vancouver Island, British Columbia, to the central Bering Sea. In midocean they are apparently distributed as far south as lat. 46°N, since eggs and larvae of *L. schmidti* were collected in 1951 and 1955 from about lat. 46°-57°N and long. 149°-179°W (Ahlstrom 1969; Moser[8]). They have apparently not been found in coastal waters off Oregon, however, as the relatively few specimens of *Leuroglossus* larvae, collected off Oregon by Oregon State University, consisted exclusively of *L. stilbius stilbius* (Richardson 1973; Washington[9]). The results of an ichthyoplankton survey conducted in October-November 1971 from off Washington (lat. 46°45′N) to Dixon Entrance, British Columbia (lat. 54°30′N), were reported by Naplin et al. (footnote 4). Eggs of *L. schmidti* were found only north of lat. 53°N off Queen Charlotte Islands, whereas only *L. stilbius stilbius* eggs were collected south of lat. 51°N off Vancouver Island and coastal Washington. The few *Leuroglossus* larvae collected during this cruise were all *L. schmidti*, and they were taken only north of lat. 54°N. Possibly the eggs identified as *L. stilbius stilbius* off Vancouver Island

[7]D. M. Cohen, National Systematics Laboratory, National Marine Fisheries Service, National Museum of Natural History, Washington, D.C. (present address: NWAFC, NMFS, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112), pers. commun. July 1980.

[8]H. G. Moser, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, pers. commun. March 1980.

[9]B. B. Washington, School of Oceanography, Oregon State University, Corvallis, Oreg. (present address: Gulf Coast Research Laboratory, Ocean Springs, MI 39564), pers. commun. November 1980.

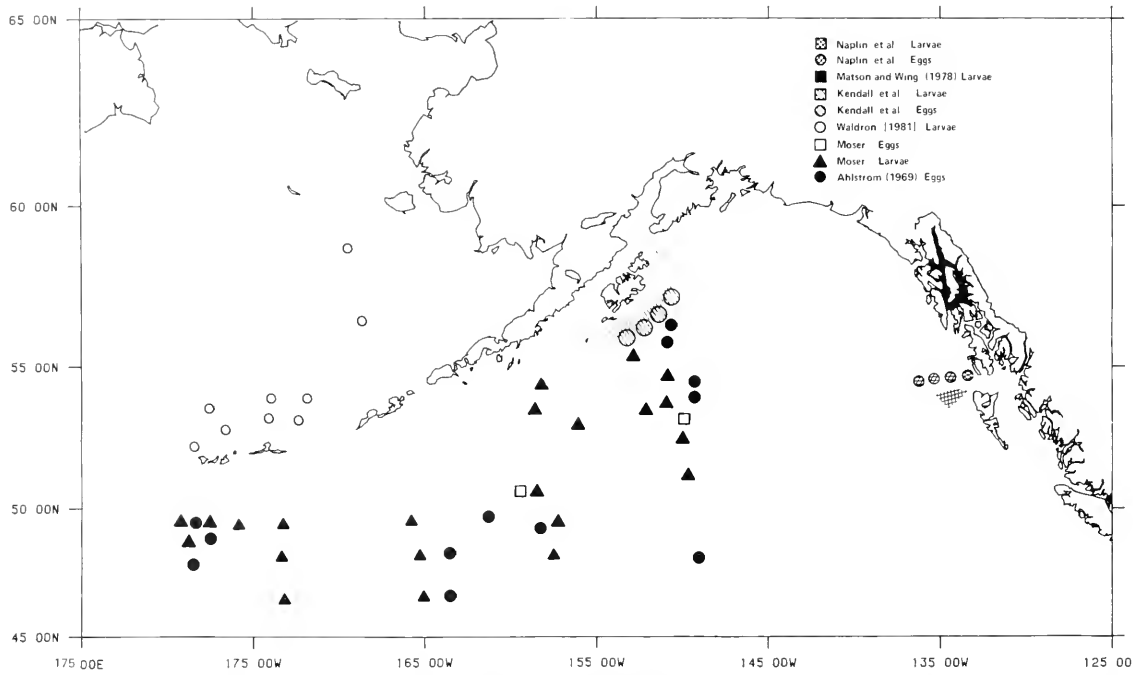


FIGURE 5.—General areas where eggs and larvae of *Leuroglossus schmidti* have been reported. Key: Naplin et al. (text footnote 4); Matson and Wing (1978); Kendall et al. (text footnote 3); Waldron [1981]; Moser (text footnote 8); Ahlstrom (1969).

could have been transported northward from more southerly spawning areas. During this cruise, surface geostrophic currents indicated a 6 cm/s northward flow offshore from about lat. 47°N to 51°N (Naplin et al. footnote 4).

Leuroglossus schmidti larvae were the third most abundant fish larvae collected in plankton samples from coastal waters of southeastern Alaska (lat. 56°50′-59°28′N, long. 133°10′-135° 23′W) in April-November 1972 (Mattson and Wing 1978). This species accounted for 4.5% of the total catch of fish larvae; abundance was high from May to August, peaking in June and July. Plankton sampling in Kodiak Island shelf waters from November 1977 through March 1979 revealed that eggs of *L. schmidti* were found principally at the shelf break (water depth >200 m); abundance was greatest in the fall, but eggs were found in small numbers in summer and winter (Kendall et al. footnote 3). Larvae were also most abundant over the shelf break in the fall, but seasonal abundance was not determined. Waldron [1981] summarized available distribution data on larvae and juveniles of *L. schmidti* occurring in the eastern Bering Sea from 1955 to 1978. Based on plankton sampling conducted by the United States, U.S.S.R., and Japan (primarily during summer) utilizing a variety of sampling devices, larvae identified as *L. schmidti* were most frequently reported over the shelf break.

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DELINEATION OF TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*, STOCKS ALONG THE UNITED STATES EAST COAST AND IN THE GULF OF MEXICO

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ABSTRACT

Tilefish, *Lopholatilus chamaeleonticeps*, are an important commercial species in the Mid-Atlantic Bight and the focus of developing fisheries in the South Atlantic Bight and the Gulf of Mexico. Attempts were made to delineate stocks over this range by analyzing for variation in morphology (28 meristic and morphometric characters) and electrophoretic migration of eye, liver, and muscle proteins. Morphological and electrophoretic data (liver isocitrate dehydrogenase and liver esterase) consistently supported a separate Mid-Atlantic Bight stock. Electrophoretic data suggested that South Atlantic Bight and Gulf of Mexico samples belonged to a separate, single stock. This was not consistently supported by the more variable morphometric characters. It was suggested that Mid-Atlantic Bight populations be treated as a separate stock and, as a working hypothesis, that South Atlantic and Gulf of Mexico populations be considered as a second stock.

Tilefish, *Lopholatilus chamaeleonticeps*, are distributed from southern Nova Scotia (Leim 1960; Markle et al. 1980) south to off Surinam, South America, (Wolf and Rathjen 1974) and throughout the Gulf of Mexico (Bigelow and Schroeder 1947; Hoese and Moore 1977) but exclusive of the Caribbean Sea (Dooley 1978). The tilefish is the basis for a valuable bottom longline fishery in the Mid-Atlantic Bight (Grimes et al. 1980), and this fishery is developing elsewhere along the east coast of the United States and in the Gulf of Mexico. This paper investigates tilefish populations to determine if separate stocks can be identified over this range.

There are several reasons to suspect that distinct stocks of tilefish may occur. Tilefish probably have a restricted habitat. They are reported from rather narrow temperature ranges (9°-14°C) at the edge of the continental shelf along the east coast (Goode 1884; Rathburn 1895; Bigelow and Schroeder 1953) and in the Gulf of Mexico (Nelson and Carpenter 1968; Wolf and Rathjen 1974). Also, preliminary tagging studies (Grimes et al. in press) suggested that individual tilefish moved <2 km in over 1 yr. These observations are supported by submersible observations which suggest that tilefish are resident in temporally stable burrows of their own construction (Able et al. 1982). In the Mid-Atlantic Bight, tilefish are caught the year-round which also suggests that these may be resident populations. In addition, the prevailing current patterns, temperature regimes, and species distribution patterns along the east coast suggest that important faunal boundaries may exist at Cape Hatteras and around the Florida peninsula (see Briggs 1974 for discussion). This study reports on morphological and electrophoretic characteristics of tilefish from the U.S. east coast and the Gulf of Mexico. The distribution of the characters were used to test the null hypothesis that there are no differences among these populations.

MATERIALS AND METHODS

Tilefish samples were obtained from commercial fishermen or collected by hook and line on exploratory fishing cruises (National Marine Fisheries Service RV *Oregon II*) during 1978 and 1979 (Fig. 1) (Katz 1982). Information on physical conditions at collection were unavailable, but temperature is known to be relatively constant throughout the range (see above). Fish were transported fresh, on ice, or frozen, depending on distance of collection from the laboratory.

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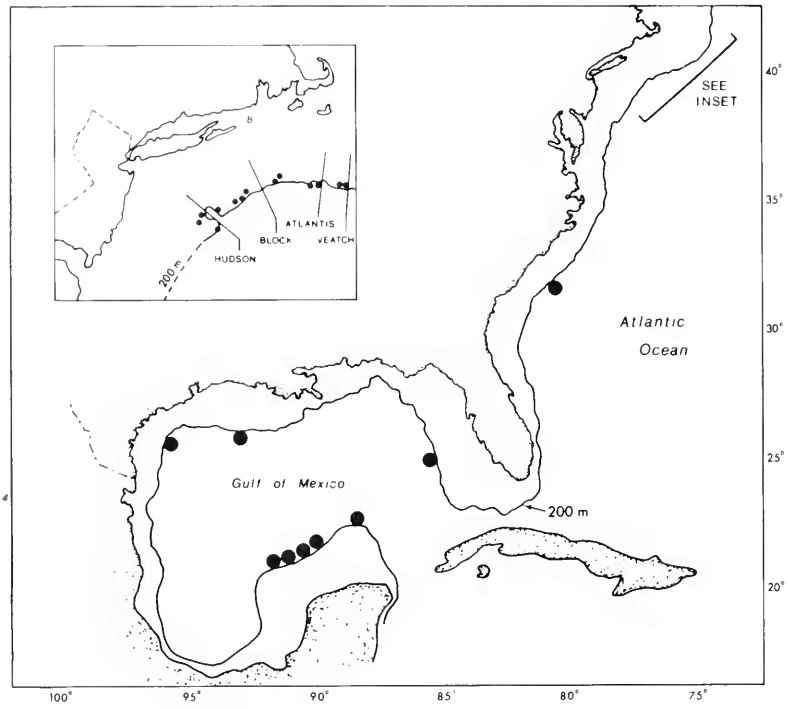

FIGURE 1.—Sample locations for tilefish along the U.S. east coast and the Gulf of Mexico. Submarine canyons are identified in the inset.

Electrophoresis

Eye, liver, and muscle tissues were removed from individual fish and frozen as soon as possible. Vertical starch gel electrophoresis was used to detect protein variation. Initially only tissues of fish from the most distant collection localities (Hudson Canyon and off Texas) were screened for 28 enzymes to maximize the chance of finding polymorphic enzymes. Of the 28 enzymes screened during the initial electrophoresis, several were scorable; however, most appeared monomorphic (malate dehydrogenase, lactate dehydrogenase, xanthine dehydrogenase, creatin kinase, adenylate kinase, peptidase, alcohol dehydrogenase, malic enzyme, 6-phosphogluconate dehydrogenase, and glyceraldehyde 3-phosphate dehydrogenase) and only two [liver isocitrate dehydrogenase (IDH) and liver esterase (EST)] were polymorphic. Liver tissues from all collections were then run for both IDH and EST with an amine citrate buffer (pH 6.0) (Clayton and Tretiak 1972) for 17 h at 140 V and 40°C, and allelic frequencies were determined for all populations. Allelic frequencies were compared with their Hardy-Weinberg expectations by a chi-square test (Spiess 1977). We evaluated differences between sample locations, by chi-square contingency tests of electromorph distribution between sample locations. This test does not assume Hardy-Weinberg equilibrium and compares n samples with k classes to determine whether the individual k classes are in the same relative proportion throughout the n samples.

Length (age)-related differences in genotype distribution were tested (chi-square) on the largest sample with a wide range of sizes ($n=40$, west side of Hudson Canyon). Fish were divided into two size classes (<550 mm fork length and >550 mm) based on the approximate size at sexual maturity.

Morphology

Seven meristic (number of dorsal fin spines and rays, anal fin spines and rays, pectoral fin rays, upper and lower gill rakers on the first arch) and 21 morphometric (fork, standard, total, pectoral fin, pelvic fin, upper jaw, snout, adipose flap, barbel, snout to vent, snout to anal origin, snout to dorsal origin, snout to incurrent nostril, lengths; orbit diameter, interorbital width, head width, height of first, second, and third dorsal fin spines, caudal peduncle depth, and suborbital depth) characters were counted or measured following Hubbs and Lagler (1967),

with two exceptions: Barbel length was measured from its posterior tip to the junction with the lower lip, and the suborbital depth was measured from the lower margin of the infraorbitals to the junction of the articular and interopercular bones. Morphometric characters were measured to the nearest millimeter with dividers and a tape measure. These characters were chosen on the basis of a preliminary study of two specimens of tilefish by Bigelow and Schroeder (1947) and a systematic study of the Branchiostegidae by Dooley (1978).

Morphological data was determined from fish of dissimilar lengths (Fig. 2), so we used analysis of covariance to remove the size effects as suggested by Atchley et al. (1976). A linear relationship to standard length (SL) was determined for most morphological characters with the exception of adipose flap length where an additional coefficient of standard length squared was included in the model because of allometry. For the final size-corrected comparisons between sample locations we used sample location least square means for each morphological character (Barr et al. 1976). Least square means are estimates of arithmetic means that would be predicted had samples with the same size composition been obtainable from each sampling location.

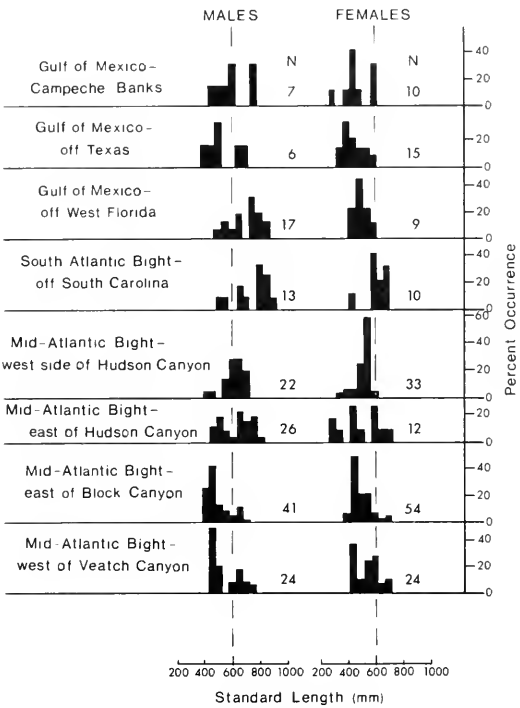

FIGURE 2.—Length-frequency histograms of tilefish samples used to conduct the morphological analysis. See Figure 1 for approximate locations.

We conducted analysis of covariance on each morphological character to test for differences between sampling locations. Sex, sample location, and all interactions were initially included in the covariance model, but all nonsignificant ($P<0.01$) interactions were removed from the final model. The difference between sample location least square means for each morphological character for each sex was tested by comparison with the west Hudson Canyon sample using a t test. Significant differences were determined conservatively, using a high significance level ($P<0.001$), because the possibility of finding differences increases with the number of tests run.

To further test for differences between sample locations we used discriminant function analysis (Jolicoeur 1959; Seal 1964) to determine the level of distinctness of fish from each location. The discriminant function was computed using both raw and size-corrected data for males and females separately, because the analysis of covariance indicated sexual dimorphism. Only linearly related morphological characters were used in the raw discriminant function (Seal 1964). Size correction of morphological characters was accomplished using the average value of standard length ($\overline{SL}$) of all samples, and linear and quadratic regression coefficients (B_1, B_2) obtained from covariance analysis for each morphological character according to the following formula:

$$\text{corrected} = \text{raw} - B_1 (\text{SL}-\overline{\text{SL}}) - B_2 (\text{SL}-\overline{\text{SL}})^2.$$

This correction removed size effects by displacing each morphological observation towards the average, while allowing sample location and interaction effects to remain.

RESULTS

Electrophoretic Data

The genetic basis of protein variation in tilefish was implied from the electrophoretic banding patterns. IDH showed a dimeric pattern (heterozygote was three banded) with medium, slow, and fast bands. The rare fast form occurred only as a heterozygote in 10 out of 226 fish in the Mid-Atlantic Bight samples; therefore it has been left out of the statistical analysis. The EST

locus exhibited a monomeric pattern (heterozygote was two banded) with fast and slow bands. Our interpretation of the dimeric and monomeric nature of these enzymes is consistent with past studies of their molecular structure (Manwell and Baker 1970). Distribution of EST and IDH electromorphs was not significantly different than expected from Hardy-Weinberg equilibrium (Tables 1, 2), which is additional support for a single-locus, two-allele genetic model. However, it should be noted that the chi-square test is not very sensitive at small sample sizes (<200) (Fairbairn and Roff 1980).

There was no significant difference in genotype distribution as a function of length (age) for both enzymes (EST $\chi^2 = 1.16$, $P>0.6$, $n = 20$; IDH $\chi^2 = 2.93$, $P>0.2$, $n = 20$) in the sample examined (west side of Hudson Canyon).

There were distinct patterns of variation among the populations sampled (Fig. 3). Chi-square contingency tests revealed no significant differences in genotype distribution within the Mid-Atlantic Bight or southern sampling locations (South Carolina, west Florida, Texas, and Campeche) (within Mid-Atlantic Bight EST $\chi^2_{5,3} = 8.77$, $0.25<P<0.5$; IDH $\chi^2_{5,3} = 9.45$, $0.25<P<0.5$: within southern locations EST $\chi^2_{4,3} = 4.12$, $0.5<P<0.75$; IDH $\chi^2_{3,3} = 7.34$, $0.1<P<0.25$). However, differences in genotype distributions between Mid-Atlantic Bight and southern samples were highly significant (EST $\chi^2_{9,3} = 45.01$, $P<0.001$; IDH $\chi^2_{8,3} = 111.76$, $P<0.001$).

Morphological Data

Gill raker numbers were the only meristic characters that were significantly different among samples. All gill raker counts (upper, lower, and total) for males and females from the Mid-Atlantic Bight samples were not significantly different from the west Hudson Canyon sample (Tables 3, 4). However, total gill rakers,

TABLE 1.—Comparison between observed genotypes and Hardy-Weinberg expectations (in parentheses) at the liver esterase locus for all tilefish sampling locations. See Figure 3 for sample sizes.

Sampling locations	A/A	A/B	B/B	χ^2
Gulf of Mexico				
Campeche Banks	4(4.51)	9(7.97)	3(3.52)	0.25 ns[2]
Off Texas	4(4.29)	11(10.40)	6(6.31)	0.06 ns
Off West Florida	9(6.78)	9(11.41)	7(4.80)	3.44 ns
South Atlantic Bight-				
off South Carolina	6(5.26)	10(11.48)	7(6.27)	0.10 ns
Mid-Atlantic Bight				
Hudson Canyon	46(45.24)	35(36.42)	8(7.33)	0.13 ns
Niche[1]	25(26.40)	22(19.13)	2(3.47)	1.13 ns
Block Canyon	45(44.27)	32(33.42)	7(6.31)	0.15 ns
Atlantis Canyon	34(36.24)	43(38.52)	8(10.23)	1.15 ns
Veatch Canyon	30(31.21)	19(16.59)	1(2.21)	1.06 ns
	χ^2 (0.05) = 3.84			

[1]Niche = name applied by fishermen to area about 50 km east of Hudson Canyon.
[2]ns = not significant.

TABLE 2.—Comparison between observed genotypes and Hardy-Weinberg expectations (in parentheses) at the liver isocitrate dehydrogenase locus for all tilefish sampling locations. See Figure 3 for sample sizes.

Sampling locations	A/A	A/B	B/B	χ^2
Gulf of Mexico				
Campeche Banks	1(0.39)	3(2.11)	12(11.40)	0.11 ns[2]
Off Texas	0(1.19)	10(7 62)	11(12.19)	2.05 ns
Off West Florida		no data, enzyme denatured		
South Atlantic Bight-				
off South Carolina	0(0.27)	5(4.47)	18(18.26)	0.12 ns
Mid-Atlantic Bight				
Hudson Canyon	29(31.65)	39(36.71)	8(10.64)	1.02 ns
Niche[1]	6(8.05)	12(9.91)	1(3.05)	3.59 ns
Block Canyon	37(34.42)	31(36.11)	12(9.47)	2.19 ns
Atlantis Canyon	14(14.77)	20(18.46)	5(5.77)	0.27 ns
Veatch Canyon	12(14.89)	25(19.23)	3(5.89)	3.71 ns
	χ^2 (0.05) = 3.84			

[1]Niche = name applied by fishermen to area about 50 km east of Hudson Canyon.
[2]ns = not significant.

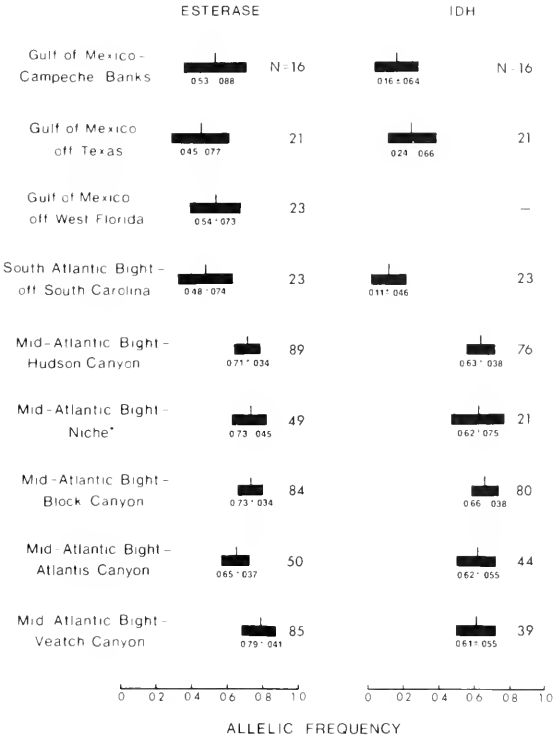

FIGURE 3.—Allelic frequencies of esterase and isocitrate dehydrogenase (IDH) for tilefish samples collected along the U.S. east coast and the Gulf of Mexico. Mean allelic frequency indicated by vertical line and bands represents 95% confidence intervals. Allelic frequency and standard error below bands. "Niche" = fisherman name of area approximately 50 km east of Hudson Canyon.

and less consistently the upper and lower gill raker number, differed significantly for the males and females from South Carolina and Gulf of Mexico samples (Tables 3, 4). These differences were not size related because there was no significant difference between fish size and gill raker number ($R^2 = 0.22$, $n = 328$).

Sexual dimorphism was apparent for several morphometric characters (Table 5); therefore all comparisons among morphometric characters were made separately for each sex.

Separate comparisons of male and female morphometric characters indicated that there were no significant differences among all of the east coast samples (Mid-Atlantic Bight and South Carolina—Tables 3, 4). The Gulf of Mexico samples, however, differed from the west Hudson Canyon site for most comparisons. In 16 of the 20 comparisons for males and 18 of the 20 for females the samples were significantly different (Tables 3, 4).

TABLE 3.—Comparison of size adjusted morphological characters (least squares means in mm) for male tilefish from sample locations by covariance analysis. Independent variable is standard length. Sample from west of Hudson Canyon is the basis for comparison. ** = $P<0.01$, *** = $P<0.001$.

Sampling locations	Pectoral fin length	Inter-orbital width	Orbit diam-eter	Caudal peduncle depth	Head length	Adipose flap length	Barbel length	2d dorsal spine length	1st dorsal spine length	No. of gill rakers		
										Upper	Lower	Total
Gulf of Mexico-Campeche Banks	141.0***	44.4	42.2***	44.4***	181.5***	16.1***	12.0	44.7***	32.0***	8.58	15.40**	23.97***
Gulf of Mexico-off Texas	140.5***	39.8***	39.8***	45.4	173.5***	10.5***	—	—	—	—	—	—
Gulf of Mexico-off west Florida	137.7***	42.9***	38.6	42.3	172.6***	19.5***	9.1***	49.6	38.1***	8.83**	15.23**	24.05**
South Atlantic Bight-off South Carolina	118.6	46.3	36.2	47.6	164.8	33.4	—	—	—	—	—	23.68**
Mid-Atlantic Bight-west of Hudson Canyon	126.7	46.6	32.8	49.6	164.5	37.7	16.1	52.0	42.0	8.11	14.65	22.76
Mid-Atlantic Bight-east of Hudson Canyon	127.4	47.3	35.7	47.6	165.0	39.6	16.0	49.9	40.1	8.53	14.74	23.26
Mid-Atlantic Bight-east of Block Canyon	125.0	44.9	34.9	47.0	166.6	44.9	16.4	51.5	39.2	8.24	14.54	22.79
Mid-Atlantic Bight-west of Veatch Canyon	126.9	44.7	34.9	47.8	166.4	40.6	17.2	50.0	39.5	8.33	14.75	23.09
R^2	0.91	0.93	0.82	0.91	0.98	0.83	0.48	0.77	0.74	0.11	0.15	0.22

TABLE 4.—Comparison of size adjusted morphological characters (least squares means in mm) for female tilefish from sample locations by covariance analysis. Independent variable is standard length. Sample from west of Hudson Canyon is the basis for comparison. ** = $P<0.01$, *** = $P<0.001$.

Sampling locations	Pectoral fin length	Inter-orbital width	Orbit diameter	Caudal peduncle depth	Head length	Adipose flap length	Barbel length	2d dorsal spine length	1st dorsal spine length	No. of gill rakers		
										Upper	Lower	Total
Gulf of Mexico–Campeche Banks	130.8	36.3***	39.2***	43.3***	172.6***	19.5***	10.5	43.6***	32.3***	8.59	15.23	23.83**
Gulf of Mexico–off Texas	138.5***	39.4***	42.9***	42.4***	170.7***	14.7***	—	—	—	—	—	—
Gulf of Mexico–off west Florida	133.2***	41.0***	41.7***	38.6***	172.1***	14.5***	5.8***	45.4***	34.2***	9.00***	15.12	24.14**
South Atlantic Bight–off South Carolina	123.9	42.6	36.8	47.0	165.4	21.0	—	—	—	—	—	24.07**
Mid-Atlantic Bight–west of Hudson Canyon	125.0	45.5	34.1	49.1	165.6	31.9	15.3	50.8	39.7	8.35	14.72	23.08
Mid-Atlantic Bight–east of Hudson Canyon	124.2	45.6	35.2	46.9	167.0	29.9	14.4	49.3	38.2	8.41	14.85	23.28
Mid-Atlantic Bight–east of Block Canyon	125.1	43.5	35.8	45.5	166.1	31.5	15.1	49.6	39.0	8.38	14.63	23.03
Mid-Atlantic Bight–west of Veatch Canyon	125.4	43.7	35.2	46.1	165.9	31.1	14.7	50.0	39.0	8.29	14.71	23.00
R^2	0.91	0.93	0.82	0.91	0.98	0.83	0.48	0.77	0.74	0.11	0.15	0.22

The nature of the variation in the morphometric characters examined varied between sexes and locations (Tables 3, 4). For several characters the least square mean values appeared to vary clinally. This was most evident for male adipose flap height and orbit diameter as seen in plots of raw data (Figs. 4, 5), female interorbital width and male head length. The values for other characters showed less consistent patterns and in some cases could be interpreted to suggest two distinct groups with the South Carolina samples most similar to Mid-Atlantic Bight groups (Tables 3, 4). This was most obvious for male pectoral fin length and female pectoral fin length, caudal peduncle depth, and head length. Clinal variation was also suggested by the increasing number of significantly different morphological characters with increasing geographic distance between compared samples.

The discriminant function analysis was conducted with both raw and size-corrected data. In each case the results were virtually identical with two exceptions (males, east Hudson Canyon - 60% correct classification with size corrected vs. 23% raw data, and Campeche - 86% correct classification vs. 43% raw data). We believe neither of these significantly affects the overall interpretation of the results, and we report the raw data results here (Tables 6, 7).

The discriminant function analysis suggests a similar clinal pattern of variation for both males and females (Tables 6, 7). There was generally low differentiation within the Mid-Atlantic Bight samples, and where misidentification occurred it was to other Mid-Atlantic Bight or South Carolina samples and infrequently to west Florida and the Gulf of Mexico off Texas. Gulf of Mexico samples naturally had higher percentage correct classification (sample locations were more widely separated geographically) and incorrect classifications were usually to other Gulf of Mexico samples. Classifications for South Carolina samples had a high correct classification, and where misclassification occurred it was to both Mid-Atlantic Bight and Gulf of Mexico locations.

DISCUSSION

For purposes of interpreting the significance in allelic frequencies observed for IDH and EST we are assuming that the genetic variation observed is neutral (Allendorf and Phelps 1981; Ihssen et al. 1981). Thus, based on the patterns

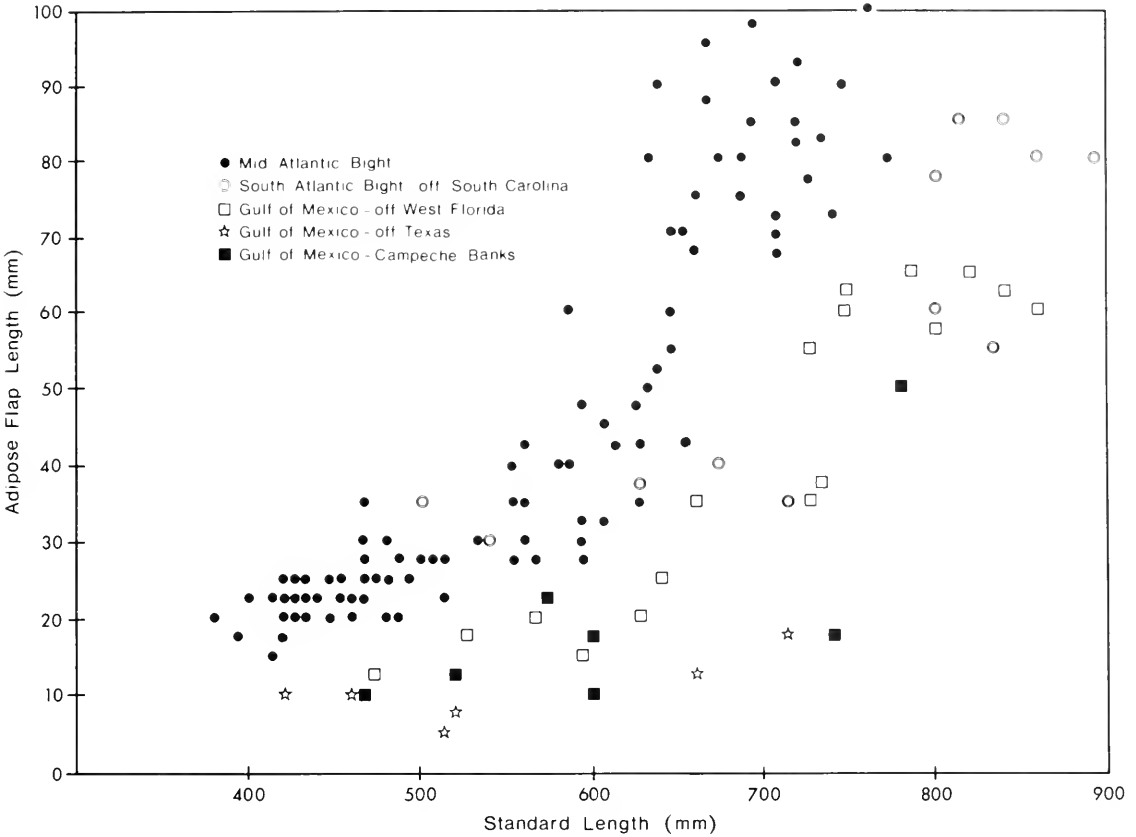

FIGURE 4.—Adipose flap length plotted against standard length for male tilefish from the U.S. east coast and the Gulf of Mexico.

TABLE 5.—Comparison of size adjusted morphological characters (least squares means in mm) for male and female tilefish by covariance analysis. Independent variable is standard length. ** = $P<0.01$.

	Inter-orbital width	3d dorsal spine length	2d dorsal spine length	1st dorsal spine length	Snout to anal origin length	Caudal peduncle depth	Barbel length	Snout to nostril length	Adipose flap length
Males	44.6**	56.6**	49.6	38.5	323.7	46.5**	14 4	47.4	30.3**
Females	42.2	54.7	48.3	37.1	328.3	44 9	12.6	46.2	24 3
R^2	0.93	0.87	0.77	0.74	0.97	0.91	0.48	0.91	0.83

observed (Fig. 3), we reject the null hypothesis and suggest that there are at least two distinct groups in the samples examined, a Mid-Atlantic Bight group and a second group composed of samples from South Carolina and the Gulf of Mexico. This is supported by concordance in the patterns of variation for both EST and IDH (Fig. 3).

The morphological data consistently support the concept of a single group of fish in the Mid-Atlantic Bight but varies for other areas. Both meristic and morphometric data for both sexes in the Mid-Atlantic Bight show little significant variation (Tables 3, 4, 6, 7), suggesting that these are freely interbreeding populations. The Gulf of Mexico samples appear completely distinct from Mid-Atlantic Bight samples by the same analysis. The morphological analyses of the South Carolina samples were contradictory with the electrophoretic results. The comparisons of least squares mean values for morphometric characters for the South Carolina samples to the Mid-Atlantic Bight samples (Tables 3, 4) consistently indicated no significant differences. However, the South Carolina samples differed significantly in total gill raker number as did the Gulf of

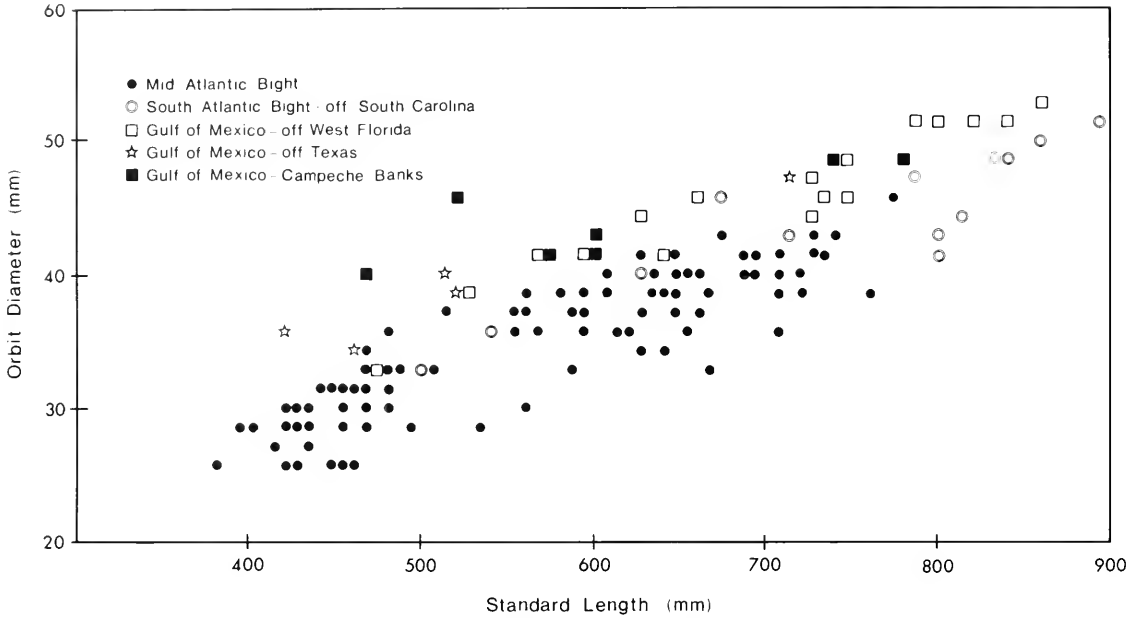

FIGURE 5.—Orbit diameter plotted against standard length for male tilefish from the U.S. east coast and the Gulf of Mexico.

TABLE 6.—Percent male tilefish classified to sample locations by discriminant function analysis.

From sample locations	To sample locations: Gulf of Mexico–Campeche Banks	Gulf of Mexico–off Texas	Gulf of Mexico–off west Florida	South Atlantic Bight–off South Carolina	Mid-Atlantic Bight–west of Hudson Canyon	Mid-Atlantic Bight–east of Hudson Canyon	Mid-Atlantic Bight–east of Block Canyon	Mid-Atlantic Bight–west of Veatch Canyon	N
Gulf of Mexico–Campeche Banks	43	14	43						7
Gulf of Mexico–off Texas	17	83							6
Gulf of Mexico–off west Florida	18	12	70						17
South Atlantic Bight–off South Carolina			9	75		8	8		12
Mid-Atlantic Bight–west of Hudson Canyon				9	55	18	9	9	22
Mid-Atlantic Bight–east of Hudson Canyon			4	15	23	23	19	16	26
Mid-Atlantic Bight–east of Block Canyon		2		5	7	5	54	27	41
Mid-Atlantic Bight–west of Veatch Canyon			12	4	4	17	50	13	24

TABLE 7.—Percent female tilefish classified to sample locations by discriminant function analysis.

From sample locations	To sample locations: Gulf of Mexico–Campeche Banks	Gulf of Mexico–off Texas	Gulf of Mexico–off west Florida	South Atlantic Bight–off South Carolina	Mid-Atlantic Bight–west of Hudson Canyon	Mid-Atlantic Bight–east of Hudson Canyon	Mid-Atlantic Bight–east of Block Canyon	Mid-Atlantic Bight–west of Veatch Canyon	N
Gulf of Mexico–Campeche Banks	20	20	50			10			10
Gulf of Mexico–off Texas		87	13						15
Gulf of Mexico–off west Florida		22	78						9
South Atlantic Bight–off South Carolina			10	70		10	10		10
Mid-Atlantic Bight–west of Hudson Canyon			3	6	45	3	33	9	33
Mid-Atlantic Bight–east of Hudson Canyon				17	17	33	33		12
Mid-Atlantic Bight–east of Block Canyon	2		4	11	6	3	67	9	54
Mid-Atlantic Bight–west of Veatch Canyon			4	17	8	5	33	33	24

Mexico populations. In the discriminant function analysis South Carolina samples of both sexes classified correctly a high percentage of the time but misclassification occurred to both Mid-Atlantic Bight and Gulf of Mexico samples. The variability in the pattern of morphological characters can be accounted for by clinal variation in these characters, or, less likely, by two distinct groups that are only weakly differentiated. The interpretation of the morphological data may also be hampered by the small samples for more southern populations and the great distances between them.

Other life history data for tilefish in the Mid-

Atlantic Bight are in accord with the concept of a separate stock. As we have previously mentioned, they are resident because they are taken year-round in the fishery (Grimes et al. 1980), apparently move short distances in the course of a year (Grimes et al. in press), and construct temporally stable burrows that may be occupied for the life of a fish (Able et al. 1982). In addition, they are known to reproduce in the Mid-Atlantic Bight because gonads show seasonal patterns of development and decline (Idelberger et al. 1981) and eggs and larvae have been collected (Fahay and Berrien 1981).

The prevailing current patterns and hydrographic regimes over the study area are consistent with our delineation of the stocks. While there is a southwesterly drift of shelf water within the Mid-Atlantic Bight (Miller 1952; Bumpus 1973) that would provide mixing of eggs and larvae, it is unlikely that egg or larval transport occurs between the Mid-Atlantic and South Atlantic Bights. The Gulf Stream turns eastward at Cape Hatteras so that its axis is located 250 km east of the shelf break in the Mid-Atlantic Bight (Emery and Uchupi 1972). This difference in Gulf Stream effects produces distinct northern and southern continental shelf water masses (Stefansson et al. 1971; Emery and Uchupi 1972). Thus it is unlikely that egg and larval transport between these two areas would commonly occur, although Cox and Wiebe (1979) have suggested that anticyclonic eddies could provide a mechanism for transporting oceanic larvae across the Gulf Stream to Mid-Atlantic Bight waters.

Prevailing current systems in the southern United States may provide the means for larval mixing between the Gulf of Mexico and the South Atlantic Bight as suggested by the similarities in allelic frequencies for samples from these two areas. The Gulf of Mexico Loop Current (Maul 1977) provides a means for tilefish larvae to be transported out of the Gulf of Mexico and into the South Atlantic Bight as it joins the Florida Current and eventually forms the Gulf Stream.

In addition to prevailing currents, periodic mass mortality may have contributed to the differences between distinct stocks. Following their discovery by a cod fisherman off southern New England in 1879, tilefish experienced a mass mortality in 1882 (a few billion fish reported floating at the surface; Bumpus 1898) probably caused by a sudden temporary intrusion of cold water (McLellan et al. 1953; Hachey 1955). This mortality may have resulted in a "founder effect" phenomenon and thus be responsible for stock differences we have noted.

In summary, we believe that the available data suggest that Mid-Atlantic Bight tilefish populations represent one unit stock and that South Atlantic Bight and Gulf of Mexico populations be considered another stock, at least as a working hypothesis. However, the wide geographic separation of the latter two areas may necessitate managing them as two stocks. Because the electrophoretic results suggest that gene flow may occur between Gulf of Mexico and South Atlantic Bight populations, this should be done with cognizance that Gulf of Mexico populations could serve as a source of recruits to South Atlantic Bight populations.

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EFFECTS OF BEHAVIORAL INTERACTIONS ON THE CATCHABILITY OF AMERICAN LOBSTER, *HOMARUS AMERICANUS*, AND TWO SPECIES OF *CANCER* CRAB

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ABSTRACT

Intraspecific and interspecific behavioral interactions may affect the probability of capturing *Cancer irroratus*, *C. borealis*, and *Homarus americanus* in lobster traps. To test this hypothesis, the catch per unit of effort (CPUE) of each of these species in traps stocked with *C. irroratus*, *C. borealis*, or *H. americanus* was compared with that obtained from empty baited traps (controls).

In traps stocked with lobsters, the catch of all three species was significantly reduced. Traps stocked with 8 lobsters caught significantly fewer crabs than traps containing 3 lobsters. The only effect of stocking traps with crabs was to increase the catch of *C. borealis* in traps stocked with 3 crabs of either species. Results of laboratory experiments comparing crab CPUE in control traps with crab CPUE in traps stocked with 8 lobsters concurred with the field results.

When *H. americanus* was stocked in the holding section (parlor) of the trap, a greater proportion of the crab catch was found in the entrance section (kitchen). This behavioral response may facilitate escape of crabs from traps containing *H. americanus*. The distribution of the lobster catch was unaffected by stocking *H. americanus* or *Cancer* crabs in the parlor.

Behavioral mechanisms underlying reductions in crab CPUE were investigated by laboratory observation of an actively fishing trap. When *H. americanus* was stocked, *C. borealis* avoided entering traps. *Cancer irroratus* entered the kitchen of traps containing *H. americanus*, but the proportion entering the parlor was reduced. The escape rate of both crab species increased in traps stocked with *H. americanus*. The position underneath the entrance to the parlor was preferred by all species. When both *H. americanus* and *Cancer* crabs were present in the trap, *H. americanus* occupied that position.

A number of environmental and biological factors are known to affect the probability of capturing crustaceans in traps. Water temperature and salinity are positively correlated with capture rates of rock lobster, *Panulirus cygnus*, (Morgan 1974), and a linear relationship between temperature and the catchability of American lobster, *Homarus americanus*, was found by McLeese and Wilder (1958). Biological rhythms and physiological changes, such as those associated with the molt cycle (e.g., Chittleborough 1975), may affect feeding and other activities (e.g., Bennett 1974; Morgan 1974) and thus cause fluctuations in catchability. In addition, behavioral attributes such as avoidance of dead conspecifics (Hancock 1974; Morgan 1974; Chapman and Smith 1979), intraspecific attraction (reviewed in Hancock 1974), or competitive relations (Bennett 1974; Ricker 1975; Caddy[3]) may affect catch rates. The potential importance of such interactions between animals converging on a trap has been recognized by several authors (Bennett 1974; Bennett and Brown[4]; Caddy footnote 3; Miller 1978, 1979a, b, 1980; Fogarty and Borden 1980).

The present study was designed to determine whether trap efficiency, the number of individuals captured as a fraction of those detecting the gear (Caddy footnote 3), for Jonah crab, *C. borealis*, rock crab, *C. irroratus*, and *H. americanus* is affected by the presence of others of these species in the traps. Additional null hypotheses were that 1) trap efficiency is independent of the density of other species in the trap, and 2) the

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[3]Caddy, J. F. 1977. Some considerations underlying definitions of catchability and fishing effort in shellfish fisheries, and their relevance for stock assessment purposes. ICES Shellfish and Benthos Committee Ref. Gear and Behavior Committee, No. 18, 22 p.

[4]Bennett, D. B., and C. G. Brown. 1976. The problems of pot immersion time in recording and analyzing catch-effort data from a trap fishery. ICES Special Meeting on Population Assessments of Shellfish Stock, No. 6, 9 p.

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location of animals within the trap is unaffected by the presence of other species. Laboratory observations of the behavior of the two crab species in and around traps were made to assess processes influencing their catch rates and to investigate the allocation of space in the trap by captured animals.

METHODS

Trap Efficiency

Field studies were carried out from 27 July to 30 August 1979 to investigate the effects of intraspecific and interspecific interactions on the catch per unit of effort (CPUE) of *C. irroratus*, *C. borealis*, and *H. americanus*. The catch obtained in lobster traps stocked with these three species was compared with the catch obtained in unstocked traps. It was assumed that equal numbers of animals were attracted to all traps; thus any differences in CPUE would be due to differences in trap efficiency caused by animals stocked in the traps.

The 18 lobster traps were $91 \times 25 \times 46$ cm, constructed from galvanized aluminum mesh (2.54 cm^2 openings) with no escape gaps (Fig. 1). Traps were set three to a string, with three strings at each of two locations in Narragansett Bay, R.I. One location was an area of coarse sand overlain with boulders, a substratum where *C. borealis* and *H. americanus* are typically found. The other location was a predominantly sand bottom where *C. irroratus* and *H. americanus* occur (Jeffries 1966; Fogarty 1976). Traps within strings were about 13 m apart, strings in each location were 15 to 60 m apart, and the locations were separated by about 1 km. Water depth varied from 8 to 14 m.

In each string of three traps, the middle trap was stocked with 8 individuals of a given species, one end trap contained 3 individuals of that species, and the other end trap was not stocked and

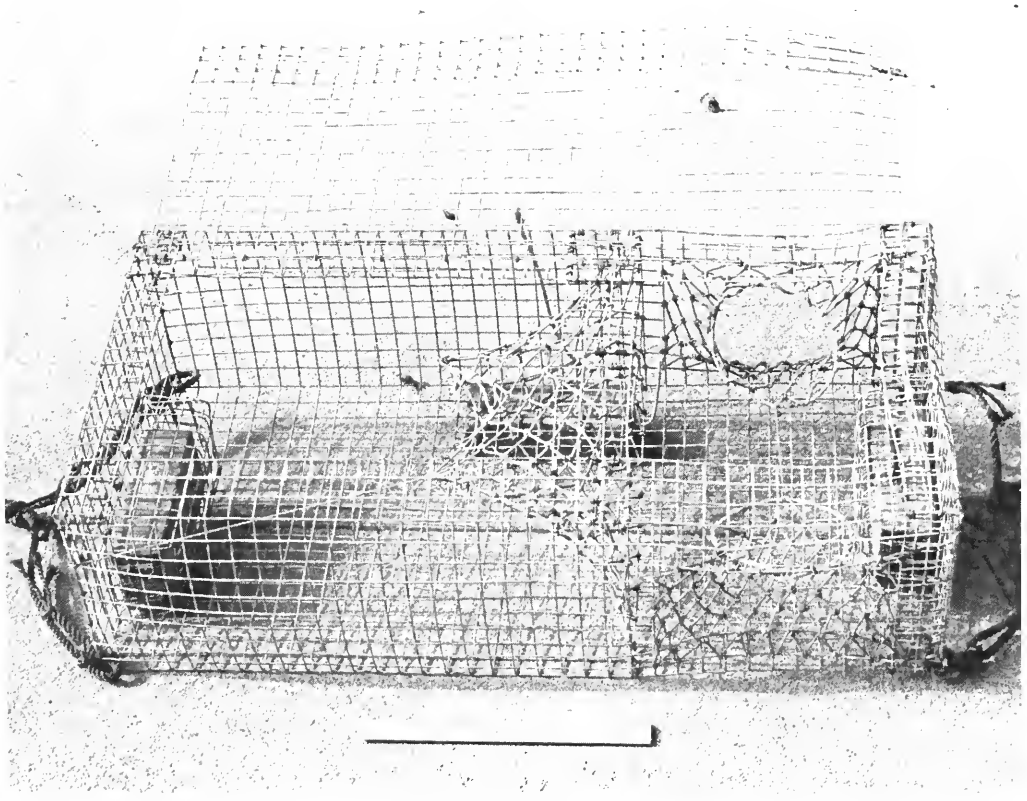

FIGURE 1.—Lobster trap used in field experiments.

served as a control. This arrangement was necessitated by poaching of the 8-lobster treatments when they were at the ends of strings. The stock rates approximated natural catch rates for lobsters, but were considerably lower than could be achieved for crabs. The use of two stocking densities allowed us to assess the effects of both the species identity and the stocking density upon catch rates.

Traps were hauled daily, weather permitting, rebaited with about 1 kg of flounder or flounder carcasses, and experimental traps were restocked if necessary. The number, size, sex, and proportion of the catch in each trap compartment were recorded for each of the three species. A total of 336 trap hauls were made.

The sizes of stocked animals were *C. borealis*, 95-115 mm carapace width (CW); *C. irroratus*, 90-115 mm CW; and *H. americanus*, 75-85 mm carapace length (CL). Carapace width of crabs was measured as the distance between the two most lateral notches on the carapace; carapace length of lobsters was the distance between the posterior edge of the carapace and the posterodorsal edge of the eye socket, parallel to the longitudinal axis. Stocked animals were assigned to traps unsystematically with respect to size and sex.

To further assess the effects of lobsters on catch rates of crabs, laboratory studies were undertaken from July through October of 1979. Two rectangular wooden lobster traps ($69 \times 34 \times 51$ cm) were covered with 2.5 cm mesh wire to simulate the mesh size of traps used in the field experiments. The baited traps containing either 8 or 0 (control) lobsters (70-85 mm CL) were placed in the center of two large indoor tanks ($3.4 \times 1.5 \times 0.5$ m and $3.1 \times 1.5 \times 0.5$ m) supplied with ambient seawater running at about 2 l/min. Inflow and outflow were at opposite ends of the tanks, thus the water flowed through the traps. Each tank was provided with 10 clay pipe shelters (10.2 cm in diameter, 31 cm long, with two open ends). For each trial, 15 individuals of *C. irroratus* (80-110 mm CW) or *C. borealis* (85-115 cm CW) were placed in the tank. After about 24 h the catch was counted and removed, and the location of animals in the trap was recorded. Crabs were used only once; stocked lobsters were used twice, in different traps. Prior to experimentation, each species was held separately in large outdoor tanks supplied with running seawater and fed every third day with a variety of species of fresh fish. Individual traps were alternated as experimental and control treatments to avoid bias due to differences between traps and tanks. Ten replicates of each experiment were performed.

Behavior

Behavioral mechanisms affecting trap efficiency were investigated by direct observation in the laboratory. A rectangular wooden lobster trap was modified to improve visibility by replacing the top with 2.5 cm mesh wire and painting the bottom white. The trap was baited with thawed whole flounder or flounder carcasses, stocked with 5 or 0 (control) lobsters (70-85 mm CL), and placed in a $3.1 \times 1.2 \times 0.6$ m tank provided with 10 clay pipe shelters and ambient seawater running at about 2 l/min. An hour after the trap was placed in the tank, 20 *C. irroratus* or *C. borealis* (80-110 mm CW) were added. Tape-recorded observations began 15 min later and continued during alternate 15-min periods. A 25-watt incandescent red light suspended 1.2 m above the tank provided the only light. Kennedy and Bruno (1961) have shown lobsters to be relatively insensitive to these wavelengths.

Observations were carried out intermittently from July through October 1979. One sunset-to-sunrise observation for each combination of stock treatment (0 or 5 lobsters) and catch species (*C. irroratus* or *C. borealis*) revealed that activity peaked between sunset and midnight. Subsequent observations were made during these hours. Lobster-stocked and control observations for each crab species were done within 2 wk of each other to minimize seasonal effects. A total of 11.5 h of observation in three separate periods was made on each combination of stock treatment and catch species.

All animals were held in conditions similar to those described previously for tank experiments, and were in captivity from 2 d to 1 mo before use. No animal was used more than once.

Data collected included frequency and nature of inter- and intraspecific interactions and trap entry and escapement. Positions of animals in the trap were recorded every 15 min.

RESULTS

Trap Efficiency

We assumed that the relative effect of the experimental treatments would not differ between

field locations. Contingency table analyses indicated no significant differences between locations in 8 of 9 tests ($P>0.05$, Table 1). Therefore the catches from both field locations were combined according to treatment. The number of trap hauls for each stock species was made equal by randomly deleting observations. The hypothesis that the CPUE of *C. irroratus*, *C. borealis*, and *H. americanus* is not affected by the presence of other animals inside traps was tested by comparing the total catch of each species in stocked traps with the total catch in control traps. Catches obtained after 24 h immersion time were compared using a χ^2 goodness of fit test (Zar 1974).

In traps containing 8 or 3 lobsters, the total catch of *C. irroratus*, *C. borealis*, and *H. americanus* was significantly reduced ($\chi^2_{(2)} = 277.8$, 35.1, 18.2, respectively, $P<0.001$) (Table 2). In addition, the catch of both species of crabs was significantly lower in 8-lobster treatments than in 3-lobster treatments (*C. irroratus*, $\chi^2_{(1)} = 22.9$, $P<0.001$; *C. borealis*, $\chi^2_{(1)} = 6.1$, $P<0.025$). The catch of lobsters was not affected by the density of stocked lobsters ($\chi^2_{(1)} = 2.42$, $P>0.05$). The only effect of stocking traps with crabs was to increase the catch of *C. borealis* in traps stocked with either 3 *C. borealis* or 3 *C. irroratus* (for both treatments, $\chi^2_{(1)} = 8.6$, $P<0.005$). Stocking traps with crabs had no effect on the catch of lobsters ($P>0.05$).

The average size of animals captured did not differ between treatments for any of the species (Student's t test, $P>0.05$) (Table 3).

The results of the laboratory experiments in which lobsters were stocked concurred with those from the field. The catch of both *C. irroratus* and *C. borealis* was significantly reduced when *H. americanus* was in the parlor (Table 4).

TABLE 1.—χ^2 values for 3×2 contingency tables comparing strings of each treatment type for *Homarus americanus* (Ha), *Cancer irroratus* (Ci), and *C. borealis* (Cb) between locations. A separate contingency table was made for each species caught. * = $P<0.05$, @ = expected frequency of one cell was <5.

	Comparison of locations for		
Species caught	Ha treatments	Ci treatments	Cb treatments
C. borealis	0.980 @	0.920	2.675
C. irroratus	3.880	48.357*	2.594
H. americanus	0.348 @	0.146	1.816

Behavior

Location Within Trap

The spatial distribution of animals caught in a trap may be affected by behavioral interactions among the trap occupants. To test this hypothesis, the proportion of the catch found in the entry section, or "kitchen," in control traps was compared with the proportion in the kitchen in stocked traps. All comparisons of proportions were made using the normal approximation for differences between two proportions (Zar 1974). Stocked animals were placed in the parlor.

In both field and laboratory experiments, a

TABLE 2.—Total numbers of *Cancer irroratus*, *C. borealis*, and *Homarus americanus* caught after 24-h immersion time in field experiments. Catch per trap haul is indicated in parentheses; control = empty baited traps; treatment refers to species stocked; n = no. of trap hauls for each treatment level.

	H. americanus-stocked			*C. borealis*-stocked			*C. irroratus*-stocked		
Species caught	Control	3	8	Control	3	8	Control	3	8
C. irroratus	319(7.60)	100(2.38)	42(1.00)	300(8.82)	371(10.91)	300(8.82)	342(9.50)	365(10.14)	355(9.86)
C. borealis	70(1 67)	36(0.86)	17(0.40)	61(1.79)	99(2.91)	78(2.29)	65(1.81)	102(2.83)	70(1.94)
H. americanus	54(1.29)	31(0.74)	19(0.45)	23(0.68)	21(0.62)	33(0.97)	29(0.81)	29(0.81)	29(0.81)
n	42	42	42	34	34	34	36	36	36 $\Sigma n = 336$

TABLE 3.—Average size (mm) and standard deviation (SD) of *Homarus americanus*, *Cancer borealis*, and *C. irroratus* caught in all traps, locations combined. Size of crabs is carapace width; size of lobsters is carapace length.

		H. americanus-stocked			*C. borealis*-stocked			*C. irroratus*-stocked		
Species caught		Control	3	8	Control	3	8	Control	3	8
C. irroratus	$\bar{X}$	91.7	91.8	92.2	90.6	91.1	92.2	91.5	89.5	92.1
	SD	(10.1)	(11.5)	(13.2)	(9.9)	(11.3)	(10.4)	(10.6)	(11.8)	(8.6)
C. borealis	$\bar{X}$	92.8	94.8	94.8	93.3	94.5	92.3	94.4	94.6	92.7
	SD	(9.5)	(9.2)	(6.5)	(10.6)	(8.4)	(8.1)	(7.9)	(6.9)	(9.0)
H. americanus	$\bar{X}$	68.3	73.4	74.8	72.2	71.1	73.2	71.2	72.2	71.8
	SD	(7.9)	(6.8)	(8.1)	(6.7)	(9.1)	(9.6)	(7.6)	(7.0)	(12.5)

TABLE 4.—Total number of *Cancer irroratus* or *C. borealis* caught in 10 laboratory trials of each treatment and catch species. ** = $P<0.001$, χ^2 goodness of fit test.

Species caught	Treatment		
	Control	8 *Homarus americanus*	χ^2
C. irroratus	49	15	23.8**
C. borealis	66	20	14.9**

greater proportion of the crab catch was found in the kitchen of 8-lobster treatments than of controls (Tables 5, 6). Stocking traps with 3 lobsters had no effect on the distribution of crabs, and lobsters were unaffected by either stock density of lobsters ($P>0.05$).

Interspecific interactions between *C. irroratus* and *C. borealis* apparently influenced the distribution of these species inside traps. In traps stocked with either 3 or 8 *C. irroratus*, the proportion of the *C. borealis* catch found in the kitchen was significantly greater than in controls ($Z = 2.50$, $P<0.01$). In traps containing 3 *C. borealis*, the proportion of the *C. irroratus* catch found in the kitchen was significantly greater than in controls ($Z = 2.50$, $P<0.01$), but no effect was seen in traps stocked with 8 *C. borealis* ($P>0.05$) (Fig. 2).

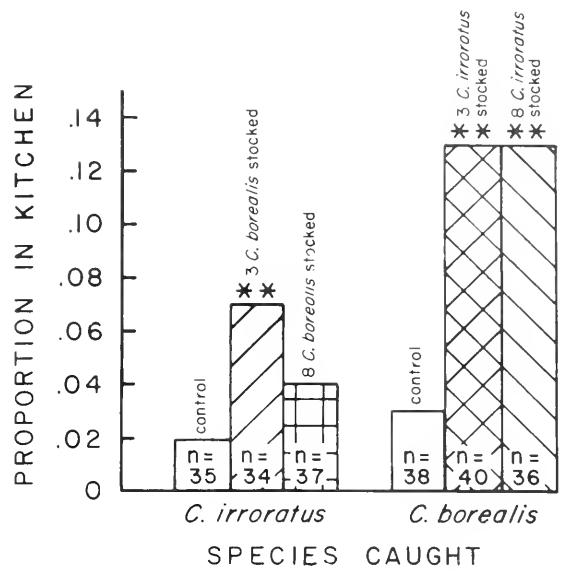

FIGURE 2.—Proportion of *Cancer irroratus* and *C. borealis* found in the kitchen of traps stocked with congeners in field experiments. All data obtained after one setover day are included. n = number of trap hauls, ** = significant difference ($P<0.01$) between treatment and control, using normal approximation for differences between two proportions (Zar 1974).

TABLE 5.—In field experiments, spatial distribution of *Cancer irroratus*, *C. borealis*, and *Homarus americanus* catch in traps stocked with *H. americanus* (Ha). All data obtained after one setover day are included. Proportion of catch found in the kitchen of stocked traps was compared with controls using normal approximation for differences between two proportions (Z) (Zar 1974). n = number of trap hauls; * = $P<0.05$, ** = $P<0.001$.

Species caught	Treatment	n	Proportion in kitchen	Z
C. irroratus	8 Ha	42	0.29	8.67**
	3 Ha	54	0.06	0.91 ns
	Control	51	0.03	
C. borealis	8 Ha	42	0.35	2.00*
	3 Ha	54	0.09	0.67 ns
	Control	51	0.13	
H. americanus	8 Ha	42	0.00	0.94 ns
	3 Ha	54	0.00	1.25 ns
	Control	51	0.03	

TABLE 6.—In laboratory experiments, spatial distribution of the *Cancer* crab catch in traps stocked with *Homarus americanus* (Ha). Proportion of catch found in the kitchen of stocked traps was compared with controls using normal approximation for differences between two proportions (Z) (Zar 1974). n = no. of trap hauls, * = $P<0.0001$.

Species caught	Treatment	n	Proportion in kitchen	Z
C. irroratus	8 Ha	10	0.27	5.19*
	Control	10	0.08	
C. borealis	8 Ha	10	0.70	5.27*
	Control	10	0.09	

Competition Inside Traps

To further investigate how the location of animals in a trap is affected by behavioral interactions, competition for preferred areas in the trap was studied in the laboratory. Frequency of occupation was used as an index of preference and was measured as the number of times a given position was occupied when censused every 15 min. The observed distribution of animals was compared with an expected uniform distribution using a χ^2 goodness of fit test. For lobsters and for each crab species in the absence of lobsters, the preferred position in the parlor was underneath the entry head (*C. irroratus*, $\chi^2_{(4)} = 202.0$, $P<0.001$; *C. borealis*, $\chi^2_{(4)} = 51.8$, $P<0.001$; *H. americanus*, $\chi^2_{(4)} = 744.2$, $P<0.001$). When lobsters were present, the number of crabs in the parlor decreased sharply, so comparisons between lobster-stocked and control traps were made using proportions. In the presence of lobsters, the preference of both crab species changed (*C. irroratus*, $Z = 2.26$, $P<0.01$; *C. borealis*, $Z = 5.97$, $P<0.001$). *Cancer irroratus* occupied the middle of the parlor, and *C. borealis* occupied the corners most frequently when *H. americanus* was

present (*C. irroratus*, $\chi^2_{(1)} = 82.3$, $P<0.001$; *C. borealis*, $\chi^2_{(1)} = 52.5$, $P<0.001$) (Table 7).

Space inside the trap was partitioned into vertical strata. Both crab species showed a significant increase in occupation of the top part of the trap when lobsters were present (*C. irroratus*, 0.47 vs. 0.79, $Z = 4.87$, $P<0.001$; *C. borealis*, 0.21 vs. 0.38, $Z = 1.76$, $P<0.05$). This contrasts with 99% occurrence of lobsters in the bottom portion of the trap.

from the parlor did not increase in lobster-stocked traps for either species (*C. irroratus*, $Z = 1.37$, $P>0.05$; *C. borealis*, $Z = 0.37$, $P>0.05$).

DISCUSSION

Trap Efficiency

The results of the field and laboratory experiments demonstrate that the presence of lobsters

TABLE 7.—Laboratory-observed frequency and relative frequency of occupation of positions in the parlor by *Cancer irroratus*, *C. borealis*, and *Homarus americanus*. Counts were weighted to compensate for unequal availability of positions due to trap design. * = significant ($P<0.01$) χ^2 values for frequency of occupation and preferred positions; + = significant ($P<0.01$) differences in occupation of a particular position in lobster-stocked traps and controls; ctl = control; lob = 5 lobsters stocked.

	Position occupied									
	Under head		Corner		Corner by head		Side		Middle	
Species caught	ctl	lob	ctl	lob	ctl	lob	ctl	lob	ctl	lob
C. irroratus										
Frequency	129*	27	12	9 3	32	8	9	8	60	57*
Relative frequency	0.53	0 25+	0.05	0.09	0.13	0.07	0.04	0.07	0.25	0 52+
C. borealis										
Frequency	93*	3	32	42.5*	42.5	17.3	23	9	42	15
Relative frequency	0.40	0.04+	0.14	0.49+	0.18	0.20	0 10	0 10	0 18	0.17
H. americanus										
Frequency	—	555*	—	204 8	—	38.6	—	109	—	471
Relative frequency	—	0.40	—	0.15	—	0.03	—	0.08	—	0.34

Trap Entry and Escapement

Laboratory observations revealed that *C. irroratus* and *C. borealis* respond differently to traps stocked with *H. americanus*. The presence of *H. americanus* did not affect the number of *C. irroratus* entering the kitchen (39 vs. 33, $\chi^2_{(1)} = 0.35$, $P>0.05$); however, significantly fewer *C. borealis* entered when *H. americanus* were stocked (35 vs. 8, $\chi^2_{(1)} = 18.2$, $P<0.001$).

The proportion of *C. irroratus* which moved from the kitchen to the parlor was significantly reduced in lobster-stocked traps (0.81 vs. 0.23, $Z = 2.73$, $P<0.0001$). The proportion of *C. borealis* entering the parlor did not decrease significantly when *H. americanus* was present (0.53 vs. 0.31, $Z = 0.58$, $P>0.05$); however, the number of *C. borealis* that had entered the kitchen was relatively low.

The proportion of both *C. irroratus* and *C. borealis* which escaped the kitchen increased significantly in the presence of *H. americanus* (*C. irroratus*, 0.23 vs. 0.55, $Z = 2.86$, $P<0.005$; *C. borealis*, 0.26 vs. 0.63, $Z = 1.97$, $P<0.025$). Escape reduces the CPUE of crabs, and provide a possible explanation for the inverse relationship between lobster and crab catches seen in other studies (e.g., Stasko 1975; Krouse 1978; Fogarty and Borden 1980). This effect appears to be density-dependent since fewer crabs were captured when a large number of lobsters were present.

Factors other than behavioral interactions could cause negative correlations between lobster and crab catch rates. *Cancer irroratus* is often spatially separated from *C. borealis* and *H. americanus* in Narragansett Bay (Jeffries 1966; Fogarty 1976). Such discontinuous distributions could result in inverse catches of *C. irroratus* and *H. americanus*, or of *C. irroratus* and *C. borealis*, but do not explain the differences seen in the catch of adjacent traps in this study. Other factors known to affect catchability (e.g., size, sex, reproductive condition, molt stage) were held constant among stocked animals used in the different treatments. Temperature changed little over the course of the study (average surface temperature, 21.9°±2.15°C). This and other environmental variables would have affected all treat-

ments equally. The nonrandom arrangement of treatment levels within strings could have biased catch rates through gear competition. However, we feel the assumption that equal numbers of animals were attracted to all traps is valid for the following reason. If gear competition caused the reduced crab catches in lobster-stocked strings, a similar pattern of catch rates would have been seen in crab-stocked strings. This was not the case.

Cancer irroratus is a prey item for lobsters (Squires 1970; Weiss 1970; Scarratt and Lowe 1972; Ennis 1973), suggesting that the decreased catch of this species in traps containing lobsters may be the result of predator-avoidance behavior. *Cancer borealis* and *H. americanus* are thought to compete for shelter space in rocky subtidal habitats (Stewart 1972; Fogarty 1976; Cooper and Uzmann 1977; Wang 1982). In laboratory studies (Fogarty 1976), *H. americanus* dominated *C. borealis* for possession of shelter. This dominance appeared to be the result of avoidance by *C. borealis* rather than overt aggressive interactions. Such behavior may cause reduced catches of *C. borealis* in traps containing lobsters.

The reduction in lobster CPUE when lobsters were stocked is not surprising since lobsters are known to be highly aggressive and generally inhabit shelter alone under natural conditions (Cobb 1971; Cooper and Uzmann 1980). Trap saturation apparently becomes important for lobsters at relatively low catch levels since traps stocked with 8 and 3 lobsters were equally effective in reducing the lobster catch. In a laboratory experiment reported by Smolowitz (1978), a reduction in trap entry was seen with only 1 or 2 lobsters in the trap. Reduced entry was probably important in the present study since escapement of stocked lobsters was low (10.1%).

Stock rates used for crabs were low compared with crab catches in control traps. At higher densities, crabs might have had a more significant effect on the catch of lobsters. An increased lobster catch might be expected in traps containing *C. irroratus*, a lobster prey item (Squires 1970; Weiss 1970; Ennis 1973; McLeese 1974). However, the presence of live prey may not significantly increase the attractiveness of an already baited trap. No evidence was seen of lobster predation on crabs in traps. Similarly a decrease in lobster catch might be expected in traps containing a competitor (*C. borealis*). However, *C. borealis* is less aggressive than *H. americanus* (Fogarty 1976; Wang 1982) and occupies mutually desirable shelters through passive means rather than active displacement, as shown in Stewart's (1972) study.

Trap saturation apparently was not an important factor for crabs at the stock levels used, since crab catches in crab-stocked traps were not reduced below the level of control traps. In laboratory observations, Miller (1978, 1979a, 1980) noted that intraspecific agonistic interactions among *C. irroratus*, *Hyas araneus*, and *C. productus* aggregating downstream from baited traps often resulted in departure from the trap area. He suggested that trap saturation in these three species was due in part to "intimidation" of crabs outside the trap by those inside. However, at relatively low catch densities, the effects of aggression may be minimal.

The increased *C. borealis* catch in traps stocked with 3 crabs of either species is difficult to explain. Release of attractants from the bait by feeding activity could enhance trap entry. As crab density inside the trap increases, such enhancement may be countered by increased aggression, reducing trap entry rates and increasing escapement. These speculations do not explain why the *C. irroratus* catch was not similarly increased by a low stock density of either crab species.

Behavior

Location Within Trap

Behavioral interactions apparently affected the spatial distribution of animals in traps. A greater proportion of the crab catch was found in the kitchen when 8 lobsters were stocked in the parlor. This may have been the result of the avoidance responses discussed above and may enhance escapement of crabs from traps containing lobsters. *Cancer borealis* shifted to the kitchen in both density levels of *C. irroratus*-stocked traps, but the distribution of *C. irroratus* changed significantly only in traps stocked with 3 *C. borealis*. Perhaps the generally greater activity of *C. irroratus* (Jeffries 1966; pers. obs.) serves as a deterrent to parlor entry by *C. borealis*. Both species may be influenced by prior residence effects in which an advantage is conferred upon the individual(s) initially utilizing a resource (e.g., Sinclair 1977; Davies 1978; O'Neill and Cobb 1979). Such an effect may have been caused by the stocking procedure.

Competition Inside Traps

During scuba diving observations of lobster traps, Pecci et al. (1978) noted an apparent dominance of crabs over lobsters in occupation of mutually desirable "niches" in traps. They reported that when both crabs and lobsters were present in traps, crabs always occupied positions that were evidently preferred by both species. The observations of this study contradict those of Pecci et al. Both crab species were displaced by lobsters. It is possible that our results reflect a prior residence advantage conferred on lobsters by the stocking procedure. However, our findings agree with what is known of the relative aggressiveness of *H. americanus*, *C. borealis*, and *C. irroratus* (Fogarty 1976; Wang 1982).

Trap Entry and Escapement

In the laboratory, the presence of *H. americanus* in a trap did not affect the number of *C. irroratus* entering the kitchen, but did decrease the number of *C. borealis* entering. Just the opposite might have been expected in light of the predator-prey relationship between *C. irroratus* and *H. americanus*. We observed no interactions between animals inside the trap and those outside; thus the sensory basis for avoidance by *C. borealis* of traps containing lobsters is unknown.

The proportion of *C. irroratus* moving from the kitchen to the parlor was reduced in lobster-stocked traps. The decrease in parlor entry rate for *C. borealis* was not statistically significant; however, the number of *C. borealis* that had entered the kitchen was relatively low. Reduced parlor entry appeared to be the direct result of interactions between animals in the two trap compartments. These typically consisted of a lobster displaying (meral spread) or lunging at a crab climbing up the parlor head, resulting in retreat to the kitchen by the crab. In several instances, crabs hanging from the parlor head contacted a lobster, which responded by displaying or attacking the crab. The crab then pulled back up into the parlor head and returned to the kitchen. General lobster activity (fighting, exploring, etc.) had a similar effect on crabs in the parlor head. Only 24% of *C. irroratus* and 10% of *C. borealis* entering the parlor head actually entered the parlor when lobsters were stocked. Parlor entrants increased to 60% and 67%, respectively, in control traps.

Escapement could be a significant factor in reducing the efficiency of traps. Skud[5] considered this the most likely explanation for declining catch rates for lobster over time. High escape rates for two species of *Cancer* have been observed by Miller (1979b) and High (1976). In this study, escape of both crab species from the kitchen increased when lobsters were present in the parlor, probably due to the behavioral interactions described above. Escape of crabs from the parlor did not increase when lobsters were stocked. This may reflect both the design of the parlor head, which makes escape more difficult, and the small sample size resulting from a low rate of entry to the parlor.

In summary, the behavioral mechanisms involved in reducing crab catches in traps containing lobsters were

1) For *C. borealis*, entry to the trap is reduced, and escapement of those that enter the kitchen is increased.
2) For *C. irroratus*, trap entry is not reduced, but entry to the parlor decreases and rate of escape from the kitchen increases.

SUMMARY

This study demonstrated that behavioral interactions between animals attracted to traps can have significant effects on the probability of their capture. The CPUE of American lobsters and of two species of commercially harvested *Cancer* crabs was significantly reduced in traps containing lobsters. Such effects may be density-dependent, since significantly fewer crabs were caught in traps containing 8 lobsters than in traps containing 3 lobsters. The proportion of captured crabs occupying each trap section changed significantly when lobsters were stocked, and behavioral observations indicated that lobsters occupy the mutually preferred positions in traps. The behavioral mechanisms responsible for decreased crab catches included both reduced entry (*C. borealis*) and increased escapement (*C. irroratus* and *C. borealis*). These results reflect the behavioral and ecological relations of the three species.

[5]Skud, B. E. 1976. Soak-time and the catch per pot in an offshore fishery for lobsters (*Homarus americanus*). ICES Special Meeting on Population Assessments of Shellfish Stocks, No. 8, 25 p.

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THE REPRODUCTIVE BIOLOGY OF THE ATLANTIC SHARPNOSE SHARK, *RHIZOPRIONODON TERRAENOVAE* (RICHARDSON)

GLENN R. PARSONS[1]

ABSTRACT

Atlantic sharpnose sharks, *Rhizoprionodon terraenovae* (Richardson), were collected in the north central Gulf of Mexico from June 1979 to May 1980. The principal sampling devices employed were longline, trawl, and rod and reel. From a total of 215 Atlantic sharpnose sharks obtained during the study, 144 were female and 71 were male, ranging from 30 to 107 cm total lengths. The reproductive anatomy of both male and female sharpnose sharks is described. Atlantic sharpnose sharks differ from other carcharhinids in that the ovary is developed on the left side in females and overlapping siphon sacs are present in males. Clasper development suggests that males mature at about 80 cm total length, while ovarian egg diameters show that female maturation occurs at about 85 cm. Matings occur primarily between mid-May and mid-July. Embryonic growth is rapid immediately after fertilization during summer and fall but declines during winter and spring. Gestation requires 10 to 11 months and parturitions probably peak in June. Pups are released near shore at an average total length of 32 cm. Statistical analyses reveal a positive relationship between adult total length and litter size, with the largest individuals being the most fecund. An inverse relationship was observed between the numbers of embryos per uterus and embryo size. Mechanical "packing" within the uterus is proposed to explain the relationship.

The seasonal distribution of sharpnose sharks was found to be determined by an inshore-offshore migration. The data indicate that during winter months in deeper offshore waters, aggregates of predominately adult female sharpnose sharks may be encountered. The sex ratio at birth was found to be 1:1 but among adults collected a 1:2.8 ratio was observed.

Studies dealing with the reproductive biology of elasmobranchs have fallen far behind the voluminous amount of data that have accumulated on reproduction in the teleostean fishes. The northern Gulf of Mexico has been an area of particular neglect with only a few rather generalized studies (Springer 1938, 1940, 1950; Baughman and Springer 1950). Springer's (1960) classic work on the natural history of the sandbar shark, *Carcharhinus milberti* (*Eulamia milberti*), contains a great deal of reproductive information that might be applied to carcharhinid sharks in general. Likewise, Clark and von Schmidt's (1965) survey of the sharks of the central gulf coast of Florida provided valuable reproductive data. The understanding of the life history of the blue shark, *Prionace glauca*, was furthered by Pratt's (1979) examination of its reproductive biology.

Data concerning the life history of *Rhizoprionodon terraenovae* are scarce. *Rhizoprionodon* species are believed to be born in the late spring and summer. Bigelow and Schroeder (1948) reported that recently born specimens can be collected from Florida in July and that they were also present off the mouth of the Mississippi River in August. Skocik (1969) reported that pups are usually born in the spring but no data were available on mating season or gestation period.

Rhizoprionodon species are viviparous, the embryos obtaining nourishment via a placental connection (sometimes called a "pseudo- or yolk-sac placenta") between mother and embryo. Fecundity in *Rhizoprionodon* has been variously reported. Baughman and Springer (1950) reported four embryos for *R. terraenovae*. Bass et al. (1975) found an average of 4.7 embryos with a range of two to eight in *R. acutus*. Skocik (1969) reported a litter size of 12 for *R. terraenovae*, while Bigelow and Schroeder (1948) reported the same number for *R. terraenovae* taken around Cuba. Clark and von Schmidt (1965) briefly surveyed *R. terraenovae* off Englewood, Fla., and found one 83 cm female with five eggs. They also reported that all adult females examined had functional left ovaries. Compagno (1978) reported a range of one to four embryos for *R. porosus*. The pups of *R. terraenovae* have been reported to be 11 to 16 in (27.9 to 40.6 cm) at birth (Baugh-

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man and Springer 1950). Bigelow and Schroeder (1948) reported that specimens from Texas showing traces of the umbilical scar were from 280 to 407 mm long.

Among *R. terraenovae* populations, adults are commonly 26 to 30 in (66 to 76 cm) total length (TL) (Baughman and Springer 1950), but the size at which male and female Atlantic sharpnose sharks mature is unknown. In his revision of the genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*, V. G. Springer (1964) reported that insufficient information was available to establish the size at which males first mature but it appeared that maturation occurs at >640 mm TL. Bass et al. (1975) reported that male *R. acutus* mature between 68 and 72 cm and females at 70 to 80 cm TL.

The present study is an attempt to clarify some of the known aspects of *R. terraenovae* reproductive biology as well as to provide additional information. The reproductive "strategy" of the Atlantic sharpnose shark is also examined.

METHODS AND MATERIALS

Atlantic sharpnose sharks, *Rhizoprionodon terraenovae* (Richardson), were collected in the north central Gulf of Mexico from June 1979 to May 1980. The principal sampling devices employed were longline, trawl, and rod and reel.

Floating longline generally gave the best results (Table 1). The technique, as used by Japanese fishermen, is described by Lopez et al. (1979). Because of the hazard to navigation that a floating longline represents, longlining operations were undertaken exclusively in deep waters offshore (Fig. 1). Longline sets were made in 10 to 28 fathom (18 to 51 m) depths, approximately due south of Dauphin Island, Ala. A trawl was used to collect specimens both inshore as well as offshore. Rod and reel, gill net, and seine were used exclusively inshore.

Specimens were immediately weighed and sexed. Total, fork, and standard lengths were measured to the nearest 0.1 cm. Lengths of the claspers and siphon sacs were measured on all male specimens. All specimens were dissected immediately in the field by an incision starting at the cloaca and extending to the midpectoral region. Notes on reproductive condition in males

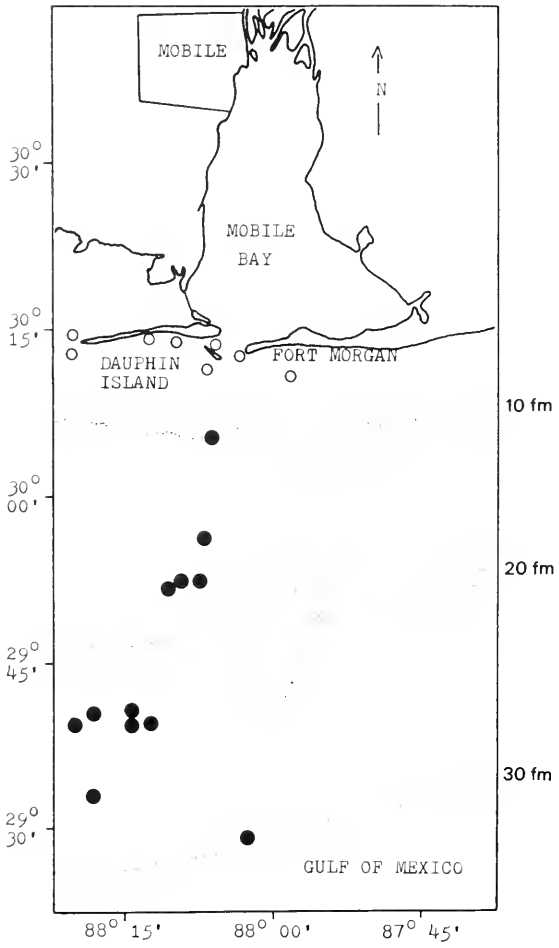

FIGURE 1.—Coastal Alabama study area of the Atlantic sharpnose shark. Offshore points (closed circles) represent longline and trawl sites. Inshore points (open circles) represent trawl, gill net, rod and reel, and seine sites.

TABLE 1.—Landings of Atlantic sharpnose sharks by month and by method. Longline and trawl produced more than 60% of the sharpnose shark specimens. Sharpnose sharks were collected in 10 of the 12 mo of the study period. — indicates no collections; 0 indicates collections attempted but no sharks landed.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Totals
Longline	—	1	—	2	0	—	—	14	—	4	19	35	75
Trawl	—	1	—	21	8	—	6	8	6	0	9	0	59
Rod/reel	—	0	—	0	8	1	38	1	2	0	0	0	50
Gill net	—	—	—	2	15	0	4	4	—	—	—	—	25
Seine	—	—	—	—	—	6	0	—	—	—	—	—	6
Totals	—	2	—	25	31	7	48	27	8	4	28	35	215

were taken, using those indicators of maturity reported by Clark and von Schmidt (1965). Dissections of males allowed examinations of the reproductive systems and measurements of testicular length, weight, and volume.

Testes and epididymides were removed from some specimens, preserved in 10% Formalin[2], and returned to the laboratory. Histological sections of testes as well as epididymides were prepared. The tissues were embedded in paraffin, sectioned at 7 μm, stained with hematoxylin and eosin, and examined with phase contrast microscopy. Sperm smears were also examined under the microscope.

After obtaining weight and total, fork, and standard lengths, female specimens were dissected and their reproductive organs examined. Ovarian lengths as well as the number of ovarian eggs and their diameters were recorded. When embryos were present, the number, sex, total length, and wet weight were determined for each uterus.

When appropriate, the data were keypunched and statistically evaluated, using the McGill University System for Interactive Computing (MUSIC) time sharing system. The STATPAK computer program, a statistical package containing 23 statistical analyses and data modification routines, was used to analyze the data.

RESULTS AND DISCUSSION

Reproductive Anatomy

Ovarian Structure

Forty-two Atlantic sharpnose shark ovaries were examined during the study period. Elasmobranchs possess a great deal of variability in the structure of the ovary (Dodd 1972). The ovary of the adult Atlantic sharpnose shark is an unpaired, tear-shaped organ, 6 to 10 cm long and 3 to 5 cm wide. Unlike other carcharhinids, the ovary of the sharpnose shark is developed on the left side only. Structure and location of the sharpnose shark ovary (aside from its position on the left side of the body cavity) are similar to that found in the blue shark (Pratt 1979). The adult sharpnose shark's ovary, during most of the year, is filled with many small (ca. 2.0 to 5.0 mm) oocytes embedded in dense connective tissue. Outside the breeding season the ovary of the adult female contains an average of about 30 oocytes greater than ca. 2 mm in diameter. These oocytes serve as a "pool" from which the next generation of eggs will be drawn. In some ovaries, unusual, bright red, fluid-filled structures were found, ranging from about 2 to 8 mm in diameter (Fig. 2). These structures are assumed to be oocytes in a state of atresia that had failed to ovulate during the most recent breeding period. These preovulatory structures may be "corpora atretica," which are derived from egg-containing follicles. In *Cetorhinus maximus* the corpora atretica are believed to arise from follicles that have attained a diameter of about 1.0 mm (Dodd 1972). The corpora atretica consist of vacuolated peripheral cells and a central cavity and are well vascularized (Dodd 1972).

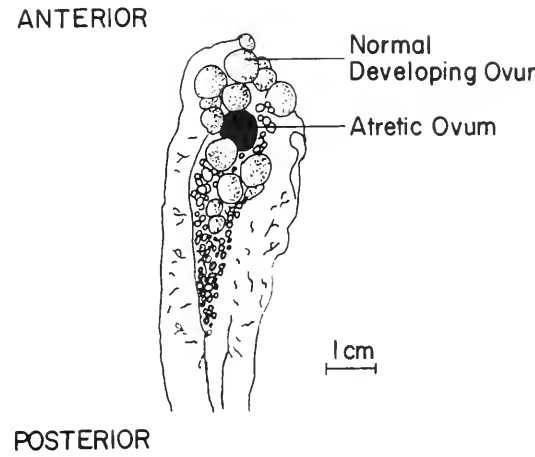

FIGURE 2.—Diagram of an Atlantic sharpnose shark ovary taken in December from a 93 cm gravid female. A red, fluid filled (atretic?) ovum can be seen in the center of the ovary.

Ovulation

As ovulation approaches, rapid yolk deposition occurs in four to eight of the many smaller oocytes. The "selected" oocytes are preferentially yolked, while the others undergo atresia. At or near ovulation the ovary appears highly vascularized and the large, yellow oocytes fill the entire ovary (Fig. 3). Measurements of both ovarian and uterine oocytes suggest that ovulation occurs at an egg diameter of about 20 mm.

After ovulation, the eggs move through the body cavity into the ostium tubae which forms the anterior end of the oviduct. In most cases

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

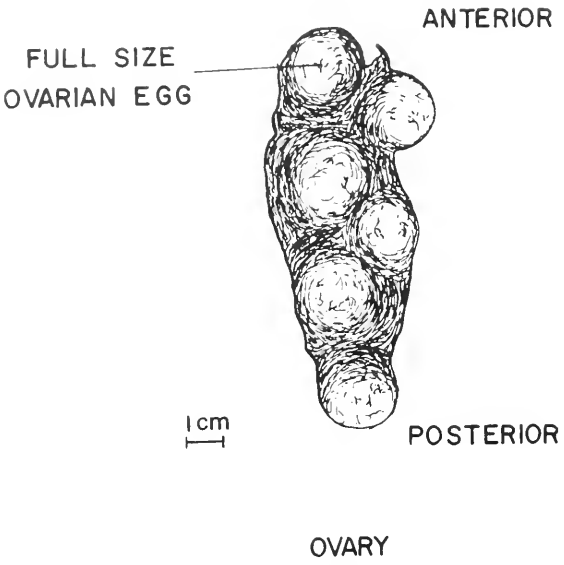

FIGURE 3.—"Ripe" ovary of an Atlantic sharpnose shark. The ovary contains ca. 20 mm ova that are ready to ovulate.

an equal number of ova enter both oviducts, although in some instances greatly disproportionate numbers of embryos were found between right and left uteri. The eggs move through the oviducts to the oviducal gland where fertilization probably takes place. The oviducal gland (Fig. 4) in the Atlantic sharpnose shark is a paired structure located at the forward end of the oviduct. The oviducal glands are the source of the egg case, and in some sharks the glands may be the site of long-term sperm storage (Pratt 1979). Viable sperm can be found within the lumen of those tubules within the gland which secretes the egg shell (Wourms 1977). As no histological sections of adult sharpnose sharks' oviducal glands were prepared, the question of sperm storage in sharpnose sharks remains unresolved. Prasad (1944), however, noted the presence of spermatozoa in the oviducal glands of *Scoliodon sorrakowah*, a closely related Indian Ocean species. This observation suggests that the oviducal gland may have at least a short-term storage capacity.

After moving through the oviducal gland the fertilized eggs then move to the uterus where they become implanted in depressions in the uterine wall. At this point the eggs are found encased in a thin, yellowish shell with pointed ends (Bigelow and Schroeder 1948). Within the uterus the eggs are elongate, averaging about 18 mm wide and about 32 mm long. Fertilization is apparently very efficient since in examination of 315 embryos only two unfertile eggs were noted (0.6%).

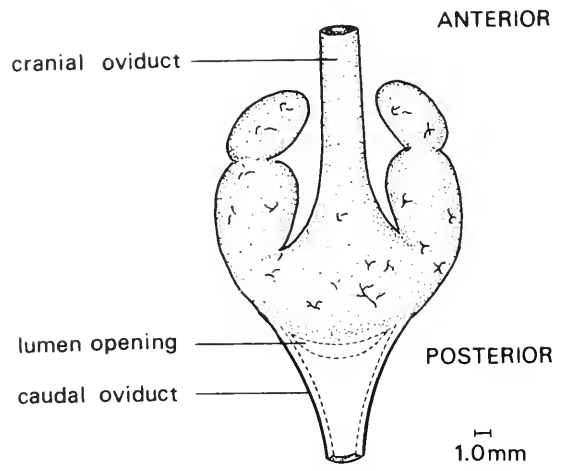

FIGURE 4.—Diagram of an oviducal gland taken from a mature female Atlantic sharpnose shark.

Placentation and Structure of the Umbilical Cord

During the first 2.5 to 3.0 mo of gestation, the Atlantic sharpnose shark embryos depend upon the yolk sac for nourishment. After about 3 mo the yolk sac has become intimately associated with the uterine wall to form a yolk-sac placenta. October embryos, i.e., 3 mo old, were ca. 16 to 20 cm and had well-developed placentas with little yolk material remaining. By November, 4 mo into gestation, embryos were 19 to 23 cm long and no yolk material remained in the placenta. In a related Indian Ocean species, *Scoliodon sorrakowah*, Mahadevan (1940) described a very thick vascularized area of the uterine wall, referred to as a trophonematous cup, which forms to receive the yolk sac of the foetus. This vascularized area was also noted in the Atlantic sharpnose shark.

Development of the umbilical cord closely parallels placentation. The umbilical cord is connected on the embryo's ventral surface in the midpectoral region. Very early in development the umbilical cord is virtually naked. By the time the embryos have grown to about 6.0 cm TL the umbilical cord has developed many knoblike appendages which give it a "pipe-cleaner" appearance. The appendages are about 1 mm long, and terminate in one or a cluster of several grapelike

distentions. Budker (1971) suggested that in addition to placentally derived nutrients, these appendages may allow the embryo to absorb directly nutritive substances that are secreted by the uterine lining. This type of nutrition is termed histotrophic. As gestation progresses the appendages of the sharpnose shark's umbilical cord lengthen and change morphologically. Full-term embryos possessed umbilical cords about 10 to 12 cm long with appendages about 10 mm. The projections at this time have a foliose appearance, i.e., flattened, extensively branched, and terminating in rounded, flat expansions. This differs from the fingerlike shape described for the projections found on the umbilical cord of *Sphyrna tiburo* (Schlernitzauer and Gilbert 1966).

Structure of Claspers and Siphon Sac

The paired claspers of the adult male Atlantic sharpnose shark are much the same as those of other carcharhinid sharks. The claspers are rigid, calcified, intromittent organs that rotate freely around their attachment base. The tip, or rhipidion, expands whereupon the rigid cartilages of the tip are directed at right angles to the main axis of the clasper. This expansion is believed to function as an anchor, holding the clasper in the oviduct during copulation. Under normal circumstances the claspers are directed posteriorly. Springer (1960) has suggested that just prior to mating the claspers of large carcharhinid sharks such as *Eulamia milberti* (*Carcharhinus milberti*) rotate in and forward. Expansion of the rhipidion occurs independently after insertion of the clasper into the oviduct of the female. This apparently also occurs in the Atlantic sharpnose shark, since a live specimen captured in December had one clasper oriented in this fashion, with the rhipidion expanded, probably a result of trauma. The clasper gradually returned to normal after about 3 min.

The siphon sac in the adult Atlantic sharpnose shark is a muscular, subdermal organ which begins at the base of the claspers, extends anteriorly along the ventral surface, and ends just short of the coracoid bar. The sac in adults ranges from about 20 to 28 cm long and 1 to 2 cm wide. Unlike other shark species which have paired separate siphon sacs, Atlantic sharpnose sharks possess overlapping sacs which communicate with the claspers via an opening located at the base of each clasper. Springer (1960) suggested that the siphon sac is filled with water just prior to mating and is used to flush sperm along the clasper groove and into the oviducts during copulation. The clasper siphon of adult spiny dogfish, *Squalus acanthias*, has been found to be a rich source of serotonin. This suggests that the siphon-sac secretion may play a role in affecting the mechanism of copulation and ejaculation in the male, or by eliciting contractions of the female reproductive tract, thus influencing passage of sperm and fertilization (Mann 1960).

Structure of the Testes and Epididymides

The testes in the adult male Atlantic sharpnose sharks are paired, elongate, flattened organs (Fig. 5). Depending on the season and the size of the adult, the testes range from 13 to 20 cm long, 1 to 2 cm wide, and 0.5 to 1.0 cm thick. The testes are located dorsal to the lobes of the liver at the anterior end of the peritoneal cavity. The organs are supported here by a mesorchium.

Microscopic examination of a mature testis of the sharpnose shark shows that the organ is filled

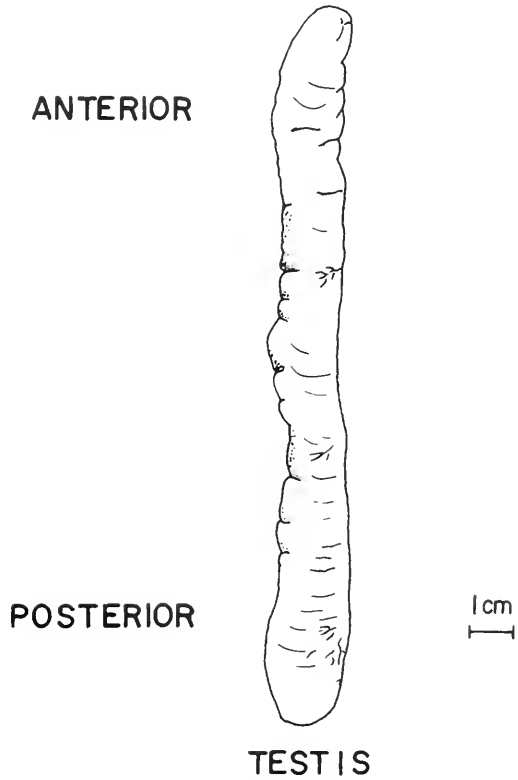

FIGURE 5.—Diagram of a "ripe" Atlantic sharpnose shark testis. The testis is turgid indicative of the reproductively active condition.

with spherical seminiferous ampullae, much the same as are found in spiny dogfish (Simpson and Wardle 1967) and blue shark (Pratt 1979). Histological sections of mature testes demonstrate that these ampullae contain spermatozoa in various stages of development (Fig. 6). Viewed in cross section, the heads of the mature spermatozoa are arranged in discrete groups around the periphery of the spherical ampullae.

The spermatozoa leave the testis by way of the efferent ductules and enter the epididymis. The epididymis is a paired organ located above the testis against the dorsal wall of the abdominal cavity. The sharpnose shark's epididymis is about 15 cm long, 1.0 cm wide, and 0.5 cm thick. Histological sections of an epididymis from a reproductively active sharpnose shark reveal great numbers of spermatozoa present in the tubules of the organ (Fig. 7).

Maturation

Males

Maturity in animals can generally be determined by comparing external secondary sex characters in adults with the same characters in smaller individuals. Using two indicators of sexual maturity (i.e., clasper growth and siphon-sac development), it was determined that maturation of the male Atlantic sharpnose shark begins at about 60 to 65 cm TL and is complete at about 80 cm.

At <65 cm TL the clasper length represents about 2.5% of the adult total length. Regression analysis shows that the claspers undergo a period of rapid growth with a major inflection in the line occurring at 65 to 70 cm TL (Fig. 8). The claspers quickly elongate, growing 3 cm within a short period of time to represent 7 to 8% of the total length. The smallest mature males examined were about 80 cm long and their claspers represented about 7.8% of total length. There were many individuals examined between 75 and 80 cm TL that possessed elongated claspers, but incomplete calcification of the claspers indicated that the specimens were not mature.

The clasper grows faster than the total length at the onset of maturation and for a short period into adult life. Regression analysis indicates that from about 85 to 95 cm TL the relationship is unchanging, but after 95 cm there is a period of

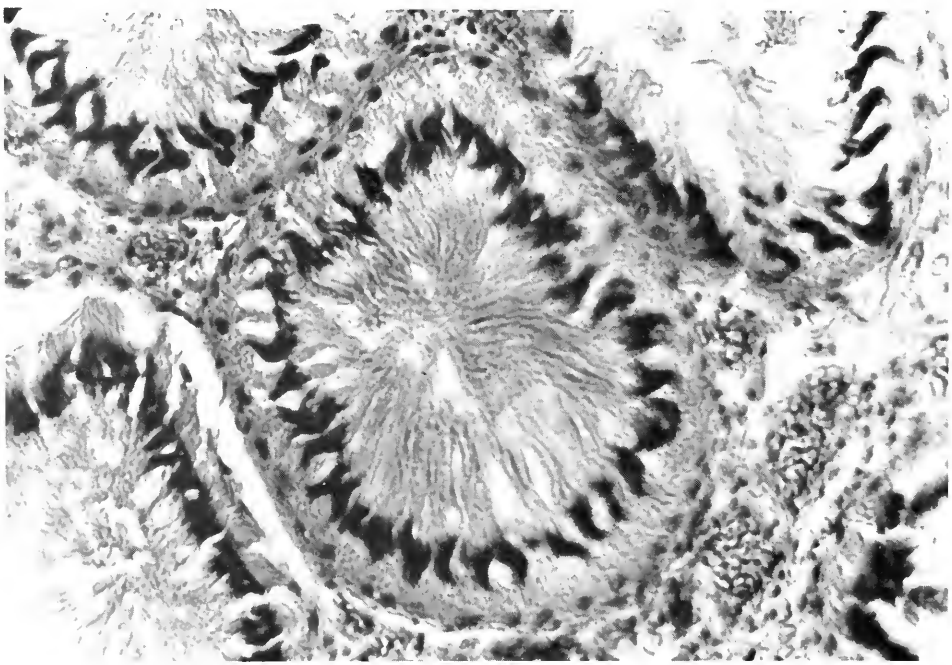

FIGURE 6.—Histological section of a testis from a mature Atlantic sharpnose shark (×440). The cross sections show that the heads of the mature spermatozoa are arranged in discrete groups around the periphery of the spherical seminiferous ampullae.

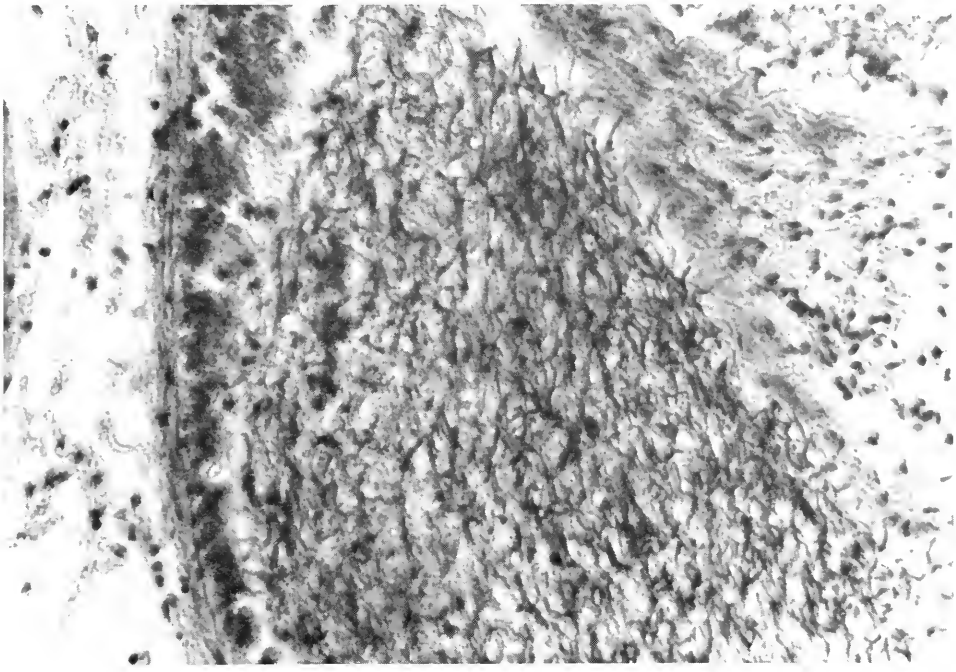

FIGURE 7.—Histological section of an epididymis from a mature Atlantic sharpnose shark (×140). Large numbers of spermatozoa are present within the tubules of the structure.

negative allometric growth. The claspers, after attaining their functional length, do not continue to grow or at least grow very little. This is a tenable hypothesis since continued growth would not necessarily enhance the claspers' utility.

Development of the siphon sacs coincides closely with the rapid increase in clasper length (Fig. 9). This muscular, subdermal organ is nonexistent until the onset of maturity. The siphon sacs develop quickly and represent about 28% of the

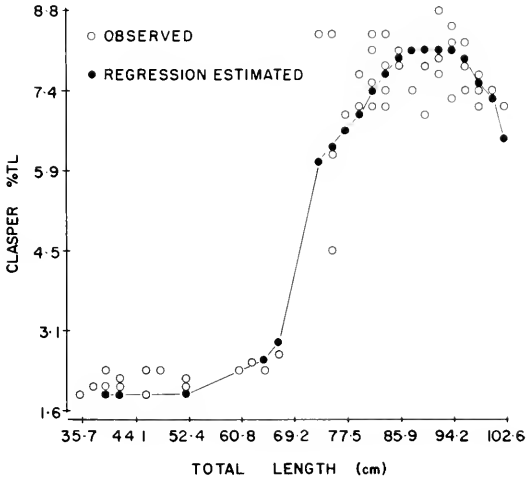

FIGURE 8.—The maturation of male Atlantic sharpnose sharks as evidenced by clasper development. The regression line indicates that maturation occurs between 80 and 85 cm total length, $N = 70$.

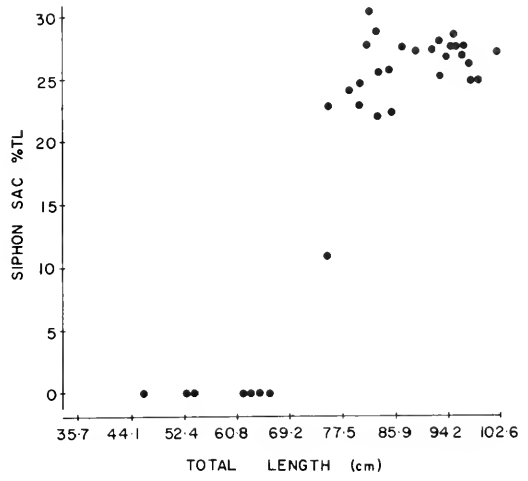

FIGURE 9.—The maturation of male Atlantic sharpnose sharks as evidenced by siphon-sac development. The scatter diagram suggests that maturation occurs at about 80 cm total length, $N = 35$.

total length at maturity. The smallest mature individuals were about 80 cm and possessed siphon sacs about 23% of total length.

Females

Maturation in females was determined by examining the developing ovary and ovarian eggs. Females were found to mature at a greater total length than males. The ovary does not begin to develop until the individual reaches about 60 cm TL. Figure 10 shows that development reaches an asymptote between 85 and 90 cm TL. Even among individuals of the same size taken during the same month there is a high degree of variation in ovarian length. For this reason ovarian length is not considered a good indicator of maturity in Atlantic sharpnose shark.

Changes in the diameter of ovarian eggs were found to be a reliable indicator of the beginning of maturation. Figure 11 shows the first generation of ovarian eggs produced by the subadult population. Increase in egg diameter begins at 60 to 65 cm TL, at about the same time the length of the ovary begins to increase. The eggs increase in diameter until the first ovulation, which occurs at about 85 to 90 cm TL. Most female sharpnose sharks mature within this size range.

Several female sharpnose sharks that had recently matured were examined. One individual of 88 cm TL, collected in late May, had full-sized ovarian eggs and had apparently recently mated due to the numerous mating scars that were observed in the region between the first and second

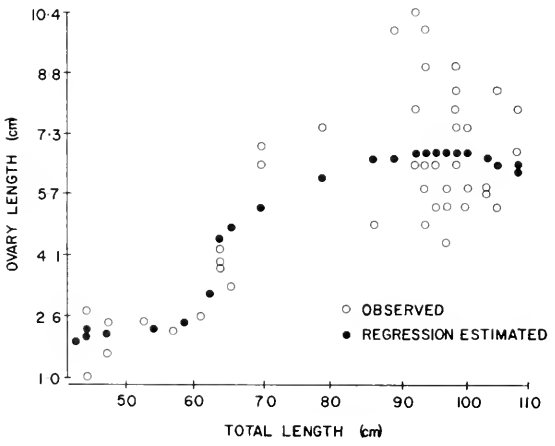

FIGURE 10.—Regression analysis showing development of the ovary in Atlantic sharpnose sharks, $N = 42$. Maturation is estimated to be complete at 85 to 90 cm total length.

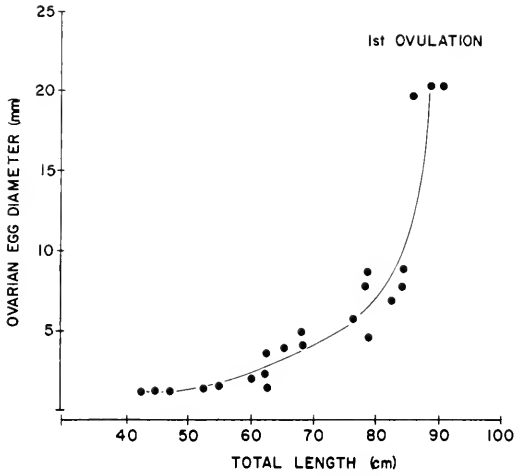

FIGURE 11.—Maturation of female Atlantic sharpnose sharks as evidenced by the increase in ovarian egg diameter. Hand-fit curve approximates the increase in ovarian egg diameter from juvenile to first ovulation, $N = 63$.

dorsal fins. An 86 cm individual, collected in early July, possessed six ova (8 to 10 cm), while another 89 cm female, collected in mid-July, possessed uterine eggs. In late August, all mature females examined contained embryos. The smallest gravid specimens were 87, 88, and 89 cm TL and contained 11, 8, and 6 cm embryos, respectively. These observations further support the 85 to 90 cm estimated size at maturity.

Mating Season

Twenty-three reproductively active male Atlantic sharpnose sharks were examined to delineate the mating season. A gonadosomatic index (GSI), testis weight expressed as percent total body weight, was found to be the best indicator of mating season.

The GSI provided a defined mating season for male sharpnose sharks (Fig. 12). Reporting on central gulf coast of Florida populations, Clark and von Schmidt (1965) suggested that small shark species (such as *Mustelus norrisi* and *Scoliodon terraenovae* = *Rhizoprionodon terraenovae*) mate and bear young in the late winter and early spring. In the north central gulf, contrary to Clark and von Schmidt's findings for Florida, male sharpnose sharks appear to be reproductively active during late spring and summer. From about September to March, the GSI was found to be low, 0.2 to 0.37. During these months specimens were observed to have reduced testes

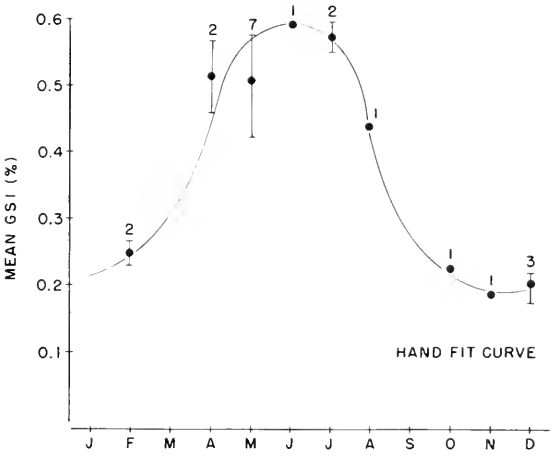

FIGURE 12.—Mating season of adult male Atlantic sharpnose sharks as evidenced by the seasonal increase in gonadosomatic index (GSI). The data suggest that male sharpnose sharks are reproductively active during late spring and summer. The closed circles represent mean values and the numbers indicate sample sizes, $N = 20$.

and no visible sperm or semen in the seminal vesicles. In late April the GSI had risen to 0.51, but there was little sperm present in the seminal vesicles. During mid- to late May the GSI averaged 0.47. All mature individuals had enlarged testes, turgid seminal vesicles, and copious amounts of sperm present in the claspers as evidenced by microscopic examination. This condition was found to persist through June and July with GSI equalling 0.59 and 0.57, respectively. Several adult males examined in August were found to have large quantities of sperm in the seminal vesicles. A single GSI determination indicated a slight decline from previous months.

The mating season in female sharpnose sharks was evidenced by an increase in ovarian egg diameter (Fig. 13). From August to December the average egg diameter increased from ca. 3.0 to 4.2 mm. In almost every ovary examined during November and December, a few eggs were beginning to visually dominate the other oocytes. In February, the mean oocyte diameter equalled 5.0 mm, with some eggs reaching 11 mm. In February, all mature ovaries contained four to eight oocytes that were noticeably larger than surrounding eggs. From mid-February to late May or June, there was a rapid increase in egg diameter to about 20 mm at ovulation.

The information indicates that the mating season for male and female sharpnose sharks in the northern Gulf of Mexico coincides, although male sharpnose sharks are reproductively active earlier in the year. Assuming that females do not mate when gravid and that ovulations occur after copulation, then the mating season must occur between mid-May and mid-July. Most adult females still carried near-term embryos in mid-May, and by mid-July all females examined had uterine eggs. Considering the peak of parturition for gravid females (see Embryonic Growth and Development section), the subsequent appearance of uterine eggs, and the occurrence of the first detectable embryos, the peak of mating most likely occurs from mid-June to mid-July.

Embryonic Growth and Development

Embryos representing various stages of development were weighed, sexed, and measured in total length. Conceptions were estimated to be at a peak in early to mid-July. At this time several sharpnose sharks that possessed recently ovulated uterine eggs but no visible embryos were examined. In late August, gravid females were collected, and they contained embryos ranging from about 4 to 11 cm TL. The smallest embryos examined were still dependent upon the yolk sac. They had prominent branchial gill filaments, undeveloped fins, and the anterior end was enlarged in relation to the rest of the body. Pratt (1979) suggested that growth of embryonic *Prionace glauca* is linear. Increase in length of sharpnose shark's embryos approximates a sigmoid curve as evidenced by polynomial regression

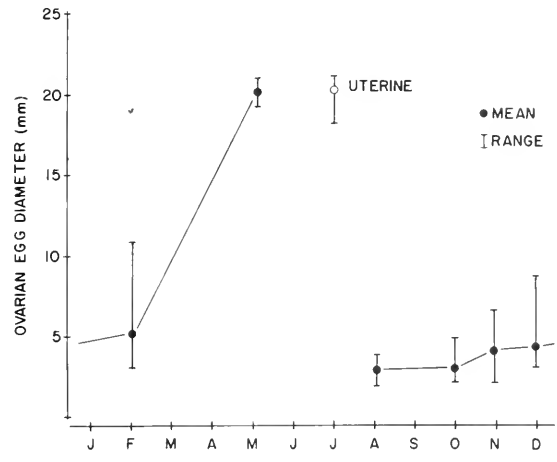

FIGURE 13.—Mating season of adult female Atlantic sharpnose sharks as evidenced by the seasonal increase in ovarian egg diameter, $N = 1,260$. The data suggest that the mating season for females occurs from mid-June to mid-July.

analysis (Fig. 14). After conception there is a period of rapid growth through the remainder of the summer and fall. By November the embryos have attained an average of 21.3 cm and appear almost completely developed. There is a noticeable inflection in the regression line in November. The increase in length declines through the winter and spring months, although a slight increase may occur just before parturition in May or June. Pups are born at an average of about 32 cm TL. Skocik (1969) reported a total length of 25 cm for sharpnose shark at birth, and Bigelow and Schroeder (1948) stated that newborn sharpnose sharks are generally about 275 to 400 mm long. The largest embryo recorded during the study period was 36 cm TL and the smallest free-living specimen was 32 cm.

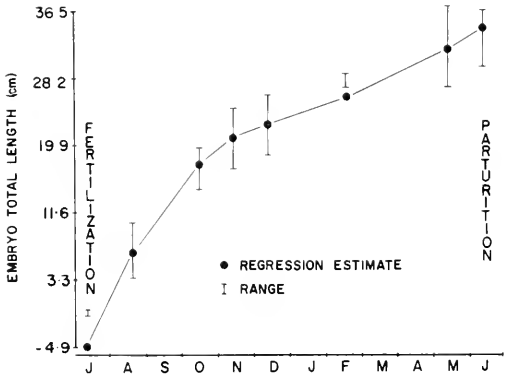

FIGURE 14.—Growth of embryonic Atlantic sharpnose shark. Regression analysis shows the increase in embryo total length from fertilization to parturition, $N = 300$.

Increases in weight of the sharpnose shark's embryo differed from the increases in total length (Fig. 15). Embryo weight increased slowly during the period from estimated conception (mid-July) to October. Thereafter, however, until parturition in late May or June, an almost linear increase of about 16 g/mo occurred. Parturition occurs most likely between about 95 and 150 g.

By using the above information, it was possible to estimate the gestation period. Atlantic sharpnose shark's embryos require a 10 to 11 mo gestation period, beginning in July or August and ending in May or June of the following year.

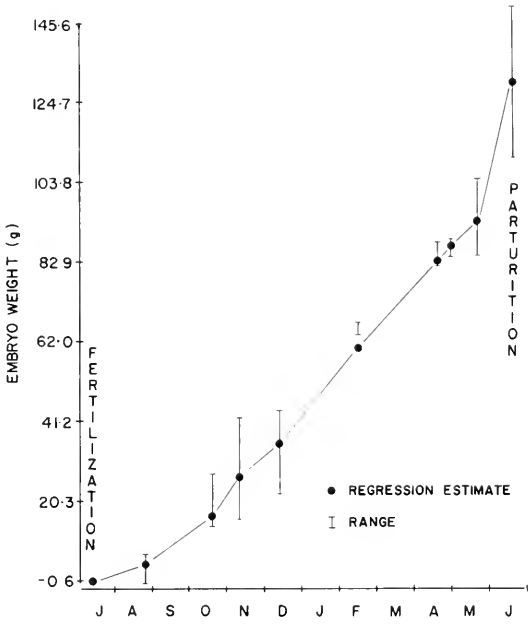

FIGURE 15.—Growth of embryonic Atlantic sharpnose shark. Regression analysis shows the increase in embryo weight from fertilization to parturition, $N = 300$.

Relationships Between Adult Females and Embryos

A significant relationship was observed between total length of the gravid female and the number of offspring produced. This is noteworthy since other works have failed to show such a relationship among carcharhinids (Springer 1960; Clark and von Schmidt 1965). Figure 16 shows that the total length of the adult is correlated with litter size (ANOVA significant at <0.01). There is a direct relationship between fecundity and the size of the adult with the largest individuals being the most fecund. Gravid females produce an average of 5 pups/litter per year (one to seven), but in most cases either four or six embryos will be present.

It was anticipated that a relationship between litter size and embryo size could be detected. An optimal clutch size has been demonstrated in some species of birds (Lack 1954, 1966, 1968). Compared with small and large clutches, intermediate-sized clutches leave proportionately more offspring that survive to maturity. Birds from large clutches are smaller in size than birds from intermediate-sized clutches. After evaluating the data, an "optimal litter size" could not be demonstrated for the Atlantic sharpnose sharks. However, when the right and left uteri of adults collected during a single sampling trip (to cancel out seasonal differences) were treated separately, an inverse relationship was observed between the numbers of embryos per uterus and

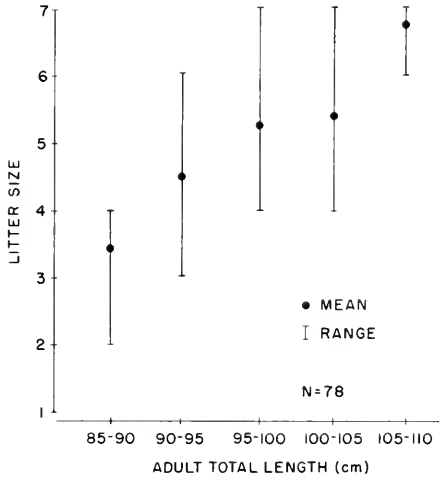

FIGURE 16.—Relationship between adult total length and litter size of the Atlantic sharpnose sharks. The plot indicates that fecundity increases significantly as adult total length increases ($F = 9.216$, $P<0.00001$).

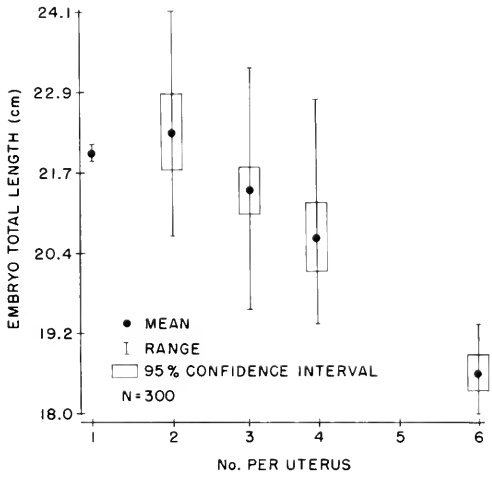

FIGURE 17.—Relationship between numbers of embryos per uterus and embryo total length of the Atlantic sharpnose sharks. Embryo total length decreases significantly with increasing number per uterus, $N = 89$.

embryo size (Fig. 17). The figure indicates that at the 95% confidence limits significant differences exist between the total lengths of the embryos. Embryos were found to be largest when one or two are present per uterus. However, in only one case was there a single embryo found within a uterus.

It is conceivable that mechanical "packing" within the uterus causes "intra-uterine competition" for nutrients. As already discussed, in addition to placentally derived nourishment, sharpnose shark embryos may be able to absorb directly nutrients which are produced by the uterine epithelium. An increase in the number of embryos within the uterus above some optimal value might result in competition for this "uterine milk" and a decrease in embryo size.

In sharpnose sharks, the parents that produce what might be termed an "optimal" number of embryos per uterus are producing the largest embryos. If we assume that these size differences are retained until birth, and thereafter, these larger embryos will result in progeny of highest individual fitness. Larger offspring cost more to produce, but they are also worth more (Pianka 1978).

It would be interesting to examine the reproductive strategy of tropical sharpnose shark populations, since these sharks have been reported to have litters with as many as 12 embryos (Bigelow and Schroeder 1948; Skocik 1969). Based on this study, it would be a logical extrapolation to predict that these litters would result in smaller offspring. A litter of 12 must be approaching maximum fecundity for sharpnose sharks.

Seasonal Distribution

In this study it was determined that migratory behavior of the Atlantic sharpnose shark is primarily limited to an inshore-offshore movement. From late April to September of 1979, 93 sharpnose sharks were collected from shallow inshore waters. During the period from late October 1979 to April 1980, despite numerous attempts, no sharpnose sharks were collected inshore. Sharpnose sharks may be encountered offshore year-round; however, the data indicate that the concentration of sharks is greatest during the fall and in particular, winter months. From October 1979 to February 1980, 59 sharpnose sharks were collected during offshore longlining. Figure 18 shows that the number of sharpnose sharks landed in deep water, as well as the catch per unit effort (CUE), is low in spring and summer (CUE = 1.2 and 2.4, respectively) and increases to a high in winter (CUE = 7.3).

The above data suggest that the migration from inshore to offshore begins around October or November. Atlantic sharpnose sharks apparently remain in deeper waters during the colder months and return inshore again in April and May.

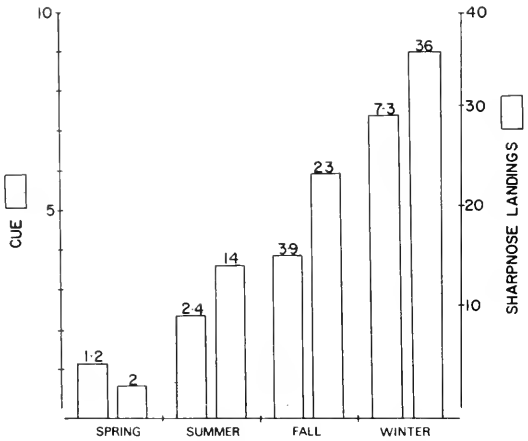

FIGURE 18.—Catch per unit effort (CUE) in sharks/100 hooks per hour and number of Atlantic sharpnose sharks landed during longline operations. Ninety percent of these offshore landings were gravid females.

Since adult female Atlantic sharpnose sharks were collected inshore only during summer months, the data suggest that females migrate inshore in late spring or summer to pup and mate, whereupon they return offshore again to overwinter. During June and July sharpnose shark pups with a fresh umbilical scar (in some cases the scar was actually an open slit) could be collected from the littoral zone. It is likely that special nursery areas exist for many shark species (Springer 1967), although the existence of specific pupping or nursery grounds for the Atlantic sharpnose sharks could not be conclusively established from this study. However, since newborn pups were never taken from deep waters in spite of intensive trawling, it is reasonable to suppose that the pups were born in shallow water. Perhaps the shallows of the northern Gulf of Mexico's extensive barrier island system serve as pupping/nursery grounds for the Atlantic sharpnose shark.

Sex Ratio

Sex of the Atlantic sharpnose sharks could be determined by clasper examination in embryos as small as 5.0 cm TL. The sex ratio through most of gestation could therefore be determined. The sex ratio early in development and of near-term embryos was found to be 1:1. One-hundred and fifty male and 155 female embryos were examined. These data suggest that the sex ratio at parturition is also 1:1.

Among adults sampled, the sex ratio was found to be one sided in favor of females. During this study 33 adult male and 91 adult female sharpnose sharks were collected representing a 1:2.8 ratio. During offshore longlining 90% of the catch consisted of gravid adult female sharpnose sharks. This condition in sharpnose shark is not without precedent, as it has been observed in other shark species. Springer (1940), discussing *Carcharhinus milberti* and *Carcharhinus obscurus*, stated that in both species females outnumber males. Clark and von Schmidt (1965) found a similar situation in *Galeocerdo cuvieri*.

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VARIATION IN THE GROWTH RATE OF *MYA ARENARIA* AND ITS RELATIONSHIP TO THE ENVIRONMENT AS ANALYZED THROUGH PRINCIPAL COMPONENTS ANALYSIS AND THE ω PARAMETER OF THE VON BERTALANFFY EQUATION

RICHARD S. APPELDOORN[1]

ABSTRACT

Age-length data and environmental parameters were obtained for 25 populations of the soft-shell clam, *Mya arenaria*. Growth rates were analyzed for 20 of the populations and variations in the growth rates were related to differences in the environment. The analysis of growth was based on Gallucci and Quinn's ω parameter for the von Bertalanffy equation. Environmental variability was analyzed, using principal components analysis which yielded three environmental factors: Northness, siltiness, and sedimentary hydrocarbons. Growth was found to be significantly related to each of the three components. A distinct latitudinal growth relationship was observed, with growth decreasing towards the north. Temperature, tidal height, tidal position, and edaphic conditions systematically varied with latitude, with temperature being the dominant factor affecting growth. Growth was negatively correlated to both siltiness and sedimentary hydrocarbons.

The growth of the soft-shell clam, *Mya arenaria*, has been studied by many investigators (Wilton and Wilton 1929; Belding 1930; Newcombe 1936; Swan 1952; Brousseau 1979; and others), and much work has been done in assessing the importance of various environmental factors in the growth process. These factors include water current and quality, food, temperature, salinity, various edaphic parameters, and pollution. In the past, investigators were obliged to study these factors individually even though it was realized that many were interrelated (Belding 1930). Because of local variations researchers often disagreed on the relative importance of each of these factors, and overall trends have not been firmly established.

The purpose of this study was to investigate various factors contributing to growth rate variations in soft clam populations and to demonstrate a methodology incorporating the analysis of multiple factors applicable to the above investigation. Of specific interest was the demonstration of a latitudinal trend in growth and the factors responsible for it, since such a relationship had yet to be quantified (Brousseau 1979). Principal components analysis was used to analyze multivariate environmental data, and the von Bertalanffy model was used for the analysis of growth, using the recently introduced growth rate parameter ω of Gallucci and Quinn (1979). This study represents one of the first applications of ω to investigate growth rate variations.

MATERIALS AND METHODS

Samples of *Mya arenaria* and environmental data were obtained from 25 sites located along the east coast of North America, from Maryland to Nova Scotia (Fig. 1). The sites were initially chosen and sampled as part of a study to investigate the relationship between environmental quality and neoplasia (Brown 1980), and as a result 1) the sites varied greatly in their environmental quality, 2) the sampling design employed was not specifically designed for the present study, and 3) it was therefore necessary to use proxy data in some cases to represent certain environmental characteristics. These drawbacks were not severely limiting, since the particular statistical techniques used could control much of the induced variability in the data. Estimates of the following environmental parameters were obtained: Salinity, tidal position, tidal range, average annual temperature, sedimentary grain size, dispersion and skewness of grain sizes, percent silt-clay, percent organic matter, and total sedimentary hydrocarbons.

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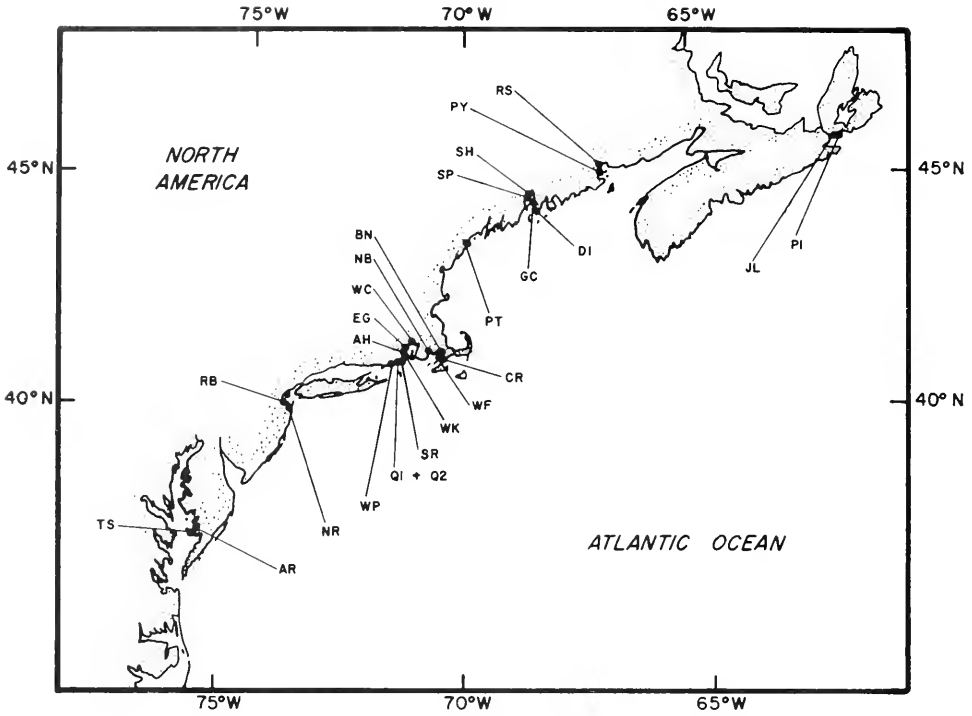

FIGURE 1.—Location of sampling sites. Site codes are given in Table 1.

Salinity, at low tide, was measured by a refractometer; tidal position was estimated on a scale of 0-1, where 0 = subtidal and 1 = full exposure. Estimates of the average annual temperature near each site were obtained from various literature sources, and estimates of the tidal range were obtained from National Ocean Survey (1978).

Sediment samples (composites of two surface cores 21 $cm^2 \times 8$ cm depth) were collected and analyzed to determine grain size distribution and organic content. The sand fraction was analyzed by dry sieving; silt-clay by the hydrometer method (American Society for Testing Materials 1963). The particle size distributions obtained from the two analyses were pooled, and the cumulative frequency versus grain size (ϕ) was plotted for each sample. From the graphs the following summary statistics were obtained: Median grain size ($Md\phi$), quartile deviation ($QD\phi$), and skewness ($Skq\phi$) (Buchanan 1971). The results were reported in phi notation rather than millimeters [$\phi = -\log_2(mm)$], as this scale is commonly used to describe grain size characteristics and because it allows for greater discrimination in the silt-clay range which may be more meaningful biologically.

The percent organic matter was determined by measuring the percent weight loss of a small aliquot upon ignition at 550°C for 4 h (Buchanan 1971). Estimates for total sedimentary hydrocarbons through infrared analysis were obtained from C. Brown.[2] The sites and their environmental parameters are given in Table 1 along with their dates of collection, latitude, and code.

Clams were sampled from one or more trenches dug by a standard clam hoe or shovel, with the exception of the Chesapeake Bay sites where a commercial hydraulic escalator dredge was used. All clams excavated were retained for analysis. For each individual, shell length (maximum shell dimension) was measured by vernier calipers to the nearest millimeter.

Age structure was determined via length-frequency analysis for 19 of the populations. Similar information for six of the sites (BN, WF, SP, GC, PY, JL) was available from Appeldoorn (1981), though only the West Falmouth (WF) growth data were used in subsequent analyses since major growth interruptions resulting from pollution events occurred at the other sites.

[2]C. W. Brown, Professor, Department of Chemistry, University of Rhode Island, Kingston, R.I., pers. commun. May 1979.

TABLE 1.—Sampling sites and their environmental parameters. — = missing value.

Sampling site	Site code	Date of sampling	Latitude (°N)	Average annual temperature (°C)	Tidal range ft (m)	Tidal position	Mdϕ	QDϕ	Skqϕ	% silt-clay	% organic matter	Total sedimentary hydrocarbons (μg/g)	Salinity (ppt)
Tangier Sound, Md.	TS	27-3-78	37.952	[1]15.0	2.5 (0.77)	0	—	—	—	—	—	—	11
Big Annemessex River, Md.	AR	27-3-78	38.051	[1]15.0	2.5 (0.77)	0	—	—	—	—	—	—	11
Navesink River, N.J.	NR	2-6-77	40.377	[2]13.0	3.5 (1.08)	0.50	1.80	0.40	−0.10	1.0	1.5	114	24
Raritan Bay, N.J.	RB	1-6-77	40.459	[2]13.0	6.0 (1.85)	0.50	2.55	0.44	−0.05	4.2	2.6	104	24
Winnapaug Pond, R.I.	WP	18-7-77	41.327	[3]12.3	2.0 (0.62)	0.50	1.97	0.62	0.01	1.5	0.7	21	31
Quonochontaug Pond-1, R.I.	Q1	22-6-76	41.333	[3]12.3	2.0 (0.62)	0.35	1.00	0.60	0.00	0.7	1.5	0	31
Quonochontaug Pond-2, R.I.	Q2	4-4-77	41.333	[3]12.3	2.0 (0.62)	0.50	3.05	0.31	−0.01	8.1	1.5	9	31
Saugatucket River, R.I.	SR	14-12-78	41.423	[3]12.3	3.0 (0.92)	0.35	1.40	1.48	−0.40	2.0	1.1	509	16
Wickford, R.I.	WK	15-3-76	41.566	[4]10.5	4.7 (1.45)	0.35	2.92	0.23	−0.02	4.6	1.4	[5]15	27
Coonamessett River, Mass.	CR	12-5-77	41.577	[6]11.0	4.0 (1.23)	0	1.10	0.59	−0.05	2.7	1.0	101	12
Allen Harbor, R.I.	AH	27-9-77	41.620	[4]12.4	4.5 (1.38)	0.50	4.20	0.48	−0.03	61.1	1.9	358	28
West Falmouth, Mass.	WF	3-5-77	41.633	[6]10.5	5.0 (1.54)	0.50	0.46	0.80	0.27	2.1	0.8	190	32
New Bedford, Mass.	NB	18-10-78	41.639	[6]10.5	4.0 (1.23)	0.35	1.39	0.72	0.07	3.0	1.5	567	22
East Greenwich Cove, R.I.	EG	3-3-76	41.656	[4]11.5	5.0 (1.54)	0.20	2.08	1.08	−0.66	3.6	1.6	[7]24	19
Bourne, Mass.	BN	22-5-76	41.682	[6]10.5	3.8 (1.17)	0.50	0.89	0.55	0.01	2.4	0.7	523	30
Watchemoket Cove, R.I.	WC	12-5-76	41.799	[4]11.1	5.7 (1.75)	0.50	—	—	—	—	—	—	25
Portland, Me.	PT	21-7-76	43.636	[8]9.1	10.4 (3.20)	0.50	1.56	1.14	0.11	16.2	2.5	209	27
Deer Isle, Me.	DI	22-9-76	44.203	[9]7.4	11.2 (3.45)	0.80	1.90	1.38	0.57	9.8	1.6	24	32
Goose Cove, Me.	GC	20-7-76	44.377	[10]7.1	11.1 (3.42)	0.80	−0.51	1.37	0.09	2.8	1.4	254	20
Long Cove, Searsport, Me.	SP	22-9-76	44.463	[10]7.1	11.5 (3.51)	0.65	1.52	1.67	0.90	15.9	2.9	135	25
Stockton Harbor, Me.	SH	13-9-78	44.464	[10]7.1	11.5 (3.51)	0.65	0.26	2.05	0.15	7.3	1.3	399	25
Perry, Me.	PY	15-8-78	44.973	[9]6.7	21.0 (6.46)	0.65	2.22	1.58	−1.38	5.2	2.4	23	30
Robinston, Me.	RS	15-8-78	45.106	[9]6.8	21.0 (6.46)	0.65	−0.41	1.53	0.27	9.6	2.2	44	28
Janvrin Lagoon, Nova Scotia	JL	18-7-78	45.458	[11]9.0	4.0 (1.23)	0.65	2.24	0.46	0.06	8.2	1.4	177	29
Potato Island, Nova Scotia	PI	18-7-78	45.589	[11]9.0	4.0 (1.23)	0.65	−0.67	1.58	0.15	10.3	4.6	20	29

[1]Beaven (1960).
[2]Jeffries (1962).
[3]Marine Research (1975).
[4]Hicks (1963).
[5]Estimated from clam tissue concentration
[6]Gilbert (1973).
[7]Estimated from gas chromatography measurement
[8]Gilfillan et al. (1976).
[9]Welch (1981) and R. L. Dow, Maine Department of Marine Resources, State House, Augusta, ME 04333, pers. commun. January 1976
[10]Shorey (1973).
[11]Sameoto (1972) and Thomas (1978).

Length-frequency analysis was chosen because it could be applied to all samples, thus facilitating the comparison between samples. The use of shell annuli is unreliable south of Cape Cod (Mead and Barnes 1904; Shuster 1951), and MacDonald and Thomas (1980) found little support for the technique in a Prince Edward Island population. Constraints on the sampling design precluded mark-recapture methods.

For each population the modes on a length-frequency histogram were broken down into a series of normal curves (Tesch 1971; MacDonald and Pitcher 1979) by a Dupont[3] 310 Curve Resolver, an analog computer which allows one to break down a complex distribution into its basic components in a graphical fashion (Appeldoorn 1981). From the resulting graphs the mean and standard deviation of the curve which represents each mode of the histogram can be obtained. The curve resolver also determines the percentage of the whole sample under each curve.

Length-frequency analysis assumes that spawning and settlement are discrete relative to growth such that the length distributions of cohorts are separable. Ropes and Stickney (1965), Pfitzenmeyer (1962), and Brousseau (1978) found that periods of both spawning and settlement of each cohort were discrete events. In the latter study, closely spaced cohorts within the same year were separable by length-frequency analysis using probability paper. In the present study, discrimination of cohorts within a year class was also possible.

By inspection of the histograms and subsequent age-length curves and through consideration of local recruitment processes and sampling efficiency, ages were assigned to each cohort (Brothers 1980; Schnute and Fournier 1980). When possible, results were corroborated by comparing them with previously published age-length data for the same or nearby areas (e.g., Belding 1930; Pfitzenmeyer 1972; Mead and Barnes 1904; Gilfillan and Vandermuelen 1978; Brousseau 1979), by comparison of adjacent areas (e.g., the two Quonochontaug Pond sites), by comparison of multiple samplings (Allen Harbor, Deer Isle), and by counts of shell annuli (Portland, Deer Isle).

The ages assigned were relative rather than absolute; the time beyond the last yearly increment represents the fraction of expected yearly growth already obtained (Appeldoorn 1981). This process results in a smoother growth curve, since it linearizes seasonal growth variations which would otherwise necessitate the use of a more complex growth model (Cloern and Nichols 1978).

The analysis of growth differences can be simplified by comparing model parameters rather than the direct age-length observations (Rao 1958). Growth was modeled by fitting the von Bertalanffy growth function (VBGF) to the age-length data. The VBGF is described by the equation:

$$L_t = L_\infty \, (1 - e^{-K(t-t_0)})$$

where t = time, L_t = length at time t, L_∞ = maximum asymptotic length, K = growth constant, and t_0 = time when $L_t = 0$. The single growth parameter of Gallucci and Quinn (1979) is obtained by $\omega = K \cdot L_\infty$.

Recent studies on the statistical comparison of VBGF's (Allen 1976; Bayley 1977; Gallucci and Quinn 1979; Kimura 1980; Misra 1980; Kappenman 1981) and on the VBGF's biological basis (Pauly 1979, 1981) have removed most of its past criticism (Roff 1980). Dickie (1971) considered the VBGF applicable for modeling population growth even when individual growth did not fit the model. The VBGF has been previously applied to *Mya arenaria* by Munch-Petersen (1973), Brousseau (1979), and Brêthes and Desrosiers (1981).

The ω parameter was chosen for analysis because, as a single parameter, it was easily calculated, tractable to further analysis, statistically comparable, interpretable in both a biological and statistical sense, and more robust than either K or L_∞ (Gallucci and Quinn 1979). A major benefit of applying the VBGF is that only estimates of length at known time intervals are required to determine K, L_∞, and hence ω. Absolute age at length is only required to estimate t_0. However, t_0 is of less importance here, since it is not a measure of growth, but only a location parameter.

The VBGF was fitted to the data according to the methods of Gallucci and Quinn (1979), using the NLIN procedure of SAS79 (Helwig and Council 1979) which yielded estimates of the parameters, their asymptotic standard errors, and the correlation coefficient of K and L_∞. From these estimates the ω parameter and its variance were calculated (Gallucci and Quinn 1979). The regression procedure incorporated the size and

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

variance of each age mode. Therefore, variation in the original data is reflected in the variance estimates of the model parameters, and poorly represented age modes, where estimates of mean length and variance might be subject to error, are weighted less. The resulting growth curves are based on the assumption that growth varies from year to year only to the extent expected owing to normal fluctuations in growing conditions. Hence, they are an estimation of "average" growth within a population, representing an integration of several variable processes affecting growth.

The environmental data listed in Table 1 were used to characterize *Mya arenaria* habitats. These data were subjected to principal components analysis (PCA) to reduce the observed variables to a more meaningful and manageable number of factors without excessive loss of information. PCA locates hidden components which have generated dependence in the observed variables (Morrison 1976). Each resulting component is a composite variable—a linear combination of the original variables. The components are independent and ordered, so that the first component accounts for most of the observed variation, the second for most of the residual variation, and so on. The loadings given for each component represent the correlation coefficient (r) between a variable and a component. The analysis was run on the Pearson product-moment correlation matrix of the environmental parameters (to allow for standardization of the units of measure) by using the CORR, FACTOR, and SCORE procedures of SAS79 (Helwig and Council 1979).

The components produced by PCA are limited by the input data and can only reflect the factors represented by those data. In the present study the selection of factors was constrained by the sampling design, and no direct measurements were made on a number of factors which would be expected to influence growth (e.g., current flow, food concentration). However, several of the factors represent an integration of processes, incorporating factors not measured directly. For example, current flow is represented to some degree by tidal range, tidal position, and sediment characteristics (see Discussion). This integration effect will help offset the limitations of the input data.

The growth rate parameter was transformed to $\log_{10}(\omega)$ for the analysis of growth variations. Since $\log_{10}(K)$ and $\log_{10}(L_\infty)$ are inversely proportional (Pauly 1979), it is felt that $\log_{10}(\omega)$ is a more suitable measure of growth (Appeldoorn in press). A difference in $\log_{10}(\omega)$ would then indicate a fundamental difference in growth—not just a reciprocal change in K and L_∞. [See Pauly 1979, 1980 for a discussion of the analogous $P = \log_{10}(K \cdot W_\infty)$ parameter of the VBGF for weight.]

Variations in growth rate were analyzed using a stepwise functional regression of $\log_{10}(\omega)$ on the components generated by PCA, where the residuals of the regression of the $\log_{10}(\omega)$ on Component 1 were regressed against Component 2 and so on. The geometric mean functional regression was deemed appropriate because of variability in both ω and the components, small sample size, and uncertainties about the distribution of the data (Ricker 1973; Laws and Archie 1981). In normal predictive regressions the regression coefficient (slope) is b; functional regression yields a coefficient of $r = b/r$ where r is the correlation coefficient. The standard error of r (SE_r) equals the standard error of b (SE_b) and 95% confidence limits on r are approximated by $r \pm 2SE_r$ (Ricker 1973). Estimates of b, r^2, and SE_b were obtained using the GLM procedure of SAS79 (Helwig and Council 1979) and used to calculate r and its 95% confidence limits. The significance of the regression is tested by determining if the confidence limits bracket $r = 0$. If not, the null hypothesis H_0: $r = 0$ is rejected.

RESULTS

The mean lengths at age as determined through length-frequency analysis are given in Appendix Table 1 for the 19 populations analyzed here. The parameters of the VBGF and $\log_{10}(\omega)$ are given in Table 2. Using the 95% confidence limits around $\log_{10}(\omega)$, statistically significant growth differences become readily apparent. A functional regression of $\log_{10}(\omega)$ on latitude yielded: $\log_{10}(\omega) = 4.8184 - 0.0878$ latitude with $r = 0.8220$. Although the regression accounts for the majority of the observed variation in growth, it does not indicate what underlying processes may be responsible for this relationship.

The results of the PCA are shown in Table 3. The terms used in the table follow the definitions in Morrison (1976). In order to simplify the table, those loadings <0.30 have been left out, although all variables contribute to all components to some degree. The first five components have been retained and account for 88% of the observed variation. Of these, the first three were examined in greater detail.

TABLE 2.—Estimates and standard errors for the von Bertalanffy constants.

Site code	K	L_∞	t_0	$\text{Log}_{10}(\omega)$	+ 95% confidence interval
TS	0.2530 (0.0597)	111.05 (11.18)	−1.188 (0.263)	1.4486	1.3839-1.5050
AR	0.2740 (0.0520)	107.13 (7.22)	−1.440 (0.268)	1.4677	1.4166-1.5134
NR	0.3016 (0.0162)	79.69 (1.10)	−0.718 (0.095)	1.3808	1.3473-1.4119
RB	0.1829 (0.0986)	81.50 (22.08)	−1.450 (0.558)	1.1734	1.1202-1.2207
WP	0.2992 (0.0114)	73.27 (0.89)	−0.400 (0.058)	1.3418	1.3253-1.3577
Q1	0.1175 (0.0194)	93.23 (9.20)	−1.104 (0.148)	1.0396	0.9848-1.0882
Q2	0.1069 (0.0134)	111.00 (6.96)	−1.205 (0.191)	1.0743	1.0045-1.1344
SR	0.2119 (0.0229)	72.34 (2.48)	−0.445 (0.225)	1.1855	1.1417-1.2253
WK	0.1811 (0.0155)	111.80 (4.21)	−0.436 (0.127)	1.3066	1.2724-1.3383
CR	0.1997 (0.0114)	97.75 (1.60)	−0.990 (0.143)	1.2905	1.2512-1.3265
AH	0.0903 (0.0184)	113.20 (13.11)	−1.668 (0.288)	1.0095	0.9147-1.0873
WF	0.0917 (0.0162)	136.73 (14.88)	−1.357 (0.184)	1.0982	1.0056-1.1746
NB	0.1532 (0.0198)	89.28 (4.30)	−1.571 (0.304)	1.1360	1.0902-1.1774
EG	0.1377 (0.0425)	91.95 (18.20)	0.914 (0.186)	1.1025	1.0439-1.1541
WC	0.1411 (0.0246)	87.18 (7.37)	−1.549 (0.236)	1.0899	0.9965-1.1668
PT	0.1468 (0.0077)	67.91 (1.39)	−0.836 (0.122)	0.9986	0.9778-1.0186
DI	0.1255 (0.0114)	67.96 (2.46)	−0.781 (0.218)	0.9311	0.8974-0.9623
SH	0.0565 (0.0083)	135.71 (12.34)	−0.980 (0.336)	0.8847	0.7663-0.9776
RS	0.1623 (0.0287)	73.13 (4.52)	−0.745 (0.434)	1.0754	1.0275-1.1167
PI	0.0986 (0.0248)	81.55 (10.78)	−0.171 (0.432)	0.9053	0.7839-0.9674

TABLE 3.—Results of the principal components analysis on environmental data. Loadings <0.30 have been omitted for clarity.

Environmental parameter	Principal components					Communality
	1	2	3	4	5	
Average temperature	−0.938					0.925
Tidal range	0.806			0.383		0.819
Tidal position	0.817					0.855
Mdϕ	−0.503	0.725				0.891
QDϕ	0.808	−0.382				0.872
Skqϕ			0.386	−0.858		0.933
% silt-clay		0.609	0.675			0.880
% organic matter	0.521				0.765	0.942
Total hydrocarbons			0.802			0.855
Salinity	0.396	0.750				0.840
Eigenvalues	3.588	1.875	1.363	1.134	0.851	
% variance	35.9	18.7	13.6	11.3	8.5	
% cumulative variance	35.9	54.6	68.3	79.6	88.0	

The first component is interpreted as representing latitude, since the major contributing variables vary with latitude. Average annual temperature, as might be expected, shows the highest correlation. It decreases with latitude. To avoid confusion the first component will be referred to as "northness." The second component is sediment siltiness. Grain size (negatively correlated) and percent silt-clay (positively correlated) are the main contributing variables. The high correlation of salinity may reflect the role of flocculation and estuarine circulation in the distribution of silts and clays in estuarine sediments (Krumbein and Sloss 1963; Knauss 1978). The third component, positively correlated with hydrocarbons and percent silt-clay, is sedimentary hydrocarbons. The higher silt-clay component (also reflected to some degree by positive skewness) provides a greater sedimentary surface area for the retention of hydrocarbons (Lytle and Lytle 1977).

The first three components were used for the further analysis of growth to try and deduce factors which could have contributed to the latitudinal trend and to point out secondary growth affecting factors. Several sites were omitted from this analysis because missing values precluded the calculation of the component scores. The results of the stepwise regression analysis are given in Table 4. As expected, growth was found to be negatively correlated with northness. The second regression showed a negative relationship between siltiness and growth. The last

TABLE 4.—Results of the stepwise regression of growth (ω) on the first three principal components. The slope of the predictive regression (b) can be found by $b = v \cdot r$.

Regression	r	Intercept	v = slope	Approximate 95% confidence limits
$\text{Log}_{10}(\omega)$ vs. northness	0.693	1.1137	−0.1653	$-0.2269 < v < -0.1037$
1st residual vs. siltiness	0.184	−0.0112	−0.1116	$-0.1682 < v < -0.0549$
2d residual vs. sedimentary hydrocarbons	0.217	0.0065	−0.1472	$-0.2214 < v < -0.0730$

regression indicated that growth was negatively correlated with sedimentary hydrocarbons.

DISCUSSION

The observed relationship between latitude and growth rate is not surprising, especially considering the range of temperatures reflected in the data. Increasing growth would be expected at higher temperatures owing to temperature's direct effect on metabolism and length of the growing season (Brousseau 1979). In addition, with increasing temperature *Mya* is found lower intertidally or even subtidally (Pfitzenmeyer 1972), thereby increasing its daily feeding period. However, Belding (1930), Dow and Wallace (1961), Newcombe and Kessler (1936), and Swan (1952) have stated that local hydrologic and edaphic conditions are more important than temperature in affecting growth, and previous studies have failed to quantify such a latitudinal relationship. Newcombe (1936) and Turner (1948) each noticed growth differences between three populations which they attributed to temperature. Brousseau (1979) showed a tendency for Massachusetts populations to grow faster than more northern ones, but the relationship was not definite. Each of these studies suffered from two deficiencies: Limited geographical range and small number of sample sites. Under these limitations, variations in growth rate due to local conditions can mask any latitudinal trends. The unaccounted variation (32%) in the regression of $\log_{10}(\omega)$ on latitude is evidence for this.

Analysis of the latitudinal trend of growth rate and its residual variation was facilitated by the PCA results. The first component, northness, correlated well with growth. Temperature and tidal position had the highest loadings for this component; their interrelationship and influence on growth have already been discussed. As with many factors, the components produced by PCA represent an integration of effects and the correlation between growth and northness may depend upon factors other than temperature.

Two other characteristics vary markedly with increasing northness. The sediment becomes coarser and more variable, and tidal range increases. The tidal range increase, due to the large tides of the Gulf of Maine and Bay of Fundy, represents to some degree an increase in tidal current. Belding (1930) considered current the most important factor affecting growth. Coarser sediments are beneficial to growth by allowing for ample water percolation, drainage, and exchange (Dow and Wallace 1961; Swan 1952). The correlation of northness with coarser, variable sediments reflects both their glacial origins and the influence of current on their deposition.

Within northness, then, there are two sets of opposing conditions which influence growth. Temperature is positively associated with growth while current and sediment characteristics are negatively associated with growth. Since northness is itself negatively correlated with growth it must be concluded that the effects of temperature are overriding and dominant.

The effect of siltiness on growth also represents an integration of processes. In small quantities silt and clay help stabilize surface sediments (Kellogg 1905), but in large quantities they become detrimental. Studies with *Mya arenaria* have shown that excessive siltation can lead to reduced feeding through clogging of the gills (Belding 1930), to growth interruptions when silt becomes trapped between the shell and mantle (Shuster 1951), and to complete smothering and death (Wilton and Wilton 1929; Dow and Wallace 1961). Silty sediments tend to be fairly consolidated, and reduced growth has been observed in such sediments (Swan 1952; Dow and Wallace 1961). High silt-clay is also indicative of a poor current regime, itself a contributing factor to reduced growth. The negative correlation found between siltiness and growth is, therefore, logical and consistent with previous reports.

Sedimentary hydrocarbons, the third component derived from PCA, were also negatively associated with growth. Many studies have shown that the growth of *Mya* is adversely affected by the presence of petroleum hydrocarbons (Dow 1975; Dow and Hurst 1975; Gilfillan and Vandermeulen 1978; Gilfillan et al. 1976; Appeldoorn 1981). Hydrocarbon pollution can adversely affect growth through direct toxicity, smothering, and sediment compaction.

CONCLUSIONS ON METHODOLOGY

PCA produced meaningful, easily interpretable variables which led to results, when further analyzed, that were lucid, rational, and consistent with other studies. Since PCA will be limited by the input data, sampling should be properly designed or controlled. One advantage of PCA is that variable integration effects can incorporate

some factors not specifically measured. However, reliance upon these effects should be avoided when possible and caution should be exercised when interpreting the results.

The ω parameter proved useful, both for its description of growth rate and ease of manipulation in further analyses. Incorporating both the sample size and variance of the age-length determinations into the nonlinear regression protected ω against random errors in the location of the age-length modes. In addition, since ω is more robust than either K or L_∞, it is further protected against inaccuracies in their estimation—an advantage over using K during the subsequent growth analyses. The trends resulting from the subsequent regressions were also protected from random inaccuracies in the estimation of ω by virtue of the large number of sample sites used. However, it is important to recognize that such random errors do exist and not to continue the analysis past its potential limits.

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APPENDIX TABLE 1.—The age (yr), length ±1 standard deviation (mm), and percent of sample in each age class. Percentages may not total 100 due to roundoff or exclusion of some outliers from the analysis. Sample size is given in parentheses. — = undefined.

Age	Length	% of sample	Age	Length	% of sample	Age	Length	% of sample
Navesink River (103)			Coonamessett River (124)			Portland (367)		
0.67	26.0±2.3	3	1.15	34.0 —	0.5	1.5	19.0±0.8	1
1.33	35.2±2.5	14	2.15	42.8±2.0	4	2.5	26.7±1.3	4
1.67	42.5±2.0	23	2.85	52.0±1.0	7	3.5	31.5±1.6	17
2.33	47.3±1.8	18	3.15	56.1±2.0	7	4.5	37.1±1.6	21
2.67	51.8±1.4	10	4.15	64.0±1.4	18	5.5	41.3±1.6	29
3.33	55.3±1.4	11	5.15	69.4±1.2	9	6.5	44.5±1.2	10
3.67	59.6±1.6	2	6.00	72.8±1.2	16	7.5	48.1±1.2	15
4.50	62.1±1.4	2	7.15	77.4±1.2	18	9.5	52.7±0.7	3
5.50	65.4±1.2	2	8.15	82.3±1.4	17	10.5	55.0±0.5	1
6.50	69.7±1.5	4	10.15	88.2±1.1	5	11.5	56.7±0.4	1
8.50	74.7±1.2	4	11.15	94.0 —	0.5	13.5	60.2±0.5	1
9.50	78.0±1.2	6	Quonochontaug Pond-2 (146)			Saugatucket River (140)		
Deer Isle (318)			2.15	33.7±2.7	41	2.0	29.0±1.3	2
3.0	25.7±1.9	4	3.15	41.6±2.0	28	2.6	33.8±0.9	5
4.0	31.2±1.1	7	4.15	49.0±1.3	6	3.0	37.6±1.6	9
5.0	35.2±1.3	21	5.15	55.1±1.8	6	3.8	43.3±2.2	42
6.0	39.2±1.3	18	6.15	60.2±1.0	4	4.8	48.9±1.5	7
7.0	42.1±1.1	9	7.15	65.8±1.3	6	5.8	52.8±1.1	12
8.0	44.6±1.0	10	8.15	70.5±0.8	4	7.0	56.1±0.7	6
9.0	47.8±1.0	12	9.15	73.5±0.8	3	8.0	60.0±1.2	6
10.0	51.5±1.0	9	10.15	79.0±1.1	4	9.0	64.5±1.2	3
Quonochontaug Pond-1 (198)			Allen Harbor (144)			Potato Island (201)		
1.33	23.9±2.1	33	1.85	30.0±1.8	11	2.5	25.3±0.7	2
2.33	30.7±2.1	43	2.85	37.7±2.6	24	3.5	30.9±1.3	8
3.33	38.3±1.9	13	3.85	44.5±1.5	15	4.5	34.6±1.6	25
4.33	44.9±1.3	7	4.85	50.4±1.8	18	5.5	39.2±1.5	41
5.33	49.6±1.2	2	5.85	55.2±1.3	14	6.5	43.7±1.0	13
6.33	54.2±1.4	3	6.85	59.7±1.4	8	7.5	47.1±0.8	6
7.33	58.6±1.4	1	7.85	65.8±1.4	9	8.5	49.4±0.9	3
Watchemoket Cove (90)			Big Annemessex River (177)			Robinston (190)		
1.15	27.6±2.9	24	1.33	57.0±1.3	14	3.67	37.9±1.6	8
2.15	34.8±2.0	31	1.80	60.9±1.8	30	4.67	42.5±1.6	16
3.15	42.4±1.7	19	2.33	68.8±2.0	33	5.67	47.2±1.6	41
4.15	48.2±2.5	11	2.80	73.7±0.8	4	6.67	51.7±1.0	20
6.15	57.1±1.4	8	3.33	77.2±1.3	7	7.67	54.6±0.9	7
7.15	62.5±1.0	6	4.33	86.8±1.5	2	8.67	57.0±1.2	4
New Bedford (180)			Stockton Harbor (164)			Tangier Sound (166)		
1.85	32.0±1.0	0.5	3.0	31.0±1.8	2	1.33	54.6±2.3	36
2.85	43.7±1.2	3	4.0	38.2±1.8	2	1.80	62.0±1.6	26
3.56	48.3±1.6	8	5.0	44.8±1.4	11	2.33	67.9±1.2	13
3.85	51.2±0.8	15	6.0	49.2±1.1	13	2.80	73.4±1.3	11
4.56	53.9±0.9	16	7.0	54.1±1.5	17	3.33	78.2±0.9	3
4.85	56.2±0.9	21	8.0	58.2±1.2	21	3.80	81.6±0.8	1
5.56	58.9±1.2	16	9.0	62.8±1.3	13	4.33	86.2±0.7	2
5.85	61.2±0.8	11	10.0	66.5±1.4	11			
6.85	64.4±0.9	6	11.0	70.3±1.2	3	Raritan Bay (200)		
7.85	69.0±0.6	3	12.0	75.0±1.3	5	1.33	30.4±0.8	3
Winnapaug Pond (229)			Wickford (203)			1.67	36.4±1.8	23
0.9	24.2±1.6	3	0.20	7.0 —	0.5	2.33	40.2±1.7	39
1.5	31.5±1.0	2	2.00	37.3±1.1	2	2.67	43.8±1.6	25
1.9	37.4±1.2	5	2.67	48.7±1.4	4	3.33	47.4±0.8	10
2.5	41.4±1.2	7	3.00	53.9±1.4	10			
2.9	46.2±1.3	14	3.80	60.4±1.8	18	East Greenwich Cove (192)		
3.5	50.6±1.8	24	4.80	68.1±2.5	36	1.0	20.8±3.5	30
4.5	56.0±1.6	29	5.80	75.1±1.8	13	2.0	30.8±1.0	9
5.5	60.5±1.2	8	6.00	80.2±1.1	7	3.0	38.4±2.8	49
6.5	64.1±1.4	4	7.00	84.7±0.9	2	4.0	45.0±1.5	11
7.5	67.2±0.7	4	8.00	88.5±0.6	2	5.0	50.9±1.1	3

BIOCHEMICAL GENETICS OF PACIFIC BLUE MARLIN, *MAKAIRA NIGRICANS*, FROM HAWAIIAN WATERS[1]

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ABSTRACT

An electrophoretic survey of 35 enzyme-coding gene loci in Pacific blue marlin was accomplished to determine levels of genetic variation and the feasibility of using electrophoresis to study stock structure in this species. Polymorphism (P_{95}) in the marlin was 0.26 and the average heterozygosity (H) was 0.06. Allele frequencies at 11 variable loci were determined for a sample of 95 fish from Kona, Hawaii. The observed levels of polymorphism and heterozygosity suggest that a biochemical genetic analysis of blue marlin stock structure is possible and may reveal stock heterogeneity.

The Pacific blue marlin, *Makaira nigricans*, is the predominant billfish species in the central tropical Pacific. As such, it is an important commercial species and the object of a considerable sport fishery. The average annual catch of this species in the Pacific exceeds 14,000 t (metric tons) (Shomura 1980). The Pacific blue marlin is primarily distributed in equatorial areas, although Japanese longliner catch records indicate that its range extends from lat. 48°N to 48°S. During the Southern Hemisphere summer (December through March) a center of concentration occurs in the western and central South Pacific (between lat. 8°S and 26°S). In the Northern Hemisphere summer (May through October) a center of concentration occurs in the central North Pacific (between lat. 2°N and 24°N). During April and November the fish appear to be concentrated equatorially between lat. 10°N and 10°S (Rivas 1975). There is currently no direct evidence of migration of blue marlin within the Pacific. However, a general movement to the northwestern Pacific during the Northern Hemisphere summer and to the southeastern Pacific during the Southern Hemisphere summer has been postulated by Howard and Ueyanagi (1965) on the basis of the shifting abundance patterns of the fish.

Little is known about spawning, other than that Pacific blue marlin appear to spawn throughout the year in an area 10°-20° on either side of the Equator, and up to 30° on either side of the Equator during the Northern and Southern Hemispheres' respective summer months. In general, the highest spawning densities occur in the western Pacific, with the density decreasing eastward (Strasburg 1970; Matsumoto and Kazama 1974; Rivas 1975). Because of the apparently single equatorial Pacific spawning area, it has been assumed that the species consists of a single unit stock (Yuen and Miyake 1980; Yoshida 1981), yet there has been no direct test of this assumed stock structure. The most recent report available on the condition of the Pacific blue marlin stock considers it to be badly overfished. Yuen and Miyake (1980) calculated that the present fishing effort (commercial longliner effort only, since no data are available on recreational fishing effort) is about twice that suitable for maximum sustainable yield. Because the catch per unit effort of Pacific blue marlin has steadily declined over the past 10 yr, in spite of a fairly constant level of effort, Yuen and Miyake (1980:19) concluded "...that continued fishing at high levels will continue to reduce the abundance of the stock and a recruitment failure will become a distinct possibility."

The importance of being able to define subpopulations or stocks of fishes with respect to the formulation of appropriate fishery management schemes has long been recognized (Marr 1957). This problem is especially acute for species (such as Pacific blue marlin) which are highly migra-

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tory, subjected to an oceanwide multinational fishery, and which, because of relatively low catches, are not well suited to tag-recapture studies. In fact, the pressing need to understand blue marlin stock structure has been recognized for some time (Shomura 1980; Yoshida 1981).

The electrophoretic analysis of protein polymorphisms in natural populations can be a powerful approach for analyzing genetic aspects of population structure in sexually reproducing organisms. For this reason, the technique has been applied to the study of racial or subpopulation differentiation in numerous invertebrates and vertebrates (Ayala 1976). Because of the basic importance of information on subpopulation or stock structure to fisheries management (Berst and Simon 1981), population genetic studies have been conducted for many species of fishes [reviewed by de Ligny (1969) and Allendorf and Utter (1979)]. Most of the fishes investigated to date have been freshwater species or marine forms which are either inshore shallow-water species or demersal species.

Stock heterogeneity for oceanic species has not generally been reported (but see Fujino 1976; Fujino et al. 1981). Although open water, pelagic species *may* be characterized by large panmictic cosmopolitan populations, this pattern has not yet been clearly established. One problem in testing this hypothesis has been the unusually low levels of genetic variability observed to date in several large marine vertebrates such as skipjack tuna (Fujino 1970) and seals (McDermid et al. 1972; Bonnell and Selander 1974). Indeed, Selander and Kaufman (1973) have even suggested that large, mobile vertebrates may generally have low levels of heterozygosity—a characteristic which, if true, would preclude definitive stock analysis using electrophoretic techniques (but see Ryman et al. 1980). The general lack of progress in defining stock structure in oceanic fishes, such as scombroids, using electrophoretic methods, is attributable to several factors. Many of the reports in the literature have been preliminary in nature dealing with small samples of fish and few variable loci. Although such small sample sizes are not unexpected given the remote, far-seas nature of many of the commercial fisheries, they severely limit the subsequent statistical treatment of the data. Similarly, the analysis of only one or two polymorphisms reduces the likelihood of demonstrating any population subdivision which may exist. Finally, the schooling and/or highly migratory nature of many of these fishes makes it difficult to plan and execute adequate sampling programs.

The study described in the present report was designed to determine the suitability of utilizing electrophoretic techniques to study stock structure in the Pacific blue marlin. Three specific questions were addressed:

1) How much and what kind of electrophoretically detectable genetic variation is there in the Pacific blue marlin? Specifically, is there enough genetic variation to allow an electrophoretic analysis of stock structure in this species?
2) What combinations of enzymes, tissues, and buffer systems can be utilized in a study of genetic variation in this species?
3) What allele frequency distributions characterize the population of Pacific blue marlin in Hawaii?

MATERIALS AND METHODS

Muscle, liver, heart, eye, and brain samples were dissected from Pacific blue marlin landed at the Hawaiian International Billfish Tournament held at Kailua-Kona, Hawaii, in August 1980. All tissue samples were taken immediately after each fish had been weighed, and all fish had been dead for at least 1 h but <8 h. The dissected tissues were initially placed on ice and subsequently transferred to a freezer within 12 h. The time delay between fish capture and the freezing of dissected tissues did not seem to adversely affect any of the polymorphic enzymes screened with the possible exception of L-iditol dehydrogenase which could only be scored in 84 of the 95 fish analyzed. Tissues were stored frozen at −20°C until extracted.

Tissue extracts were prepared by homogenization using a loose-fitting, motorized stainless steel pestle in polycarbonate centrifuge tubes. The extraction buffer consisted of 0.1M Tris-HCl pH 7.0 containing 1×10^{-3}M EDTA and 5×10^{-5}M $NADP^+$. After homogenization, the extracts were centrifuged at $25{,}000 \times g$ for at least 30 min. Supernatants were transferred to individually labeled glass vials, capped, and stored at −75°C until the electrophoretic analysis was completed.

The supernatants were subjected to horizontal starch gel electrophoresis (modified from Selander et al. 1971), using some 15 different buffers. The gels were made using Lot 60F-0558 starch

(Sigma Chemical Co., St. Louis, Mo.) at a concentration of 12% w/v. After electrophoretic separations, enzyme patterns were visualized using standard histochemical staining recipes modified from Shaw and Prasad (1970), Selander et al. (1971), and Siciliano and Shaw (1976). All zymograms were photographically recorded.

Patterns of enzyme variation which were consistent with the subunit structure of the enzyme (when known) and simple models of Mendelian inheritance were scored and recorded as genotypes. Names of enzymes and Enzyme Commission numbers follow the recommendations of the Commission on Biochemical Nomenclature (1973). For multilocus enzyme systems, loci were given alphabetic designations when appropriate (e.g., Gpi-A) or were simply assigned a number beginning with 1 for the most anodally migrating isozyme. The most common allele at each locus was designated 100, and all other alleles at that locus were numbered according to their electrophoretic mobility relative to the 100 allele. Negative numbers refer to alleles with cathodal migration. The putative genotype data were summarized as genotype and allele frequency distributions. The genotype distributions were examined for internal consistency with the Mendelian inheritance model by chi-square testing of goodness-of-fit of observed genotype ratios with those expected for a single random mating population in the absence of differential selection among the alleles. The expected ratios were computed from observed allele frequencies using Levene's (1949) unbiased method for small samples. Heterozygosity for each locus (h) was calculated as $h = 1 - \Sigma Xi^2$ where Xi is the frequency of the ith allele. Average heterozygosity (H) was calculated as the mean of h over all loci examined.

RESULTS

Tissue samples from 95 Pacific blue marlin were analyzed. A total of 23 enzyme systems representing 35 gene loci were satisfactorily resolved using extracts of muscle, liver, and eye (Table 1). Heart and brain tissue did not add significantly to this total. Eleven loci exhibited detectable genetic variation in the sample of 95 fish analyzed. The enzymes adenosine deaminase (Ada), mannosephosphate isomerase (Mpi), and phosphoglucomutase (Pgm) all behaved as monomers with two-banded heterozygotes. Aspartate aminotransferase (Aat-1), alcohol dehydrogenase (Adh), glucosephosphate isomerase (Gpi-A), muscle glycerol-3-phosphate dehydrogenase (G-3-Pdh-2), liver isocitrate dehydrogenase (Idh-1), phosphogluconate dehydrogenase (Pgdh), and umbelliferyl esterase (Umb) behaved as dimers exhibiting triple-banded heterozygous patterns. L-iditol dehydrogenase (Iddh), often referred to as sorbitol dehydrogenase in the literature, appeared to be a tetramer as heterozygotes exhibited a five-banded phenotype.

Two of the 11 variable loci were represented by only a single heterozygous individual out of the 95 fish screened. The remaining nine loci were

TABLE 1.—Electrophoretic analysis of *Makaira nigricans* from Hawaii. M = muscle, E = eye, L = liver.

Enzyme			Loci	
Name (Enzyme Commission number)	Abbr	Tissue	Invariant	Variable
aspartate aminotransferase (2.6.1.1)	Aat	L	1	1
adenosine deaminase (3.5.4.4)	Ada	M	—	1
alcohol dehydrogenase (1.1.1.1)	Adh	L	—	1
creatine kinase (2.7.3.2)	Ck	M+E	2	—
enolase (4.2.1.11)	Eno	M	1	—
esterase (3.1.1.—)	Est	L	2	—
glyceraldehyde-phosphate dehydrogenase (1.2.1.12)	Gapdh	M	2	—
glutamate dehydrogenase (1.4.1.2)	Gdh	L	1	—
glucosephosphate isomerase (5.3.1.9)	Gpi	M	1	1
glycerol-3-phosphate dehydrogenase (1.1.1.8)	G-3-Pdh	M+L	1	1
hexose diphosphatase (3.1.3.11)	Hdp	L	1	—
L-iditol dehydrogenase (1.1.1.14)	Iddh	L	—	1
isocitrate dehydrogenase (1.1.1.42)	Idh	M+L	1	1
lactate dehydrogenase (1.1.1.27)	Ldh	M+E	3	—
malate dehydrogenase (1.1.1.37)	Mdh	M	3	—
malate dehydrogenase ($NADP^+$) (1.1.1.40)	Mdh($Nadp^+$)	M	1	—
mannosephosphate isomerase (5.3.1.8)	Mpi	M	—	1
peptidase (3.4.11.—)	Pep	M	2	—
phosphogluconate dehydrogenase (1.1.1.44)	Pgdh	M	—	1
phosphoglucomutase (2.7.5.1)	Pgm	M	—	1
superoxide dismutase (1.15.1.1)	Sod	L	1	—
umbelliferyl esterase	Umb	M	—	1
xanthine dehydrogenase (1.2.1.37)	Xdh	L	1	—

polymorphic by the normal criteria (common allele at a frequency of 0.99 or less) with five loci (Ada, Mpi, Pgdh, Pgm, and Umb) having the most common allele at a frequency of between 0.95 and 0.99 and four loci (Aat-1, Adh, G-3-Pdh-2, and Iddh) having the most common allele at a frequency of <0.95 (Table 2). All 11 variable loci exhibited two or three alleles except for Aat-1 which had five different alleles, three of which were reasonably common.

Heterozygosity values for the individual loci ranged from zero for all of the apparently monomorphic loci to 0.494 for G-3-Pdh-2. The average heterozygosity (H) across all 35 loci was 0.0605.

Where possible, the observed genotype distributions were tested for goodness-of-fit to Hardy-Weinberg equilibrium expectations (Gpi-A, Idh-1, Mpi, and Pgm were not tested because of the very small number of observed variants in the sample). Where necessary, rare alleles were pooled prior to the tests. All tests were nonsignificant except that for Adh ($\chi^2 = 6.97$, df = 1; $P<0.01$) where there was a significant deficiency of heterozygotes.

Further analysis of the Adh data was undertaken to attempt to identify the major contributor(s) to this significant chi-square value. Since sex linkage of a locus can result in a deficiency of heterozygotes, the sample of blue marlin was subdivided into males and females. A chi-square test of the Adh genotypes of the 81 male fish also revealed a significant deficiency of heterozygotes ($\chi^2 = 9.36$, df = 1; $P<0.005$). Another possible source of the deficiency of heterozygotes could be the pooling of different year classes which actually had different frequencies of the Adh alleles. Indeed, year class fluctuations of allele frequency have been reported in other fishes (Williams et al. 1973; Mitton and Koehn 1975; Smith et al. 1978; Smith 1979). In the absence of growth data for this species, the only subdivision we could make was on the basis of size. The 95 blue marlin were subdivided into two groups: 1) 100-200 lb total weight and 2) 201-450 lb. There were 74 fish in the 100-200 lb group and the statistical analysis of this group once again revealed a deficiency of heterozygotes ($\chi^2 = 9.95$, df = 1; $P<0.005$). The similarity of the results for small fish and for males is not unexpected since all of the female fish ($N = 13$) were in the large size class (>200 lb). Therefore, the deficiency of heterozygotes seems to characterize the overall sample and cannot be attributed to sexual or gross age (= size) differences.

TABLE 2.—Allele frequencies and heterozygosities for 11 variable loci in *Makaira nigricans* from Hawaii.

Locus[1] (heterozygosity)	Allele	Frequency
Aat-1	250	0.016
(h = 0.4497)	145	0.145
	100	0.720
	27	0.102
	–30	0.016
Ada	107	0.005
(h = 0.0716)	100	0.963
	92	0.032
Adh	–220	0.344
(h = 0.4556)	–100	0.656
Gpi-A	100	0.995
(h = 0.0099)	86	0.005
G-3-Pdh-2	100	0.595
(h = 0.4944)	75	0.389
	60	0.016
Iddh	147	0.006
(h = 0.4219)	100	0.702
	22	0.292
Idh-1	100	0.995
(h = 0.0099)	84	0.005
Mpi	104	0.005
(h = 0.0316)	100	0.984
	90	0.011
Pgdh	155	0.016
(h = 0.0529)	100	0.093
	67	0.011
Pgm	144	0.011
(h = 0.0316)	100	0.984
	33	0.005
Umb	100	0.953
(h = 0.0896)	87	0.047

[1]Sample size = 95 fish for each locus except for Mpi where $N = 94$, Aat-1 and Adh where $N = 93$, and Iddh where $N = 84$.

DISCUSSION

In spite of the low levels of genetic variation reported in the literature for skipjack tuna (Fujino 1970; Fujino et al. 1981; Lewis 1981; Richardson in press) and suggested by Selander (1976:34) that "...levels of variability are unusually low in large marine vertebrates such as tuna fish and porpoises," the above data clearly indicate that the Pacific blue marlin does not have abnormally low levels of genetic variation. The level of polymorphism ($P_{.99}$) observed for marlin in the present study ($P = 0.26$; i.e., 9 out of 35 loci), although slightly lower than the average for fish ($P = 0.31$) reported by Selander (1976), is higher than the averages for reptiles, birds, and mammals (0.23, 0.15, and 0.23, respectively). Furthermore, the average heterozygosity (H) of 0.0605 for the 35 loci screened in the Pacific blue marlin is greater than the average of 0.0494 calculated by Nevo (1978) for 135 species of vertebrates and the average of 0.0478 calculated by Winans (1980) for 82 species of fishes. Although perhaps somewhat un-

expected, the relatively high level of genetic variation reported above for blue marlin is not unique among large marine vertebrates as several other scombroid fishes (e.g., white marlin, southern bluefin tuna, and Spanish mackerel) exhibit similar or even higher levels of variation (Edmunds 1972; Smith and Jamieson 1980; Lewis 1981; Shaklee unpubl. data).

The observed pattern of genetic variation can be used to subdivide the 11 variable loci into two general categories. Four loci (Aat, Adh, G-3-Pdh-2, and Iddh) form one group characterized by high heterozygosities (0.4219-0.4944) due to the presence of at least two relatively common alleles. The second group, which is composed of the remaining seven variable loci (Ada, Gpi-A, Idh-1, Mpi, Pgdh, Pgm, and Umb), is characterized by low heterozygosity per locus (0.0099-0.0896) and the presence of a single common allele at a frequency of at least 0.95. In reality, both groups of loci are of utility in population analyses because the power of the statistical tests for detecting significant differences in allele frequency between pairs of samples actually increases somewhat as the frequencies approach the extremes (i.e., 0 and 1.0) compared with samples having frequency distributions close to 0.5.

The close agreement between observed and expected genotypic frequencies for all but one of the variable loci is consistent with all 95 fish analyzed belonging to a single panmictic population. However, the significant ($P<0.01$) deficiency of heterozygotes observed at the Adh locus is not. Although this observation may be due to selection or simply be an anomaly, another potential explanation is that this heterozygote deficiency is due to the mixing of two or more different stocks of blue marlin which have different frequencies of the two Adh alleles (Wahlund effect). Such potential stock mixing would not be unreasonable given the presumed migratory nature of Pacific blue marlin.

The fundamental significance of the above observed levels of genetic variation is that they are adequate to allow a biochemical genetic analysis of stock structure in Pacific blue marlin. We are now in the process of initiating just such an analysis and are employing an experimental design which should allow us to detect stock heterogeneity which has either a stable geographical basis or a temporally shifting geographic basis. The former basis for stock heterogeneity, namely the localization of two or more stocks in different regions of the species' range is by far the most commonly observed form of population subdivision among organisms. We will be testing for this type of heterogeneity by analyzing samples from different localities (Hawaii, Guam, Samoa, etc.) throughout the range of the Pacific blue marlin. However, this type of analysis is complicated by limited access to marlin caught in many areas of the range, by the shifting patterns of abundance which characterize this species, and by the virtual impossibility of obtaining simultaneous samples of blue marlin from multiple localities throughout the range. Indeed, it is the apparent migratory nature of the species which suggests that the second type of population structuring, that based on both temporal and geographic isolation, may be occurring in this species. Our approach to this problem is to sample continuously in the Hawaiian Islands to look for significant seasonal shifts in allele frequency such as might be expected if different stocks of blue marlin migrate past the Hawaiian Islands at different times of the year. Given the present potentially overfished nature of billfish stocks and the difficulties associated with alternative forms of stock analysis such as tag-recapture studies, this biochemical genetic approach may well represent the only practical means of gathering information on stock structure in a time frame compatible with the urgent need for the formulation of meaningful management programs for this species.

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STOCHASTIC AGE-FREQUENCY ESTIMATION USING THE VON BERTALANFFY GROWTH EQUATION

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ABSTRACT

The method of estimating age frequency from length frequency via the von Bertalanffy growth equation is deterministic and yields biased results. Most of the bias can be removed by incorporating a stochastic element in the von Bertalanffy relationship. The stochastic element is based on estimated probabilities of lengths by intervals at age, the probabilities being estimated from variances in lengths-at-age. Based on age-length samples from the Pacific bonito fishery the stochastic method gives improved age-frequency estimates over those obtained by the deterministic method. The stochastic application may be generalized to all growth models including discontinuous growth such as in crustaceans.

Complex population dynamics techniques rely heavily on age-structure information. Frequently, appropriate assessment techniques for a stock require an estimate of the age frequency of that stock. For example yield-per-recruit analysis (Ricker 1958) is computed on the dynamic relationship between growth and mortality: Mortality rates when computed via cohort analysis (Murphy 1965) are based on estimated age frequency.

For some species accurate aging methods are not available. When feasible, determining the age of fish and consequently computing an age frequency are most accurately accomplished by visual inspection of scales, otoliths, or other structures (Ricker 1958). Such visual inspection is time consuming and often expensive. To reduce the cost and time of estimating the age structure of a fisheries catch, age frequency is usually estimated from sampled length frequency, the age-length relationship being described by either an age-length key or a growth curve such as the von Bertalanffy growth curve (Ricker 1958). The growth curve method is used when there are insufficient data to construct an age-length key.

Age-length keys work on the principle that age can be estimated from length using information contained in a previously or concurrently aged sample from the population. As long as the proportion of length-at-age remains the same for all ages, then the age-length key will yield unbiased estimates of age for any sampled lengths from that population. However, since the estimated parameters of an age-length key—proportions of age-at-length—are dependent on the sampled population used to construct the key, the application of the key to the population with altered age structures can yield inaccurate results. Kimura (1977) and later Westrheim and Ricker (1978) demonstrated that under conditions of varying year-class strength and substantial overlap of lengths between ages, age-length keys can yield nearly useless estimates of numbers-at-age.

Clark (1981) effectively removes age-length key bias by first proportioning numbers in length intervals at age over time and then using the matrix of these proportions standardized over time to compute least-squares estimates of age frequency from the vector of length frequency. Effective applications of many stock assessment growth and mortality based methods require that ages are expressed in fractions of years (Ricker 1958; Lenarz et al. 1974). The large number of aged fish required to construct a sufficient key for a large number of ages is difficult and expensive to attain. Even with Clark's bias correction procedure, the construction of a sufficient key can present difficulties due to data needs.

In this paper we deal specifically with the von Bertalanffy growth equation and the application of stochastic methods to reduce or eliminate biases. However, it should be noted that the method presented here may be applied to any growth equation as well as to cases where no growth equation has been fitted or where growth is discontinuous as in crustaceans.

The von Bertalanffy growth equation mathe-

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matically models the relationship between age and length, length being the dependent variable (see Equation (1)). As suggested by Gulland (1973), age is estimated from length by algebraically rearranging the growth equation so that age is the dependent variable (see Equation (2)). Regardless of whether length or age is the dependent variable, the von Bertalanffy relationship is deterministic: There is a one-to-one correspondence between age and length.

For the von Bertalanffy growth equation, age frequency is estimated from a length sample as follows:

1) For each length compute the corresponding age.
2) For each age interval, usually the interval between midpoint ages of adjacent ages, sum the number of aged fish falling within the interval.
3) The age frequency is then the total number of aged fish falling within each age interval.

Use of the von Bertalanffy growth equation for age-frequency estimation results in several types of biases, different from those inherent in age-length keys. This paper documents these biases and proposes a method for their resolution.

BIASES

When growth is modeled according to the von Bertalanffy age-length relationship (Brody 1945; Ricker 1958),

$$L_t = L_\infty\ (1 - \exp[-k(t - t_0)]), \qquad (1)$$

then age, t, can be converted to length:

$$t = t_0 + \ln\ (1 - L_t/L_\infty)/(-k) \qquad (2)$$

where L_t = length at age t
L_∞ = the asymptotic length
k = the rate at which length reaches L
t_0 = hypothetical age at which fish would have zero length.

When computing numbers-at-age from Equation (2), estimation bias occurs. One bias is due to L_∞ being a fitted parameter. Thus, all numbers-at-length greater than L_∞ must either be eliminated or arbitrarily distributed to older ages. Bias also results when lengths approach L_∞ and are mathematically allocated to ages above those attainable by fish within the stock. As lengths (L) approach L_∞, Equation (2) will yield unreasonably old ages.

Additional bias results from the deterministic nature of the von Bertalanffy equation: Back calculations of length to age, Equation (2), are on a one-to-one basis. Thus, for any length there is a determined age. In reality, there can be a number of possible ages for any given length, the most probable age-at-length being that with the highest relative contribution of numbers-at-length. Since these back calculations are without probabilistic arguments, the determined age is not necessarily the most probable for the given length.

Back calculations of length to age also result in a mathematical estimation bias due to the switching of independent and dependent variables in going from Equation (1) to Equation (2). The degree of bias is likely to be a function of the amount of residual error in fitting Equation (1). The bias will probably not be consistent between cases and the degree of bias will have to be considered separately for each case. Consequently this bias is not specifically dealt with in this paper.

A computer model can readily demonstrate this bias. For von Bertalanffy parameters: L_∞ = 90.0 units, $t_0 = 0.0$ units, and $k = 0.30$, predetermined numbers-at-age are arbitrarily distributed normally with a standard deviation equal to 3 units about the von Bertalanffy length-at-age, Equation (1), for ages I through X. A length-frequency vector is then generated by 1) multiplying the number-at-age times the probability of age occurring within each 0.5 unit length interval, thus for each age generating a vector of number-at-length for length intervals between 0 and 100 units, and 2) accumulating numbers-at-length for each length interval over all ages. The numbers-at-age are then deterministically estimated from Equation (2) by accumulating numbers-at-length over the length intervals at age.

The bias from this model is illustrated in Table 1. Input and back-calculated numbers-at-age and their differences are listed in columns 2, 3, and 4, respectively. The input numbers-at-age represent a sample age distribution where either catchability, recruitment, mortality, or some combination thereof, are age-class variant. Differences, column 4, indicate a strong bias which increases with overlap of length distributions at age. One hundred and eleven fish were aged to be

TABLE 1.—Input and estimated numbers-at-age for both the deterministic (col. 3) and stochastic (col. 5) models, with the input numbers-at-age in column 2. The differences between the input numbers-at-age and the deterministic estimates are given in column 4.

	Numbers-at-age			
Age (1)	Input (2)	Deterministic (3)	Difference (4)	Stochastic (5)
I	200	199	1	200
II	400	399	1	400
III	800	760	40	800
IV	200	267	67	200
V	600	441	159	600
VI	300	378	78	300
VII	400	320	80	400
VIII	300	258	42	300
IX	100	164	64	100
X	100	68	32	100
X	—	111	111	—
Inf	—	35	35	—

greater than the maximum age, 10. Thirty-five had lengths greater than L_∞ and, consequently, were not classifiable.

BIAS RESOLUTION

With estimated variance of length-at-age a stochastic model can be built from the von Bertalanffy relationship: For any age the probability of a specific length interval is the probability of that interval taken over all length intervals containing that age. Thus for all ages a probability matrix ("P"-matrix) of dimension r by c can be computed, where r = the number of rows, or length intervals, and c = the number of columns, or ages, then $P(1,1)$ = (max. length, min. age). If the number-at-age vector is "a" (a_1 = (min. age)) and the number-at-length vector is L (L_1 = (max. length)), then

$$P\,a = L. \tag{3}$$

And as long as $r > c$ then the numbers-at-age vector can be uniquely solved via least-squares:

$$a = (P'P)^{-1}P'L. \tag{4}$$

Applying this stochastic method (Equation (4)) to the previous example, the numbers-at-age generated from the number-at-length vector are given in column 5 of Table 1. Since the probabilities of the P-matrix are the same as those used to generate the number-at-length vector, it is not surprising that the solution yields unbiased results. This computed example illustrates that the stochastic method yields unbiased estimates of age frequency.

PACIFIC BONITO

For the Pacific bonito, *Sarda chiliensis*, of the eastern tropical Pacific, Campbell and Collins (1975), using ages determined from otoliths, estimated the von Bertalanffy growth parameters to be $L_\infty = 76.87$ cm, $t_0 = -0.785$ yr, and $k = 0.6215$. Numbers-at-length for 1 cm intervals for ages I through V are shown in Figure 1 with the corresponding length-frequency plot in Figure 2. These numbers represent the 1973 catch from California waters and are a subset of the data used to estimate the von Bertalanffy parameters. This example serves to demonstrate bias and illustrate application of the stochastic method. If desired a variance-covariance matrix can be generated (Draper and Smith 1981) to estimate precision in the resulting age structure.

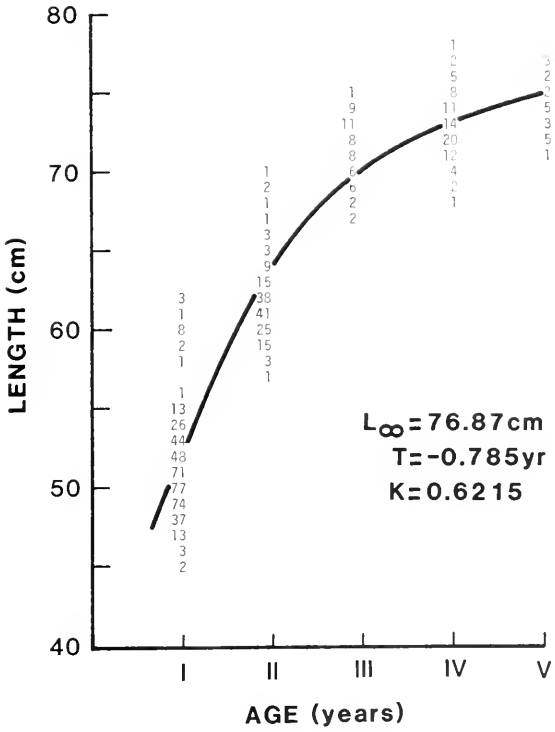

FIGURE 1.—Numbers-at-age by length in 1 cm intervals for the Pacific bonito, *Sarda chiliensis*. Data from 1973 California landings (Campbell and Collins 1975).

The length-frequency information and von Bertalanffy parameters are used to generate both deterministic and stochastic estimates of numbers-at-age. The estimated length-at-age

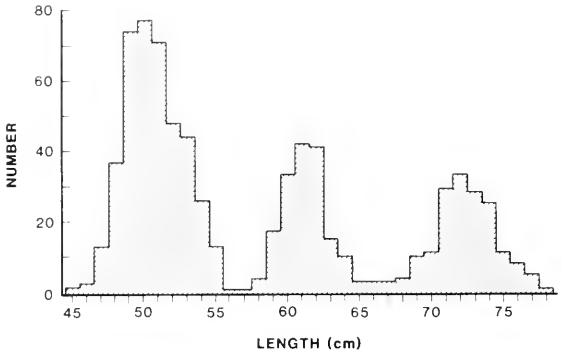

FIGURE 2.—Length frequency for the Pacific bonito, *Sarda chiliensis*, from 1973 California landings (Campbell and Collins 1975).

and sample standard deviations are

Age	*Length*	*Standard deviation*
I	51.5 cm	2.7 cm
II	63.3 cm	2.1 cm
III	69.5 cm	2.3 cm
IV	72.9 cm	2.0 cm
V	74.8 cm	1.9 cm

Deterministic estimates were made on lengths rounded to the nearest 0.1 cm. From Equation (2) the deterministic numbers-at-age are shown in column 3 of Table 2 with the difference between the true and estimated numbers in column 4. While the estimates are reasonably close over the first two ages, they become increasingly disparate for older ages. Thirteen fish had lengths greater than those at the maximum age. Seven had lengths greater than L and consequently were unclassifiable.

Quarter centimeter intervals were used to compute the stochastic estimates of age frequency. The results are shown in column 6 of Table 2, with the difference between true and estimated numbers in column 7. For all ages, especially the older ages, the stochastic estimates are closer and less biased than those of the deterministic method (column 3).

Some insight into the improvement of the stochastic age estimates over the deterministic age estimates can be gained by inspection of Figure 1. Lengths of age I fish overlap those of age II fish and vice versa. Since the deterministic cutoff point for age I fish is 58.7 cm (1.5 yr), all overlap is lost in the deterministic model. In contrast, for the stochastic model, overlaps in lengths-at-age are shared between ages, the degree of sharing being relative to the probabilities of length intervals at the respective ages.

With increasing age, the extent of relative overlap and, consequently, misaging increases for the deterministic model; allocation of lengths to ages becomes more sensitive. Only if the degree of overlap between adjacent ages is equal do accurate estimates of numbers-at-age result from the deterministic model. In the present example varying year-class strength and random variability in lengths-at-age offset this sensitive compensatory mechanism needed for accurate estimation with the deterministic model.

Fish lengths above 75.3 cm, the length at age 5.5 yr, are misclassified either as older or of infinite ages for the deterministic model. Since for the stochastic model probabilities of length intervals at age exist for all ages and lengths, even for lengths above L_∞, fish at lengths above the 75.3 cm cutoff point are distributed to all ages relative to their respective probabilities for length intervals.

DISCUSSION

Calculations of age from length via the von Bertalanffy growth equation result in several

TABLE 2.—Deterministic (col. 3) and stochastic (col. 6) estimates of numbers-at-age with their respective differences from the true numbers-at-age in columns 4 and 7 for the Pacific bonito, *Sarda chiliensis*, from 1973 California landings (Campbell and Collins 1975).

	Numbers-at-age						
Age (1)	True (2)	Deterministic (3)	Difference (4)	% Difference (5)	Stochastic (6)	Difference (7)	% Difference (8)
I	424	411	13	3.1	415	9	2.1
II	158	167	−9	−5.7	162	−4	−2.5
III	54	39	15	27.8	49	5	9.3
IV	80	71	9	11.3	85	−5	−6.3
V	21	29	−8	−38.1	26	−5	−23.8
>V	—	13	−13	Inf.	—	—	0.0
Inf	—	7	−7	Inf.	—	—	0.0

types of bias. The degree of bias is proportional to overlap in lengths-at-age and changes with weak or strong year classes. When overlap increases with age, age-frequency estimates will generally be more biased for older than younger ages. When overlap occurs, biases will always result, since the numbers-at-length will be allocated to unreasonably old ages. Any numbers-at-length for lengths greater than L_x will be undetermined in age estimation, resulting in downward biases for those ages contributing such lengths.

Age estimation biases can be effectively removed by creating a stochastic model based on a matrix of length interval probabilities at age. The probability matrix (P-matrix) is independent of year-class strength and will effectively remove all sources of estimation bias except that due to random variation in length-frequency estimation. As long as the von Bertalanffy growth parameters remain the same over time, the stochastic method based on accurate estimates of variance in length-at-age will always yield unbiased results.

A probability model of the distribution of length-at-age with estimated parameters is necessary for estimating probabilities of length intervals at age for the P-matrix. If age information is unavailable then variances can be estimated from visually separable length-frequency modes. In the case where modes are separable for the first few ages only, there will be a problem in estimating variances for older ages: A model relating the variance in length-at-age with age can be used in estimating variances for these older ages. Ricker (1969) proposed that while distributions in lengths-at-age remain normal, variances increase during the first few years, stabilize, and then decrease over the final years. The trend in variances with age for a similar species might also be substituted in cases where variances are unavailable.

The principal strengths of the stochastic method are that few fish are required to be aged to estimate the P-matrix and that existing von Bertalanffy growth relations can be used. Accurate estimates of variance in length-at-age can probably be achieved with as few as 20 to 30 fish/age, which is likely to be a much smaller number of fish than needed to estimate accurate proportions of age-at-length necessary to construct an age-length key.

Von Bertalanffy growth parameters have been estimated for many species. Since most stocks have variant year-class strength, overlaps in lengths-at-age, and lengths exceeding the upper bound for the last age attainable, conversion to a stochastic model may be necessary, if unbiased estimates of age frequency are desired. Reexamination of age-length data used to estimate the von Bertalanffy parameters may be useful in estimating variances in lengths-at-age for the P-matrix. Taking additional age-length samples may be a cost-effective way of improving age-frequency estimation.

In fishery management, the overestimation of maximum age by the deterministic von Bertalanffy equation may produce underestimates of mortality rates which may result in overestimates of population size and recruitment. Further, the deterministic method tends to "fill in" weak year classes which results in underestimates of year-class variability and overestimates of recruitment stability. In general, all of these affect accuracy of a stock assessment and contribute to improper advice for fishery management.

Application of the stochastic method shown here to cover other growth equations and situations, such as discontinuous growth, is handled by simply estimating appropriate elements in the P-matrix for each case.

ACKNOWLEDGMENTS

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AGE, GROWTH, AND MORTALITY OF KING MACKEREL, *SCOMBEROMORUS CAVALLA*, FROM THE SOUTHEASTERN UNITED STATES[1]

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ABSTRACT

Age, growth, and mortality of king mackerel, *Scomberomorus cavalla*, from the southeastern United States were studied. Otoliths from 1,449 fish were used to estimate age composition, growth rates, and mortality rates of this species.

Age composition varied between locations (Texas, Louisiana, Florida, South Carolina, and North Carolina). The majority of older fish were found in Louisiana waters. The oldest females were 14+ years old and the oldest males were 9+ years old. Compensatory growth was found in both sexes. The von Bertalanffy growth equations were as follows: Males (all areas) $l_t = 965\,(1 - e^{-0.28(t+1.17)})$; females from Louisiana $l_t = 1{,}529\,(1 - e^{-0.14(t+2.08)})$; and females (excluding Louisiana) $l_t = 1{,}067\,(1 - e^{-0.29(t+0.97)})$ where l = fork length (mm) and t = years. The mean annual mortality rate determined by six methods of analysis ranged from 0.32 to 0.42. The length-weight relations of king mackerel were for males: $W = 0.8064 \times 10^{-5} L^{2.9928}$; for females: $W = 0.8801 \times 10^{-5} L^{2.9827}$, where W = weight in grams and L = fork length in millimeters.

King mackerel, *Scomberomorus cavalla*, is a major recreational and commercial fisheries resource in the southeastern United States (Manooch 1979). Age, growth, and mortality information has been based on small specimens collected from a limited geographical area (Beaumariage 1973). A need has existed to reexamine age, growth, and mortality from broader geographically based samples.

King mackerel of Brazil have been studied intensively, but the great distance separating these Brazilian fish from those in the United States makes application of their results to king mackerel in United States waters a questionable practice (see Manooch et al. 1978 for annotated bibliography on this species).

A geographically comprehensive sampling of king mackerel in U.S. waters was initiated by us in 1977. Recreational landings were sampled because the sport fishery is less localized than the commercial fishery. We utilized samples from Texas to North Carolina to meet our objectives of determining the age composition, growth rates, length-weight relationships, and mortality rates of king mackerel from U.S. waters.

METHODS AND MATERIALS

King mackerel (7,723 fish) were collected from Texas, Louisiana, Florida, South Carolina, and North Carolina from June 1977 through August 1979 (Fig. 1). They were caught by recreational hook and line, except for some small individuals, which were caught in shrimp trawls at Cape Canaveral, Fla., in December 1978. The trawl-caught fish were used in determining the relation between otolith radius and fish length. In 1979, 121 fish samples were taken only in northwest Florida and were used to supplement existing samples for the marginal increment analysis.

Processing the fish samples involved several steps. The fish were sexed when possible, measured to the nearest millimeter of fork length (FL), and weighed to the nearest gram. Otoliths were removed from the fish, cleaned, and stored either dry or in 100% glycerin.

The otoliths were examined under reflected light in a black-bottomed watch glass containing 100% glycerin with a binocular dissecting microscope at 28×. The otolith radius (OR) was measured on the posterior surface from the focus to the distal margin along the axis approximating the extension of the sulcus acousticus. All measurements were made in ocular micrometer units (1 omμ = 0.0363 mm). Marks were counted and measured along the radius to their distal edge. The marks were opaque (light) under re-

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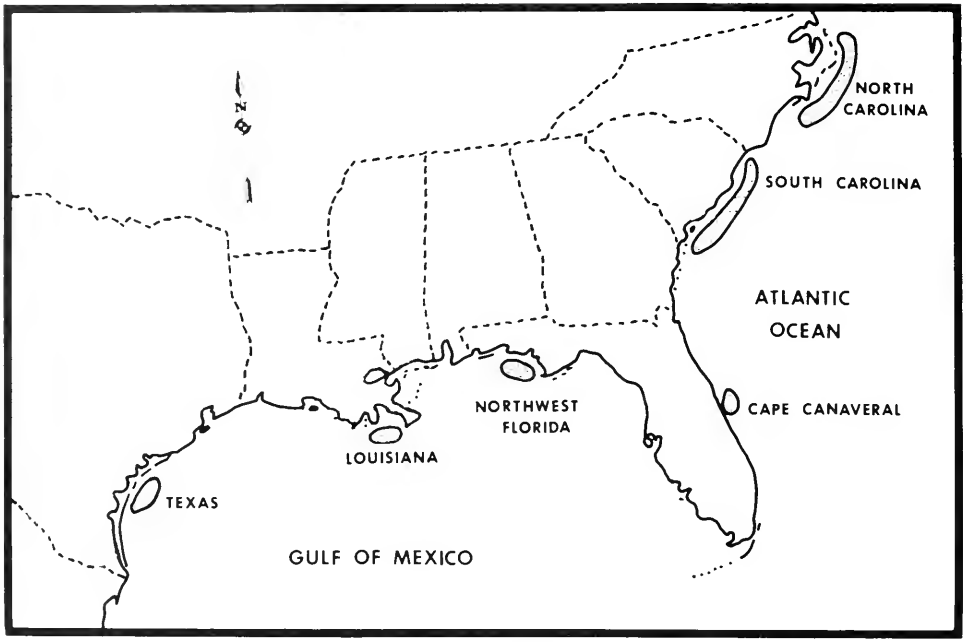

FIGURE 1.—Location of king mackerel, *Scomberomorus cavalla*, sampling sites.

flected light, while the interspaces were hyaline (dark).

Otoliths were classified into age groups according to the number of opaque nonmarginal marks (following the method of Beaumariage 1973). Each otolith was examined by two readers. If the readers did not agree on the age of a fish, data for that fish were not used.

We determined the time of mark formation by comparing frequency per month of otoliths with opaque margins. A high percentage of opaque margins indicated recent mark formation.

Comparison of age estimations was made, based on surface (whole) and internal (sectional) examination of 133 otoliths. Three to 10 otoliths from each age (0+ through 14+) were used for the comparison. Three to six sections, each 0.15 mm thick, were made through the focus of each otolith, using a Norton[3] diamond blade (SD519-N50m-1/8) rotating at about 285 rpm on an Isomet low-speed saw. The otolith was mounted in thermoplastic (quartz) cement (No. 70C Lakeside) and cooled with mineral spirits during sectioning. Later the cement was dissolved by soaking in 50% isopropanol. The free sections were then mounted on glass slides using Piccolyte cement and examined with a binocular dissecting microscope.

The relationship of the size of the aging structure (OR) to the size of the fish (FL) was determined by using least-square regressions with both linear and power curves. Once the relationship was established, fork lengths at earlier ages were back-calculated from surface otolith measurements, using methods adopted from Tesch (1971), Ricker (1975), and Everhart et al. (1975).

Otolith measurements were analyzed for implications of compensatory growth. A frequency distribution of otolith lengths from the focus to the proximal edge of the first opaque mark was developed. Both slow- and fast-growing fish were separated from those that grow at intermediate rates, and lengths at earlier ages were back-calculated for both the slow and fast growers.

A computer program by Abramson (1971) was used to fit von Bertalanffy theoretical growth curves. Each age was given equal weight, and mean back-calculated lengths were used in the computations.

Length-weight equations were developed for the entire king mackerel collection, and for males and females separately, by a computer program following Ricker's (1975) suggestions. Nonlogarithmic length intervals (50 mm) and

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

weight intervals (computed by the program) were used. A maximum of 20 length-weight values was randomly selected for the analysis within each qualifying length and weight interval. If any length or weight interval contained fewer than 20 values, all were utilized.

Estimates of annual mortality rate A (after Ricker 1975) were developed by catch-curve analysis of south Florida length-frequency data. These data were used because they best represented the king mackerel in U.S. waters according to Trent et al. (1981). Since these data were not separated by sex, two age-length keys were developed, one combining males and females assuming a 1:1 sex ratio and the other assuming a 1 male:2 female ratio (the approximate ratio in our collection). The length-frequency data were converted to age-frequency distributions (N = number of fish caught in age-class i) by applying each of the combined age-length keys. Age classes I through X of the resultant catch curves were analyzed by

1. Heincke's (1913) method;
2. Jackson's (1939) method;
3. Rounsefell and Everhart's (1953) method;
4. Beverton and Holt's (1957) method, using the mean of values computed with their equation 13.4 between successive age groups;
5. Robson and Chapman's (1961) method, uncorrected for possible age-length key bias; and
6. finding the slope (m) of a regression line fitted to ln (N_i) and i and substituting in the equation $A = 1 - e^m$.

RESULTS AND DISCUSSION

Age

The validity of using otoliths for estimating the age and past growth history depends on these structures being directly correlated with the growth of the fish and on otolith mark formation being periodic. We found the otolith radii to be closely correlated to fork lengths, especially when the data were transformed to represent a "power" function. The "power curve" equation, $FL = 1.232\ OR^{1.331}$ with correlation coefficient $r = 0.987$, had a better fit than the linear equation, $FL = 5.559\ OR + 84.818$ with $r = 0.847$. This close correlation of OR and FL satisfied the first criterion for validation of otoliths as an age determination structure. The second criterion, mark formation of known periodicity, needed further investigation. Beaumariage (1973) found king mackerel with opaque margins during 8 mo of the year (February-September); the highest percentage of otoliths with opaque margins occurred in May. He concluded, "Most otolith margins become opaque (form annuli) during April, May, and June...." Fish in our collections exhibited opaque margins in 11 mo of the year with the peak during May (54%); however, few fish were collected during the winter months (November-February). No month had a high percentage (over 75%) of fish with opaque margins, and only one month (March) lacked fish whose otoliths had opaque margins (Table 1).

In recent years the use of whole otoliths for estimating the age of fish has been questioned. Beamish (1979) indicated that a fish's age may be underestimated using surface examination and that otolith sections are more reliable. However, we found 96.5% agreement between king mackerel age estimates (number of opaque marks) comparing surface and sectional readings. This indicates that our age estimations for whole otoliths are similar to those of sectioned ones.

The agreement between two readers about the number of marks on king mackerel otoliths was 98%. The number of otoliths found to be usable was 1,449.

Age and Size Composition

Age composition of king mackerel varied greatly among the areas (Table 2). Younger fish were taken in northwest Florida, while older fish were caught off Louisiana, particularly in 1978. Fish of intermediate age were landed primarily in Texas, South Carolina, and North Carolina. The oldest females in our sample were 14+ yr (over 1,400 mm FL) and the oldest males were 9+ yr (970 mm FL).

Much age variation occurred within a single length group in our data (Tables 3, 4) as it did in Beaumariage's (1973) data. For example, we found females 850-899 mm FL were 1-8 yr old (Table 3).

Back-Calculated Growth

The weighted means of the back-calculated fork lengths for male and female king mackerel from all areas and years sampled in this study are shown in Tables 5 and 6. Differences in mean

TABLE 1.—Percentages by month, area, and year of king mackerel otoliths having opaque margins. ( ) = total number of fish.

Area	Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec.
Texas	1977	—	—	—	—	—	26 7 (15)	28 6	0 0 (5)	—	—	—	—
	1978	—	—	—	—	—	0 0 (5)	0.0 (17)	2 5 (40)	—	—	—	—
Louisiana	1977	—	—	—	—	—	0 0 (4)	—	—	0 0 (15)	0 0 (22)	0 0 (18)	—
	1978	0 0 (7)	16 7 (6)	0 0 (43)	40 6 (32)	0 0 (2)	15 4 (26)	6 5 (62)	13 5 (37)	0 0 (5)	0 0 (51)	5 0 (20)	14 3 (7)
NW Florida	1977	—	—	—	—	—	18 2 (11)	9 4 (64)	3 1 (65)	0 0 (73)	4 3 (46)	—	—
	1978	—	—	—	—	—	0 0 (15)	0 0 (160)	0 0 (97)	0 0 (107)	11 1 (135)	—	—
	1979	—	—	—	—	61 2 (62)	20 0 (20)	19 2 (27)	0 0 (12)	—	—	—	—
SE Florida	1978	—	—	—	—	—	—	—	—	—	—	—	50 0 (6)
	1979	83 3 (6)	—	—	—	—	—	—	—	—	—	—	—
South Carolina	1978	—	—	—	—	—	—	—	—	—	2 9 (104)	—	—
North Carolina	1978	—	—	—	—	0 0 (5)	63 6 (22)	38 5 (13)	26 7 (15)	3 8 (53)	8 9 (313)	—	—
Total		38 5 (13)	16 7 (6)	0 0 (43)	40 6 (32)	54 3 (70)	23 7 (118)	7 2 (364)	4 4 (271)	0 8 (253)	7 2 (671)	2 6 (38)	33 3 (13)

TABLE 2.—Percentages of king mackerel by area and year within each age group, developed from age-length keys and length-frequency distributions.

Area	Year	Age in years															No fish
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Males																	
Texas	1977	—	—	6 9	24 1	24 1	27 6	3 5	6 9	6 9	—	—	—	—	—	—	29
	1978	—	2 6	1 9	13 5	16 5	20 6	32 5	3 6	3 3	5 8	—	—	—	—	—	533
Louisiana	1977	—	—	—	—	—	100 0	—	—	—	—	—	—	—	—	—	10
	1978	—	—	—	—	—	20 0	24 0	36 0	8 0	12 0	—	—	—	—	—	25
NW Florida	1977	—	26 9	31 3	16 7	20 5	2 0	2 6	—	—	—	—	—	—	—	—	498
	1978	1 8	93 1	2 7	1 2	0 4	0 8	—	—	—	—	—	—	—	—	—	1,107
South Carolina	1978	—	21 1	8 8	21 8	13 6	13 6	19 7	—	—	1 4	—	—	—	—	—	147
North Carolina	1978	—	5 2	5 2	18 3	35 7	20 0	8 6	3 5	3.5	—	—	—	—	—	—	115
Total males		0 8	48 8	8 6	10 5	12 6	7 7	6 5	1 7	1 4	1 4	—	—	—	—	—	2,507
Females																	
Texas	1977	—	—	27 9	48.8	7 0	9 3	4 7	2 3	—	—	—	—	—	—	—	43
	1978	—	4 1	8.5	5 8	37 3	23 6	9 9	10 8	—	—	—	—	—	—	—	780
Louisiana	1977	—	0 4	0 8	12.6	28 9	30.1	10 9	6 7	2 9	6 7	—	—	—	—	—	239
	1978	—	—	0 4	1.3	6 0	14 4	24 4	11.9	7 7	7 7	10 9	8 8	4 4	1 3	0 8	479
NW Florida	1977	—	39 6	30 4	12.5	10 0	5 8	0 6	0 6	0 4	—	0 1	—	—	—	—	1,393
	1978	2 0	85 0	5 9	2 5	2 1	1 6	0 8	—	—	—	0 1	—	—	—	—	1,463
South Carolina	1978	—	17.3	3.6	26 5	21 7	5.6	11 2	—	4 4	5 6	2 4	0 8	0 9	—	—	249
North Carolina	1978	—	4 5	3.7	19 7	20 4	19 2	16 4	8 5	4 0	3 2	—	—	0 4	—	—	402
Total females		0 6	37 9	10 9	9 9	11 1	8 6	0.3	4 0	2 2	1 7	1.7	1 1	0 7	0 2	0 1	5,216

length occurred from year to year and from area to area. Only data for Louisiana, however, where five or more individuals were used in computing a mean, showed the range of means within an age group to vary more than 100 mm.

In 2 yr of sampling in Louisiana, over 300 females were sampled, but too few males were collected to back-calculate size at previous ages. Generally, the Louisiana fish were also much larger than those taken elsewhere, and we concluded that this must be an anomalous group of fish. We separated Louisiana females from other females for growth computations, except those dealing with compensatory growth.

TABLE 3.—Length composition (%) of female king mackerel by age group (locations combined).

Length group (mm FL)	Age in years															Total no fish
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
350-399	100 0															1
400-449	33 3	66 7														6
450-499	43 5	56 5														23
500-549		100.0														48
550-599		100 0														90
600-649		96 4	3 6													112
650-699		77 5	19 7	2 8												71
700-749		25 3	65 1	7 2	1 2	1 2										83
750-799		3 0	36 0	43 0	16 0	2 0										100
800-849		2 4	11 0	36 2	31 5	13 4	3 9	1 6								127
850-899		1 6	0 8	18 9	33 6	32 0	9 8	2 5	0 8							122
900-949			1 0	11 0	22 0	25 0	28 0	9 0	4 0							100
950-999				2 5	23 4	31 2	26 0	14 3	1 3		1 3					77
1,000-1,049					16 7	23 1	34 6	11 5	6 4	3 8	2 6		1 3			78
1,050-1,099					4 1	28 6	26 5	10 2	10 2	16 3	4 1					49
1,100-1,149					1 9	11 5	40 4	13 5	19 2	7 7	5 8					52
1,150-1,199						11 9	21 4	33 3	9 5	9 5	7 1	4 8	2 5			42
1,200-1,249						2 9	15 2	21 2	21 2	9 1	15 2	6 1	9 1			33
1,250-1,299							12 5	8 3	4 2	16 7	33 3	8 3	16 7			24
1,300-1,349							4 3	4 3	13 0	8 7	21 7	26 3	13 0	8 7		23
1,350-1,399									5 0	15 0	30 0	35 0	5 0	5 0	5 0	20
1,400-1,449										26 7	13 3	33 3	20 0		6 7	15
1,450-1,499											14 3		57 1	14 3	14 3	7
1,500-1,549																0
1,550-1,599												50 0	50 0			2

TABLE 4.—Length composition (%) of male king mackerel by age group (locations combined).

Length group (mm FL)	Age in years													Total no fish
	0	1	2	3	4	5	6	7	8	9	10	11	12	
400-449		100 0												4
450-499	15 2	84 8												33
500-549		100.0												51
550-599		98 3		1 7										60
600-649		93 0	5 3		1 7									57
650-699		37 5	37.5	14 6	10 4									48
700-749		11 9	35 7	31 0	16 6	2 4	2 4							42
750-799			11 1	27 8	46 3	13 0	1 8							54
800-849			2 0	15 4	34 6	21 2	19 2	3 8	3 8					52
850-899				15 0	5 0	35 0	30 0	10 0	5 0					20
900-949					14 2	42 9	42 9							7
950-999							25 0	25 0	25 0	25 0				4
1,000-1,049								25 0		75 0				4
1,050-1,199														0
1,200-1,249									100 0					1

TABLE 5.—Weighted means of back-calculated fork lengths (mm) for female king mackerel from all areas, 1977-78.

Age class	Texas		Louisiana		NW Florida		South Carolina	North Carolina
	1977	1978	1977	1978	1977	1978	1978	1978
I	487	457	504	502	463	443	415	393
II	688	673	718	714	670	687	638	627
III	777	748	824	824	755	764	750	738
IV	847	811	906	909	805	838	809	798
V	[1]805	853	970	983	866	895	864	844
VI	[1]849	937	990	1,045	[1]897	[1]934	916	891
VII	[1]932	[1]885	[1]1,097	1,096	[1]963		941	939
VIII			[1]1,203	1,148			996	992
IX			[1]1,361	1,202			1,033	[1]1,000
X				1,252			[1]1,034	
XI				1,311				
XII				1,332				
XIII				[1]1,350				
XIV				[1]1,399				

[1]Lengths based on less than 5 samples

TABLE 6.—Weighted means of back-calculated fork lengths (mm) for male king mackerel from all areas, 1977-78.

Age class	Texas		Louisiana		NW Florida		South Carolina	North Carolina
	1977	1978	1977	1978	1977	1978	1978	1978
I	414	413	—	—	473	407	373	385
II	588	574			635	665	607	614
III	659	658			686	[1]734	715	702
IV	703	720			736	[1]746	746	747
V	747	790			[1]798		[1]769	781
VI	[1]754	829			[1]850		[1]821	795
VII	[1]803	[1]896						[1]810
VIII	[1]789	[1]951						
IX		[1]943						

[1]Lengths based on less than 5 samples

Back-calculations for male king mackerel from all areas combined are shown in Table 7. Growth is rapid until the third year of life, after which time the annular growth increment decreases and stabilizes at an average 42 mm FL.

Females from the combined areas (Table 8), excluding Louisiana, also showed rapid growth in the first 3 yr, after which the annual growth increment decreased to an average 40 mm FL. Females were larger than males for all ages.

Fish from Louisiana (all females) exhibited an impressive growth rate (Table 9). They averaged 69 mm longer than other females at age 1, and by age 10 were 218 mm longer than their counterparts. The yearly growth increment was over 60 mm to age 6, an increment not maintained by other females, or males, past age 3 in other locations.

Our combined back-calculated data were compared with those from Beaumariage (1973) (Table 10). His data were converted to fork lengths from standard lengths (SL) using his equation: $FL = 1.096\ SL - 17.143$. Disregarding Louisiana females, both male and female mean

TABLE 7.—Average back-calculated fork lengths (mm) at age for male king mackerel from all areas, 1977-78.

Age class	Mean length at capture (mm FL)	N	Age in years								
			1	2	3	4	5	6	7	8	9
I	570 3	206	425 0								
II	708 6	41	422 6	667 3							
III	767 0	41	408 5	618 7	737 6						
IV	772 5	44	403 3	594 6	677 5	747 9					
V	820.4	22	375 1	590 5	669 0	733 9	796 1				
VI	832 6	16	349 2	559 4	641 9	700 1	755 8	808 3			
VII	852 3	3	389 6	579 3	648 6	717 7	752 7	802 1	838 3		
VIII	920 0	2	415 2	578 8	649 2	714 5	773 1	817 3	862.5	896.0	
IX	970 0	1	476 6	560 3	623 3	754 1	796 2	830.2	864 7	899 4	943 4
Weighted mean		376	414 1	613 4	689 2	734 0	777 4	809 3	850 8	897.1	943.4
Annual increment				199 3	75 8	44 8	43.4	31 9	41 5	46 3	46 3

TABLE 8.—Average back-calculated fork lengths (mm) at age for female king mackerel from all areas except Louisiana, 1977-78.

Age class	Mean length at capture (mm FL)	N	Age in years									
			1	2	3	4	5	6	7	8	9	10
I	604 8	315	456.4									
II	741.2	112	427.9	693 8								
III	809 6	105	435 8	645.4	774 4							
IV	858 7	100	426 2	648.9	753 5	830 2						
V	897 1	79	499.3	635 3	729 6	800 7	865.4					
VI	933 7	44	405 1	630.3	727.2	791.6	848 2	908 3				
VII	960 2	21	363.0	613.3	703.3	760 5	827 4	884 5	937 5			
VIII	1,028 0	8	392.4	635 0	732.5	796.6	852.2	910.0	955 3	1,020 9		
IX	1,056 0	6	337 4	609 2	732 0	790.9	847 3	893 9	938.1	987.7	1,034 6	
X	1,062.1	2	325.5	557 8	683.1	747 4	796.9	833.9	883.6	934.7	978.4	1,033.6
Weighted mean		792	433 9	652.0	747.1	806.5	853.5	899 4	938.5	997.7	1,020.6	1,033 6
Annual increment				218 1	95.1	59 4	47.0	45 9	39.1	59.2	22.9	13 0

TABLE 9.—Average back-calculated fork lengths (mm) at age for Louisiana female king mackerel, 1977-78.

Age class	Mean length at capture (mm FL)	N	Age in years												
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
I	635.0	1	571.5													
II	815.8	4	500.3	767.1												
III	890.3	16	523.0	745.3	852.0											
IV	955.9	30	525.9	725.9	829.4	927.8										
V	1,039.2	48	517.9	728.0	838.4	926.9	1,011.2									
VI	1,079.5	78	520.7	727.8	840.7	923.6	992.2	1,057.7								
VII	1,159.1	24	495.2	711.5	834.9	924.0	997.8		1,129.3							
VIII	1,204.5	16	443.0	668.9	793.7	878.3	960.9	1,033.7	1,100.2	1,170.2						
IX	1,261.7	16	462.8	689.0	800.2	885.8	959.9	1,032.6	1,099.8	1,168.0	1,234.5					
X	1,273.3	22	473.1	674.0	765.9	851.8	925.3	991.1	1,057.6	1,121.9	1,182.4	1,244.8				
XI	1,369.5	11	505.0	715.1	810.2	900.4	976.8	1,052.6	1,121.0	1,182.8	1,235.9	1,288.0	1,345.6			
XII	1,369.0	11	469.3	681.6	790.0	869.5	941.3	1,014.5	1,081.0	1,135.5	1,193.9	1,243.9	1,295.0	1,340.8		
XIII	1,404.1	2	380.4	656.5	764.9	843.1	931.4	988.8	1,055.3	1,117.5	1,172.5	1,227.7	1,278.4	1,327.0	1,357.0	
XIV	1,419.5	2	387.0	631.9	738.3	814.5	888.2	967.0	1,022.1	1,074.1	1,130.2	1,195.0	1,241.3	1,259.8	1,343.5	1,399.1
Weighted mean		281	502.6	714.5	823.7	908.8	981.3	1,041.4	1,095.6	1,149.7	1,204.7	1,251.7	1,311.0	1,332.3	1,350.2	1,399.1
Annual increment				211.9	109.2	85.1	72.5	60.1	54.2	54.1	55.0	47.0	59.3	21.3	17.9	48.9

TABLE 10.—Mean back-calculated fork length (mm) at ages, from Beaumariage (1973) and this study. Beaumariage's data were transformed from standard length by his formula FL = 1.096 SL − 17.143.

Age	Males		Females (except La.)	
	Beaumariage	Johnson et al.	Beaumariage	Johnson et al.
1	457	414	491	434
2	643	613	703	652
3	705	689	793	747
4	752	734	857	807
5	795	777	928	854
6	822	809	986	899
7	839	851	1,033	939

fork lengths at age were smaller in our study than in his in all cases but one (7-yr-old males). Several explanations for the differences seem reasonable. First, our back-calculations employed a power curve, whereas his employed a linear equation. Secondly, our fish were sampled from a wide geographical range, which yielded fish with wide variation in age composition, whereas Beaumariage sampled from a more restricted area. Lastly, our sampling occurred almost 10 yr after his, and various changes may have occurred in the population owing to exploitation or other influences.

Compensatory Growth

Compensatory growth (Ricker 1975) appeared to occur in both male and female king mackerel. Length-frequency distributions of otolith measurements from the focus to the proximal edge of the first opaque mark in both sexes showed a normal distribution of values. After examination of the distributions, we defined slow-growing fish (both sexes) as those with an increment of 50 omμ or less, fast-growing males as those with an increment of 81 omμ or more, and fast-growing females as those with an increment of 86 omμ or more.

Back-calculated lengths for these fish are shown in Table 11. While fast-growing males grew 525 mm in year 1, they grew only 135 mm in year 2. The slow-growing males grew 303 mm in their first year, but made up some of their size difference by growing 285 mm in their second year. Females showed a similar trend, with fast-growing fish having a first-year increment of 559 mm and a second-year increment of 184 mm. The slow-growing females grew 282 mm in year 1 and 334 mm in year 2. Beyond age 2, yearly growth increments were similar within each sex.

Growth compensation in king mackerel is

TABLE 11.—Annual fork length increments (mm) computed from back-calculations on fast- and slow-growing male and female king mackerel (from all areas combined).

	Males		Females	
Age	Fast	Slow	Fast	Slow
1	525	303	559	282
2	135	285	184	334
3	87	85	101	99
4	53	72	89	67
5	104	63	75	63
6		49	64	66
7			46	75
8			52	65
9			53	47
10			44	47
11			51	67
12			34	10
13			67	35
14			11	100

probably the result of an extended spawning season. Long spawning seasons and multiple spawns are discussed by Beaumariage (1973) and would result in great size variation in young-of-the-year king mackerel. Some of that size variation would be decreased as the smaller fish continue to grow at a higher rate in their second year than do larger fish in their second year. Although the slow-growing fish make up some difference in size during year 2, they remain smaller than the fast growers throughout their lives.

Theoretical Growth

The von Bertalanffy theoretical growth parameters computed from back-calculated fork lengths are shown in Table 12, along with those reported by other authors. The von Bertalanffy (1938, 1957) growth equation is the following:

$$l_t = L_\infty \left(1 - e^{-k(t - t_0)}\right)$$

where l_t = length at age t,
L_∞ = asymptotic length,
k = growth coefficient, and
t_0 = time when length would theoretically be zero.

TABLE 12.—von Bertalanffy growth parameters for king mackerel.

Author	k value	L_∞ (mm FL)	t_0 (yr)
Males			
Johnson et al., all areas	0.28	965	−1.17
Beaumariage (1973)	0.35	903	−2.50
Nomura and Rodrigues (1967)	0.18	1,160	−0.22
Females			
Johnson et al., excl. La.	0.29	1,067	−0.97
Johnson et al., La.	0.14	1,529	−2.08
Beaumariage (1973)	0.21	1,243	−2.40
Nomura and Rodrigues (1967)	0.15	1,370	−0.13

Our theoretical growth parameters are between those calculated by Beaumariage (1973) and Nomura and Rodrigues (1967). Beaumariage's theoretical growth parameters were calculated by employing observed sizes of fish at each age, while Nomura and Rodrigues apparently combined both back-calculated lengths and empirical lengths in their calculations. We employed mean back-calculated lengths at age in our computations, which may account for some of the differences between our values and those of the other investigators.

Length-Weight Relationship

The length-weight values for king mackerel computed for the equation $W = a\ L^b$, where W is weight in grams and L is fork length in millimeters, are presented in Table 13. Male length-weight values from our study were within the confidence intervals set by Beaumariage (1973), but for both our female and combined sexes, length-weight values were below his lower confidence intervals.

Mortality

Mortality estimates are presented in Table 14. The mean annual mortality rate (A = 0.37) is lower than Beaumariage's (1973) estimate (A = 0.54). We feel that our results are more concordant with generally accepted techniques of catch-curve analysis, in that our catch-curves were developed from age-frequency data, as opposed to the length-frequency catch-curve used by Beaumariage. We also feel that our results are less influenced by the effects of gear selectivity than Beaumariage's results, since Trent et al. (1981) stated that commercial hook-and-line gear excludes small and large king mackerel to a greater extent than does recreational hook-and-line gear. Nevertheless, there are many difficulties in using catch-curve analysis in our study. Specific problems are related to the Beverton and Holt (1957) and Robson and Chapman (1961) techniques. The first technique involves using several consecutive years of data, which were unavailable in our study. With the second technique, we used age-length keys as the basis for our catch-curves but were unable to make corrections for the bias when such keys were used (Rob-

TABLE 13.—Summary of length-weight relations of U.S. king mackerel. W = weight in grams; L = fork length in millimeters.

Sex	No. fish	Range (mm FL)	$W = a\ L^b$ a	$W = a\ L^b$ b	95% confidence interval Lower	95% confidence interval Upper	Correlation coefficient (r)
Male	701	428-1,355	0.8064×10^{-5}	2.9928	2.9572	3.0284	0.9909
Female	2,023	351-1,554	0.8801×10^{-5}	2.9827	2.9562	3.0092	0.9910
Sexes combined	2,821	351-1,554	0.8464×10^{-5}	2.9881	3.0153	3.0153	0.9899

TABLE 14.—Estimated annual mortality rate (A) by estimation technique, assuming 1:1 and 1:2 male:female ratios.

Male:Female ratio	Estimation technique: Heincke (1913)	Jackson (1939)	Rounsefell & Everhart (1953)	Beverton & Holt (1957)	Robson & Chapman (1961)	Regression analysis	Mean A
1:1	0.35	0.34	0.42	0.42	0.32	0.35	0.37
1:2	0.34	0.35	0.42	0.42	0.33	0.36	0.37

son and Chapman 1961). This was a result of the age-length keys being developed for a different fish sample than the one being analyzed for mortality rates. The difficulties in applying Robson and Chapman's technique resulted in an implication that king mackerel are not fully recruited into the south Florida recreational fishery until age 7, after which the annual mortality rate is 0.53. This mortality estimate is similar to Beaumariage's (A = 0.54), but the age at recruitment was found by Beaumariage to be 2-3. His estimate was based on a smaller age range (0-7) than was ours. This difference probably influenced the resulting mortality estimates.

Many difficulties are also involved in the basic concept of using catch-curve analysis to estimate mortality in king mackerel. Rounsefell and Everhart (1953) emphasized that catch-curve analysis is based on false assumptions when applied to most pelagic species, including mackerel. Robson and Chapman (1961) reiterated this warning, stating, "if year classes...vary in strength and survival rates vary from year class to year class and age to age, then the age-frequency distribution in the catch of a single season provides no identifiable information whatsoever regarding [mortality rates]...." These comments force us to state our mortality findings with some wariness.

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ADDENDUM

Fischer (1980) reported on the length-weight relationship of king mackerel off Louisiana. His length-weight values are similar to ours.

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REVIEW AND ANALYSIS OF THE BLUEFIN TUNA, *THUNNUS THYNNUS*, FISHERY IN THE EASTERN NORTH PACIFIC OCEAN

DOYLE A. HANAN[1]

ABSTRACT

Northern bluefin tuna migrate from waters near Japan to the eastern North Pacific where they are fished primarily by purse seine. While annual catches fluctuate greatly, two major periods are identified. The average annual catch in the second period (1950-present) is nearly double that for the first period (1921-50) and is attributed to increased fishing effort by the "high-seas" tuna fleet operating off Baja California. The declining catch per unit effort in the second period and declining catches after 1963 are assumed to indicate declining abundance of bluefin tuna in the eastern North Pacific.

Length-frequency analysis reveals 1) significantly smaller bluefin tuna in U.S. waters than in waters off Baja California and 2) significant variation in mean lengths among years.

Analysis of tag-recapture data confirms seasonal northward migration and vulnerability to the fishery for as many as three fishing seasons. A catchability coefficient of 1.66×10^{-4}/boat-day and an annual instantaneous total mortality rate of 2.07, both estimated from the tag-recapture data, are used with summaries of fishing effort to calculate an average annual exploitation rate of 30% for bluefin tuna in the eastern North Pacific.

Purse seining for northern bluefin tuna, *Thunnus thynnus* Linnaeus, in the eastern North Pacific Ocean began about 1914, with the first large commercial landings in 1918 (Whitehead 1931). Prior to the development of this purse seine fishery, a sport fishery existed off southern California at Santa Catalina Island; and since bluefin tuna are difficult to catch by hook and line, elaborate fishing methods evolved such as using a kite to make the bait (flying fish) skip across the water (Clemens and Craig 1965). The Tuna Club of Avalon at Santa Catalina Island even awarded "blue buttons" to its members for catching the large and wary prize. Because of this difficulty in hooking bluefin, the commercial "high-seas" fleet did not fish for bluefin until the late 1950's, when most of the fleet had converted from pole-and-line gear to purse seines (Bell[2]).

Currently the bluefin fishery consists of a "wet-fish" fleet, principally out of San Pedro, Calif.; a high-seas fleet mostly out of San Diego, Calif.; and since 1975, an expanding Mexican fleet mostly out of Ensenada, Baja California. The bluefin fishery extends along the coast of North America from Cabo San Lucas, Baja California, to Point Conception, Calif., and occasionally farther north (Table 1). The bluefin catch is composed mainly of 1-, 2-, and 3-yr-old fish, which appear to migrate to the eastern North Pacific from the western Pacific near Japan (Schultze and Collins 1977); however, older and much larger bluefin are reported and occasionally caught in the eastern North Pacific.

This paper reviews and analyzes the bluefin tuna fishery in the eastern North Pacific, using data collected by the California Department of Fish and Game (CFG) in cooperation with the Inter-American Tropical Tuna Commission (IATTC), and the National Marine Fisheries Service (NMFS) of the U.S. Department of Commerce.

CATCH AND EFFORT ANALYSIS

Although annual bluefin catches have fluctuated considerably in the eastern North Pacific (Table 2), two major periods are identified in the catch by a plot of a 10-yr running average (Fig. 1). During the first period, about 1921-50, total landings averaged 5,066 t (metric tons)/yr and were declining toward the end of the period. During this time, bluefin were landed almost ex-

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TABLE 1.—Total number of months in which bluefin tuna catch exceeded 50 t within a 1° area of latitude and longitude for the years 1957-69 and 1974. Each latitude and longitude indicates the southeast corner of the 1° area of consideration. Asterisks indicate the coastline.

Latitude	Longitude											
	125	120	119	118	117	116	115	114	113	112	111	110
40	1*											
34		1	*									
33		1	3	7	2*							
32			7	12	14*							
31				3	11	5*						
30					8	11	*					
29					3	6	2	*				
28			7			3	7	*				
27						1	8	4*				
26							2	10	7	*		
25								1	12	6*		
24									6	8	1*	
23										4	3	1*

TABLE 2.—Total landings of bluefin tuna by commercial (in metric tons (t)) and sport fisheries (no. fish) in the eastern North Pacific Ocean, 1918-81. Asterisks indicate no data available.

Year	Landings		Year	Landings	
	Commercial (t)	Sport (no. fish)		Commercial (t)	Sport (no. fish)
1918	2,722		1950	1,242	27
1919	6,800		1951	1,752	7,142
1920	4,776		1952	2,076	145
1921	894		1953	4,433	4,276
1922	1,275		1954	9,537	966
1923	1,460		1955	6,173	8,179
1924	1,470		1956	5,727	34,187
1925	1,725		1957	9,215	6,428
1926	2,960		1958	13,934	884
1927	2,222		1959	6,914	1,330
1928	6,215		1960	5,422	97
1929	3,414		1961	9,603	2,268
1930	9,943		1962	14,651	2,453
1931	1,603		1963	14,189	737
1932	486		1964	10,642	693
1933	254		1965	7,556	92
1934	8,327		1966	16,846	1,998
1935	11,418		1967	6,601	3,166
1936	8,584	2,920	1968	6,063	1,231
1937	5,758	4,020	1969	7,172	1,470
1938	8,041	11,927	1970	4,024	1,833
1939	5,369	9,909	1971	8,415	749
1940	9,058	6,878	1972	13,390	1,470
1941	4,318	*	1973	10,576	5,347
1942	5,826	*	1974	5,748	5,765
1943	4,617	*	1975	9,578	3,348
1944	9,228	*	1976	10,561	2,040
1945	9,341	*	1977	5,151	1,838
1946	9,993	528	1978	5,903	479
1947	9,452	2,194	1979	6,743	1,087
1948	2,961	104	1980	3,128	729
1949	1,991	1,841	1981	1,016	

clusively by the San Pedro wetfish fleet, which seasonally targets fishing effort on sardines, anchovies, mackerel, bonito, bluefin tuna, and other fishes, depending on fish availability, market price, and market demand (cannery orders).

During the second period, about 1950-present, annual landings increased to 16,846 t in 1966, then declined to 1,016 t in 1981, averaging 9,076 t for the period. At the beginning of this period, many of the high-seas boats that had converted to purse seining began catching large numbers of bluefin off Baja California, although they targeted their fishing on yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*.

Two sources of data were used in summarizing total catch by area. The first, landings reported by CFG, separates pounds landed in California for 1918-79 into those caught in California waters and those caught south of California waters. These data reveal an overall decreasing trend in bluefin catch north of the international border; and, until about 1963, there was an overall increasing trend in total catches south of the international border (Fig. 2).

The second source of catch data also includes effort information and was compiled into a data base for summary and analysis. These data, representing about 87% of the catch during the periods 1954-69 and 1971-74, came from summaries of skippers' logs, from interviews with skippers and engineers, from CFG landing receipts, and from IATTC summaries of the high-seas fleet. Catch and effort in the data base are recorded by 1° areas of latitude and longitude. For this study, one boat-day or part of a boat-day of effort is assigned to a seiner for each day or partial day of purse seining or searching for tuna in the bluefin fishing range (north of lat. 22°N) during months in which bluefin were caught. Catch data, summarized by areas north and south of lat. 32°N (the parallel nearest the international border), show trends similar to the reported California landings for the same years (Fig. 3).

For comparison with the CFG reported California landings and for future consideration of the effects of Mexican regulations concerning

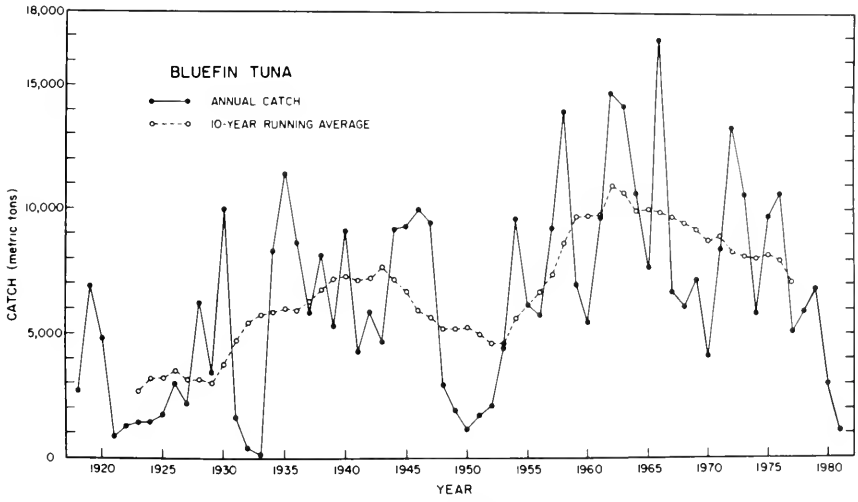

FIGURE 1.—Annual catches of northern bluefin tuna in the eastern North Pacific Ocean for the years 1918-81.

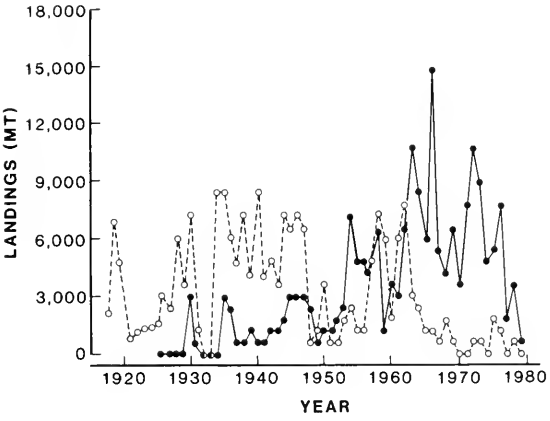

FIGURE 2.—Annual California landings (metric tons) of northern bluefin tuna caught north and south of the United States-Mexico international border, 1918-79. South is represented by solid circles and lines, north by open circles and broken lines.

the 200-mi exclusive economic zone, much of the data in this paper are separated into areas north and south of lat. 32°N. A better division from a biological standpoint would be north and south of lat. 29°N (Fig. 4).

The increase in California landings of bluefin caught south of the border during the 1957-66 period can be attributed to increased fishing effort, but the decline in catch north of the border cannot be explained by declining effort, since effort remained comparatively level throughout the period (Fig. 5). Because bluefin are valuable ($1,180/short ton in 1981) and because fishing effort north of the 32d parallel remained fairly constant, the decline in northern catches is attributed to a decrease in abundance in that area. During this period, increased catches south of the border appear to have offset the decline in catches to the north and to indicate the fish were intercepted before migrating northward. If this is true, the recent catch decline south of the border indicates declining bluefin abundance in the eastern North Pacific.

Catch and effort data summarized by latitude show a bimodal distribution centering just north of the 25th and 32d parallels (Table 3). The catches are concentrated in the period June-September, with the largest catches shifting northward during the fishing season (Fig. 4). Early in the

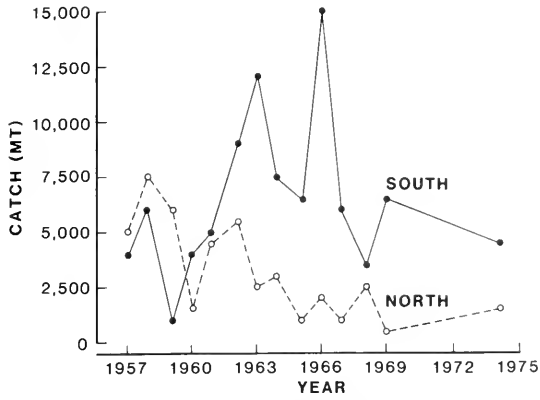

FIGURE 3.—Logged annual catches (metric tons) of bluefin tuna north and south of lat. 32°N for 1957-69 and 1974.

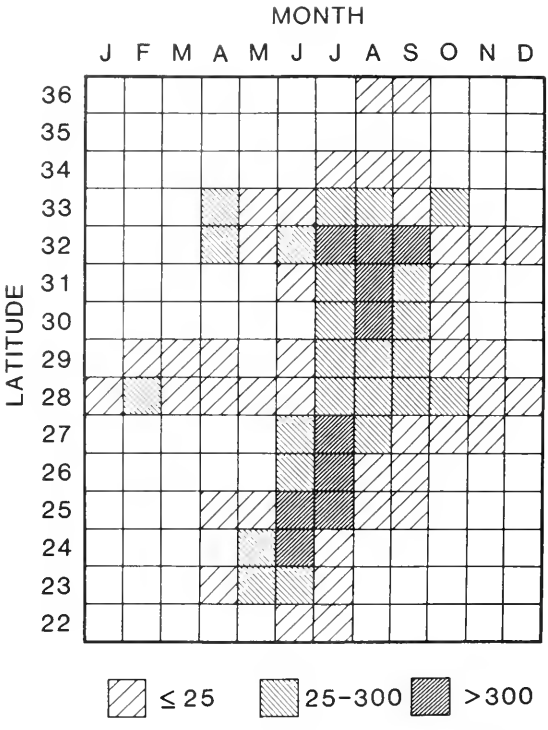

FIGURE 4.—Mean monthly catches of bluefin tuna ($\frac{\Sigma c}{13}$) for the period 1957-69 in metric tons per latitude. Totals are for areas between a given parallel and the next higher parallel.

TABLE 3.—Mean catch of bluefin tuna (metric tons (t)) and mean effort (boat-days) per latitude for the years 1957-69 and 1974.

Latitude	Mean catch (t)	Mean effort (boat-days)
36	3.29	1.16
35	0.00	0.29
34	23.06	6.67
33	452.60	75.27
32	2,160.34	460.39
31	1,048.67	214.39
30	622.63	155.11
29	544.82	135.96
28	561.82	170.37
27	615.46	253.89
26	734.33	359.86
25	981.61	629.56
24	543.07	348.16
23	234.57	353.10
22	0.44	122.02

season there are catches both in northern and southern parts of the bluefin range, whereas there are relatively few catches late in the season in the southern part of the range, thus indicating northward movement. This shift is also apparent in the number of occurrences of recorded bluefin

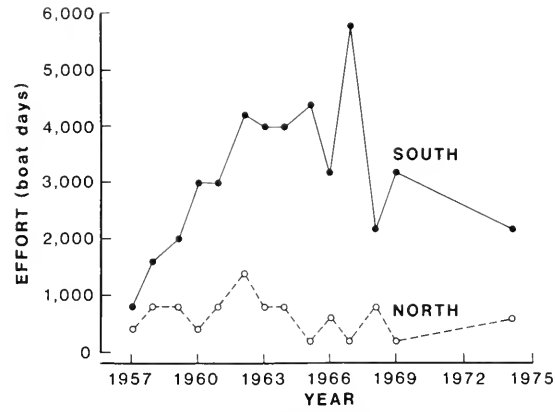

FIGURE 5.—Logged annual effort (boat-days/year) for bluefin tuna north and south of lat. 32°N for 1957-69 and 1974.

catch per month and latitude during the 1957-69 period (Table 4). The northward shift in location of the largest catches does not reflect a shift in fishing effort, since effort remains high in the south throughout the season (Fig. 6). Apparently, bluefin move northward or there is a shift in bluefin vulnerability towards the north during the fishing season.

Catch and effort data for 1957-69 summarized by vessel size indicate that seiners of 101-300 ton capacities accounted for more than 70% of bluefin landings and that smaller vessels tended to be phased out of the fishery and replaced by larger ones (Table 5).

CATCH-PER-UNIT-EFFORT ANALYSIS

Catch per unit effort (CPUE) is calculated for each year as total catch divided by total effort (Table 6). The relationship between the CFG data and the IATTC data (Bayliff and Calkins 1979) is expressed as a ratio which includes the origin. The ratio estimator $\Sigma y/\Sigma x$, obtained from years for which both CFG and IATTC measures of CPUE are available (1966-74), yielded a value of 1.01, by which the CFG values (1954-65) were multiplied to obtain IATTC equivalents. These equivalent CPUE values were then plotted, and a regression line fit to them reveals a decline in CPUE with time (Fig. 7). This observed decline is probably conservative because fishing effort, which was not standardized, has most likely become more effective with time (Pella and Psaropulos 1975).

CPUE values were highest in the northern

TABLE 4.—Total occurrences of recorded bluefin tuna catch per latitude and month during 1957-69 and 1974. Totals are for the areas between a given parallel and the next higher parallel.

Latitude	Month												Total
	J	F	M	A	M	J	J	A	S	O	N	D	
36								1	1				2
35													0
34							2	2	1				5
33				2	1	5	9	9	4	2			32
32	1			3	2	6	11	13	12	4	2	1	55
31						2	9	11	8	1			31
30							8	10	6	2			26
29		3	1	1		3	9	6	1	2			26
28	7	5	4	5	7	9	11	7	4	1	3	2	65
27						3	9	7	2	1	1		23
26						9	10	1	1				21
25				1	3	11	11	3	1				30
24					3	10	7						20
23				1	3	6	4						14
22						1	1						2
Total	8	8	5	13	19	65	101	70	41	13	6	3	

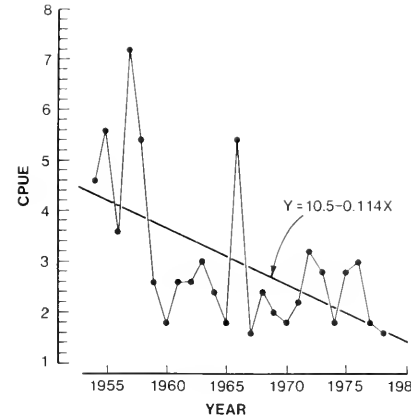

FIGURE 7.—Annual catch per unit effort (metric tons/boat-day) of bluefin tuna plotted by year (1954-78) with a regression line fitted to the curve.

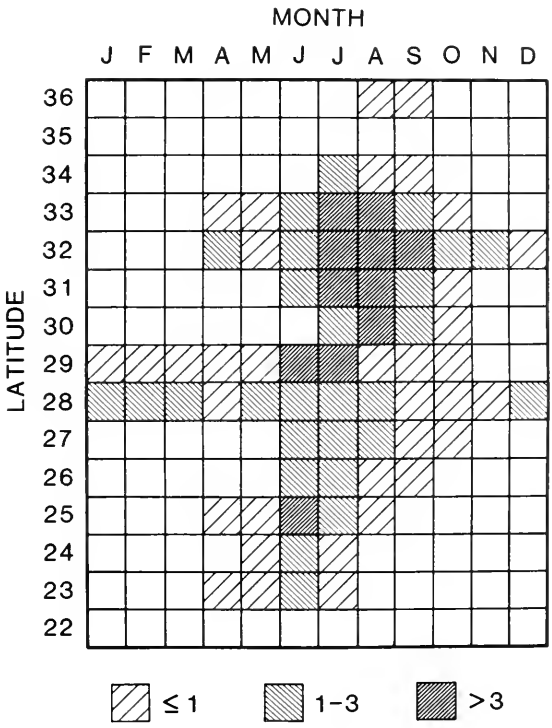

FIGURE 6.—Mean monthly effort for bluefin tuna ($\frac{\Sigma f}{13}$) for the period 1957-69 in boat-days per latitude. Totals are for areas between a given parallel and the next higher parallel.

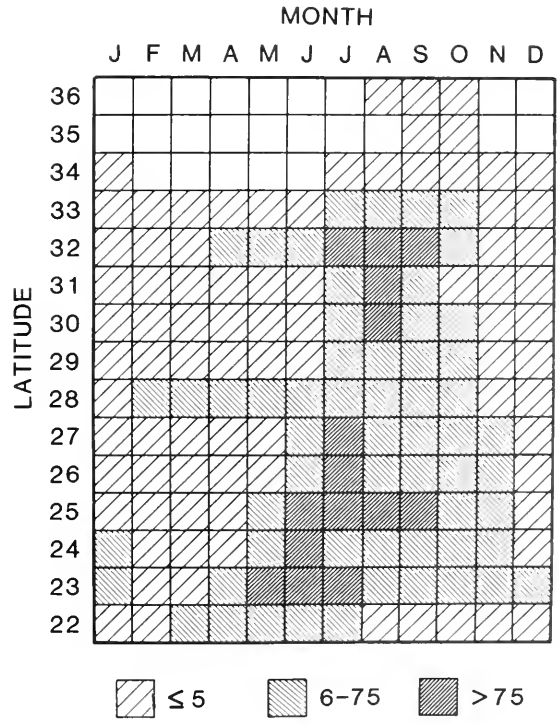

FIGURE 8.—Mean monthly catch per unit effort of bluefin tuna $\left(\frac{\Sigma \frac{c}{f}}{13}\right)$ per latitude (metric tons/boat-day) for the period 1957-69. Totals are for areas between a given parallel and the next higher parallel.

part of the bluefin range (Figs. 8-10), and is attributed to differences in searching and fishing methods between the wetfish and the high-seas fleets.

Because effort data are not available for the 1979-81 period, the rapid decline in total catches during those years cannot be explained by direct

TABLE 5.—Yearly catch (metric tons) of bluefin tuna and effort (in parentheses) by vessel size class for 1957-69 and 1974, from logbook data. Hold capacity in short tons: 0-50 = Class 1; 51-100 = Class 2; 101-200 = Class 3; 201-300 = Class 4; 301-400 = Class 5; over 400 = Class 6.

	Vessel class						
Year	1	2	3	4	5	6	Total
1957	205	2,537	4,614	35	—	—	7,391
	(20)	(328)	(679)	(24)	(—)	(—)	(1,051)
1958	276	1,840	6,767	646	—	—	9,529
	(37)	(433)	(1,266)	(42)	(—)	(—)	(1,778)
1959	164	1,912	2,468	522	330	—	5,396
	(29)	(408)	(1,352)	(267)	(117)	(—)	(2,173)
1960	5	287	2,318	1,067	1,081	69	4,827
	(33)	(194)	(1,495)	(730)	(341)	(39)	(2,832)
1961	21	526	5,325	2,331	1,015	4	9,222
	(4)	(171)	(2,222)	(925)	(352)	(12)	(3,686)
1962	14	959	7,061	2,840	1,498	—	12,372
	(8)	(185)	(2,447)	(1,515)	(603)	(32)	(4,790)
1963	—	544	5,483	4,228	3,055	87	13,397
	(—)	(85)	(1,667)	(1,729)	(1,051)	(56)	(4,588)
1964	18	523	3,641	2,937	1,565	—	8,684
	(4)	(77)	(1,367)	(1,577)	(749)	(19)	(3,793)
1965	60	294	2,538	2,242	1,312	36	6,482
	(12)	(51)	(1,641)	(1,338)	(753)	(13)	(3,808)
1966	21	429	5,576	5,400	3,107	561	15,094
	(16)	(112)	(1,479)	(1,299)	(580)	(38)	(3,524)
1967	60	289	1,318	2,530	1,804	51	6,052
	(10)	(33)	(1,103)	(1,936)	(1,435)	(270)	(4,787)
1968	—	399	2,038	1,481	1,300	293	5,511
	(—)	(69)	(1,162)	(895)	(493)	(71)	(2,690)
1969	32	175	3,370	2,338	605	448	6,968
	(7)	(40)	(1,200)	(1,280)	(479)	(232)	(3,238)
1974	60	257	1,712	905	719	677	4,330
	(3)	(81)	(672)	(450)	(500)	(251)	(1,957)
Total	936	10,971	54,229	29,502	17,391	2,226	115,255
	(183)	(2,267)	(19,752)	(14,007)	(7,453)	(1,033)	(44,695)
Total	1%	10%	47%	26%	15%	2%	100%
	(0.4%)	(5%)	(44%)	(31%)	(17%)	(2%)	(100%)

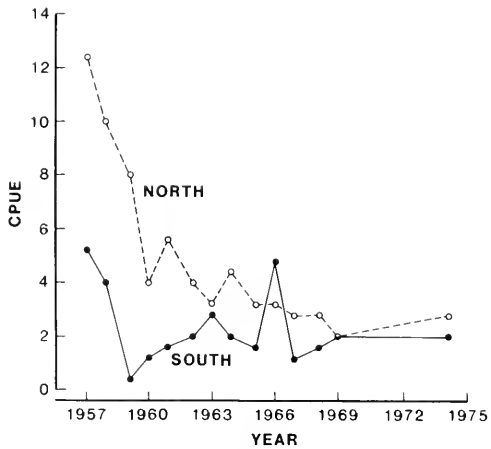

FIGURE 9.—Annual catch per unit effort of bluefin tuna (metric tons/boat-day) for 1957-69 and 1974 north and south of lat. 32°N.

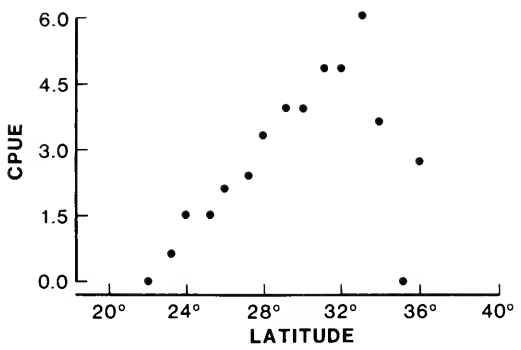

FIGURE 10.—Bluefin tuna catch per unit effort (metric tons/boat-day) by latitude for 1957-69 and 1974. Latitude area is that lying between a given latitude and the next higher latitude.

CPUE evidence. However, if it is assumed that effort remained at about the same levels, CPUE would have declined by an even greater rate than that predicted by the trend in Figure 7. This indicates that bluefin abundance in the eastern North Pacific has declined severely.

TABLE 6.—Bluefin tuna CPUE values from this study (CFG) for the years 1954-74 and from IATTC (Bayliff and Calkins 1979) for the years 1954-78. CFG values converted to IATTC equivalent values are in parentheses.

	CPUE values			CPUE values	
Year	CFG	IATTC	Year	CFG	IATTC
1954	4.49	(4.55)	1967	1.26	1.63
1955	5.44	(5.52)	1968	2.05	2.35
1956	3.59	(3.64)	1969	2.15	1.96
1957	7.03	(7.13)	1970	—	1.71
1958	5.36	(5.44)	1971	2.31	2.11
1959	2.48	(2.52)	1972	3.61	3.23
1960	1.70	(1.72)	1973	3.15	2.89
1961	2.50	(2.54)	1974	2.21	1.75
1962	2.58	(2.62)	1975		2.73
1963	2.92	(2.96)	1976		2.98
1964	2.29	(2.32)	1977		1.86
1965	1.71	(1.73)	1978		1.62
1966	4.28	5.40			

LENGTH-FREQUENCY ANALYSIS

Length-frequency data summaries (Figs. 11-14) were obtained from two CFG data sets of fork-length samples taken as frozen bluefin were unloaded at Terminal Island, Calif., canneries. Set 1 (1952-65) represents random samples of 50 fish/seiner; set 2 (1963-71 and 1974) represents random samples of 20 fish for every 200 short tons landed from each 1° area of latitude and longitude. Set 2 samples were taken for an age determination study. Although a smaller number of bluefin were sampled, they appear to represent the same population as the first data set,

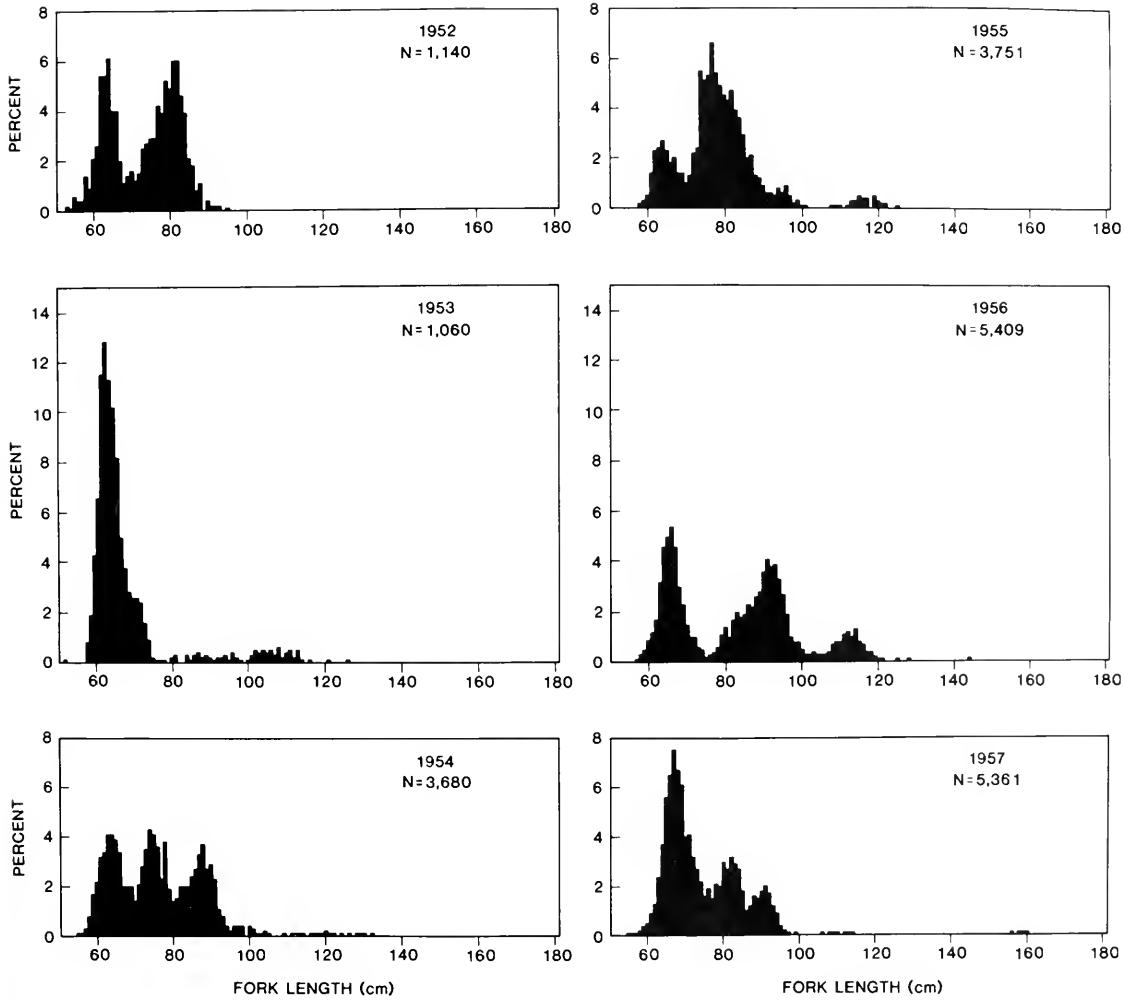

FIGURE 11.—Bluefin tuna percent length frequencies, 1952-57.

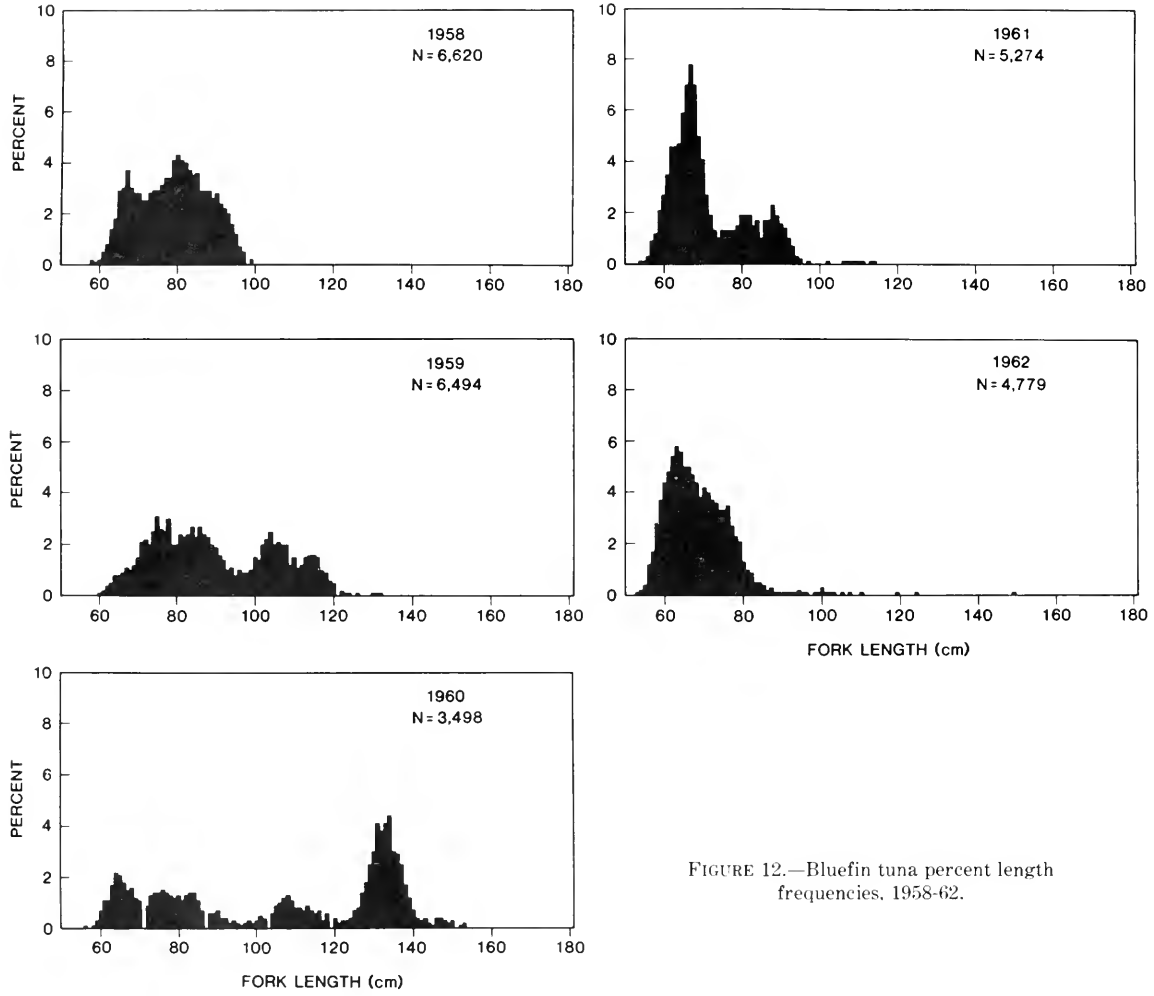

FIGURE 12.—Bluefin tuna percent length frequencies, 1958-62.

TABLE 7.—Mean length frequencies of bluefin tuna, north and south of lat. 32°N, 1952-65.

Year	Mean length		
	South	North	Combined
1952	73.7	70.2	73.2
1953	67.1	63.8	68.1
1954	79.7	66.3	76.3
1955	83.1	72.3	78.8
1956	90.4	65.8	83.1
1957	83.7	71.5	73.0
1958	81.3	77.7	78.6
1959	85.8	90.6	90.3
1960	112.1	96.8	105.6
1961	72.3	71.2	71.7
1962	73.5	64.0	68.8
1963	80.3	68.9	76.4
1964	70.4	62.8	67.9
1965	79.8	65.8	76.0

when overlapping years (1963-65) and composite samples for both data sets are compared (Fig. 15).

Analysis of fish lengths from the first data set shows a decrease in mean length with increasing latitude. These data (1952-65) were also summarized by year for areas north and south of the 32d parallel (Table 7) for a two-way analysis of variance. The analysis shows significant differences ($P<0.01$) among years and between areas. These results show that bluefin caught in the north are smaller than those to the south (Fig. 16) and that mean lengths vary considerably, as much as 39.8 cm/yr.

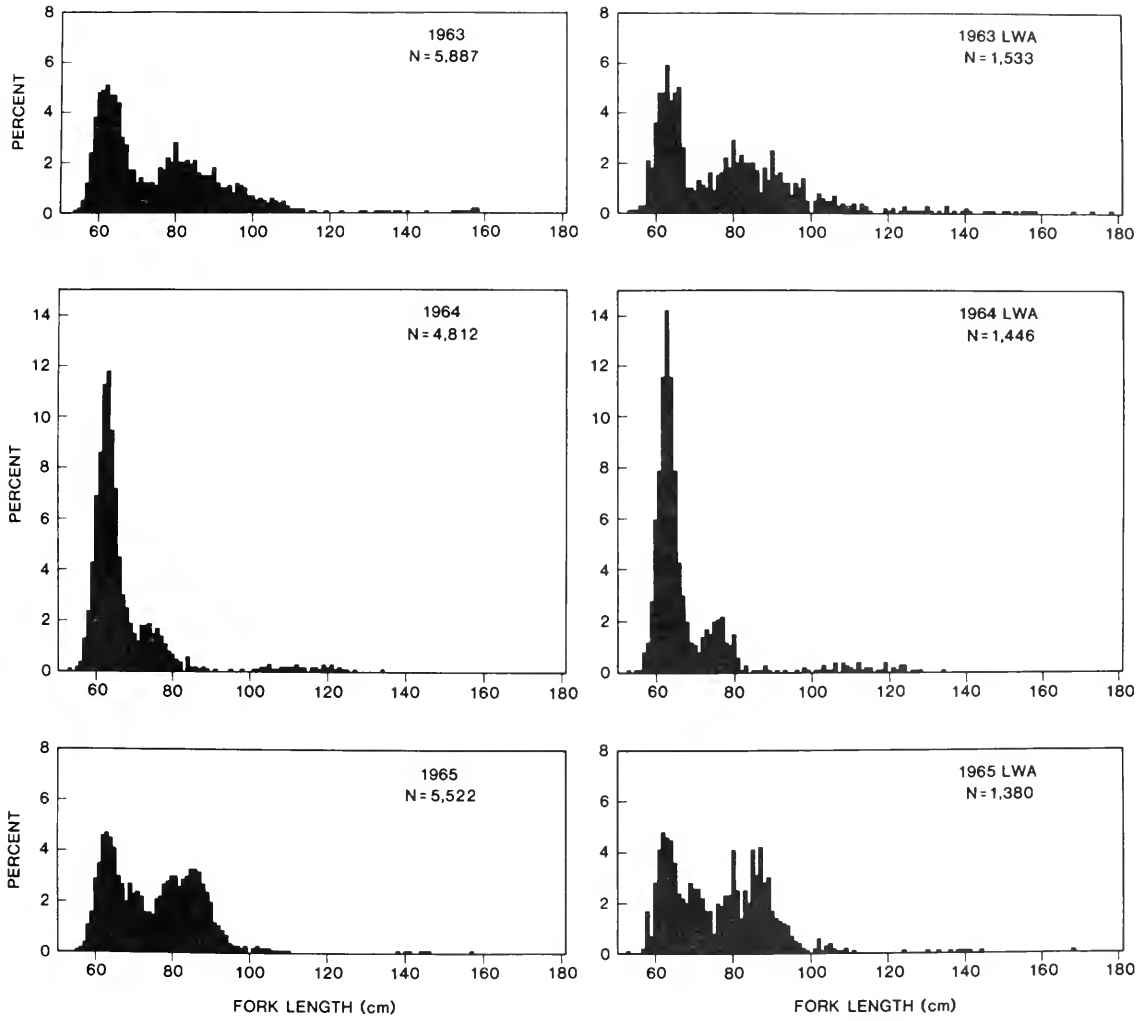

FIGURE 13.—Bluefin tuna percent length frequencies, 1963-65. Graphs to the left are based on length-frequency samples only, whereas those to the right are based on length-weight-age frequency samples.

TAGGING DATA ANALYSIS

From 1953 to 1958, 186 bluefin were tagged and released by CFG and IATTC in the eastern North Pacific incidental to tagging other species. From 1962 to 1968 a tagging cooperative of CFG, U.S. Bureau of Commercial Fisheries (NMFS), and the Mission Bay Research Foundation of San Diego tagged and released 2,836 bluefin. Of these, 565 (20%) were recaptured in the eastern North Pacific, including 7 by sport fishing and 9 in the western Pacific (Clemens and Flittner 1969). Bluefin for tagging were caught by purse seine and tagged with spaghetti-loop tags prior to 1960 and with spaghetti-dart tags since then.

Bluefin are caught within about 200 mi of the coast, thus spatial analysis of tag returns is expressed only by latitude. Of the 565 tagged bluefin caught in the eastern North Pacific, recovery latitude information is available for 540 returns. Data from tagged fish recovered during the season in which they were released (62%) show a general movement northward (Table 8); however, many were caught near the release point and to the south (Table 9). Tagged fish recaptured during the second and third fishing seasons after tagging were well dispersed throughout the fish-

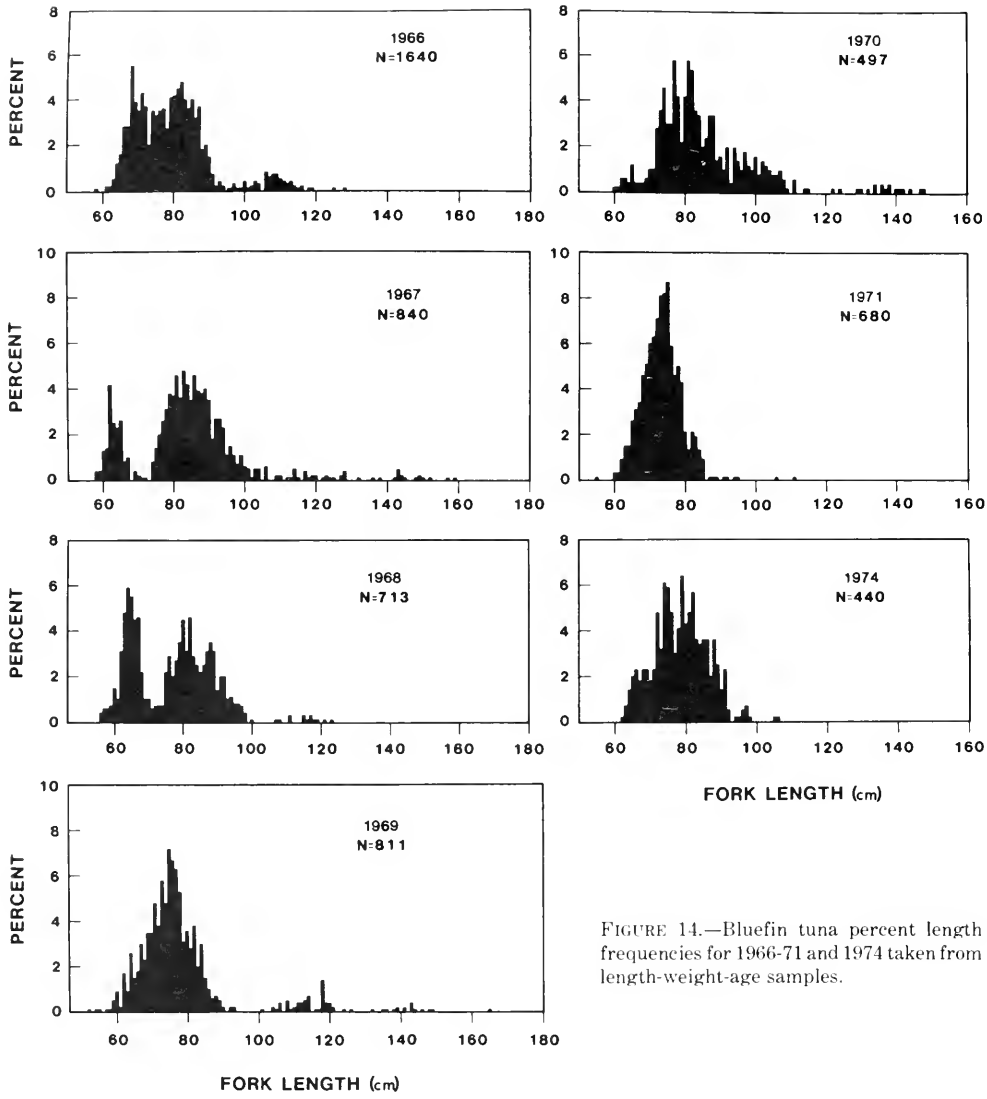

FIGURE 14.—Bluefin tuna percent length frequencies for 1966-71 and 1974 taken from length-weight-age samples.

TABLE 8.—Bluefin tuna tags returned during tagging season (1958-68) summarized by latitude of release and of return. Totals are for areas between a given parallel and the next higher parallel.

Release latitude	Return latitude										
	33	32	31	30	29	28	27	26	25	24	Total
33	13	28									41
32		85	28	1		1					115
31		20	16	2		2					40
30		16	19	7	4	2					48
29		1		2	1	3					7
28		2	1		1	5	1				10
27		2	8	5		1	1				17
26											
25											
24				1	1	2	7	23	2	22	58
Total	13	154	72	18	7	16	9	23	2	22	336

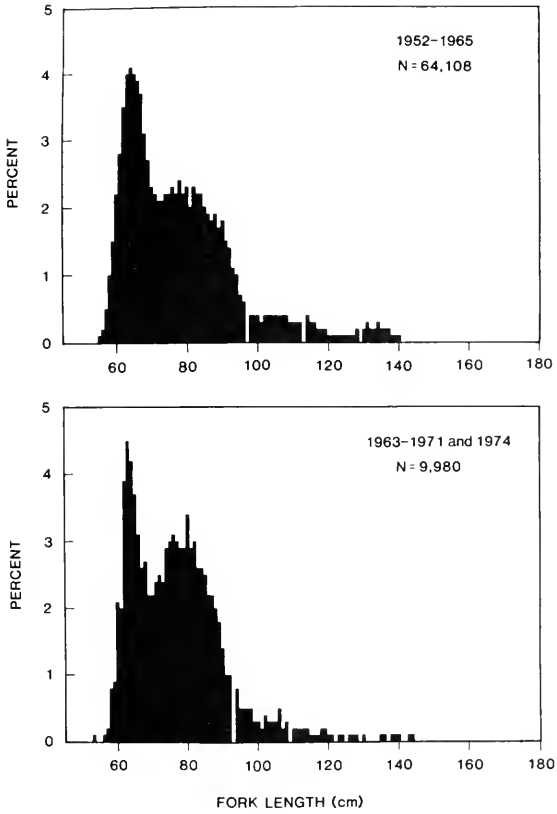

FIGURE 15.—Composite bluefin tuna percent length frequencies. Upper graph summarizes length-frequency samples for 1952-65, and lower graph summarizes length-weight-age samples for 1963-71 and 1974.

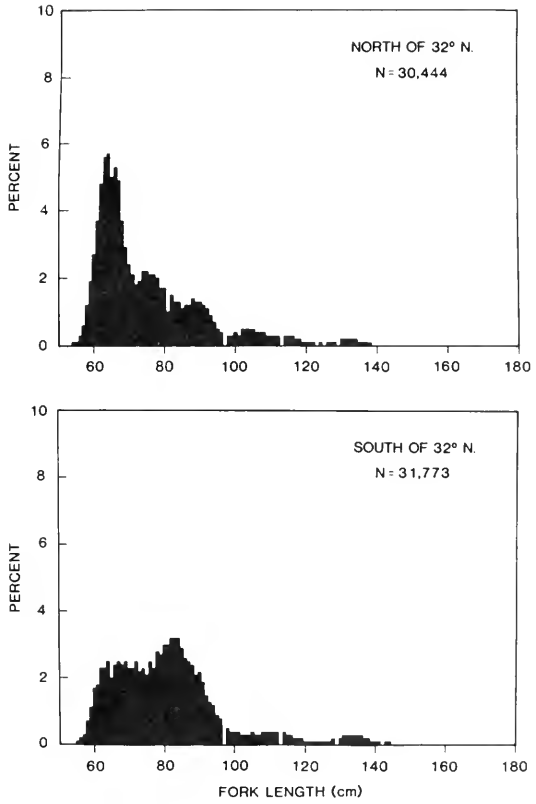

FIGURE 16.—Bluefin tuna percent length-frequency composites for 1952-65, north (top) and south (bottom) of lat. 32°N.

ing grounds and fishing season, indicating good mixing with the untagged population.

Gulland (1963) described a method of estimating fishing mortality from tagging experiments; this method was modified and applied to the bluefin data. It was assumed that the number of tags returned per unit of effort is proportional to the CPUE, and no provision was made for immigration or emigration. For any period following tagging, an estimate of catchability (q) would be the number of tags returned per unit of effort divided by the initial number released. When these

TABLE 9.—Total number of returned bluefin tags summarized by latitude of release and of return. Totals are for areas between a given parallel and the next higher parallel.

Release latitude	Return latitude											Total
	33	32	31	30	29	28	27	26	25	24	23	
33	13	28	1	4	3	4	3		9	3		68
32		87	30	5	9	5	7	6	20	7	1	177
31		21	17	3	2	4	1	2	8	1	1	60
30		17	27	14	10	3	2	6	8	3		90
29		3	2	9	2	8			4			28
28		5	2		7	7	8		5	2		36
27		2	8	5		4	1		1			21
26												
25												
24				1	1	2	7	25	2	22		60
Total	13	163	87	41	34	37	29	39	57	38	2	540

estimates are plotted against time, the intercept at time zero is an estimate of q for bluefin in the eastern North Pacific.

As tagged bluefin were not fully dispersed during the season of tagging, monthly estimates of q were calculated as the monthly mean, per 1° area of latitude and longitude, for 1° areas from which tagged fish were caught. For the second and third seasons, when tagged fish appeared to be fully dispersed, monthly estimates were calculated for the entire bluefin range; then, the natural logarithms of these values and those for the first season were plotted (Fig. 17). Effort and therefore $\hat{q}$ are expressed in boat-days. The regression line fitting these points ($Y = -8.7363 - 0.1725\,X$, $R^2 \approx 68\%$) was weighted by the number of tagged fish released each year, since the number of tagged fish varied between 35 and 960/yr.

The best estimate of q from the tag-recapture data is the antilogarithm of the regression line intercept, 1.66×10^{-4}/boat-day with a 95% confidence interval of 0.99×10^{-4} to 2.63×10^{-4}/boat-day corrected for geometric mean bias (Beauchamp and Olson 1973). The slope of the regression (-0.17, $S^2 = 0.02$) is an estimate of the monthly instantaneous mortality coefficient (Z), and was expanded to estimate the yearly instantaneous mortality ($Z = 2.07$, $S^2 = 0.24$) including immigration and emigration. This estimate compares favorably with Bayliff and Calkins' (1979) and Bayliff's (1980) estimates ($\overline{Z} = 2.08$, $S^2 = 0.8$) for 1962-66. They call these estimates "rates of attrition," since immigration and emigration are included.

The ratio of fishing mortality to instantaneous total mortality is an estimate of the exploitation ratio (Ricker 1975) and was calculated as a mean for the period 1962-70 because $\hat{q}$ was also calculated for that period. The mean annual fishing effort in that period was 4,215 boat days which, multiplied by $\hat{q}$, estimates a fishing mortality of 0.7/yr. Dividing this value by estimated Z (2.07/yr) yields an exploitation ratio of 0.34, and then multiplying by the annual mortality or "attrition" (0.87) yields a 30% exploitation rate.

DISCUSSION

The review and analysis of data concerning the bluefin tuna fishery in the eastern North Pacific show large fluctuations in the catch to be a major part of two important phases. The decline in catch near the end of the first phase (1921-50) is offset by the development of a "high seas" purse seine fleet and the resultant increased catch of bluefin off Baja California. The current decline (1963-present) is probably due to a decline in the abundance of bluefin as indicated by CPUE evidence. The effect on the resource of Mexico's 200-mi regulations was not assessed at this time; however, the apparent decline in catch and CPUE cannot be attributed to such regulation since it has been enforced only recently.

The declines in catch and CPUE in the eastern North Pacific are significant and are reflected by an even greater decline in catch and nominal CPUE in the western Pacific (Figs. 18, 19).

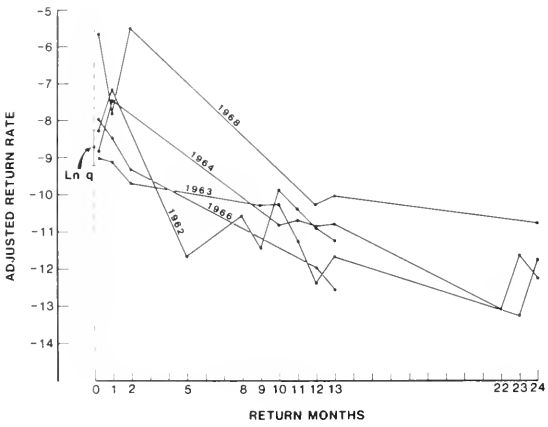

FIGURE 17.—Natural logarithms of adjusted return rates for tagged bluefin tuna plotted against number of months between tagging and recapture, for the years 1962-64, 1966, and 1968. The predicted catchability coefficient ($\hat{q}$) from straight-line regression and the 95% confidence interval around ($\hat{q}$) are shown at the zero-month intercept.

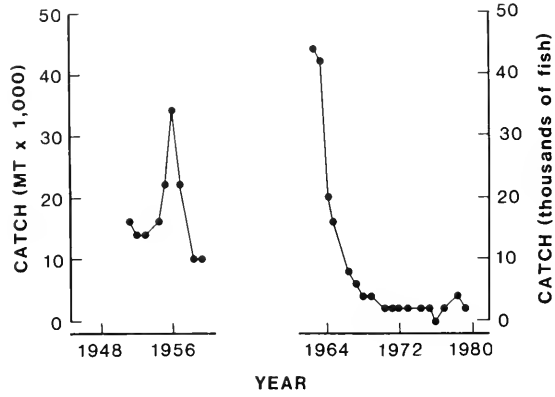

FIGURE 18.—Annual Japanese landings of northern Pacific bluefin tuna for the years 1951-59 (metric tons × 1,000) and 1962-79 (thousands of fish).

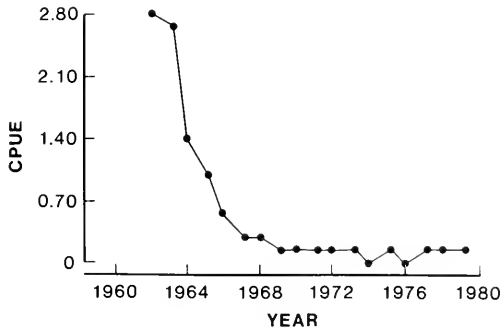

FIGURE 19.—Annual Japanese catch per unit effort (metric tons/boat-day) from longline catches of northern bluefin tuna for the years 1962-79.

Although those data (Anonymous 1981; Yamanaka and Staff 1963) represent only a portion of the fishing effort in the western Pacific, they indicate a need for more extensive and explicit data from that area. With improved data, mathematical models for estimating sustainable yields can be used to describe the status of the bluefin resource throughout the North Pacific Ocean.

Based on strong evidence of declining stock abundance, the bluefin tuna fisheries in the Pacific Ocean should receive an extensive analytical review, and nations fishing bluefin, especially Japan, Mexico, and the United States, should consider needed actions. If management to conserve this valuable resource is to be taken, it should be soon, so that the resource can return to an optimal level of abundance.

ACKNOWLEDGMENTS

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INTERACTIONS BETWEEN FUR SEAL POPULATIONS AND FISHERIES IN THE BERING SEA

GORDON L. SWARTZMAN AND ROBERT T. HAAR[1]

ABSTRACT

In this paper we consider fur seal-fisheries interaction in the Bering Sea by asking whether the slower than originally predicted recovery of the fur seal stock from female fur seal harvest during 1956-68 might be a result of a reduction in carrying capacity because of the large fishery harvest of walleye pollock and Pacific herring—fish which are important fur seal prey.

The changes we found occurring in the fur seal population did not support the hypothesis that fur seal carrying capacity was reduced by the fisheries. In fact the population parameters changed little, or changed in a direction opposite to that proposed by the hypothesis.

Study of the fur seal diet data indicated that walleye pollock comprised a larger part of the fur seal diet in the 1970's, after the establishment of the fishery, than earlier, although average pollock size appeared to drop significantly. This trend may have been induced by an increased harvest of older fish. Since walleye pollock are cannibalistic, the removal of the older fish by the fishery could result in lower mortality among the younger pollock stocks, the outcome being an increase in the pollock resource available to both the fishery and the fur seal.

In this paper we assess and clarify possible relationships between fur seals and fisheries in the Bering Sea. The event most prominent in focusing concern on fur seal-fisheries interactions was the failure of the Pribilof Islands' fur seal herd to recover as predicted from large female harvests during 1956-68. While the present herd appears to have stabilized, it has stabilized at a population 30% below the maximum sustained productivity estimates made in 1955 (York and Hartley 1981). A number of possible explanations for this have been presented, including reduced fur seal carrying capacity.

In this paper we 1) briefly summarize and highlight the available fur seal and fish data, including studies of cases of other known marine mammal-fish interactions, 2) consider the evidence about fur seal population dynamics and seal-fish interactions, and 3) suggest analyses of existing data and further field sampling needed to clarify the effect of the Bering Sea fishery on fur seal populations.

AVAILABLE DATA

The relevant data may be divided into fur seal data, Bering Sea fish stock and fishery data, and anecdotal marine mammal-fish interaction data.

The fur seal data consist of 1) annual fur seal collections at sea during 1958-74 in the eastern North Pacific Ocean and the eastern Bering Sea conducted jointly by the United States and Canada under terms of the Fur Seal Interim Convention (Kajimura et al. 1979,[2] 1980[3]); 2) harvests from 1950 to 1978 on the Pribilof Islands of subadult males (Lander 1981) and counts of harem and nonharem bulls from 1905 to 1978 on other island rookeries; 3) estimates of pup production on the Pribilof Islands from 1912 to 1924 and from 1951 to 1979 (Johnson 1975; Lander 1981), and counts of dead pups from 1950 to 1979 (Lander 1981); and 4) studies of fur seal rookery behavior (Bartholomew and Hoel 1953; Gentry[4]), food habits (Spalding 1964; May 1937; Wilke and

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[2]Kajimura, H., R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg. 1979. Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958-74. Report submitted to the 22d Annual Meeting of the Standing Scientific Committee, North Pacific Fur Seal Commission, 247 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[3]Kajimura, H., R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg. 1980. Further analysis of pelagic fur seal data collected by the United States and Canada during 1958-74. Part 1. Submitted to the 23d Annual Meeting of the Standing Scientific Committee, North Pacific Fur Seal Commission, 94 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[4]R. Gentry, Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115, pers. commun. May 1980.

Kenyon 1957; Fiscus 1979; Kajimura et al. footnotes 2, 3), and fertility (Abegglen and Roppel 1959).

Bering Sea groundfish and pelagic fisheries data, which give estimates of relative abundance, life history parameters, and migratory patterns of important fish stocks, are contained in a number of Northwest and Alaska Fisheries Center (NWAFC) reports (Pereyra et al. 1976[5]; Favorite et al. 1979[6]; Pruter 1973; Bakkala et al. 1979[7]). These data cover the period of development of the large foreign groundfish fishery in the eastern Bering Sea (1954-78) and include catch, catch per unit effort (CPUE), mortality, seasonal migration patterns, and diets for a number of commercially important fish, including walleye pollock and Pacific herring, important food sources for the fur seal in the eastern Bering Sea.

Fur Seal Data Synopsis

Seal Data Collected at Sea

Fur seal migration patterns were deduced from fur seals sampled at sea from 1958 to 1974. Adult males remain year-round in the Bering Sea and Gulf of Alaska, while females migrate south in winter, with smaller (younger) females tending to migrate the farthest south. Many subadult males also migrate south, but not nearly so far as the females. Females begin returning to the rookeries of the Pribilof Islands in June, and the rookeries are almost completely established by the end of July (Kajimura et al. footnotes 2, 3).

Pelagic data were also used to construct a fur seal life table (Lander 1981) which, along with a pup production estimate, gave an overall fur seal biomass estimate for the Pribilof Islands stock of 29,000 t or 1.25 million animals. Seasonal patterns of growth were also computed from the pelagic survey data (Lander 1981). Stomach content data were pooled over years by region and by month, and were presented as the frequency of occurrence (proportion of stomachs containing a particular food item), the volume and the percent of total food volume comprised by each prey type, and the number of specimens of each prey type and their percent of the total diet. Diet composition of fur seal stomachs by percent volume (which we consider to be the most reliable measure of prey abundance in predator stomachs) in the eastern Bering Sea is given in Table 1 (modified from Kajimura et al. footnote 3) pooled by month over all years of data collection.

TABLE 1.—Major species in fur seal diets in the eastern Bering Sea (percent volume), June-September. (Kajimura et al. footnote 3).

Species	June	July	August	September
Herring	—	0.2	13.2	0.2
Capelin	69.9	16.4	17.0	15.2
Pollock	4.1	50.9	26.1	38.3
Deepsea smelt	—	4.0	3.5	8.6
Atka mackerel	19.4	1.5	1.7	1.8
Squid	4.9	22.0	29.4	17.5

Fur seals are pelagic feeders and are highly opportunistic (Kajimura 1981[8]), feeding on a wide variety of species. Of their major prey only pollock and herring are target species for a fishery. Data on fur seal diets outside the eastern Bering Sea corroborate the pattern of fur seals feeding primarily on schooling fish. South of British Columbia, hake replaces pollock in seal stomachs and herring and sand lance are increasingly important, while capelin decreases in importance. Anchovy is the most important fur seal food off California. Since fur seals and fisheries both tend to exploit schooling species, a possible competitive relationship may exist between fur seals and fisheries. Most fur seal feeding in the Bering Sea is done by lactating females during the summer pupping period, so the importance of food during this period cannot be overemphasized. Since this is the period of rapid pup growth and is also the period of maximum growth for nonpregnant females and subadult males (Fig. 1), food limitation during this period could have drastic consequences to pup survival, especially after they leave the rookeries.

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[6]Favorite, F., W. J. Ingraham, Jr., K. D. Waldron, E. A. Best, V. G. Wespestad, L. H. Barton, G. B. Smith, R. G. Bakkala, R. R. Straty, and T. Laevastu. 1979. Fisheries oceanography — eastern Bering Sea Shelf. Proc. Rep. 79-20, 481 p. Northwest and Alaska Fisheries Center Seattle Laboratory, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[7]Bakkala, R., L. Low, and V. Wespestad. 1979. Condition of groundfish resources in the Bering Sea and Aleutian area. NMFS Northwest and Alaska Fisheries Center report submitted to the International North Pacific Fisheries Commission, 106 p.

[8]Kajimura, H. 1981. The opportunistic feeding of northern fur seals off California. Unpubl. manuscr., 46 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

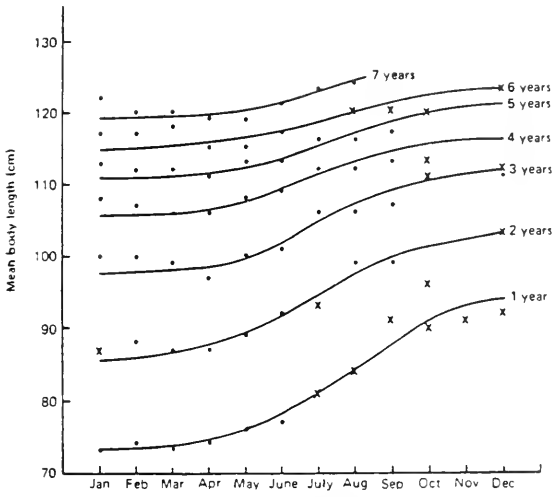

FIGURE 1.—Seasonal pattern of growth in mean length (cm) of nonpregnant female fur seals of age 1-7. Curves are drawn by inspection with the restriction of no downward curvature. An x designates <10 seals. From Lander (1981).

Sampling on the Fur Seal Rookeries

The herds on the Pribilof Islands (St. Paul and St. George Islands and Sea Lion Rock) are estimated to comprise 80% of the total world fur seal population. Every year from 1912 to 1924 and since 1950 some census of pup births has been made. Dead pup counts have also been made. Harvests of subadult males on the island hauling grounds have yielded information on weights, lengths, and age composition of these animals as well as limited food data from stomach samples. An estimate has also been made annually of numbers of harem bulls.

From 1956 to 1968 almost 300,000 females were harvested from St. Paul and St. George Islands, presumably to increase the sustained productivity of the herds. The herd subsequently failed to achieve a higher sustained productivity as was postulated from higher pregnancy and survival rates predicted from population projections (Abegglen et al. 1956[9]).

From 1912 to 1924, pup populations were estimated from direct counts. Fur seal populations increased steadily over this period at an 8% annual rate, as they recovered from heavy losses due to pelagic sealing in the late 19th and early 20th centuries. Direct counts were discontinued from 1924 to 1948, but an 8% annual population increase was assumed. However, estimates of pups in 1948 showed that the 8% increase had not continued. In 1947, tagging studies were set up to estimate pups and were continued until 1961. In 1960 an estimation procedure involving pup shearing and direct counts was initiated to replace the tagging method. Estimates of the number of pups born were computed by adding live pup estimates to dead pup counts.

The 1951-61 tagging studies are presently thought to have greatly overestimated actual pup abundance because of procedural difficulties and lost tags (Chapman 1973). The pup shearing procedure, although shown to be unbiased by comparing pup estimates with direct counts on small rookeries (Chapman and Johnson 1968), may be biased for large rookeries in such a way as to underestimate actual pup numbers (Fowler[10]).

Age-specific survival and weight at age were estimated from the weighing and aging of the preadult males harvested annually on the rookeries. Male harvest was discontinued on St. George Island in 1972 to study the effect of the male population density on seal population dynamics. Recent pup survival on St. George Island appeared lower than on St. Paul Island (Lander 1981), and this has been linked to the increased abundance of idle males on the rookeries (Fowler footnote 10).

Bering Sea Fish Data

Data on commercially important Bering Sea fish stocks by species have been compiled by the NWAFC. Catch data from Japanese, Russian, Korean, Polish, United States, and Canadian fishing operations have been included. The major species (in order of magnitude of catch) are walleye pollock, *Theragra chalcogramma*; yellowfin sole, *Limanda aspera*; Pacific herring, *Clupea harengus pallasi*; Pacific salmon, *Oncorhynchus* spp; Pacific cod, *Gadus macrocephalus*; sablefish, *Anoplopoma fimbria*; Pacific halibut, *Hippoglossus stenolepis*; other flatfish (rock sole, flathead sole, Alaska plaice, Greenland turbot,

[9]Abegglen, C. F., A. Y. Roppel, and F. Wilke. 1956. Alaska fur seal investigations, Pribilof Islands, Alaska. Manuscr. rep., 143 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[10]C. W. Fowler, Head, Fur seal investigations group, Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115, pers. commun. June 1980.

and arrowtooth flounder); and Pacific ocean perch, *Sebastes alutus*. Pacific herring and walleye pollock (hereafter referred to as herring and pollock) are the most important of these species in the diet of fur seals in the Bering Sea, and have been heavily fished (as have yellowfin sole, halibut, and Pacific ocean perch). The intensity of fishing on herring and pollock suggests the possibility of fur seal stock depletion due to decreased food abundance, although stock depletions can also have other causes.

Figure 2, adapted from Pereyra et al. (footnote 5) and Favorite et al. (footnote 6), gives the total catch for pollock and herring as well as an index of relative abundance (CPUE) based on research trawl surveys conducted by the International Pacific Halibut Commission, the National Marine Fisheries Service (NMFS), and the Japanese Fishery Agency.

Pollock stocks have been heavily fished since 1964, with peak yields coming in the early 1970's. A steady increase in CPUE between 1964 and 1968 may have been due in part to improvements in fishing gear and tactics, but must also have been due to higher levels of recruitment of young fish (Pruter 1973), possibly because of reduced cannibalism. Pruter (1973) pointed out that, since only a few age groups of pollock are utilized in any given year, poor recruitment could have a disastrous effect on the fishery.

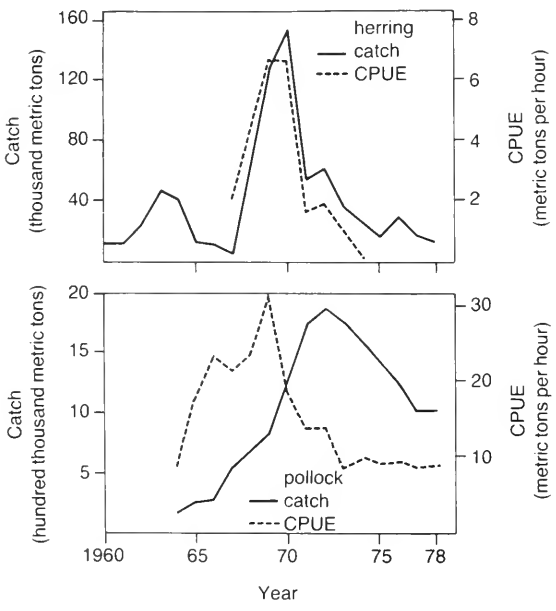

FIGURE 2.—Catch and relative abundance of walleye pollock and Pacific herring in the eastern Bering Sea. Adapted from Pereyra et al. (text footnote 5) and Favorite et al. (text footnote 6).

Herring harvest in the Bering Sea before 1968 was mostly west of long. 170°W. However, when stocks there declined, effort was shifted to the eastern Bering Sea, where the stocks were heavily exploited for 3 yr before abundance levels fell.

Relating stock abundances to fur seal food availability requires examining the overlap between Pribilof rookery feeding grounds and the area of the fishery. Since both fur seals and fishermen concentrated on areas of high fish density, we might expect competition for those fish species they both pursue.

Herring is a preferred food of fur seals, and evidence for heavy feeding on herring by fur seals in the Bering Sea was obtained from stomach samples taken in 1964 (Perez[11]). Since no large herring fishery exists in the eastern Bering Sea, we cannot be sure whether 1964 was a year of herring abundance or the high diet incidence of herring that year was just a local effect. Fur seals heavily exploit herring off Washington (Kajimura et al. footnote 3) where they are usually abundant. Heavy feeding on herring by fur seals has also been observed near Sitka, Alaska (Wilke and Kenyon 1957).

Schooling species such as herring, pollock, and squid provide a spatially heterogeneous, or patchy, feeding environment, making it difficult to interpret feeding patterns by average stomach content data. Pollock populations are patchy and mobile (Pereyra et al. footnote 5). The distribution of pollock between 1965 and 1970, generally warmer years, was more concentrated on the inner shelf than in the relatively colder years, 1971-75 (Pereyra et al. footnote 5). However, the region of the lower shelf between the Pribilof Islands and Unimak Island has consistently provided a large proportion of the Japanese catch of pollock throughout the history of the fishery in all months of the year (Pereyra et al. footnote 5). Thus, it may be that the fishery and the fur seal are most closely in competition for the pollock on the outer shelf. While fur seals are capable of taking relatively large prey, most pollock taken seem to be in the 6-20 cm range, while the fishery takes fish averaging 35 to 40 cm (Salveson and Alton 1976).

[11]M. A. Perez, Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115, pers. commun. May 1980.

Since there were no stomach content data for fur seals near the Pribilofs from 1968 to 1970, the years of the major herring fishery in the eastern Bering Sea, it was not possible to estimate how much interaction there was between fur seals and the herring fishery. Although herring is sometimes a food of fur seals, it may not be common in stomachs of the nursing female fur seals, because in summer the herring are not common in fur seal feeding areas but mostly remain in coastal waters (Wespestad 1978[12]).

Studies on Related Systems

Marine mammals are integrally tied to their environment. They can respond to reduction in competition by increases in abundance, which implies that many marine mammal populations are existing at or near their carrying capacities. Many marine mammals are opportunistic and voracious predators and can strongly affect trophic dynamics of lower trophic levels (Simenstad et al. 1978). Marine mammals are also frequently in food competition with each other. This is demonstrated 1) by the reduction in age of maturity of minke whales in the Antarctic Ocean after drastic reduction through harvest of sei and blue whales (Hofman[13]), 2) by the increase in ringed seal populations after depletion of bowhead whales in the Beaufort Sea (Lowry[14]), 3) in the fairly heavy predation of sea lions on fur seal pups (3.5 to 5.5% annually on St. George Island according to Gentry footnote 4), and 4) in the feeding overlap on hake by a large number of marine mammals (Fiscus 1979).

Work by Fowler (1981) showed that *K*-selected (low fecundity) animals demonstrate density dependence when near their carrying capacities, and from the above arguments it seems probable that most marine mammals exhibit density dependence in at least some of their population or growth parameters. Also, temporary reductions of a marine mammal population might provide an opportunity for a food competitor to reduce the carrying capacity of that marine mammal population. An important question in this case is whether the density-dependent effects experienced by a population at or near its carrying capacity are primarily a behavioral or a physiological phenomenon. The term "density-dependent" generally means that a population variable varies nonlinearly with changing population density. This does not, in itself, imply a direct cause or mechanism for this response. However, it may occur through increased mortality, reduced fecundity, reduced weight gains, or changes in animal condition. Each of these population parameters may be affected by a variety of density related factors.

In the case of the fur seal it has been hypothesized that reduction in fur seal populations due to female harvest gave the competing fishery an opportunity to increase harvest rates and thereby reduced the fur seal's carrying capacity. If this hypothesis is true, we should see a change in one or several of the population parameters discussed earlier.

EVIDENCE OF CHANGES IN FUR SEAL CARRYING CAPACITY

Fur Seal Population Trend

The fur seal population appears at present to be dropping. After the female harvests from 1956 to 1968, an increase in pregnancy rate and survival was expected. This expected response of the population did not materialize, and population numbers are reduced over model population projections.

Hypotheses to explain the reduction since 1956 (Fowler footnote 10) are:

1) The discrepancy is mainly due to overestimates of pup abundance during the tagging studies (1951-61) and underestimates in the subsequent pup shearing studies.

2) There has been a reduction in carrying capacity because of reduced available food in the Bering Sea, resulting from overfishing of major food sources for the fur seal—pollock and herring—in the feeding areas of the rookery seals.

3) The reduced pup abundance may be a transient effect of the female harvest. This is in spite of the observation that the direct effect of the animals removed has by now largely passed through the population (Lander 1981).

4) Increased abundance of nonharem adult males and an increase in ratio of these males to harem bulls on St. Paul Island may have reduced

[12]Wespestad, V. G. 1978. Exploitation, distribution and life history features of Pacific herring in the Bering Sea. Proc. Rep., 26 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[13]R. Hofman, Marine Mammal Commission, 1625 Eye Street NW., Wash., DC 20006, pers. commun. May 1980.

[14]L. Lowry, Alaska Department of Fish and Game, Fairbanks, AK 99701, pers. commun. May 1981.

land survival of pups. In pinniped populations on other islands—fur seals on the Commander Islands, Robben Island, and St. George Island, and elephant and grey seal populations on other islands—total adult populations are increasing and pup survival is going down. Thus, although pup production is increasing due to increased numbers of adult females, pup survival is reduced.

5) There may be reductions in survival and birth rates caused by pollutants and entrapment in fishing gear.

Among the most serious alternatives (from the standpoint of its implications for man) is that increased fishing intensity in the Bering Sea during the female harvest period has reduced the carrying capacity of the Bering Sea for fur seals. In our discussion of the Bering Sea fishery data we noted that the most probable link, if any, is in depletion by the fishery of pollock and herring in the feeding area of nursing females. Demonstration or corroboration of this hypothesis directly requires showing that pollock and herring stocks have been reduced in rookery fur seal feeding areas and that this has resulted in reductions of these foods in female fur seal diets, and reductions in lactating fur seal feeding rates and consequently in pup growth and survival. Present data available on fur seals, while substantial, is not sufficient to attempt so conclusive a test of this hypothesis. For example, fish surveys were not made in conjunction with pelagic fur seal surveys, so we do not know how selective fur seals are in their feeding or how dependent their feeding rates are on prey density and relative prey abundance. Also, we do not have direct estimates of the abundance of noncommercial species such as capelin and squid, which comprise large portions of the seal's diet and may be abundant in the absence of pollock and herring.

We suggest, and others have suggested before (Fowler 1980; Eberhardt and Siniff 1977), that there is a need to examine the changes in a number of behavioral and physiological indices of fur seal populations which might have presaged or reflected reduced carrying capacity. Measures that we considered are 1) the age at which females attain sexual maturity, 2) the weight at age for harvested preadult males, 3) the number of pup deaths on land compared with total pup births, 4) the average time spent at sea by lactating females (or some composite index of the time at sea plus the time suckling pups), 5) the survival rate of pups to age 3 computed from harvest of 3-yr-old males and pup counts 3 yr earlier, and 6) changes in diet composition after the development of the pollock fishery. We also used estimates of fur seal abundance, fish stock, and daily food intake to see how great an impact the fur seals actually made on this stock and whether estimated fishery reductions in the stock were sufficient to impact the fur seals.

Fur Seal Population Indices

Age at Sexual Maturity

Kajimura et al. (footnote 3) used a method modified from Lett and Benjaminsen (1977) to compute an average age of maturity for year classes from 1954 to 1964 (from the 1958-74 pelagic cruises). These are graphed in Figure 3 (from Kajimura et al. footnote 3). The average age at maturity increased sharply for the 1956 year class, the first year the females were harvested. Age at maturity subsequently dropped and remained stable, though at a higher average age than before 1956. The graph in Figure 3, as well as the results of other studies done before 1956 on age at maturity, suggests that post-1956 age at maturity was greater than pre-1956 averages.

There are a number of alternative explanations for the apparent increase in age of maturity in addition to the carrying capacity of fur seals being reduced. First, the increase may also have been due to the female harvest on the Pribilofs, selecting a higher fraction of mature females at a given age than actually existed in the population. Since the Pribilofs are a rookery, the presence of mature females in higher proportion than in the

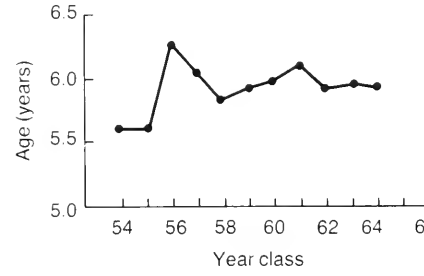

FIGURE 3.—Estimated average age at first reproduction of female northern fur seals based on females pregnant at least once for the 1954-64 year classes. From Kajimura et al. (text footnote 3).

entire population would leave the nonrookery population with a higher proportion of immatures which would then affect the samples taken at sea. Another difficulty with these data is that only 2 yr of pre-1956 age class data were available from the pelagic cruises, and the other pre-1956 data reported by Kajimura et al. (footnote 3) may not have used the same index of maturity as Kajimura et al. (footnote 3). Other possible sources of bias in the age at maturity estimate were the tendency of the pelagic fur seal samples to contain a higher number of older individuals than expected, and the underlying assumption that survival rates of pregnant and nonpregnant females are the same (Kajimura et al. footnote 3).

Growth With Age

Preliminary analysis by the National Marine Mammal Laboratory (NMML) (Fowler footnote 10) of the data from 3-yr-old males harvested on the Pribilof Islands showed a statistically significant increase in weight over time from 1964 to 1970 in contrast to growth rate reductions to be expected under a reduced fur seal carrying capacity.

Kajimura et al. (footnote 2) plotted the average length of pregnant females against age for the time periods 1958-62, 1963-68, and 1969-74. Their results (Fig. 4) indicate that growth rates were greater from 1963 to 1974 than from 1958 to 1962. These results raise the possibility that the fur seal might actually have experienced an increase in carrying capacity since 1963. However, Berdine[15] noted that if fur seal population density and carrying capacity both decline, growth rate could still show an increase. As mentioned earlier, changes in carrying capacity can result from a variety of causes, and until stronger links are established between fur seal populations and their controlling processes, arguments that carrying capacity changes are reflected by certain changes in population parameters will be incomplete.

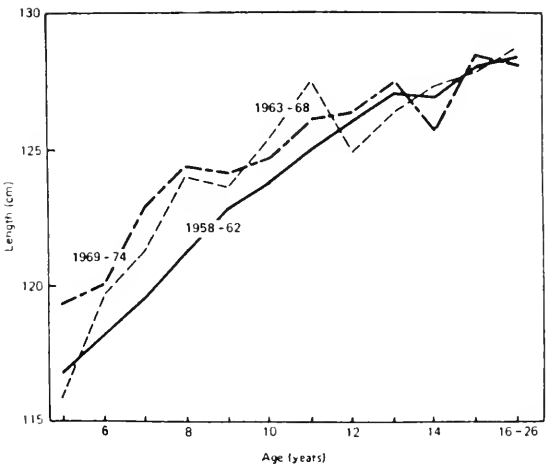

FIGURE 4.—Comparison of average lengths of pregnant fur seal females age 5 to 16-26 for combined months of January to April 1958-62, 1963-68, and 1969-74. Sample size ≥10 seals. From Kajimura et al. (text footnote 2)

Pup Deaths on the Rookery

Counts of dead pups on the rookeries of the Pribilof Islands are an indication of the survival rate of pups, when these are used in conjunction with total pup birth estimates. Gentry (footnote 4) estimated that dead pup counts include around 95% of the actual dead pups on the islands. From 1970 to 1979 pup death estimates on the Pribilof Islands varied between 4,500 and 54,000, averaging about 25,000—about 7% of the average pup population (Lander 1981). Earlier pup count data indicated extremely high pup mortality in 1954, 1956, 1960, and 1961; the last three years were also the years when mature females were harvested—this may account for the high pup mortalities.

Several facts about the dead pup counts are: 1) Large pup losses appeared more frequently before 1956 than after, although this bears further corroboration; 2) the year-to-year variability in pup mortality was large; and 3) pup mortality on St. Paul Island did not appear to be correlated with that on St. George Island, while temporal patterns of pup mortality from one rookery to the next on either island were more closely correlated with each other. The last fact seems to argue against food limitation as the controlling factor for pup survival through the rookery period and suggests, instead, some more local effects on the populations.

Average Time at Sea for Mother Seals

Bartholomew and Hoel (1953) recorded time at sea and nursing for 12 nursing fur seals in 1952

[15]J. Berdine, Judson Hall, Room 621, 53 Washington Square South, New York, NY 10012, pers. commun. August 1980.

on St. Paul Island. Gentry (footnote 4) made similar observations on nursing fur seals in the late 1970's and found no significant change in time at sea from those of Bartholomew's study.

Pup Survival to Age 2

Lander (1981) calculated early survival rates to age 2 for male fur seals from the 1950-70 year classes. York and Hartley (1981) analyzed these estimates, using Mann-Whitney and Student's *t* tests, and found pre-1956 rates to be significantly lower than post-1956 rates (0.32 vs. 0.40 average). This does not appear to support the hypothesis of reduced carrying capacity.

Time Trends in Fur Seal Diets

Fur seal stomach contents taken in 1960, 1962-64, 1968, and 1973-74 cruises were used to investigate trends in fur seal diets to see whether these might have changed after development of the pollock fishery. These data were summarized by month.

Figure 5 indicates that the age composition in catch in the pollock fishery shifted from a mode of 4 yr in 1964 to 3 yr in 1974 with the 2-yr-old catch also being strongly represented. H. Kajimura, who was present on the cruises, suggested that the size of pollock in fur seal stomach samples decreased from 1964 to 1974. Examination of average volume per pollock specimen in fur seal stomachs (Unpubl. data[16]; Table 2) corroborates this observation, with average specimen size decreasing significantly between 1968 and 1973-74. We also note that the percentage volume of the total stomach content comprised of pollock was consistently high in 1973-74 (>48%), while earlier, especially before 1968, pollock comprised a variable and usually low percentage of the diet (<20% in 8 of the 11 mo sampled).

These data indicate that there may have been an interaction between fur seal diets and the pollock fishery. As fishing pressure on pollock increased, fishing out of older age classes reduced the average size of the fish and increased the average growth rate of the pollock. Furthermore, young pollock survival may have been increased through reduced cannibalism. These increased

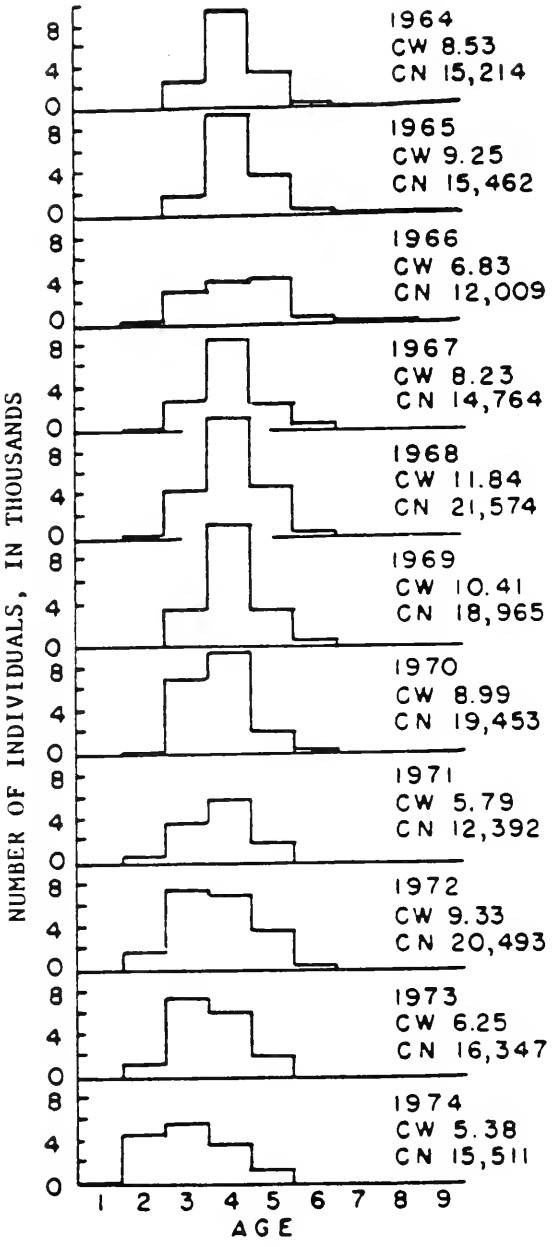

FIGURE 5.—Age composition in catch per unit effort (CPUE) of walleye pollock from the Japanese trawl fishery in the eastern Bering Sea. Japanese trawl fishery includes the mothership fishery and the North Pacific trawl fishery, but not land-based-dragnet fishery. From Salveson and Alton (text footnote 12). CW = CPUE in weight in metric tons; CN = CPUE in number.

stocks of smaller fish were reflected by the increase in abundance of pollock in fur seal diets after 1968 and by a marked decrease in the average size of fish taken by the fur seals. This in-

[16]Data obtained from Dr. M. Tillman, Director, Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

TABLE 2.—Fur seal diet of walleye pollock from pelagic samples in the eastern Bering Sea. (Unpubl. data (text footnote 16).)

Date	Number of stomachs with food	Volume of pollock in diet		Number of pollock in diet	Percent of total numbers	Pollock volume/ specimen (cm^3)
		cm^3	Percent			
June 1960	4	385	12 3	19	5 2	20 26
July 1960	152	39,807	61	403	9.8	98.7
Aug 1960	61	37,124	75	148	10	251
June 1962	53	295	2 4	2	0.16	147.5
July 1962	137	4,343	12 6	45	1.1	96.5
Aug 1962	277	17,266	18 3	323	3 1	53 45
Sept. 1962	111	10,342	28	235	5 4	44.0
July 1963	256	11,188	14 16	62	0 56	180.45
Aug 1963	536	9,758	5	163	0.59	59.9
Sept. 1963	17	700	11.06	1	0 11	700
July 1964	97	2,354	9 5	7	0 27	336
Aug 1964	213	29,296	15.4	792	9 8	37
July 1968	78	31,901	76 9	384	14 3	83
Aug 1968	53	11,206	37.4	30	1.21	373.5
July 1973	148	72,427	90 7	1,418	33.0	51.07
Aug 1973	191	36,564	60 7	1,305	15 1	43.34
Sept. 1973	178	32,511	48 5	2,172	23.7	14.9
July 1974	52	13,658	87.4	244	58.6	36.0
Aug 1974	110	15,198	63.2	390	20 2	38.9

crease in total stock biomass, mostly in the younger age classes, can account both for the increased fur seal diets on (mostly smaller) pollock and the continued high yield of the fishery after over 10 yr of heavy fishing pressure.

Table 2 indicates that both fur seals and the fishery may have exploited the same pollock resource, since both show a drop in size of "catch" over time. We suspect that the trend toward greatly increased abundance of pollock juveniles in the Bering Sea has also resulted in larger schools (patches) of juvenile pollock, which has made them an easier target for the fur seals and also the fishery, than previously. One possible, dangerous consequence of future increased fishing pressure on pollock, however, is that most of the catch will be of premature individuals. With continued heavy fishing pressure, this might result in inadequate recruitment to maintain the stock.

A possible alternative explanation for why pollock were so consistently taken by fur seals in 1973-74 is that these were relatively cold years with pollock aggregating more on the outer shelf than in warmer years (Pereyra et al. footnote 5). Another possible explanation is that the Pribilof area, where the bulk of the 1973 and 1974 stomach samples were taken (unlike the earlier samples which did not focus as heavily on this area), is a nursery area for young-of-the-year pollock, which may account for the reduced average size and increased abundance of pollock in fur seal stomachs during 1973 and 1974. Despite these possible alternatives, the most plausible hypothesis is that pollock has increased in importance in fur seal diets since the initiation of the pollock fishery.

Energetics Approach to Fur Seal Food Consumption

The total amount of food consumed by fur seals (and other marine mammals as well) in the eastern Bering Sea has been estimated by a number of individuals (Laevastu and Larkins 1981; McAlister and Perez 1976[17]; Anonymous 1979[18]). McAlister and Perez (footnote 17) estimated that fur seals eat 378,000 t of fish and squid every year. They used an estimated feeding rate of 7.5% body weight daily while Miller (1978)[19] suggested that 14% body weight daily may be more appropriate to support seals at 7°C, the average summer temperature in the Bering Sea. Miller based his arguments on metabolic studies in which he recorded oxygen consumption at different temperatures in the laboratory for a number of juvenile seals and also conducted feeding studies using food most commonly found in the diet of

[17]McAlister, W. B., and M. A. Perez. 1976. Preliminary estimates of pinniped-finfish relationships in the Bering Sea. Background paper for the 19th meeting of the North Pacific Fur Seal Commission, 29 p. Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[18]Anonymous. 1979. Draft environmental impact statement of the Interim Convention on Conservation of North Pacific Fur Seals. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Seattle, Wash., 39 p.

[19]Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. U.S. Marine Mammal Commission Report MMC-75/08, 27 p.

fur seals in the Bering Sea. Using Miller's estimate for consumption would give an estimate of 705,000 t eaten annually by fur seals. Laevastu and Larkins (1981) gave an estimate of 513,000 t taken by fur seals annually in the eastern Bering Sea, with an additional 368,000 t taken in the Aleutian region. The latter estimates were based on runs of the PROBUB (prognostic bulk biomass) model. Estimates of fur seal populations of the Bering Sea and the Aleutian Islands and their mean consumption rates, given in Table 3 (Anonymous footnote 18), were used to compute a total fur seal consumption of 219,000 t.

These estimates can be compared with annual fish catches in the eastern Bering Sea and Aleutian Islands (North Pacific Fishery Management Council[20]). Between 1968 and 1976, annual fish catches varied between 750,000 and 2,100,000 t in the eastern Bering Sea and between 40,000 and 80,000 t near the Aleutian Islands. These figures indicate that fish harvests by marine mammals and by man in the Bering Sea are comparable and that the marine mammals' harvest exceeds man's in the Aleutian Islands' area. It is important to note, however, that fur seals prey on a larger number of species than man, and thus a part of their harvest is not in direct competition with man's. As a consequence of the fur seals' greater ability to switch prey when abundances of preferred prey species are low, total fur seal consumption is probably fairly steady from year to year, while man's is highly variable.

It has been estimated (Anonymous footnote 18: table 12) that 9.8% of fish standing stock in the eastern Bering Sea and the Aleutian Islands is consumed annually by marine mammals, 5% by man, and 1.8% by birds (1.9% by fur seals). Laevastu and Larkins (1981) estimated a total commercial fish standing stock of 24,880,000 t in the Bering Sea and Gulf of Alaska, which implies that 3.5% of all commercial fish stocks are taken by fur seals annually and 10.7% by all marine mammals. The fur seal figures are deceptive, since fur seal impact on fish stocks is relatively localized. Thus, fur seals near the Pribilof Islands are probably consuming considerably more fish than man is, though man may be harvesting some different species than fur seals. This energetics computation is inconclusive with respect to fur seal-fishery interaction, except to show that competition between the two is possible.

DISCUSSION

Suggested Analyses of Existing Data

Population Indices

Following Eberhardt and Siniff's (1977) suggestion that a population's response to impact may be reflected by various indices, we suggest

[20]Data available from North Pacific Fishery Management Council, 333 W. Fourth Ave., Suite 32, P.O. Box 3136DT, Anchorage, AK 96813.

TABLE 3.—Fur seal population estimates at sea (June-November) in the eastern Bering Sea and Aleutian area (Anonymous text footnote 18).

Age class	Population[1] total	June-Nov. eastern Bering Sea and Aleutian	Estimated percent of time at sea (June-Nov.)	Estimated population at sea (June-Nov.)	Mean[2] weight (kg)	Mean[3] daily consumption rate (%)
Pups	349,000	[4]321,000	10	32,100	10.00	14.00
M+F, age 1	174,000	67,000	[5]90	78,300	9.54	13.76
M+F, age 2	122,000	61,000	[5]75	45,750	16.69	12.32
F, age 3	55,000	23,000	[5]80	22,400	18.80	12.53
F, >age 4	582,000	46,000	[6]79	368,140	35.64	11.76
M, age 3-7	101,000	71,000	[7]10	7,100	32.60	7.60
M, >age 7	11,000	9,000	[7]10	900	105.25	7.01
Total	1,394,000	1,043,000 [8](754,100)		554,690	29.92	11.71

[1]Average 1969 to 1974.
[2]Based on National Marine Mammal Division, NMFS pelagic research data, 1958-74, N = 13,772, except average weight for pups (10 kg) based on observations in the Pribilof Islands during September; total mean weight based on an effective fishery population 754,000, on time spent on land and at sea for each class during June and September.
[3]Weighed by mean animal weight of estimated body weight for animals weighing <10 kg or <45 kg in waters colder than 15°C; 7% for >10 kg on land or >45 kg at sea.
[4]Based on the ratio of males to females (0.085) in the eastern Bering Sea during June-November from National Marine Mammal Division, NMFS pelagic research data, 1958-74 (N = 4,451).
[5]8% mortality, pups estimated to feed at sea only 18 d (10% of time) during September-November
[6]These percentages represent proportions of the total population of the respective age class not on the rookeries during the breeding season.
[7]Based on percent of time out of 130 d not on rookery.
[8]Effective fishery population (June-November).

that the available data from which these indices are computed be also studied for trends. Indices that are most easily obtained for the fur seal are pup birth estimates, dead pup counts, male survival to age 3 (from male harvest data), and length at age for preadult males (from harvested males).

Fur Seal Diet Trend

We have suggested a relationship between fur seals and the fishery via greatly increased abundance of juvenile pollock (Table 2). The data used, however, were already combined in such a way that we were unable to separate the data by region where the data were collected and the degree of digestion of the prey. We suggest that the original data be used to conduct a complete statistical analysis with corrections made for the area in which the sample was taken and, if possible, the time of day the samples were taken (assuming that the correlations found between the proportion of the stomachs empty and time of day the samples were taken also applies to the percentage of food digested). Variance estimates can also be computed and used to make statistical tests for time trends both in the average size of pollock in fur seal stomachs and in the percentage of the total diet comprised of pollock.

Role of Patchiness in Seal Feeding

Although we suspect from survey data on pollock (Smith 1979) that pollock are quite patchily distributed in the eastern Bering Sea, the survey data need to be reexamined for an indication of the size of patches or degree of aggregation. An attempt should be made to represent this patchiness stochastically (in terms of probability). One important question to be considered with these data is whether or not there has been a trend in pollock school size from 1963 to 1974 in the eastern Bering Sea. Another approach to consider patchiness is to use the abundance of pollock in fur seal stomachs collected at different locations as an index to the spatial separation and size of pollock schools.

Suggested Future Data Collection

We suggest that a fish trawl survey targeting on pollock be conducted between the Pribilof Islands and Unimak Pass from June to September with study designed to focus on areas of high pollock density to determine the size distribution of pollock, the size of the schools, and, if possible, to observe fur seal feeding intensity around the schools. The pollock and fur seals might be tracked by using multibeam sonar techniques. Additional stomach samples of fur seal taken in conjunction with the trawl survey would give useful insight into fur seal food selectivity.

CONCLUSIONS

In summary, we see rookery fur seal behavior and multispecies, age-classed, patch-feeding models as directions for future study. Before proceeding in this direction we recommend further detailed analyses of the fur seal stomach content data, to explore more fully the interaction between the fur seal and the walleye pollock fishery (Table 2), and to elucidate other interactions with fisheries of which we may be unaware at this time.

The available fur seal and fishery data, while limited, appear to be the best mammal-fishery data in the world and as such deserve to be fully archived and fully utilized.

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AGE, SIZE, GROWTH, AND CHEMICAL COMPOSITION OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, FROM NARRAGANSETT BAY, RHODE ISLAND

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ABSTRACT

Age and size were determined for 2,015 Atlantic menhaden caught in Narragansett Bay, R.I., during 1976. Atlantic menhaden were predominantly age 2 and age 3, and in all age groups were significantly smaller than fish caught from Long Island Sound to the Gulf of Maine during 1955-71. The chemical composition of the Atlantic menhaden, as determined from analysis of selected subsamples, was ash—10.94, carbon—56.61, and nitrogen—8.03% of dry weight; kilocalories—6.238 per gram dry weight and 7.002 per gram ash-free dry weight; and dry weight—33.4% of wet weight.

Instantaneous annual growth rates during the years 1970-75 were estimated from back-calculated fork lengths and wet weights at the time successive scale annuli were formed. Instantaneous daily growth rates of Atlantic menhaden in Narragansett Bay during 1976 were estimated from the growth of the scale margin beyond the 1976 annulus, and from the increase in mean fork length and wet weight of the fish as the season progressed. Growth rates of age 2 and age 3 Atlantic menhaden in 1976 were considerably greater than the respective average growth rates estimated for previous years, suggesting significant differences in age-specific growth rates of Atlantic menhaden in different regions and different years.

The Atlantic menhaden, *Brevoortia tyrannus*, is a schooling, plankton-feeding clupeid which ranges inshore along the Atlantic coast from Florida to Maine. It makes extensive seasonal migrations, moving north during spring and south during fall (Nicholson 1971, 1972, 1978). Atlantic menhaden are usually present in Narragansett Bay, R.I., from April to November, with peak abundance from June to mid-September. Here we report measurements of age, size, and chemical composition of menhaden caught in Narragansett Bay during 1976. We also report the first calculations of instantaneous growth rates in fork length and wet weight, as measured from scale annuli of individual fish. These data are part of a larger study to determine the energy budget of adult menhaden in Narragansett Bay.

METHODS

Atlantic menhaden were sampled from the catch of two purse seiners, operating from Point Judith, R.I. During 1976, fishing activity fluctuated considerably, according to abundance and availability of Atlantic menhaden in Narragansett Bay. Most of the catch was obtained during early June and from late July to early September. All samples were collected during these two periods, with two additional samples collected on 7 October and one on 4 November.

Random samples of fish from a purse seine set were stored on ice and returned to the laboratory at the end of the day. A total of 2,262 fish were sampled from 24 purse seine sets. An average of 94 fish were collected per set, with a maximum of 2 sets sampled on a given day. About 11% (247 fish) that had regenerated scales, and therefore could not be aged, were excluded from further analysis.

Wet weight and fork length were recorded, and several scales were collected for age determination (June and Roithmayr 1960). Every fifth fish from each sample was collected into a subset of five fish and frozen for dry weight determination or chemical analysis. Dry weights, for the calculation of wet weight:dry weight ratios, were determined by drying groups of these frozen fish at 105°C to constant weight. Fish used for chemical analysis were homogenized, while still frozen, with an equal volume of distilled water. Ash, carbon, nitrogen, and caloric contents were determined for subsamples of the freeze-dried homogenate. The ash content was measured by combusting samples at 475°C

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for 4 h (4-8 replicates). The carbon and nitrogen contents were determined with a Hewlett-Packard[2] Model 185B CHN Analyzer (3 replicates) and the caloric content with a Parr adiabatic bomb calorimeter (4 replicates).

Five scales from each fish were mounted dry between acetate sheets and examined under a Wild M5 dissecting microscope at 18×. Annuli were counted, and distances from the focus to each annulus and to the scale margin were measured with an optical micrometer on the most symmetrical and clearly marked scale.

Condition factor (CF) was calculated from the following equation:

$$CF = \frac{\text{wet weight (g)} \times 10^5}{\text{fork length (cm}^3\text{)}}. \quad (1)$$

Length-weight relationships were determined from functional regression of $\log_{10}$ wet weight on $\log_{10}$ fork length (Ricker 1973, 1975b; Jolicoeur 1975). Functional regressions were used because experimental error existed in both the x and y values. Growth of the fish during 1976 was determined by regressing the size of the fish (y) against the date of capture (x). Here, ordinary regressions were used because error was associated only with the y values.

RESULTS AND DISCUSSION

Atlantic Menhaden Age Structure, Size, and Condition Factor

Atlantic menhaden taken from Narragansett Bay during 1976 were predominantly age 2 and age 3 (Table 1), and the relative proportions of the different age groups in the catch remained approximately constant throughout the sampling period. The high proportion (31.4%) of age 2 menhaden taken in the Narragansett Bay catch during 1976 was unusual, based on records from previous years. During 1955-71, age 2 menhaden usually did not migrate in significant numbers north of Long Island, although in some years large numbers were observed in New England waters (June and Reintjes 1959, 1960; June 1961; June and Nicholson 1964; Nicholson and Higham 1964a, b, 1965a, b; Nicholson 1975). Also, the age distribution in the 1976 Narragansett Bay catch (Table 1) was quite different from that in 1975 (Ganz 1975), where, in a sample of 1,100, age 1 = 0.2%, age 2 = 14.6%, age 3 = 70.7%, age 4 = 13.4%, and age 5 = 1.6%.

TABLE 1.—Size and condition of Atlantic menhaden caught in Narragansett Bay, R.I., during 1976, compared with those caught in the North Atlantic during 1955-71. Means and 95% confidence limits are shown for the Rhode Island data. Size of menhaden during the years 1955-71 are taken from June and Reintjes (1959, 1960); June (1961); June and Nicholson (1964); Nicholson and Higham (1964a, b, 1965a, b); Nicholson (1975).

	Narragansett Bay All fish 3 June-4 Nov	North Atlantic 1955-62	North Atlantic 1955-71
Age 1			
Fork length (mm)	233		
Wet weight (g)	238		
Condition factor	1.87		
No. of fish	2		
Age 2			
Fork length (mm)	233±1.5	272	268
Wet weight (g)	241±4.8	363	—
Condition factor	1.86±0.011	1.89	—
No. of fish	633		
Age 3			
Fork length (mm)	238±1.4	296	288
Wet weight (g)	260±3.6	452	—
Condition factor	1.89±0.008	1.89	—
No. of fish	1,224		
Age 4			
Fork length (mm)	249±3.7	312	306
Wet weight (g)	303±14.4	545	—
Condition factor	1.91±0.023	1.90	—
No. of fish	134		
Age 5			
Fork length (mm)	272±10.3	321	317
Wet weight (g)	384±39.7	604	—
Condition factor	1.89±0.068	1.90	—
No. of fish	18		
Age 6			
Fork length (mm)	274±1.2	329	325
Wet weight (g)	407±1.6	657	—
Condition factor	1.94±0.295	1.91	—
No. of fish	4		

Age 4 and older menhaden contributed significantly in numbers and in biomass to the North Atlantic catch prior to 1966 (Nicholson 1975). However, during the mid-1960's these older age groups dwindled until they became a negligible part of the catch (Nicholson 1975). Small numbers of age 4+ menhaden in Narragansett Bay catches of 1975 (15.0%) and 1976 (7.7%) indicate that the relative abundance of these age groups continues to be low.

Menhaden caught in Narragansett Bay in 1975 (mean weight 297.6 g (Ganz 1975)), and in 1976 (this study), were considerably smaller than fish of the same age caught during 1955-71 in the North Atlantic area (Long Island Sound to Gulf of Maine) (Table 1). However, the condition factor of the 1976 fish was similar to that of fish previously caught in the North Atlantic (Table 1), implying that the basic length-weight relationship was the same.

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

The relationship between wet weight and fork length in the 1976 fish was determined by regressing $\log_{10}$ wet weight on $\log_{10}$ fork length. The functional regressions determined for age groups 2-5 were not significantly different in slope or elevation ($P<0.05$), and a common relationship for all ages combined was therefore determined; where W = wet weight (g) and L = fork length (mm):

$$\log_{10} W = -5.3055 + 3.2441 \log_{10} L \qquad (2)$$
$$r = 0.9615$$
$$n = 2{,}015.$$

Back-Calculated Size-at-Age and Growth Rate

The fork length, at the time a menhaden formed each of its scale annuli, was calculated by direct proportion by:

$$\frac{L_i}{S_i} = \frac{L_c}{S_c} \qquad (3)$$

where L_i = fork length (mm) at the time scale annulus i was formed
S_i = width of scale (mm) from focus to annulus i
L_c = fork length (mm) of the fish at time of capture
S_c = width of scale (mm) from focus to outer margin, at time of capture.

Mean back-calculated fork lengths of each age group at the time of annulus formation are presented in Table 2. The overall length-weight relationship (Equation (2)) was used to convert the back-calculated fork lengths of each fish to wet weight; mean values for each age group are presented in Table 2.

These back-calculated lengths and weights were then used to calculate the annual instantaneous growth rate of each fish during previous years (Table 3), where

$$G_i(L) = \log_e L_{(i+1)} - \log_e L_{(i)} \qquad (4)$$

where $G_i(L)$ = instantaneous yearly growth rate

TABLE 2.—Mean back-calculated fork length and wet weight of Atlantic menhaden caught in Rhode Island waters during 1976, using the overall length-weight relationship (Equation (2)).

Age (1976)	Year class	n	Mean ± 95% confidence limit, back calculated at annulus at age					
			1	2	3	4	5	6
Fork length:								
2	1974	633	103.5±1.9	179.0±1.2				
3	1973	1,224	91.4±1.0	150.8±1.0	191.3±1.0			
4	1972	134	90.4±3.2	146.5±3.9	185.0±4.0	217.3±4.6		
5	1971	18	100.9±10.3	161.4±10.6	193.5±11.6	220.7±13.2	248.5±12.5	
6	1970	4	114.2±18.7	163.9±30.6	186.6±34.6	214.6±36.4	236.7±48.2	252.0±52.5
Wet weight:								
2	1974	633	20.4±1.2	103.5±2.4				
3	1973	1,224	13.1±0.5	60.9±1.4	129.1±2.5			
4	1972	134	12.8±1.8	57.3±5.0	118.7±8.4	199.7±14.0		
5	1971	18	18.0±6.2	76.2±15.2	136.1±25.9	208.4±37.4	302.0±45.5	
6	1970	4	24.1±12.1	78.4±42.5	119.4±70.9	186.9±95.6	260.6±170.1	319.5±208.7

TABLE 3.—Mean annual growth in fork length (L)[1] and in wet weight (W)[2] of each age group of Atlantic menhaden during previous years. These individual growth rates were then averaged to provide an estimate of the mean growth of each age group during successive years of its life.

Age (1976)	Year class	n	Mean ±95% confidence limit, instantaneous yearly growth at age				
			1	2	3	4	5
Fork length:							
2	1974	633	0.5745±0.0189				
3	1973	1,224	0.5129±0.0092	0.2406±0.0047			
4	1972	134	0.4906±0.0267	0.2385±0.0148	0.1608±0.0103		
5	1971	18	0.4814±0.0923	0.1831±0.0408	0.1313±0.0244	0.1207±0.0269	
6	1970	4	0.3600±0.1317	0.1299±0.1024	0.1407±0.1479	0.0964±0.0525	0.0620±0.0282
Wet weight:							
2	1974	633	1.8636±0.0614				
3	1973	1,224	1.6639±0.0300	0.7805±0.0152			
4	1972	134	1.5917±0.0865	0.7737±0.0480	0.5218±0.0335		
5	1971	18	1.5617±0.2993	0.5941±0.1325	0.4260±0.0791	0.3917±0.0872	
6	1970	4	1.1678±0.4272	0.4213±0.3322	0.4563±0.4799	0.3128±0.1702	0.2011±0.0914

[1]Growth was calculated individually for each fish from its back-calculated fork length at the time of annulus formation in 2 successive years, where instantaneous yearly growth rate, $G_i(L) = \log_e L_{(i+1)} - \log_e L_{(i)}$.
[2]Growth was calculated individually for each fish from its back-calculated wet weight at the time of annulus formation, where instantaneous yearly growth rate, $G_i(W) = \log_e W_{(i+1)} - \log_e W_{(i)}$.

in fork length for a fish age i

$L_{(i)}$ = back-calculated fork length at the time annulus i was formed

$L_{(i+1)}$ = back-calculated fork length at the time annulus $i+1$ was formed.

The instantaneous annual growth in wet weight, G_i (W), was similarly calculated from back-calculated wet weight of each fish at the time each annulus was formed (Table 3).

Growth calculated in this way is the "true growth rate" of the individual fish, as opposed to the "population growth rate" derived from the mean size-at-age of a fish population and which generally underestimates the true rate (Ricker 1975a). However, individual growth rates calculated according to Equation (4) may still underestimate growth of the average individual in prior years, if the back-calculations of size-at-age are affected by Lea's Phenomenon. Although Lea's Phenomenon has been observed in menhaden (June and Roithmayr 1960; Nicholson 1972), we are unable to assess the importance of this potential bias in Tables 2 and 3, because we lack the necessary information on actual mean size and seasonal growth rates of the menhaden population during 1970-75.

Among age groups 3-6 (1970-73 year classes), the mean back-calculated size-at-age and the annual instantaneous growth rates of fish of equivalent age were not significantly different ($P<0.05$) (Tables 2, 3). Annual growth rates declined with increasing age of the fish. The mean back-calculated size-at-age of age 2 menhaden (1974 year class) was, however, significantly larger ($P<0.05$) than that of fish of earlier year classes (Table 2), indicating that age 2 menhaden had grown significantly more at age 0 and age 1 than fish from the older age groups.

Further information on total menhaden population movements and on age and size structure during 1976 is needed in order to evaluate the Narragansett Bay data in terms of the population as a whole. However, some preliminary conclusions may be drawn, based on comparisons with data from 1955 to 1971.

The summer distribution of the Atlantic menhaden is discontinuous, with a southern group ranging from Florida to Virginia and a northern group (composing the main body of the population) ranging from Chesapeake Bay to Maine (June and Reintjes 1959, 1960; June 1961; June and Nicholson 1964; Nicholson and Higham 1964a, b, 1965a, b; Nicholson 1971, 1975). During summer the northern group is age-stratified along the coast, with younger fish in the more southern part of the range and older fish predominating in the north. Nicholson (1971) concluded that age 1 menhaden were most abundant from Chesapeake Bay to New Jersey; age 2 from New Jersey to the south shore of Long Island; age 3 from Long Island Sound to Nantucket Sound; and age 4+ from Nantucket Sound to Maine. The average size of individuals within each age group also increased with latitude, especially with age 1 and age 2 fish. This size stratification was much less pronounced for age 3 and older menhaden.

Since Rhode Island is located within the summer population center of age 3 menhaden, Rhode Island landings should provide a good estimate of the mean size of age 3 menhaden in the population. However, since Rhode Island is near the northern limit of the age 2 fish, we would expect the landings to represent only the larger members of this age group.

Records from 1955 to 1971 suggest that age 2 menhaden caught in Narragansett Bay during 1976 were probably the larger members of the 1974 year class and were not representative of the year class as a whole. The comparatively large size-at-age and the growth rates back-calculated for the age 2 menhaden at age 0 and age 1 (Tables 2, 3) are consistent with this suggestion.

Menhaden of all ages (including age 2) caught in Narragansett Bay during 1976 were among the smallest fish for their age ever recorded, and resembled the very small menhaden typically caught in Chesapeake Bay in earlier years (June and Reintjes 1959, 1960; June 1961; June and Nicholson 1964; Nicholson and Higham 1964a, b, 1965a, b; Nicholson 1971). The back-calculated fork lengths of the 1976 fish demonstrated that they had been small since age 1. Size differences between age groups were also greatly reduced (Tables 1, 2, 3).

The reason for the small size of menhaden caught in Narragansett Bay during 1975 and 1976 is not known. Present results are open to two interpretations: 1) Migratory patterns during 1976, and possibly 1975, did not follow the pattern observed in earlier years, and therefore the size of the menhaden from Narragansett Bay was not representative of any age group in the overall population; or, 2) there has been a significant, overall reduction since 1971 in size-at-age within the Atlantic men-

haden population. Such a reduction in size-at-age could result from a number of factors, including poor growth during age 0 only, followed by normal growth rate; an overall decline in the mean growth rate of all age groups; or a shift in the relative proportions of different spawning groups within the population (see June 1965; Nicholson 1972), where faster growing individuals have declined and been replaced by slower growing individuals.

Growth During 1976

Instantaneous Daily Growth Rate

Mean instantaneous daily growth rates of menhaden caught in Narragansett Bay during 1976 were estimated from the seasonal increase in mean size of the fish. Such estimates, based on successive samples from a population, assume that the fish were initially of similar size and that there was no significant influx of new fish, with different growth histories, into the region during the study period; these conditions are difficult to meet with a free-ranging fish such as the menhaden. However, we have evidence that these conditions were met, at least for a 1-mo period during the study. First, back-calculated fork lengths at the most recent annulus indicated that menhaden caught in Narragansett Bay were of similar length at the start of the 1976 growing season (Fig. 1). Second, daily observations by the menhaden spotter pilots suggest that our samples collected between 3 August and 1 September were derived from a single group of menhaden. Many large schools were observed moving into Narragansett Bay during the week of 26 July. No significant additional movement of schools into or out of the bay was observed until 7 September, when large schools were again seen entering the bay. Uniformity of the back-calculated fork lengths of the menhaden sampled during this period (Fig. 1) supports the fishermen's opinion that the same group of fish was being sampled. The influx of new fish into the area, observed by the commercial fishermen on 7 September, was accompanied by an abrupt shift in the mean and variance of back-calculated fork lengths of age 3 menhaden on 7-8 September, presumably because of the mixing of new arrivals with those already present (Fig. 1).

Daily growth rates of age groups 2 and 3, the most abundant age groups in the samples, were estimated for the period 3 August-1 September

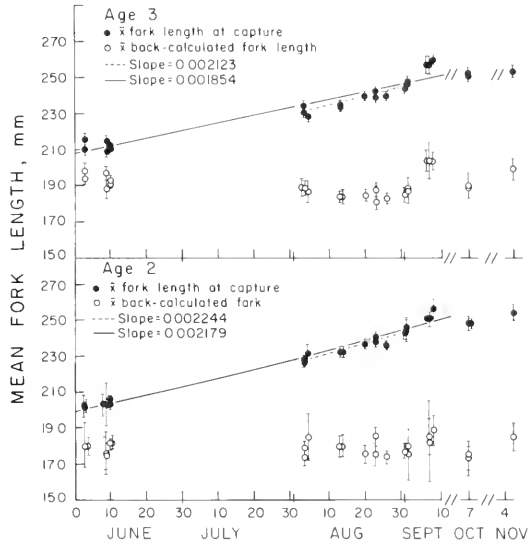

FIGURE 1.—Mean fork length ±95% confidence limits of Atlantic menhaden collected from Narragansett Bay during 1976. Curves depict the instantaneous daily growth in length (Table 4, Equations (9)-(12)).

from 1) rates of increase in mean fork length and wet weight during this period (Figs. 1, 2) and 2) growth rate of the scale margin beyond the 1976 annulus (Fig. 3).

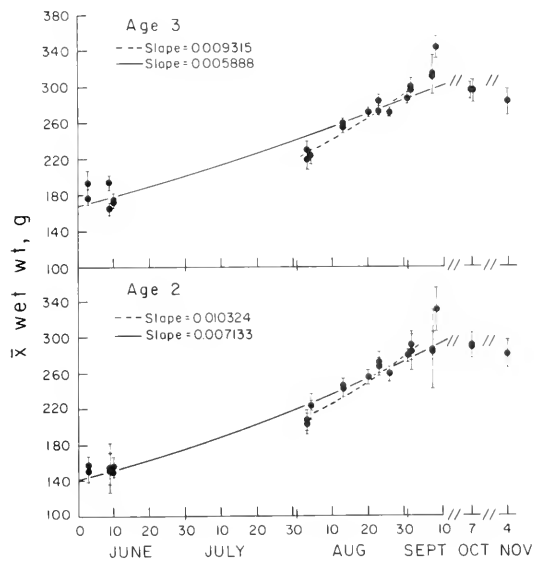

FIGURE 2.—Mean wet weight ±95% confidence limits of Atlantic menhaden collected from Narragansett Bay during 1976. Curves depict the instantaneous daily growth in wet weight (Table 4, Equations (13)-(16)).

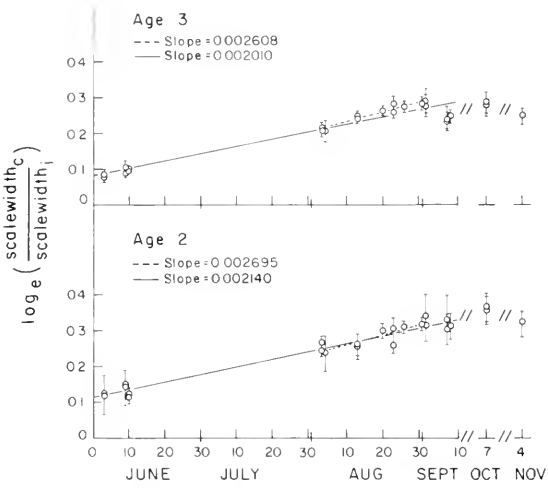

FIGURE 3.—Seasonal growth of the scale margin beyond the 1976 annulus in Atlantic menhaden collected from Narragansett Bay during 1976. Means ±95% confidence limits are shown. Curves depict the instantaneous daily growth of the scale margin (Table 4, Equations (5)-(8)).

Growth rates in fork length and wet weight were determined by regressing $\log_e$ fork length and $\log_e$ wet weight vs. the date of capture (Figs. 1, 2; equations are in Table 4). Mean instantaneous daily growth rates were equal to the slopes of the relationships. Growth of the scale margin was determined for each fish from

$$G = \log_e \frac{S_c}{S_i} \qquad (4)$$

where G = instantaneous growth increment
S_c = total width (mm) of the scale at time of capture
S_i = width (mm) to the most recent (1976) annular ring.

The value of G provides an independent estimate of the total amount of growth by that fish during 1976, up to the time of capture. If the exact date were known when fish resumed growth during the spring of 1976, the mean daily growth rate for the entire season could be determined for each individual fish. However, since this date is unknown, the mean daily growth rate can be estimated only for the overall population, by repeatedly sampling that population and regressing the individual values of G against the date of capture (Fig. 3). This approach is analogous to that already described for estimating daily growth in fork length and wet weight.

Instantaneous daily growth rates of age 2 and age 3 menhaden caught within the bay during 3 August-1 September were 0.27 and 0.26%/d in the growth of the scale margin, 0.22 and 0.21%/d growth in fork length, and 1.03 and 0.93%/d growth in wet weight (Table 4). There were no significant differences ($P<0.05$) between these measures of growth for age 2 and age 3 menhaden, probably because the two age groups were very similar in size. The mean daily growth rate of the scale margin did not differ significantly ($P<0.05$) from that of fork length, indicating that both grew in the same proportion.

Daily growth was also estimated, as described above, for all fish collected between 3 June and 8 September (Table 4). These growth estimates were lower than those derived from fish thought to have remained within the bay during August, but only growth estimates in wet weight were significantly different ($P<0.05$).

TABLE 4.—Linear regressions from which the instantaneous daily growth rates of Atlantic menhaden in Narragansett Bay during 1976 may be calculated, where x = date of capture (1 June = day 0 and 8 Sept. = day 100) and (A) $y = \log_e\left(\frac{\text{scale width}_c}{\text{scale width}_i}\right)$; (B) $y = \log_e$ fork length (mm); and (C) $y = \log_e$ wet weight (g). y values are the means of each sample of fish; n = the number of samples. The instantaneous daily growth rate equals the slope of each regression relationship.

	Regression statistics									
	Age 2					Age 3				
	Eq no.	Intercept	Slope±95% C.L.	r	n	Eq no.	Intercept	Slope±95% C.L.	r	n
(A) Growth of scale margin										
3 June-8 Sept.	(5)	0.11201	0.002140±0.000203	0.9810	21	(6)	0.08157	0.002010±0.000265	0.9641	21
3 Aug.-1 Sept.	(7)	0.06990	0.002695±0.001058	0.8767	12	(8)	0.04600	0.002608±0.000562	0.8767	12
(B) Growth in fork length										
3 June-8 Sept.	(9)	5.29509	0.002179±0.000147	0.9902	21	(10)	5.33835	0.001854±0.000225	0.9693	21
3 Aug.-1 Sept.	(11)	5.28420	0.002244±0.000490	0.9541	12	(12)	5.30698	0.002123±0.000520	0.9468	12
(C) Growth in wet weight										
3 June-8 Sept.	(13)	4.96608	0.007133±0.000638	0.9830	21	(14)	5.12665	0.005888±0.000815	0.9606	21
3 Aug.-1 Sept.	(15)	4.69906	0.010324±0.001949	0.9650	12	(16)	4.82850	0.009315±0.001729	0.9660	12

The mean dates on which growth was initiated during 1976 were calculated as 10 April and 21 April for age 2 and age 3 menhaden, respectively (Equations (5) and (6) in Table 4). These estimates fell within the time period (March-early May) during which growth is believed to resume and the annular ring is formed (June and Roithmayr 1960).

Seasonal Growth Rate

In addition to these short-term estimates of daily growth rate described above, the total seasonal growth increment was determined for individual fish from the amount of growth of the scale and from back-calculations of growth in fork length and wet weight, since the 1976 annulus was formed. By early June, age 2 and age 3 menhaden had already grown considerably since their 1976 annulus was formed (Table 5). Age 2 menhaden had grown more in length and weight, and showed a greater exponential increment in size, than age 3 menhaden. These results mean that during the spring of 1976, either the age 2 fish had a higher instantaneous daily growth rate than age 3 menhaden, or they resumed growth in the spring earlier than the age 3 fish, or both.

By 8 September the mean growth of age groups 2 and 3 during 1976 was considerably greater than the average yearly growth rates of age 2 and age 3 menhaden in other years, as estimated from the back-calculations of size-at-age (Tables 2, 3). For example, during 1976 the scale annuli of age 3 menhaden indicated that when these fish were age 2, their total exponential increments in fork length and wet weight (i.e., their instantaneous yearly growth rates) were 0.2406 and 0.7805, respectively. In comparison, by 8 September the mean exponential increments in fork length and wet weight of age 2 menhaden during 1976 were 0.3256 and 1.0644. Similarly, age 4 menhaden caught during 1976 increased in fork length by 0.1608 and in wet weight by 0.5218 as age 3 fish during 1975. During 1976, the increments in fork length and wet weight of age 3 menhaden were 0.2700 and 0.8440 by 8 September. Some additional growth may have taken place after 8 September; June and Roithmayr (1960) found that growth of the scale margin in Atlantic menhaden continued until September or October.

Results indicate that significant differences in the growth rate of menhaden occur, probably because menhaden, found over an extensive geographic area during the summer, experience a wide range of temperature and food conditions that could affect growth. Further investigation into regional and annual differences in the instantaneous growth rates may provide a basis for determining which geographic regions can potentially contribute most to menhaden productivity and could provide considerable insight into ways of maximizing the yield from this fishery.

TABLE 5.—Seasonal growth of age 2 and age 3 Atlantic menhaden caught in Narragansett Bay during 1976. Absolute growth (in mm fork length and g wet weight), and the instantaneous growth increment since the formation of the 1976 annulus are shown.

Date of capture	Age 2 $\bar{x}\pm$95% C.L.	Age 3 $\bar{x}\pm$95% C.L.
3-10 June		
fork length at capture (mm)	203.7±1.5	212.2±1.2
back-calculated fork length at 1976 annulus (mm)	180.3±1.9	193.3±1.4
growth (mm)	23.4	18.9
exponential increment	0.1220	0.0933
wet weight at capture (g)	153.0±3.9	179.0±3.9
back-calculated wet weight at 1976 annulus (g)	102.0±3.6[1]	132.4±3.1[2]
growth (g)	51.0	46.6
exponential increment	0.4055	0.3016
8 September		
fork length at capture (mm)	247.9[3]	250.6[4]
back-calculated fork length at 1976 annulus (mm)	179.0±1.2[5]	191.3±1.0[5]
growth (mm)	68.9	59.3
exponential increment	0.3256	0.2700
wet weight at capture (g)	292.8[6]	303.5[7]
back-calculated wet weight at 1976 annulus (g)	101.0±2.4[1]	130.5±2.4[2]
growth (g)	191.8	173.0
exponential increment	1.0644	0.8440

[1]Using the length-weight relationshp for age 2 menhaden, where $\log_{10}$ fork length = −5.4799 + 3.3166 $\log_{10}$ wet weight, r = 0.963, and n = 633.
[2]Using the length-weight relationship for age 3 menhaden, where $\log_{10}$ fork length = −5.2138 + 3.2062 $\log_{10}$ wet weight, r = 0.956, and n = 1,224
[3]Average size on this date (Table 4, Equation (9)).
[4]Average size on this date (Table 4, Equation (10)).
[5]Based on data from all fish (Table 2).
[6]Average size on this date (Table 4, Equation (13)).
[7]Average size on this date (Table 4, Equation (14)).

Chemical Composition

The mean carbon, nitrogen, caloric, and ash contents and dry weight of menhaden from Narragansett Bay are summarized in Table 6. The ratio of dry weight:wet weight remained fairly constant in all samples; otherwise, there was a consistent trend in those fish with a high caloric content toward high carbon content and low nitrogren and ash content as a percent of dry weight (Fig. 4).

Ash, caloric, and moisture contents of the men-

TABLE 6.—Chemical composition of Atlantic menhaden collected from Narragansett Bay, R.I., between 3 June and 8 September 1976. Determinations were made on groups of five fish.

Constituent	$\bar{x} \pm 95\%$ C.L.	No. of samples
Dry wt/wet wt	0.334 ±0.018	19
Ash, proportion of dry wt	0.1094 ±0.0292	21
C, proportion of dry wt	0.5661 ±0.0671	18
N, proportion of dry wt	0.08028 ±0.00349	18
Kcal (g dry wt fish)$^{-1}$	6.238 ±1.006	20
Kcal (g ash-free dry wt fish)$^{-1}$	7.002 ±0.942	20

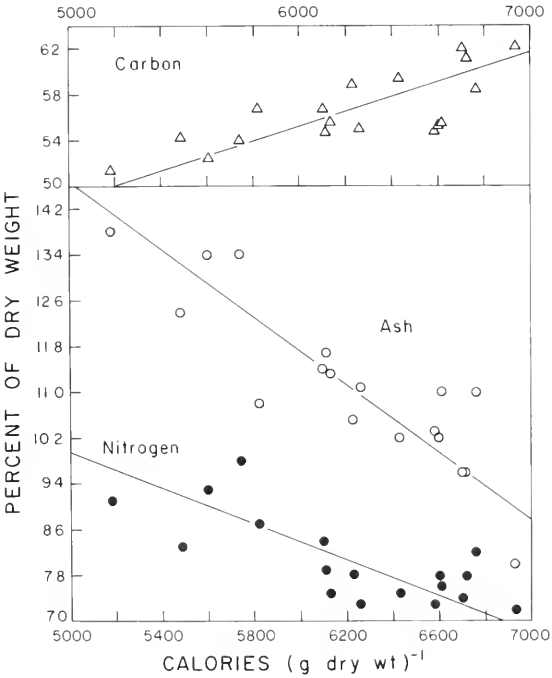

FIGURE 4.—Carbon, nitrogen, and ash contents (percent of dry weight) as a function of caloric content in Atlantic menhaden collected from Narragansett Bay.

haden in the present study are similar to those reported for Atlantic menhaden from Beaufort, N.C., (Thayer et al. 1972) and Chesapeake Bay (Dubrow et al. 1976). Menhaden are comparatively higher in percentage of dry weight and in caloric content than most other fish species (Dahlberg 1969; Perkins and Dahlberg 1971; Mayer et al. 1973; Sidwell et al. 1974; Small 1975; Kitchell et al. 1977; Foltz and Norden 1977).

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NOTES

HOMING AND FISHERIES CONTRIBUTION OF MARKED COHO SALMON, *ONCORHYNCHUS KISUTCH*, RELEASED AT TWO COLUMBIA RIVER LOCATIONS

In 1970 we conducted an experiment to determine if coho salmon, *Oncorhynchus kisutch*, released away from the rearing site would return to the release area and contribute to the fisheries there (Vreeland et al. 1975). We found the coho salmon returned almost exclusively to the release area and contributed to the fisheries near the release site. However, because the single fin marks applied were duplicated by other experimenters on the Pacific coast, we could not evaluate the contribution of the two groups to the ocean fisheries. We also surmised a possible detrimental effect of transportation on the survival of the group released downstream from the hatchery.

In 1972 we initiated a study with 1971-brood coho salmon to 1) confirm the homing results of the previous study, 2) eliminate possible differences in survival due to transportation, and 3) determine the contribution of the release groups to the Pacific coast fisheries.

Methods

We chose coho salmon originally from Klaskanine Hatchery in Oregon, the same fish stock used in the previous study. Hatchery personnel collected adults and took eggs at Little White Salmon National Fish Hatchery, located near Cook, Wash., on the Little White Salmon River about 1.5 km (1 mi) upstream from its confluence with the Columbia River and 242 km (150 mi) from the Pacific Ocean (Fig. 1). Coho salmon were reared at Willard National Fish Hatchery, 4.5 km (3 mi) up the Little White Salmon River from Little White Salmon Hatchery.

The two groups of fish were hatched and raised under uniform conditions in hatchery ponds. Fin clipping took place in September 1972 at Willard Hatchery. We applied two marks to the fish: adipose right ventral (Ad-RV) and adipose left ventral (Ad-LV).

Youngs Bay (Fig. 1) was selected as the release site, situated about 19 km (12 mi) upstream from the mouth of the Columbia River and fed by four small rivers: Lewis and Clark, Walluski, Youngs, and Klaskanine Rivers. We transported the Ad-RV marked coho salmon 253 km (157 mi) in about 4 h to Youngs Bay on 14 and 15 May 1973, where they were released at a public launch ramp. We transported the fish in two tank trucks, each 3,785 l (1,000-gal) capacity. Each truck was loaded with 462 kg (1,018 lb) of fish at 57.8 fish/kg (26.2 fish/lb) or about 26,700 fish. During the 2 d, we transported 106,852 Ad-RV marked coho salmon weighing 1,847 kg (4,072 lb) from Willard Hatchery to Youngs Bay (Table 1).

To maintain similar handling procedures and equalize any possible effects of transportation on survival, we transported the Willard Hatchery release for a time and distance similar to the Youngs Bay release. On 16 and 17 May 1973, we hauled 107,707 Ad-LV marked coho salmon weighing 1,835 kg (4,045 lb) in the same two tank trucks used for the Youngs Bay release. The fish were transported about 161 km (100 mi) for 3 h and 35 min on 16 May and 182 km (113 mi) for 3 h and 50 min on 17 May. Each truck contained about 458 kg (1,010 lb) of coho salmon. The hatchery crew released all the coho salmon from Willard Hatchery into the Little White Salmon River on 17 May.

We used catches of marked coho salmon in the fisheries and hatchery return data to determine the effect of release site on contribution and homing. Sampling for fin-marked coho salmon took place in 1973 and 1974 in the major Pacific coast salmon fisheries of Alaska, Washington, Oregon, and California, the Columbia River fisheries, and at potential hatchery return sites on the Columbia River. State fishery personnel sampled the Alaska troll fishery, the California, Oregon, and Washington ocean sport and troll fisheries, and the Columbia River gill net fishery. Personnel from National Marine Fisheries Service sampled catches from the Youngs Bay gill net fishery at two fish processing plants.

TABLE 1.—Numbers of marked coho salmon released in the Columbia River for the homing experiment. Ad-RV = adipose right ventral; Ad-LV = adipose left ventral.

Fin mark	Releases		Fish/kg	Release date	Release location
	No.	kg			
Ad-RV	106,852	1,847	57.9	14-15 May 1973	Youngs Bay
Ad-LV	107,707	1,835	58.7	17 May 1973	Willard Hatchery

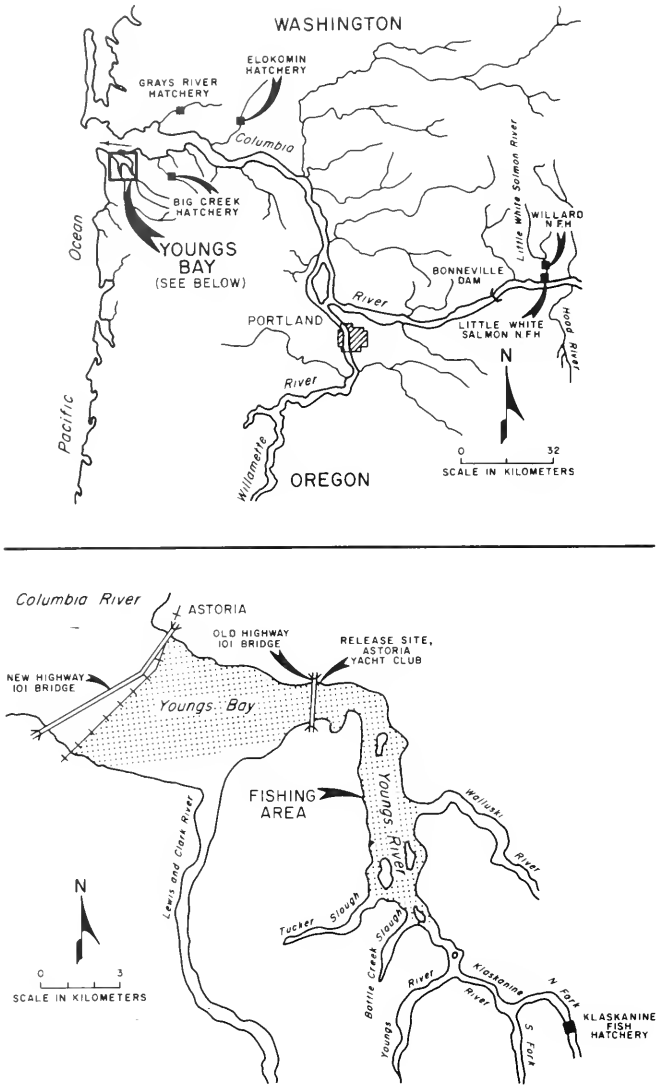

FIGURE 1.—Columbia River study area showing location of Willard and Little White Salmon National Fish Hatcheries and detailed features of the Youngs Bay region.

Returns of coho salmon to hatcheries near the two release sites were examined for marked fish to assess the effect of release site on homing. Hatchery personnel examined all returns to Little White Salmon National Fish Hatchery for marked coho salmon in the fall of 1973 and 1974. A series of waterfalls blocks access to Willard Hatchery; therefore, coho salmon released from Willard return to Little White Salmon Hatchery. In addition, State personnel examined all returns at the following hatcheries for marked coho salmon: Klaskanine Salmon Hatchery on the Klaskanine River (a tributary of Youngs Bay); Big Creek Salmon Hatchery on Big Creek near Knappa, Oreg.; the Elokomin Salmon Hatchery on the Elochoman River near Cathlamet, Wash.; and the Grays River Salmon Hatchery on the Grays River near Grays River, Wash. (Fig. 1).

Results

Homing

We compared 1) the location of catch within the Columbia River and 2) return sites of the two marked groups to determine the accuracy of homing to the release site.

The fish in this study returned almost exclu-

sively to the area of release, similar to fish in previous studies (Rounsefell and Kelez 1938; Taft and Shapovalov 1938; Donaldson and Allen 1957; Ellis 1968[1]; Jensen and Duncan 1971; Mahnken and Joyner 1973; Vreeland et al. 1975; Scholz et al. 1976). No Willard Hatchery release fish were caught in the Youngs Bay fishery, but 199 Youngs Bay release fish were caught in the fishery. Only two Youngs Bay releases were seen in hatchery returns, one at Klaskanine Hatchery and the other at Little White Salmon Hatchery (Table 2). Hatchery personnel observed only 26 Willard releases at Little White Salmon Hatchery. Construction in 1974 of a new barrier dam and fish ladder at the hatchery may have prevented some coho salmon from entering the hatchery ponds. However, the hatchery biologist at Little White Salmon Hatchery believed most fish entered the adult holding ponds prior to the ladder closure.[2]

The specificity of the homing we observed is apparently linked to the physiological stage of parr-smolt transformation. Work by Hasler (1966) and Carlin (1968) indicated the imprinting process occurs rapidly at the time of parr-smolt transformation. With steelhead trout, *Salmo gairdneri*, Wagner (1969) hypothesized the homing imprint is acquired rapidly before and/or during downstream migration. Mighell (1975)[3] found fish exposed to a new water source for as little as 4 h will imprint on the new source. Coho salmon released in a Lake Michigan tributary strayed extensively (Peck 1970). Hasler et al. (1978) postulated that this was due to releasing the fish after smolting had taken place. Jensen and Duncan (1971) described accurate homing with coho salmon released at "smolt size." Cooper et al. (1976) found a 2-d exposure to morpholine at the onset of smolting imprinted fish to the chemical as well as did a 30-d exposure. W. S. Zaugg (1975),[4] who has attempted to define more closely the onset of the parr-smolt transformation, feels the imprinting will not occur until a certain stage of the transformation is reached. Unfortunately, none of the authors (nor do we) indicate a stage of the parr-smolt transformation at time of release. Time of smolting and imprinting has yet to be defined closely enough to predict the homing location of fish released in different areas. Until more is learned, we expect varying results could occur with homing studies depending on when the fish are released.

TABLE 2.—Number of 1971-brood Youngs Bay and Willard Hatchery release coho salmon recovered at five Columbia River hatcheries, 1973 and 1974. Ad-RV = adipose right ventral; Ad-LV = adipose left ventral.

Hatchery	Youngs Bay release (Ad-RV)			Willard Hatchery release (Ad-LV)		
	1973	1974	Total	1973	1974	Total
Klaskanine	0	1	1	0	0	0
Big Creek	0	0	0	0	0	0
Grays River	0	0	0	0	0	0
Elokomin	0	0	0	0	0	0
Little White Salmon	1	0	1	2	24	26
Total	1	1	2	2	24	26

Fishery Contribution

We examined ocean and Columbia River catches of coho salmon to determine the contribution of both release groups to the Pacific coast fisheries. Fishery samplers saw 350 Youngs Bay releases and 78 Willard releases in 1973 and 1974 (Table 3). No coho salmon from either release were observed in the catches of Alaska commercial fisheries. Fisheries samplers in Canada did not examine coho salmon for multiple fin marks; however, on the average, Canadian fishermen land only 6% of all Columbia River hatchery coho salmon (Wahle et al. 1974). Catches of the two marked groups occurred primarily in the Washington, Oregon, and California marine fisheries and the Columbia River gill net fishery.

Total estimated catches for 1973 and 1974 of Youngs Bay and Willard release groups are 2,455 and 598, respectively. Catches in the Oregon and California troll fisheries contained over 50% of both marked groups (55% Ad-RV, Youngs Bay and 61% Ad-LV, Willard releases). Washington marine recoveries occurred primarily near the Columbia River, except for catches of Willard release coho salmon at LaPush on the north Washington coast. Landings of Willard release fish at LaPush comprised nearly one-half of the release caught in the Washington troll fisheries.

[1]Ellis, C. H. 1968. A return of adult coho salmon demonstrating a high degree of selectivity in homing. *In* Proceedings of the Northwest Fish Culture Conference, December 4-6, 1968, Boise, Idaho, p. 40-42. Unpubl. manuscr. Wash. Dep. Fish., 115 Gen. Admin. Bldg., Olympia, WA 98504.

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[3]Mighell, J. 1975. Some observations on imprinting of juvenile salmon in fresh and saltwater. *In* Summary notes from papers presented at homing workshop. Unpubl. manuscr., p. 11-12. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[4]W. S. Zaugg, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112, pers. commun., November 1975.

TABLE 3.—Observed (in parentheses) and estimated catches of marked 1971-brood coho salmon released from the two Columbia River sites and recovered in Pacific coast fisheries, by fishery type and year of capture.[1] Ad-RV = adipose right ventral; Ad-LV = adipose left ventral.

Location	Fishery type	Youngs Bay release (Ad-RV)				Willard Hatchery release (Ad-LV)			
		1973	1974	Total	Percent	1973	1974	Total	Percent
Alaska	Commercial	([2])	0	0	0	([2])	0	0	0
British Columbia	Commercial	([3])	([3])	([3])	—	([3])	([3])	([3])	—
	Sport	([3])	([3])	([3])	—	([3])	([3])	([3])	—
Washington									
Ocean	Troll	0	144(18)	144	6	0	47(9)	47	8
	Sport	0	219(32)	219	9	0	65(11)	65	11
Puget Sound	Commercial	0	0	0	0	0	0	0	0
	Sport	0	0	0	0	0	0	0	0
Oregon	Troll	0	668(84)	668	27	0	229(29)	229	38
	Sport	0	117(24)	117	5	12(1)	41(7)	53	9
California	Troll	0	694(65)	694	28	0	139(18)	139	23
	Sport	0	49(7)	49	2	0	5(1)	5	1
Columbia River	Gill net	0	365(14)	365	15	0	60(2)	60	10
	Indian[4]	0	0	0	0	0	0	0	0
	Sport	0	0	0	0	0	0	0	0
Youngs Bay	Gill net	6(2)	193(104)	199	8	0	0	0	0
Total		6(2)	2,449(348)	2,455	100	12(1)	586(77)	598	100

[1]Data obtained from: "1973 fin-mark sampling and recovery report for salmon and steelhead from various Pacific Coast fisheries" and "1974 Wire tag and fin-mark sampling and recovery report for salmon and steelhead from various Pacific Coast fisheries," Fish Commission of Oregon, Clackamas, Oreg.
[2]Not sampled.
[3]No sampling for multiple fin-marked coho.
[4]Setnet and dip net fisheries.

Overall fishery contribution rates for this study are lower than rates reported in studies conducted in the 1960's with coho salmon from Columbia River hatcheries. For all fisheries combined, the Youngs Bay release contributed 23.0 fish/1,000 released, and the Willard release contributed 5.6 fish/1,000 released. In a diet test at Washougal Hatchery (Senn and Noble 1968), the contribution of 1961-brood coho salmon, fed a diet similar to that fed the 1971-brood, was 51 fish/1,000 releases to the Pacific coast fisheries. Wahle et al. (1974) found the average contribution to the fisheries of 1965 and 1966 brood coho salmon was 55 fish/1,000 releases at Columbia River hatcheries. Fishery contributions of marked groups of 1967-, 1968-, and 1969-brood coho salmon at Cowlitz Hatchery ranged from 21 to 52 fish/1,000 releases.[5] In the earlier 1968-brood study, the Willard Hatchery release contributed 7.7 fish/1,000 releases to the Columbia River and Youngs Bay fisheries. We do not know the reasons for the poorer survival of the 1971-brood fish.

The release site significantly affected fishery contribution despite the low survival. We believe the Youngs Bay release survived at a higher rate than the Willard release fish because the Youngs Bay release contributed more heavily to all fisheries sampled than did the hatchery release. The contribution ratios of the Youngs Bay release to the Willard Hatchery release by fishery are 3.2:1 for Washington marine fisheries, 2.8:1 for Oregon ocean fisheries, 5.2:1 for California ocean fisheries, 9.4:1 for the Columbia River fisheries, and 4.1:1 overall. Differences between contribution rates when all fisheries are combined are significant ($\chi^2 = 137.36$).

We postulated two possible reasons for the higher fishery contribution of the Youngs Bay release. The Youngs Bay release possibly had a higher survival to the estuary than did the Willard hatchery release because the former group avoided downstream-migration mortalities from predation, gas bubble disease, and from passing over spillways or through turbines at the Bonneville Dam. A number of authors have reported the adverse effects of Columbia River dams on survival of juvenile salmonids (Schoeneman et al. 1961; Bell et al. 1967[6]; Long et al. 1968[7]; Bell and DeLacy 1971[8]; Ebel et al. 1973; Slatick et al.

[5]Hopley, C. W. 1975. Informal interim report on portions of 1967-, 1968-, and 1969-brood Cowlitz River coho stock timing evaluation. *In* Coho marking program on the lower Columbia River. Unpubl. manuscr., p. 9-43. Wash. Dep. Fish., 115 Gen. Admin. Bldg., Olympia, WA 98504.

[6]Bell, M. C., A. C. DeLacy, and G. J. Paulik. 1967. A compendium on the success of passage of small fish through turbines. Unpubl. manuscr., 268 p. U.S. Army Corps Eng., Portland Dist., Fish Eng. Res. Program, P.O. Box 2946, Portland, OR 97208.

[7]Long, C. W., R. F. Krema, and F. J. Ossiander. 1968. Research on fingerling mortality in Kaplan turbines—1968. Unpubl. manuscr., 7 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[8]Bell, M. C., and A. C. DeLacy. 1971. A compendium on

1975; Collins et al. 1975[9]; Collins 1976; Ebel and Raymond 1976). Ebel (1970) found groups of fall chinook salmon, *Oncorhynchus tshawytscha*, released below Bonneville Dam, had over twice the survival rate to the Columbia River estuary compared with a group released above the dam. The low flow of the Columbia River in 1973 caused a particularly serious passage and survival problem for juvenile salmon because most of the river flowed through the turbines at the dams.[10]

A second possible reason for the higher contribution of the Youngs Bay release is that the bay may provide a better rearing area than the hatchery release site because food is more abundant. A large concentration of the amphipod *Corophium salmonis* occurs in Youngs Bay, particularly in May, and is a major food item for coho salmon in the bay.[11] Abundant food could have given the Youngs Bay release an initial survival advantage.

Summary

We conducted this study to confirm previous results on the feasibility of creating or enhancing a fishery in a specific area by releasing hatchery salmon into that area. We compared the location of return and contribution with the Pacific coast fisheries of coho salmon released at two locations on the Columbia River. Two groups each of about 100,000 1971-brood coho salmon at Willard National Fish Hatchery were fin clipped: In May 1973 one group was released at Youngs Bay near Astoria, Oreg., and the other at Willard Hatchery. Both groups were transported an equal time and distance prior to release to equalize any possible effects of transportation on survival.

Marine sport and commercial salmon fisheries of the Columbia River and Youngs Bay, as well as Columbia River hatchery returns, were sampled for marked coho salmon in 1973 and 1974. Over one-half of both groups of marked fish were caught by Oregon and California marine sport and commercial fishermen. Recoveries of the remaining marked fish occurred in Washington, Columbia River, and Youngs Bay fisheries. The Youngs Bay release contributed 23 fish/1,000 releases to the Pacific coast fisheries, and the Willard Hatchery release contributed 5.6 fish/1,000 releases. The fish homed to the release site with little straying. Only one Youngs Bay release returned to Little White Salmon National Fish Hatchery.

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the survival of fish passing through spillways and conduits. Unpubl. manuscr., 144 p. U.S. Army Corps Eng., Portland Dist., Fish Eng. Res. Program, P.O. Box 2946, Portland, OR 97208.

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[10]Columbia River Fisheries Council. 1978. Recommendations of Columbia River Fisheries Council for in-stream flows in the Columbia and Snake Rivers. Unpubl. manuscr., 24 p. Columbia River Fish. Counc., Suite 1240, Lloyd Bldg., 700 N.E. Multnomah St., Portland, OR 97232.

[11]Durkin, J. T., S. J. Lipovsky, G. R. Snyder, and M. E. Tuttle. 1977. Environmental studies of three Columbia River estuarine beaches. Unpubl. manuscr., 78 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

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MOVEMENT PATTERNS OF BONEFISH, *ALBULA VULPES*, IN BAHAMIAN WATERS

The regular daily movement patterns of fishes appear closely related to predictable changes in their environment. Factors such as tidal fluctuations (Dodson and Leggett 1973; Stasko et al. 1973), light levels (Yuen 1970; Collette and Talbot 1972; Standora et al. 1972; McFarland et al. 1979), and temperature (Coutant 1975; Kelso 1976; Haynes et al. 1978; Langford et al. 1979) have been found to influence the cyclic movement of fishes. Until recently, most information on such movement patterns has been obtained primarily through direct observation. However, there are many situations in which direct visual methods are not feasible. An alternate means of obtaining such information has been provided by recent advances in the use of ultrasonic telemetry as a research tool.

Ultrasonic telemetry has become a valuable technique both in freshwater and deep marine environments. However, the use of ultrasonics in coastal waters is still in the early developmental stages. Rapid signal attenuation occurs under such conditions because of combined effects of the high conductivity of the water, vegetative growth, turbulence, and bottom reflection (Stasko and Pincock 1977).

This research attempted to use ultrasonics to determine movements and daily activity patterns of the bonefish, *Albula vulpes*, in Bahamian waters. The only prior attempt at scientifically studying bonefish movements in the western Atlantic region was by Bruger,[1] who initiated a

[1]G. E. Bruger, Research Biologist, Florida Department of Natural Resources, Marine Research Laboratory, 100 Eighth Ave. SE., St. Petersburg, FL 33701, pers. commun. May 1980.

comprehensive conventional tagging program on Florida bonefish. He met with no success, however, presumably due to the failure of the dart tags used. This current research thus represents the first attempt to use ultrasonic telemetry for this purpose.

Methods and Study Sites

This investigation was conducted in waters around a series of small islands or "cays" at the East End of Grand Bahama Island. The general environment here consists of mangrove, sand flats, creeks, lagoons, and offshore reefs. The north shores of these cays border the shallow waters of the Little Bahama Bank, while their south shores merge with the waters of the Northwest Providence Channel. Areas in which bonefish populations were frequently observed were selected as tagging and tracking sites; these areas are locally known as McLean's Town, Big Harbor, Little Harbor, Thrift Harbor, and Big Creek (Fig. 1). Each site represents a somewhat different habitat type: Portions of several are situated in protected lagoon areas between Abaco Islands and Grand Bahama Islands, and portions of others are located in shallow backwaters of East End, Grand Bahama, while two other locations are adjacent to open ocean and coral reefs.

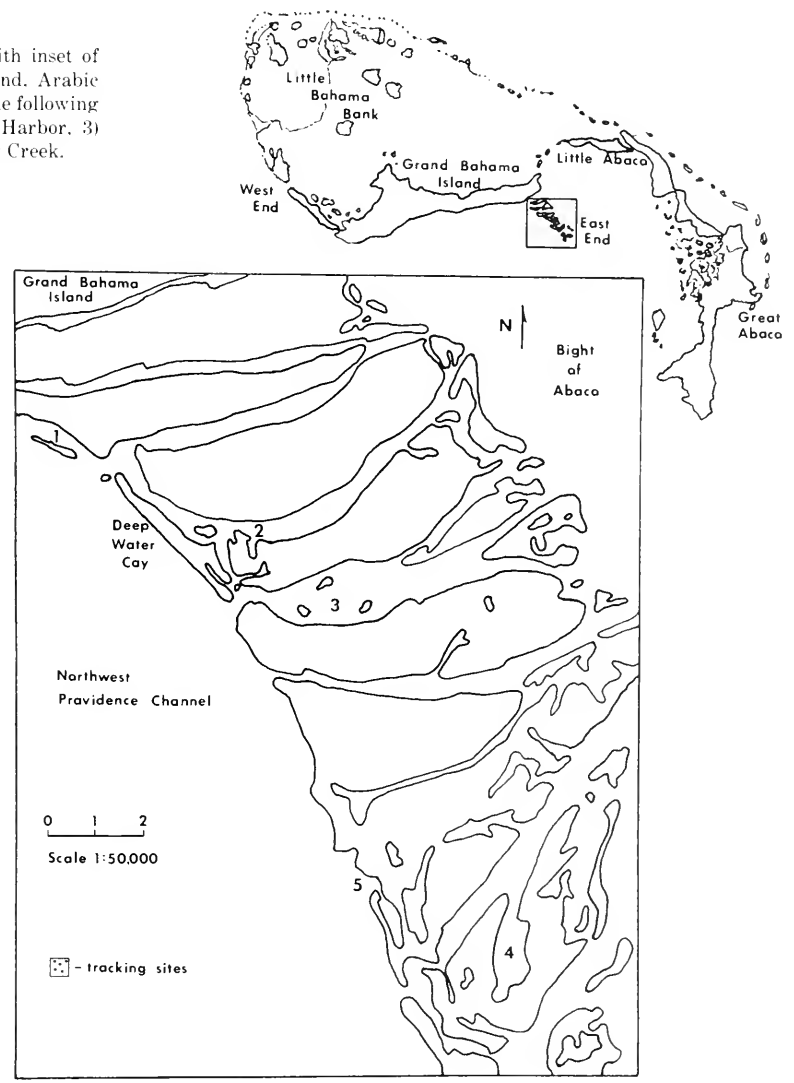

FIGURE 1.—Grand Bahama Island with inset of study areas in the vicinity of East End. Arabic numerals represent tracking sites at the following locations: 1) McLean's Town, 2) Big Harbor, 3) Little Harbor, 4) Thrift Harbor, 5) Big Creek.

The short-term (daily) movements of bonefish were monitored by an ultrasonic tracking system. Fish were captured by angling and gill nets. Bonefish were only minimally injured by the netting procedure, since the mesh size of 6.25 cm was chosen to restrain the fish without injury to the gills. Captured fish were removed by hand from the gill net and were held in a hand net for further treatment. Individuals, selected according to size (>2 kg) and physical condition, were equipped with ultrasonic transmitters. In tracking studies prior to 1981, the transmitter was placed in the stomach with a glass plunger (Henderson et al. 1966; Yuen 1970). During 1980, this technique often resulted, 3 out of 5 times, in disgorgement of the transmitter. Therefore, surgical implantation of the transmitter in the body cavity was used during 1981. Here, the fish was restrained ventral side up. Several scales were removed posterior to the pelvic fins and lateral to the midline, and an incision of 3-4 cm was made with a surgical scalpel. The transmitter was then inserted, and the incision sutured. This procedure is similar to that used by Hart and Summerfelt (1975). To aid in recovery, the fish was slowly worked forward and back in the water by hand to aerate the gills. The majority of the fish appeared to survive the implant and recovered without noticeable effect, provided predators of the bonefish were not in the immediate vicinity at time of release. Several individuals held in a saltwater holding tank for periods of 24-96 h showed no noticeable ill effects. Conclusions drawn from the observed movements of fish immediately after release are of questionable value, since behavior and movements may be strongly influenced by the process of capture and handling. Thus, only tracks initiated 24 h or more after release were considered to reflect normal behavior.

The transmitters were 58 mm long and 15 mm in diameter, weighed 3-4 g in water, and operated at a frequency range of 74-77 kHz. They were manufactured by either Smith Root Inc. or Sonotronics,[2] and were pulsed at different intervals (1-2 pulses/s), so that individual fish could be distinguished when several transmitters were operating in the same general area. Power for the pulse intervals was supplied by mercury batteries with a useful life of about 7-14 mo. Range was as wide as 0.5 km at times, but much narrower when the water was turbulent.

A Smith Root TA-50 and a Sonotronics digital (pulse/frequency display) receiver, with their respective hydrophones, were used to receive the signals. All tracking was conducted from a 4.5 m skiff equipped with two foot-controlled variable-speed electric motors. The hydrophones were mounted off the bow about 0.5 m below the surface, allowing the direction of a transmitting fish to be ascertained by pointing the bow in the direction of the strongest signal. Data recorded during tracking included location, water depth and temperature, tide state, time, and wind speed and direction. This information was generally recorded at about 30-min intervals, but more frequently when a tracked fish was moving rapidly. Location was accurately recorded on Bahamian land survey maps by using chartered landmarks in conjunction with depth.

To investigate long-term movements, a conventional tag and release program was initiated in February 1980. At the outset, Monel metal strap tags were crimped into the lower jaw. This method was replaced (January 1981) by the use of dart tags (FD 68B PVC) inserted adjacent to the dorsal fin, a procedure requiring less time and handling of the fish. These tags were of much heavier construction than those used by Bruger (1974). Tagging was concentrated in areas frequently fished and/or areas in which schools of bonefish were consistently seen.

Monthly collections of 20-30 bonefish were obtained from the study areas by nets and angling from June 1980 through December 1981, except September 1980. These data provided information on size distribution of captured individuals over the yearly cycle. Collections were obtained each month from the same general areas (indicated in Fig. 1).

Results

Between August 1980 and November 1981, 13 bonefish were implanted with ultrasonic transmitters and released. Of these, only three fish were relocated more than 24 h from time of release. Two of these fish, from McLean's Town Creek (50.5 and 53.5 cm FL (fork length)), were tracked for a period of 5 d each, with total tracking times of 16 and 30 h, respectively. The fish from Big Creek Lake (61.0 cm FL) was followed over a 100-d period for a total tracking time of 32 h (Fig. 2). Water depths in these areas ranged

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

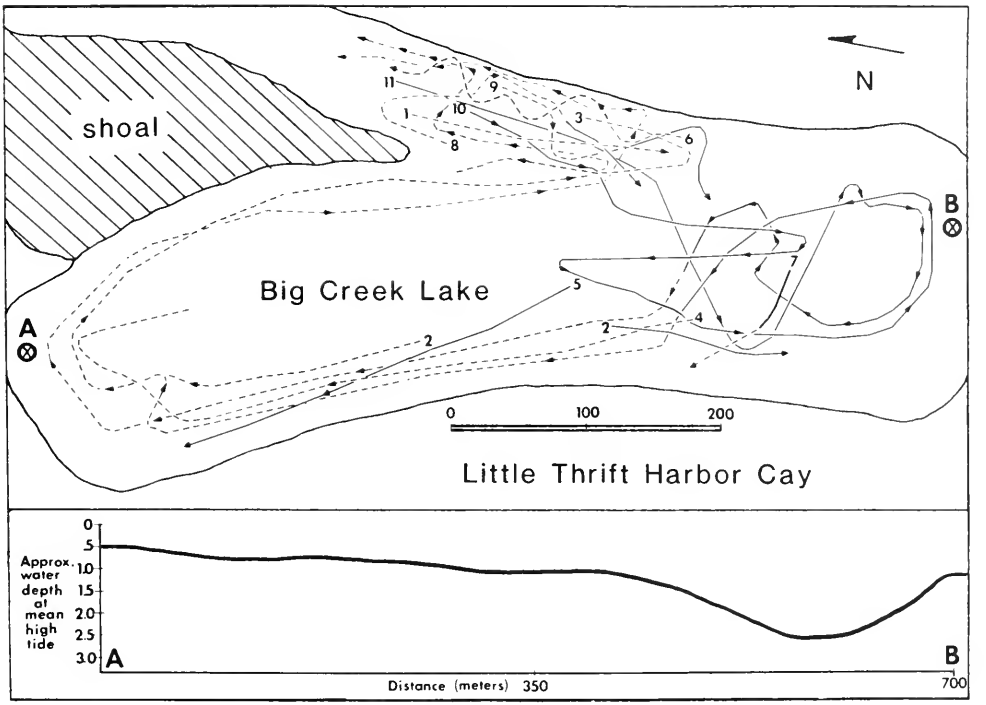

FIGURE 2.—Movements of a 61.0 cm FL bonefish in Big Creek Lake during 1981. The solid line denotes movement during falling tides, and the dashed line movement during a rising tide. The Arabic numerals denote the starting point and day of track, with ½-h intervals and direction of movement indicated by arrows. The time periods and dates of the individual tracks are: 1) 1630-1700, 14 April; 2) 0855-0925, 1615-1650, 15 April; 3) 1350-1435, 16 April; 4) 1557-1640, 18 April; 5) 1600-1700, 21 April; 6) 1200-1300, 22 April; 7) 1500-1530, 16 May; 8) 1200-1300, 20 May; 9) 0900-1000, 20 June; 10) 1200-2400, 23 June; 11) 1220-2420, 23 July.

from 0.1 to 4 m. Tracking occasionally extended into areas of <0.1 m depth, at which times movements were visually monitored by observing the exposed dorsal and caudal fins. Visual observations indicated that the fish generally remained near the substrate (<1 m). The range of water temperatures measured during a single track of any fish was no more than 8°C, with a low of 24°C and a high of 32°C.

The general pattern of daily movements was a retreat to deeper water on an ebbing tide and a movement into shallow water on a rising tide. This pattern can be clearly seen in the track of the fish from Big Creek monitored for 100 d (Fig. 2). A similar pattern was obtained by tracking the other two fish for 5 d each at McLean's Town. However, some variability was noted in the observed depth of fish movements as compared with the depth range available at the two locations. The fish at Big Creek was observed to move consistently into very shallow water (<1 m) with the rising tide. In contrast, the McLean's Town fish showed a variable response in depth-related movement. Also, "mudding" (a common term used to describe the turbidity resulting from fish feeding in bottom sediments) was observed only during low tide at Big Creek, but throughout the tidal cycle at McLean's Town. Nocturnal movements closely followed the same pattern.

From January 1980 through December 1981, 214 bonefish were tagged with Monel metal or dart tags and released in the same channels, bays, and flats of Deep Water Cay as they were captured. None of these fish were recaptured more than 24 h from time of release. Only a single collection resulted in recapture of tagged fish; this was made 4 h after the fish had been tagged.

Collection data provided a record of fish lengths and weights for each month (excluding September 1980) over a 19-mo period (June 1980-December 1981). The proportion of large fish (>55.5 cm FL) in these collections showed a pronounced regular seasonal change, with a strong

inverse relation to inshore water temperature (Fig. 3). That this change represents a movement of large fish rather than small fish from the flats during summer is strongly supported by numerous conversations with the guides, managers, and avid anglers of the Deep Water Cay Club. All of these persons made it clear that the catching of large (>55.5 cm FL) bonefish on the flats, although not common in winter months, is extremely rare in summer. The measurement of 55.5 cm FL, used in this paper to distinguish large from small fish, corresponds to the division between the fifth and sixth age-class of bonefish from the Florida Keys (Bruger 1974).

Discussion

Information gained from extended ultrasonic tracking of three individuals in two different areas suggests that bonefish display a regular pattern in daily movements in response to tidal changes. These movement patterns, although monitored on individuals, are probably representative of school movement because transmitter-implanted fish generally returned and remained with schools of bonefish (3-20 individuals) within 24 h of release. The observed differences in daily movements of bonefish in the two different areas may indicate the effects of differences among the two locations in such factors as bottom topography, food resource distribution, and predation. However, this point is in need of further research.

Information derived from ultrasonic tracking, conventional tagging, and repetitive collecting effort in specific areas indicates that movements of bonefish on a long-term basis are highly variable and without apparent pattern. Ultrasonic tracking has indicated that individual fish usually remain in a given localized area for less than a week. The two fish tracked for 5 d apparently left the McLean's Town area after that time, since extensive searching on the sixth day, up to 2 km from the area last observed, resulted in no relocation of the fish or the transmitter. Subsequent searches of the same area weeks and months later also were unsuccessful. Six other fish equipped with transmitters and released in apparently good condition were never relocated 24 h after release.

Another strong indication of the transient nature of bonefish movements is the lack of return of conventionally tagged fish, although a concentrated tag and recapture effort was made

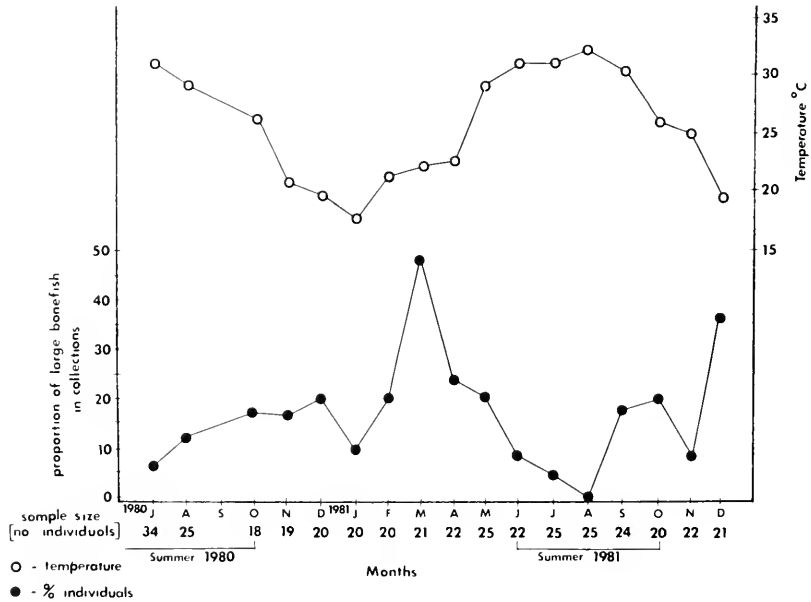

FIGURE 3.—Proportions of large individuals found in monthly collections of bonefish in the waters around Deep Water Cay, Grand Bahama. Each data point represents the percent of individuals collected each month exceeding 55.5 cm FL. No collection was obtained in September 1980. Open circles = temperature, solid circles = percent individuals.

in relatively restricted areas over a period of 18 mo. On one occasion only, fish (three individuals released 4 h prior to recapture) that had been previously tagged and released were recovered again. Failure to relocate fish conventionally tagged or fitted with transmitters could be the result of factors other than fish leaving the general area, such as mortality due to predation or shock of capture and handling, or tag failures. However, none of the evidence gained in this study suggests these factors were responsible.

The observed reduction in the proportion of large bonefish present on the flats during warm-water periods may correspond to a general offshore movement in preparation for spawning. Summer temperatures in the shallow areas of Thrift Harbor Creek have exceeded 34°C (Fig. 3). Although thermal requirements for *Albula vulpes* have not yet been experimentally determined, abnormally high temperatures are known to be deleterious to gamete formation among vertebrates (Guyton 1976; Langman 1981). Among fishes, it has been generally established that thermal requirements are even more restrictive for the reproductive process than for either growth or survival (Brett 1956). The hypothesis that large bonefish move offshore during summer is supported by the lore of the local Bahamian fishermen. They believe that larger individuals undergo a regular movement into deeper (15-25 m) waters at this time. During fall (October-November), these fish return inshore and aggregate in large numbers to spawn in shallow creeks. Erdman (1960[3]) reported a similar observation by commercial fishermen in Puerto Rico. At the time of this inshore movement, the fish are said to be lighter in color, with a highly silvery appearance. Personal examination by the senior author of fish collected by anglers from such aggregations revealed that nearly all individuals were sexually ripe. Additional evidence of seasonal offshore movements of bonefish comes from scuba divers in the Freeport area (pers. commun.), who have reported observing schools of thousands of bonefish suspended above the reefs. Böhlke and Chaplin (1968) cited a similar observation occurring off the Tongue of the Ocean, Green Cay, Bahamas.

[3]Erdman, D. S. 1960. Notes on the biology of the bonefish and its sports fishery in Puerto Rico. Paper prepared for the 5th Int. Game Fish Conf. Miami Beach, Fla., 11 p.

Summary

Bonefish appear to remain in a specific location (e.g., creek, small bay, channel, etc.) for a period usually not exceeding several days, and then move on to other locations. While at a given location, there is a distinct pattern to daily movements in response to tidal fluctuations, but long-term movements appear to be highly variable, with no definable pattern seen. In summer, larger individuals are rarely found on the flats. Their reappearance in the fall concurs with a rapid drop in water temperature at that time of the year.

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ANALYSES OF FEEDING IN TWO MARINE COPEPODS FROM SANTA MONICA BAY, CALIFORNIA

Understanding the feeding strategies of herbivorous, planktonic copepods is an important step in determining how primary production is partitioned in coastal marine food webs. The conditions under which selective feeding occurs among these animals vary, and are defined both by the species and the environment (Poulet 1974; Poulet and Marsot 1980; Donaghay 1980).

Although it is desirable to study feeding behavior in natural zooplankton assemblages, this is often difficult. Identification of phytoplankton in the gut by standard dissection and microscopic techniques is labor intensive, and usually qualitative. Furthermore, it is impossible to identify many of the soft-bodied organisms which might have been consumed. For this reason, much of the work on food selection in copepods has been restricted to the laboratory, where cultivated foods (Frost 1972) or natural particles (Poulet 1978) have been offered to the animals. While such studies have provided valuable information, they have been limited by the variety of foods which can be offered and by other technical problems (Mullin 1963; Harbison and McAlister 1980). Studies employing gut contents analysis of animals collected in the field using gut fullness (Hayward 1980; Huntley 1980) or chlorophyll a fluorescence as an estimate of total phytoplankton biomass in the gut (Mackas and Bohrer 1976; Boyd et al. 1980) have answered questions about when and where certain zooplankton feed, but usually provide only indirect data on the kinds of phytoplankton actually ingested. Dagg and Grill (1980) showed that the rate of particle ingestion is often not solely a function of concentration and suggested that food quality may be important in explaining the variability observed in the relation between feeding rate and particle concentration.

To understand the processes involved in food selection it is necessary to determine directly the types of materials in the guts of the copepods being studied. Such an analysis must be capable of detecting soft-bodied phytoplankton as well as diatoms and armored dinoflagellates, and of providing some indication of the relative importance of different taxa in the diet at a given time. We have been especially interested in the importance of the green algae to zooplankton feeding in coastal waters. Information in this area is rela-

tively scarce despite the periodic importance of green algae in the coastal flora (C. Lorenzen unpubl. data).

In September 1980, the cyst (phycoma) stage of *Halosphaera* sp. (Prasinophyceae) was observed in Santa Monica Bay, Calif., providing an opportunity to study its importance in the feeding of two calanoid copepods, *Acartia tonsa* and *Calanus pacificus*. Since chlorophyll b is present only in the green algae (Chlorophyceae, Prasinophyceae, Euglenophyceae) and chlorophyll c is present in the diatoms, dinoflagellates, chrysomonads, Haptophyceae, and Cryptophyceae (Meeks 1974; Parsons et al. 1977), we sought to compare water column concentrations of chlorophyll pigments with those in the guts of animals collected in various parts of the bay.

Methods

Samples were collected at two of three stations in Santa Monica Bay (Fig. 1) on 12 and 26 September 1980. On 12 September, stations 7B and N6 were sampled. On 26 September, stations 7B and N4 were occupied. All samples were taken between 0700 and 1200 h.

Depth integrated water samples were collected by lowering a submersible pump through the water column (to the same depth as zooplankton were collected; see below) at a constant rate and by pumping into a 122 l plastic container. The contents were mixed thoroughly, and 1 l samples were withdrawn and fixed in 3% buffered Formalin[1] for phytoplankton counting and identification, using the method of Palmer and Maloney (1954). Five hundred ml water samples were frozen for pigment analysis. In the laboratory, these were passed through 0.45 μm filters (Nucleopore) at low vacuum (<100 mm Hg), and pro-

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

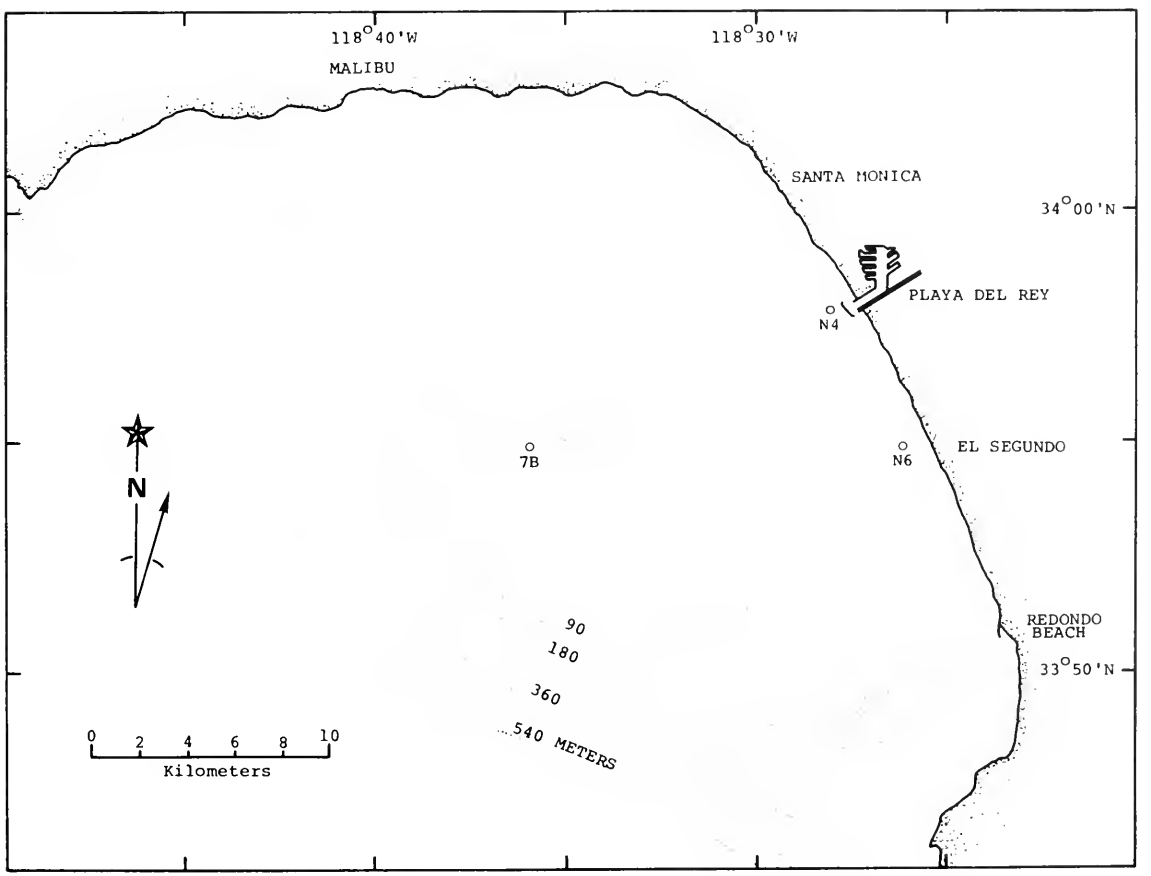

FIGURE 1.—Station locations.

cessed for chlorophylls a, b, and c by the trichromatic method (Strickland and Parsons 1972), using the equations of Parsons and Strickland (1963). Unfortunately, these equations do not give accurate estimates of chlorophyll b or c, and despite numerous attempts to improve their accuracy, no set of equations has been completely satisfactory (Jeffrey 1968, 1981; Jeffrey and Humphrey 1975). However, if the errors for gut and water samples are assumed to be the same, then comparisons can be made between pigment concentrations in guts and water. To test this, *Acartia tonsa* were starved for 24 h and a sample of animals was examined microscopically to ensure that the guts were empty. Pure cultures of the diatom *Thalassiosira fluviatilis* were added to half of the flasks containing the copepods. The animals in the remaining flasks were not fed. After 4 h, the animals in all of the flasks were processed for chlorophyll pigments as described below. We chose to feed a diatom in this experiment to find out if chlorophyll a or c might, during digestion, be converted into a product absorbing at the wavelengths used in measuring chlorophyll b (not found in diatoms). Table 1 suggests that this did not occur. Low levels of chlorophyll b were detected both in the culture and the fed animals but not in the starved animals, indicating that there was some contaminant in the culture or a small error in the equation at high chlorophylls a and c concentrations. Pigment ratios in the culture and the guts of animals fed from the culture were fairly stable.

Copepods for gut contents analysis were collected from 7 to 10 vertical tows of a CalCOFI vertical tow net (335 μm mesh). Tows were made from 70 m at station 7B and from near-bottom at stations N4 and N6. The tows took 2-3 min each to complete and were made in rapid succession. The ship was kept on station during the entire sampling period. On the cruise of 12 September, adult *A. tonsa* and *C. pacificus* were immediately separated from the rest of the catch. Half of each sample was washed in filtered (0.5 μm) seawater and frozen, and the other half was maintained in aerated, filtered seawater for 24 h allowing them to clear their guts of food prior to freezing. This empty gut group was used to detect absorbance at wavelengths used in chlorophyll analysis that was not due to chlorophyll. On 26 September, collections were made in a similar manner, except that half of the entire catch was washed with filtered seawater and frozen and the other half was maintained alive for 24 h in filtered seawater prior to freezing. Specimens for analysis were separated from the rest of the catch in the laboratory.

Chlorophyll a analysis of gut contents was conducted by macerating 50-200 animals of each species of full and empty gut groups in 90% acetone and by reading absorbances in triplicate at wavelengths of 750, 665, 645, and 630 nm on a Beckman model 34 spectrophotometer. Chlorophylls a, b, and c concentrations were computed by the trichromatic equations of Parsons and Strickland (1963). Chlorophyll degradation products (pheopigments) in the gut contents were computed as described by Strickland and Parsons (1972) and were considered as part of the total chlorophyll because the processing of food in the gut rapidly degrades chlorophylls. Since our interest was in how much plant material was present and not in the rate of food processing, we include both chlorophyll and its degradation products as a single indication of plant biomass in the gut.

Gut fullness was estimated in *A. tonsa* collected on 26 September. The animals were "cleared" by immersion in 85% lactic acid for 30 min and then examined under 25× magnification (Hayward 1980). Gut fullness was estimated independently by each author and the average of the two estimates was recorded. Attempts were made to estimate gut fullness in *C. pacificus*, but there was disagreement between estimates because the lactic acid did not clear the animals well.

TABLE 1.—Ratios of chlorophyll pigments in a culture of *Thalassiosira fluviatilis* and in *Acartia* guts when the animals were starved or fed the phytoplankton culture.

Chlorophyll pigments	Culture	*Acartia* guts	
		Starved	Fed
a/b[1]	56.91	ND	60.00
a/c	1.21	0.30	1.09
b/c	0.02	0	0.02

[1]Chlorophyll a levels per milliliter of culture = 0.24 μg, per animal = 12 ng
ND = a ratio that could not be computed, since chlorophyll b was not detected.

Results

Phytoplankton density and community structure were similar at station 7B on both sampling dates. Cell density averaged 8-10 × 10^3 cells/l. The majority of phytoplankton species found were dinoflagellates (35% of the community), dominated by *Gymnodinium* spp., and diatoms

(35% of the community), dominated by *Skeletonema costatum*. Cysts of *Halosphaera* sp. composed about 20% of the community on both dates; the motile form was not detected. Coccolithophorids composed about 10% of the cells counted. Mean chlorophyll a concentrations at the station were 0.56 and 1.16 μg/l on 12 and 26 September, respectively.

At stations N4 and N6 there were about 10^5 phytoplankton/l on each occasion. About 60% of the phytoplankton in the samples were diatoms of the genus *Chaetoceros*. Other diatom species composed about 25% of the community, and dinoflagellates made up 10%. *Halosphaera* cysts, small unidentifiable spherical cells (some of which probably contained chlorophyll b) and coccolithophorids made up about 5% of the community. Mean chlorophyll a concentrations were 1.54 and 1.92 μg/l on 12 and 26 September, respectively.

Figure 2a, b summarizes gut fullness estimates for 50 *A. tonsa* from stations N4 and 7B. At station N4 (Fig. 2a), 70% of the animals exhibited >40% gut fullness; mean gut fullness was 55.5%. At station 7B (Fig. 2b), about 20% of the animals exhibited >40% gut fullness; the mean was 31% fullness.

Gut chlorophyll a concentrations (corrected for the absorbance of empty gut animals) are shown in Table 2. Comparative water column data are also provided. The concentration of chlorophyll a in the gut contents of *A. tonsa* increased with seaward distance. Animals collected at station 7B had, on average, 40 times more chlorophyll in their guts than the same species at nearshore locations.

The chlorophyll b and c content of the water column diminished slightly with distance from shore (Fig. 3a). In the guts of *Acartia* these pigments increased sharply from nearshore to offshore stations (Fig. 3b).

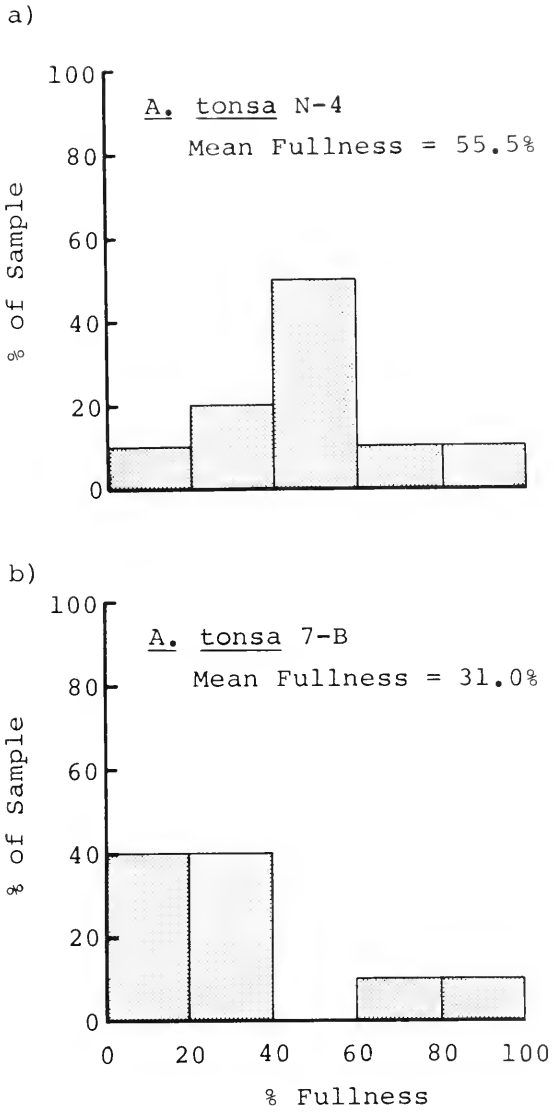

FIGURE 2.—Percent gut fullness of *Acartia tonsa* at stations a) N4 and b) 7B on 26 September 1980. $N = 50$.

TABLE 2.—Chlorophyll a in two copepod species, *Acartia tonsa* and *Calanus pacificus*, at stations of varying distances from shore, with comparative water column[1] values.

Station	Distance from shore (km)	Species (sample size)	Chlorophyll a		
			Gut (±SD) (ng per animal)	Background (ng per animal)	Water (±SD) (μg per liter)
[2]N4	0.6	*A. tonsa* (200)	0.12 (0.01)	0.16	1.92 (0.36)
[3]N6	0.9	*A. tonsa* (160)	0.18 (0.01)	0	1.54
[3]7B	18.0	*A. tonsa* (200)	6.10 (0.003)	0	1.16 (0.15)
[2]7B	18.0	[4]*C. pacificus* (55)	13.24 (0.003)	0.001	0.56

[1]Water column chlorophyll a values are mean ± standard deviation (in parentheses) from water column composite samples. On 12 September only one sample was analyzed, on 26 September, 5 subsamples of the water column composite were analyzed.
[2]Data from cruise on 26 September 1980.
[3]Data from cruise on 12 September 1980.
[4]Numbers of *C. pacificus* at the nearshore stations were too low (<5 animals/tow) for the analysis to be conducted.

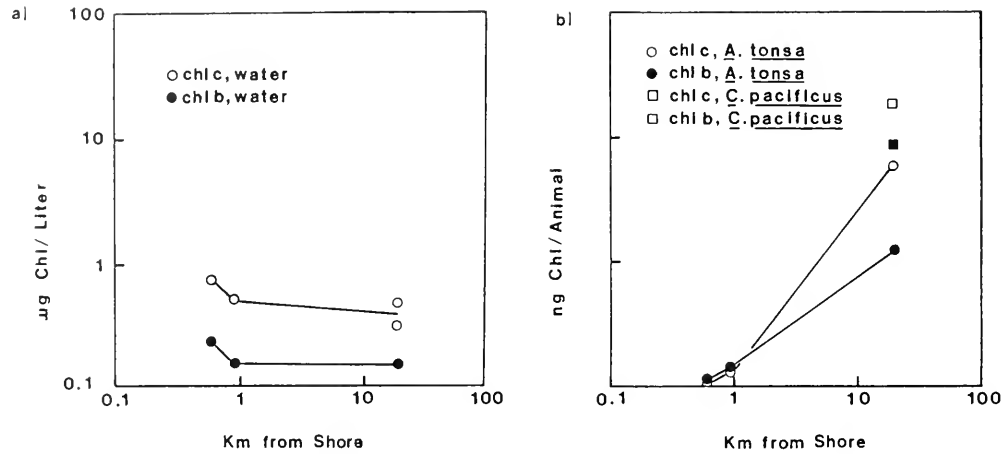

FIGURE 3.—a) Mean chlorophyll b and c concentrations in water samples plotted relative to distance from shore. b) As in a) but for pigments in the gut contents of *Acartia tonsa* and *Calanus pacificus*.

If the ratio of the chlorophyll b or c to its sum, T (= b + c), is the same in the gut of a copepod as it is in the water, then it might be reasoned that feeding on phytoplankton was not selective. Variations from unity would be interpreted as an indication of food selectivity. We define relative selectivity indices for chlorophyll b (RSI_b) and chlorophyll c (RSI_c) as:

$$RSI_b = \frac{(b/T)_g}{(b/T)_w} \quad (1)$$

$$RSI_c = \frac{(c/T)_g}{(c/T)_w} \quad (2)$$

where g and w represent the ratios in the gut and water, respectively.

RSI values, presented in Table 3, indicate selectivity for chlorophyll b-bearing organisms by *Acartia* at stations N4 and N6. At station 7B, *Acartia* evidenced a weak selection of chlorophyll c-bearing organisms and *Calanus pacificus* selected for chlorophyll b-bearing organisms.

TABLE 3.—Relative selectivity indices for chlorophyll b (RSI_b) and chlorophyll c (RSI_c) by *Acartia tonsa* and *Calanus pacificus*.

Station	Species	RSI_b	RSI_c
[1]N4	*A. tonsa*	2.04	0.62
[2]N6	*A. tonsa*	2.48	0.61
[2]7B	*A. tonsa*	0.73	1.08
[1]7B	*C. pacificus*	1.20	0.93

[1]Data from cruise on 26 September 1980.
[2]Data from cruise on 12 September 1980.

Discussion

There were clear differences in the gut contents of *Acartia* from near- and offshore locations. Gut fullness was higher in copepods from nearshore than from those offshore (Fig. 2), but the amount of chlorophyll a in the guts of animals collected nearshore was substantially lower than in the guts of animals from offshore locations (Table 2). Apparently materials other than phytoplankton composed a relatively large portion of the diet of the nearshore animals. Evidence from laboratory studies (Poulet 1973; Heinle and Flemer 1975; Richman et al. 1977; Roman 1977) suggests the possibility of a detrital or animal component in the diet of *Acartia* when these foods are available.

The RSI indicates that *C. pacificus* was feeding selectively on phytoplankton containing chlorophyll b at station 7B. The only green alga detected by microscopic analysis of water samples at this location was *Halosphaera* sp. Although it is possible, even likely, that other green algae were present, the typical chlorophytes and euglenoids were not observed, and, unlike the nearshore stations, nanoplanktonic green algae appeared to be absent. We assume, therefore, that *Halosphaera* was at least the dominant source of chlorophyll b in the water, and constituted the greater portion of the chlorophyll b signal in the *C. pacificus* gut. Since we cannot test this assumption, what follows must be considered somewhat speculative. However, we suggest that under the conditions observed in Santa Monica Bay at the time, selective feeding by *Calanus* on *Halosphaera* cysts

would be energetically advantageous to the animal.

Although many calanoid copepods, including *C. pacificus*, are recognized omnivores (Landry 1980), there have been numerous reports that *C. pacificus* will remove certain types of particles from the water, apparently in preference to others (Gifford et al. 1981). Therefore, the indication of selective feeding is not surprising. It is difficult, however, to explain the mechanisms driving this selection. It has been held that food selection is often passive in nature. For instance, the intersetal distance may facilitate the capture of certain-sized particles over others (Frost 1972; Wilson 1973), and accidental encounter may result in the most abundant particles being most commonly ingested (Poulet 1974). However, explanations based on passive feeding modes have been inadequate in several situations (Huntley 1980), and the work of Poulet and Marsot (1980) and Friedman (1980) suggests that morphological adaptations exist among the copepods which would permit a high degree of food selection based on the active detection of mechanical and chemical stimuli.

Most enlightening have been the cinematic evidence and physical arguments of Koehl and Strickler (1981) that copepods used the feeding appendages as paddles to move water to the second maxillae, rather than as strainers to filter it. This being the case, the selection of large particles, observed by Frost (1972), Gifford et al. (1981), and many others, would seem due to an active preference for these particles under certain conditions rather than the passive collection of material in the appendages. This is not to imply that copepods never ingest nanoplankton or feed passively, as we know they do. Rather, we suggest that active food selection may be quite common, even typical, in *C. pacificus*.

To understand the adaptive significance of selective feeding on large particles, it is necessary to consider the circumstances under which this sort of feeding might be most useful. Landry (1981) suggested that when the abundance of diatoms decreases in the water, adult *C. pacificus* begins to prey on copepod nauplii. An explanation of this behavior would be that when small particles (diatoms) become scarce and nauplii relatively abundant, it is energetically efficient to capture the larger biomass units (nauplii).

The low phytoplankton density observed during the present study is characteristic of Santa Monica Bay in the fall (Kleppel and Manzanilla 1981). We can extend Landry's (1981) argument somewhat by suggesting that the waning of diatom-sized particles might cause a shift in feeding to large biomass units represented by the cysts of *Halosphaera*. To get a feeling for the advantage of feeding on these cysts in relation to diatoms, we can compare rough estimates of the carbon in a diatom with that of the *Halosphaera* cyst and its rosettes (the individual units of the cyst which will mature into 200-550 motile cells), using equations based on cell volume (Strathmann 1967). We stress that such estimates have wide confidence intervals and should be considered on the basis of scale rather than accuracy.

The diameter of a mature *Halosphaera* cyst ranges from 200 to 800 μm, depending on species (Parke and den Hartog-Adams 1965; Boalch and Mommaerts 1969). The cysts we observed were somewhat smaller, 100-150 μm, indicating that they were not mature. This may explain why no motile cells were detected. Using the smaller measured diameter (100 μm), we calculate a carbon content of 0.031 μg/cyst. Considering only the rosettes (diameter based on literature values = 15-20 μm for the smallest units; Parke and den Hartog-Adams 1965) and assuming them to be round discs, 2 μm thick, we calculate the carbon content of one rosette to be 56-92 pg. If there are 200 rosettes/cyst, then the carbon content of the rosettes in one cyst is 0.011-0.018 μg.

Using the volume of *Skeletonema costatum* (the dominant diatom at station 7B) equal to 1,390 μm^3 (Parsons et al. 1961), the cellular carbon content estimated by the Strathmann equation is 91 pg. Since *S. costatum* typically forms chains 4-10 cells in length, the carbon content of a chain would be 3.7×10^{-4} to 9.1×10^{-4} μg. This is nearly two orders of magnitude lower than the carbon content of one *Halosphaera* cyst or its rosettes.

Although we stress that these estimates are crude and we recognize that numerous factors will affect the actual carbon content of a cell, the magnitude of the difference between the estimated carbon in *Halosphaera* and *Skeletonema* nonetheless seems significant. It would appear that selective feeding on *Halosphaera* would have a distinct advantage for *C. pacificus* by providing a large energy ration with each capture. This would seem of obvious value in ecosystems characterized by patchy food supplies.

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DISTRIBUTION, SIZE RELATIONSHIPS, AND FOOD HABITS OF JUVENILE KING-OF-THE-SALMON, *TRACHIPTERUS ALTIVELIS*, CAUGHT OFF THE OREGON COAST

The king-of-the-salmon is a strikingly colored ribbonfish of the family Trachipteridae that occurs in the oceanic and coastal waters of the eastern Pacific Ocean, from Chile to Alaska. Captures have been recorded from the coastal regions and offshore halfway to the Hawaiian Islands. Specimens have also been taken in coastal waters and estuaries along the United States and Canadian shores on rare occasions (Hart 1943; Walker 1953). Their lower depth limit is not known, but individuals have been taken from the surface down to at least 650 m (Fitch 1964).

Spawning apparently occurs in the open ocean throughout the year, but is probably concentrated in the spring. Plankton surveys off California have recorded the largest catches of larvae during the months of June and July (Fitch 1964). Bongo net and neuston net collections from northern California, Oregon, and Washington frequently contained eggs in April and May 1980, but larvae were rarely taken (Kendall and Clark[1]). August 1980 samples contained relatively few eggs (Kendall and Clark[2]). Egg densities during the spring sampling reached 25 eggs/10 m^2, and the eggs were found from 5 to 320 km offshore (Kendall[3]).

Throughout the early life stages, allometric growth reduces the proportionate size of the fins and alters the body form by increasing the relative size of the posterior portion of the fish (Sette 1923; Hubbs 1926). Fitch (1964) examined the otoliths of five individuals to determine their ages. His fish ranged from a 400 mm juvenile with an estimated age of 1 yr to a 1.5 m adult with an age of 7 yr.

The stomach contents of several adults show that these fish eat whole micronectonic organisms (e.g., small squid, epi- and mesopelagic fishes) as well as macrozooplankton such as euphausiids (Fitch 1964). Roedel (1938) presented a qualitative list of the gut contents of five juveniles (about 100-200 mm long) taken from the stomach of a longnose lancetfish, *Alepisaurus ferox*, caught off Santa Monica, Calif. Copepods were found in three of the stomachs, while polychaetes and fish larvae were each found in one stomach.

During 1980 and 1981, 44 juvenile king-of-the-salmon were collected with a purse seine during a study of the ecology and migration of juvenile salmonids off the Oregon coast. This paper presents an analysis of the spatial distribution, size relationships, and the feeding habits of these unusual fish.

[1]Kendall, A. W., Jr., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and Northern California April-May 1980. Northwest and Alaska Fish. Cent. Process. Rep. 82-11, 44 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.
[2]Kendall, A. W., Jr., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and Northern California August 1980. Northwest and Alaska Fish. Cent. Process. Rep. 82-12, 43 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.
[3]Arthur W. Kendall, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112, pers. commun. January 1983.

Materials and Methods

In June 1980 and May, June, July, and August 1981, 10-d sampling cruises were conducted. In 1980, 44 collections were made with a purse seine. Six sets were made during the night at two stations in 2,100-2,200 m of water about 100 km offshore from the mouth of the Columbia River. Thirty-five sets were made during the day along three transects located north and south of the mouth of the Columbia River and off the mouth of the Yaquina River. These transects extended from the 40 m isobath to 40 km offshore. An additional three sets were made along the shore 40-50 km south of the Columbia River. During the 1981 cruises, 273 sets of the purse seine were made along 12 transects, from north of the Columbia River to south of Coos Bay (Fig. 1). Transects were sampled from the 40 m isobath to distances ranging from 10 to 50 km offshore. Because of time constraints, not all 12 transects were sampled on each cruise. Both day and night samples were taken in 1981. Secchi depths were determined during day hauls made in June, July, and August 1981.

Samples were collected with herring purse seines operated from chartered commercial fishing vessels. The cruises in 1980 and in May and June 1981 used a 457 m long purse seine borrowed from the National Marine Fisheries Service in Seattle. This net fished about 9 m deep and sampled about 150,000 m^3 of water. A 457 m long commercial herring seine was used in July and August 1981; it fished about 15 m deep and enclosed about 250,000 m^3 of water. Both nets were constructed of 30 mm stretched mesh.

Immediately after capture, king-of-the-salmon were preserved in 10% Formalin[4] and returned to the laboratory. Preserved lengths and weights were then measured, and stomachs were removed for analysis. Stomach contents were sorted to the lowest practical taxonomic level. Prey were then counted, blotted dry, and weighed to the nearest 0.001 g.

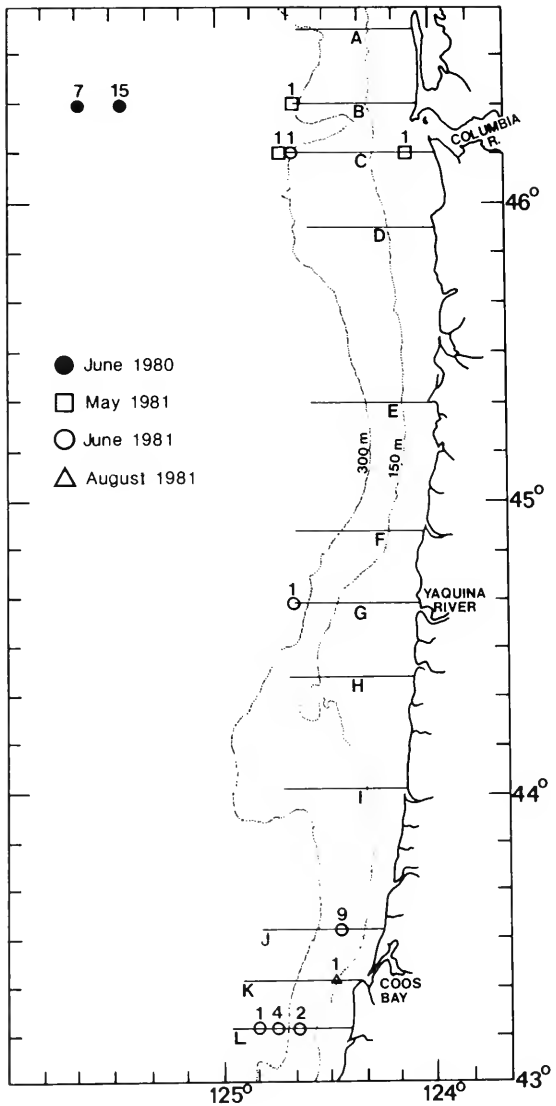

FIGURE 1.—Transects off the Oregon coast sampled during 1980 and 1981, and locations of capture of juvenile king-of-the-salmon. Numbers above symbols indicate how many juveniles were taken at that station.

Results and Discussion

In June 1980, 22 juvenile king-of-the-salmon were collected in five of the six night sets made 100 km offshore from the mouth of the Columbia River. No other specimens were collected in any of the sets made closer to the shore in 1980. In 1981, specimens were taken in both day and night sets. Sixteen juveniles were taken from the Coos Bay region in June and one was taken in August, which were the only months that this area was sampled. Four juveniles were taken offshore from the Columbia River in May and June, and a single fish was caught at the westernmost station of the Yaquina River transect in June (Fig. 1).

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

Forty-three of the 44 juveniles collected throughout this study were taken in May and June, while none were caught in July, and only one was taken in August. The high abundance of these fish in the late spring and early summer samples may indicate the presence of seasonal variation in their distribution.

During the sampling of each transect, a distinct boundary separating green coastal water from blue oceanic water was generally observed. All but one of the juveniles were taken west of this front, on or beyond the 150 m isobath. Secchi depths at the locations of capture of juveniles in June and August 1981 ranged from 11 to 25 m. In contrast, Secchi depths in the green coastal water were generally <10 m. The abundance of juveniles in the Coos Bay region is probably a reflection of the narrow continental shelf there and the steep depth gradient within several kilometers of shore. Blue oceanic water with Secchi depths of 10-25 m was found to extend to within 5-10 km of the coast in June, and right up to the beach in August.

The fish taken offshore in 1980 ranged in size from 68 to 509 mm SL, and weighed from 1.0 to 78.4 g. Juveniles collected inshore in 1981 ranged in length from 70 to 245 mm SL and weighed from 1.8 to 17.5 g. All 11 of the specimens >250 mm SL were taken offshore. The preserved length-weight relationship of 40 undamaged specimens can be summarized by a power curve regression equation: $W = 2.04 \times 10^{-4} L^{2.06}$ ($r^2 = 0.99$; Fig. 2).

The specimens collected offshore in 1980 and inshore in 1981 relied, as would be expected, on

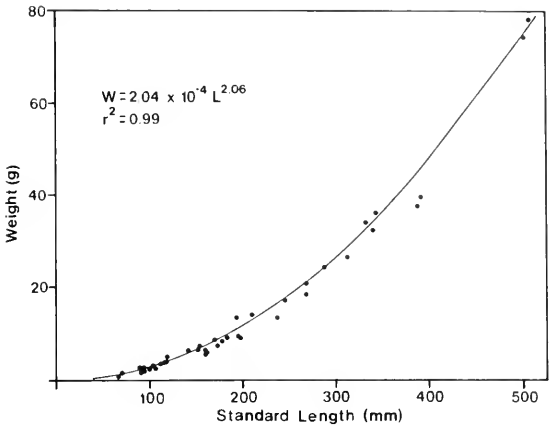

FIGURE 2.—Length-weight relationships of 40 undamaged, preserved juvenile king-of-the-salmon.

different planktonic food sources. All specimens contained at least some items in their stomachs, but the total biomass per stomach was generally <0.20 g and never exceeded 0.85 g. These low weights are more a reflection of the size and morphology of the fish than of low feeding rates. Many of the specimens had their simple, tubelike stomachs fully packed with prey.

The offshore specimens fed extensively on an hyperiid amphipod, *Phronima* sp. (Table 1). Prey identified as *Phronima* were found in 15 of the 21 stomachs examined, with a maximum of 16 *Phronima* per stomach. Crustacean parts were found in 20 of these stomachs. These parts, particularly leg and chela segments, generally closely resembled *Phronima*. Other hyperiids

TABLE 1.—Frequency of occurrence of prey taxa and maximum abundance of prey taxa in juvenile king-of-the-salmon stomachs collected at offshore stations (1980; $N = 21$) and inshore stations (1981; $N = 20$) off the Oregon coast.

Prey taxa	1980			1981		
	Number of stomachs	Maximum number per stomach	Maximum biomass per stomach (g)	Number of stomachs	Maximum number per stomach	Maximum biomass per stomach (g)
Unidentified material	21	—	0.220	17	—	0.087
Crustacean parts	20	—	0.512	2	0	0.027
Amphipods						
Phronima	15	16	0.495	1	1	0.001
other	6	4	0.029	2	1	0.001
Copepods	12	12	0.002	18	184	0.215
Euphausiids	3	2	0.003	10	37	0.148
Shrimp larvae	1	1	0.001	0	0	0
Crab megalops	1	1	0.044	3	5	0.021
Squid (tentacle)	1	1	0.027	0	0	0
Chaetognaths	0	0	0	2	5	0.011
Fish						
larvae	0	0	0	13	19	0.241
scales	11	6	0.004	0	0	0

were occasionally eaten, but did not constitute a major component of the diet. Copepods were present in 12 stomachs, but were in low numbers and probably were not very important as a dietary item. Fish scales were taken from 11 stomachs. The scales did not appear to come from other fish collected in the same net hauls and may indicate that these small-toothed juveniles consume scales floating free in the water. One fish stomach contained a piece of a squid tentacle, further suggesting that these fishes occasionally act as scavengers by picking up debris from predation events.

This reliance on *Phronima* as the dominant food organism is notable because of the parasitoid relationship between the Phronimidae and gelatinous zooplankton. Laval (1980) summarized the data known about this relationship and showed that *Phronima* spp. generally mature and live within the bodies of pelagic salps and siphonophores. Both the hosts and the amphipods are virtually transparent, and exceptional visual acuity is probably necessary to locate these prey. Traces of the hosts were not found in the fish stomachs, indicating that the fish either rapidly digest the host, pick the amphipods from the host, or eat the amphipods while the amphipods are moving between the hosts.

The inshore fishes caught in 1981 consumed a more varied range of prey (Table 1). Copepods were the most important prey item and were found in 18 of the 20 stomachs analyzed, in numbers ranging up to 184 copepods per stomach. Fish larvae were another important component of the diet and were found in 13 stomachs. These larvae ranged from tiny (2-3 mm) unidentifiable fish to 20 mm flatfish larvae (*Hippoglossoides* sp.). Up to 19 larvae were taken from a single stomach. Juvenile and a few adult euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*) were taken from 10 stomachs, in numbers up to 35 euphausiids per stomach. Unlike the oceanic specimens, the inshore fish rarely ate hyperiid amphipods and never consumed fish scales.

The dietary differences observed between the offshore and inshore collected specimens are an expected feature that reflects the availability of different prey taxa in different environments. The offshore stations had blue, clear water of relatively low particulate content, while the inshore stations were influenced by higher coastal productivity as well as river and estuarine input. The 1981 juveniles were collected in the transition zone between the oceanic and coastal environments. Utilization of this ecotone perhaps enabled these fish to take advantage of a portion of the coastal productivity and yet remain in a relatively clear oceanic habitat.

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NOTES ON THE MARINE LIFE OF THE RIVER LAMPREY, *LAMPETRA AYRESI*, IN YAQUINA BAY, OREGON, AND THE COLUMBIA RIVER ESTUARY[1]

The river lamprey, *Lampetra ayresi*, although uncommon in Oregon, is collected occasionally in the surface waters of the ocean and in estuaries. The species appears to be most abundant in the Columbia River estuary and is often found in Yaquina Bay. Systematic sampling programs in those two estuaries, carried out by the National Marine Fisheries Service (NMFS) in the Columbia River estuary and by Oregon State University in Yaquina Bay, have provided sufficient specimens (225) so that a preliminary assessment of the saltwater life of the species in Oregon can be attempted and comparisons made with its life history in British Columbia as reported by Beamish (1980).

The capture of river lampreys and the sampling program by which specimens were obtained are described or outlined by Dawley et al.,[2] Durkin et al.,[3] and Myers (1980). River lampreys were usually caught incidentally in studies of other species and were taken by means of beach seine, purse seine, lampara net, and bottom trawl. Mesh sizes of the nets employed were usually 6.5 mm or 9.5 mm bar measure, thus selection for larger individuals was probable. Additional specimens were obtained from a variety of sources. Specimens are held in the fish collection of the Department of Fisheries and Wildlife, Oregon State University (OS).

Downstream Migration

In British Columbia, river lampreys entering saltwater from late April to early July averaged 110 mm total length (TL); the range of lengths was 40-190 mm (Beamish 1980). We have no downstream migrants from freshwater, but we have two lots (OS 7320-1) that include specimens 115 mm long taken in marine waters on 21 May 1980. The earliest collection of the year of marine specimens in Oregon was made 5 May. One specimen measuring 161 mm long (OS 7370) from the Pacific Ocean and another measuring 206 mm (OS 4630) from Yaquina Bay were collected on that day. Both were immature and had been feeding. Because early May corresponds to the spawning season, the two feeders must have migrated early and apparently would have matured after the summer feeding season.

From mid-May to mid-June, specimens taken from Yaquina Bay with a 9.5 mm-mesh seine ranged in length from 141 to 245 mm (Table 1). In the same period, specimens taken by various nets (including some of 6.5 mm mesh) from the Columbia River estuary ranged from 115 to 278 mm. Specimens captured in the Pacific Ocean between mid-May and 25 June ranged from 145 to 237 mm. The distribution over the size range is sparse so that modes are difficult to recognize, except that in the Columbia estuary series (OS 6852, 6856, 6857) for 4 June (n = 110) 62% of the specimens fall between 160 and 210 mm.

[1]Technical Paper No. 6201, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, OR 97331.

[2]Dawley, E. M., C. Sims, R. D. Ledgerwood, D. R. Miller, and J. G. Williams. 1981. Study to define the migrational characteristics of chinook and coho salmon in the Columbia River estuary and associated marine waters. Progress report of coastal zone and estuarine studies. Pacific Northwest Regional Commission and Coastal Zone and Estuarine Studies Division. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98195.

[3]Durkin, J. T., T. C. Coley, J. T. McCabe, Jr., W. D. Muir, K. Verner, and R. L. Emmett. 1981. Non-salmonid, salmonid fishes. *In* Columbia River Estuary Data Development Program, 1979-80 Annual Report, Vol. 2, p. 1-24. Pacific Northwest River Basins Commission. National Marine Fisheries Service, NOAA, Hammond, OR 97121.

TABLE 1.—Ranges and means of total length of river lampreys captured in saltwater off Oregon (by half-month periods, all years combined).

	Columbia estuary			Yaquina Bay			Pacific Ocean		
Period	n	Range	$\bar{x}$	n	Range	$\bar{x}$	n	Range	$\bar{x}$
5/1-15	2	157-200	178.5	4	160-206	179.0	1	161	161
5/18-31	22	115-285	157.7	2	184-185	184.5	3	124-187	163
6/1-15	110	120-278	186.0	3	141-245	192.7	—	—	—
6/16-30	2	163-167	165.0	1	255	255	4	145-237	198
7/1-15	9	125-171	214.3	4	159-231	179.0			
7/16-31	—	—	—	8	133-241	179.6			
8/1-15	5	192-310	243.1	4	193-255	217.8			
8/16-31	25	176-304	236.1	8	184-247	215.9			
9/1-15	6	259-282	267.7	1	260	260			
9/16-30				1	240	240			
10/1-15				—	—	—			
11/1-15				1	205	205			

Maturation

Individuals captured May through August in saltwater show little development of the gonads, except for specimens >250 mm taken 31 August 1979 (OS 6858). These specimens have gonads visibly larger than those of smaller individuals. In addition, at least one of the allometric changes associated with sexual maturity is evident. The eyes of this 250-304 mm group constitute <25% of the preorbital length, whereas in 181-245 mm specimens from OS 6858 the eye constitutes between 25 and 33% of preorbital length. One specimen (OS 17) of 205 mm TL captured 14 November 1949 in Yaquina Bay had developing gonads. The season of spawning in the Columbia and Yaquina systems is deduced to be April and May, based on four specimens as follows: OS 112, 267 mm, March 1940, mature migrant, Bonneville Dam, Columbia R.; OS 343, 263 mm, 30 April 1958, mature migrant, Tongue Point, Columbia R.; OS 537, 181 mm, 15 April 1959, spawner, Yaquina R.; OS 471, 203 mm, 9 May 1959, spawner, Simpson Cr. (trib. Yaquina R.). Vladykov and Follett (1958) suggested that spawning of the species took place in April and May. Beamish (1980) reported spawning in holding tanks during May.

Growth and Upstream Migration

Although occasional adult specimens of the river lamprey have been taken from Yaquina Bay during October and November, no river lampreys have been captured in the Columbia River estuary from early September to May. The Pacific lamprey, *Lampetra tridentata*, has appeared December to June in catches from the Columbia estuary, intimating that the gear used during the winter is capable of capturing lampreys and that the absence of the river lamprey from the catch indicates their absence from the estuary. We suggest the absence means that river lampreys move into freshwater in early autumn.

Judging from the specimens caught from mid-August on, adult river lampreys must move into freshwaters of the Columbia system at lengths of of about 200 mm to >300 mm. Those that feed in Yaquina Bay probably leave saltwater at similar sizes, although the largest specimen captured there was 260 mm. Specimens up to 255 mm have been taken in Yaquina Bay in June, thus lengths of 300 mm could be reached by September or October if these animals grow at the rate observed by Beamish (1980) in British Columbia. In that study, an increase of 100 mm from mid-June to mid-August was noted. In the present study, a rough estimate of growth in the Columbia can be made by comparing early June samples (n = 110), which had a mean length of 186 mm, with combined samples from 31 August and 2 September (n = 31), which averaged 242 mm.

In a system such as the Columbia, assessment of size and growth is complicated by factors other than sampling problems. Some individuals may spend more years as larvae than others, some may transform and migrate to saltwater earlier in the year than others, some may feed in freshwater before entering saltwater (Beamish 1980), and those destined to migrate back to distant tributaries might have the genetic capacity for rapid growth and early departure from the feeding grounds. Kan (1975) noted that Pacific lampreys showed a rough correlation between size and distance of migration in the Columbia, but in that species large size can be reached not only by fast growth but by spending up to 3 or 4 yr in marine waters, rather than the few to several months spent by the river lamprey.

Ecological Observations

All but two of the eight ocean-caught river lampreys were taken in tows or hauls made within 34 m of the surface. The remaining two were taken close to the surface by anglers. Specimens from Yaquina Bay were taken by seine (3 m deep), but usually by lampara net (21 m deep) from subtidal channels. Specimens from the Columbia estuary were taken from shallow water by purse seine and beach seine. "Pelagic" coloration of blue to black on the back and silver on sides and belly appears to be typical of actively feeding *L. ayresi*, as reported by Kan (1975) and Beamish (1980). This contrasts sharply with the grey coloration of the deep-dwelling Pacific lamprey.

Water temperature in Yaquina Bay at times of capture of river lampreys ranged from 13° to 21°C. Salinity ranged from 12 to 29‰ (Myers 1980). Associated fishes in Yaquina Bay were usually American shad, *Alosa sapidissima*; Pacific herring, *Clupea harengus pallasi*; juvenile coho salmon, *Oncorhynchus kisutch*; juvenile chinook salmon, *O. tshawytscha*; surf

smelt, *Hypomesus pretiosus*; and shiner perch, *Cymatogaster aggregata*. Scars from attacks by lampreys were occasionally seen on juvenile salmonids, usually just below the dorsal fin. Scars were noted less commonly on other species, but some were noticed on a wide range of sizes of fish, including adult pile perch, *Rhacochilus vacca*. Two of the ocean-caught lampreys were taken while attached to a herring and a smelt of unknown species that anglers were using for bait.

Feeding Habits

Beamish (1980) presented data on the feeding habits of the river lamprey, mentioning salmonids and *Clupea* as common prey. Miller[4] observed what he considered significant predation by the river lamprey on chinook salmon 60-120 mm long in Elliott Bay, Wash.

In the present study, 141 of the 225 specimens from marine water were examined for evidence of feeding. Only four had empty guts. Gut contents of 30 specimens (OS 6857) captured 4 June 1979 from the Columbia River estuary were examined for identifiable material. Fragments of muscle tissue, intestine, liver, ovary, scales, and bones were present in some combination in all guts examined. Scale and bone fragments identified as clupeid were found in 14 guts, one of which also contained a worn lamprey tooth lamina and a scale from a salmonid. The salmonid scale had an ocean-type nucleus and resembled scales of chum salmon, *Oncorhynchus keta*. Clupeid scales from five guts were identified as being from American shad, which migrate up the Columbia in great numbers during June. Scale fragments from six guts were thought to represent Pacific herring. One gut had no recognizable clupeid remains, but held a small salmonid scale with two freshwater annuli, thus probably being from a smolt steelhead, *Salmo gairdneri*.

The guts of 9 of 10 specimens (OS 6858) taken 31 August 1979 from the Columbia estuary contained recognizable clupeid remains. One contained an American shad scale and three held fragments thought to be from Pacific herring scales. Seven contained forked intermuscular bones. In addition to clupeid remains, two guts held fragments of unidentified salmonid scales.

[4]Denny M. Miller, formerly Research Assistant, University of Washington, Seattle, WA 98195, pers. commun. April 1968.

Acknowledgments

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AN ECONOMIC EVALUATION OF THE ST. LAWRENCE RIVER-EASTERN LAKE ONTARIO BASS FISHERY

The St. Lawrence River-eastern Lake Ontario bass fishery has long been known as one of the finest sport fisheries in North America. Despite its well-documented popularity, there has been little research on this recreational fishery's economic value. Furthermore, recent interest has focused on the fishery's trout and salmon angling opportunities, which have been significantly enhanced since the early 1970's through the management efforts of New York's Department of Environmental Conservation. This study provides information on the economic importance of the bass fishery, considered by many to be one of the best smallmouth bass fisheries in the world. The economic value of this recreational fishery should be taken into account in decisions affecting use of the St. Lawrence River and for planning and evaluating management of this resource.

The current study estimated the economic value of the St. Lawrence River-eastern Lake Ontario bass fishery to licensed New York resident anglers. Benefits to out-of-state anglers (including Canadians) and nonlicensed anglers were not evaluated, nor were Canadian sites in the region included in this study. In addition, general recreational benefits of the fishery to tourists and others were not considered. Though a recreational fishery may be of value from a number of perspectives, it has long been established on conceptual grounds that economic evaluation of recreation benefits should be based on the willingness of users to pay for services provided. However, willingness to pay for outdoor recreation facilities cannot be estimated through the normal procedure of observing market demand because the typical practice is to provide these facilities to users free of charge.

This study used the so-called travel cost method to estimate demand for the angling services of the St. Lawrence River-eastern Lake Ontario bass fishery. The first section of this article discusses the method that was used to estimate the fishery's economic value. It includes a description of the fishery and a discussion of the travel cost method and the data. The second section presents the empirical findings. The concluding section discusses the implications of the results for management policy.

Methods

Determining the Value of Recreation Facilities

There is a substantial body of literature on estimating economic value to users of outdoor recreation. Two approaches have been widely used to obtain information for estimating economic value. The first asks individuals to reveal directly their willingness to pay for use of a recreation site. An important problem with this approach is the incentive to misstate true preferences, possibly leading to inaccurate estimates of economic value (Freeman 1979). The other procedure for estimating economic value is the travel cost method, first applied to outdoor recreation by Clawson (1959) and Clawson and Knetsch (1966). The hypothesis of the travel cost method is that outdoor recreation demand can be estimated by observing how visitation to a specific site varies with differences in costs of traveling to the site. Travel costs are viewed as a charge for use of a resource's services, and the pattern of visitation by geographical area indicates the willingness to pay for its use.

The travel cost method is a two-stage estimation procedure. The first stage predicts site visitation as a function of travel costs and other explanatory factors. Then a demand curve is derived showing how visitation would vary in response to a price (or entrance fee) charged for use of the site, assuming that users view an increase in price as equivalent to the additional costs needed to travel greater distances to the site. The site's net economic value (NEV) in its current use is equal to the area under the demand curve above the level of travel costs (Clawson and Knetsch 1966; Dwyer et al. 1977).[1]

The Participation Equation

Visitation patterns to the St. Lawrence River-eastern Lake Ontario area (Fig. 1) during the 1976-77 year form the basis for this analysis. The equation for predicting visitation to the fishery was based on a survey of licensed New York resident anglers (New York Department of Environmental Conservation 1976). The sample was limited to 904 anglers (from 51 of New York's 62

[1]The travel cost method assumes that users derive benefits from the recreation site itself rather than the trip (Brown et al. 1965).

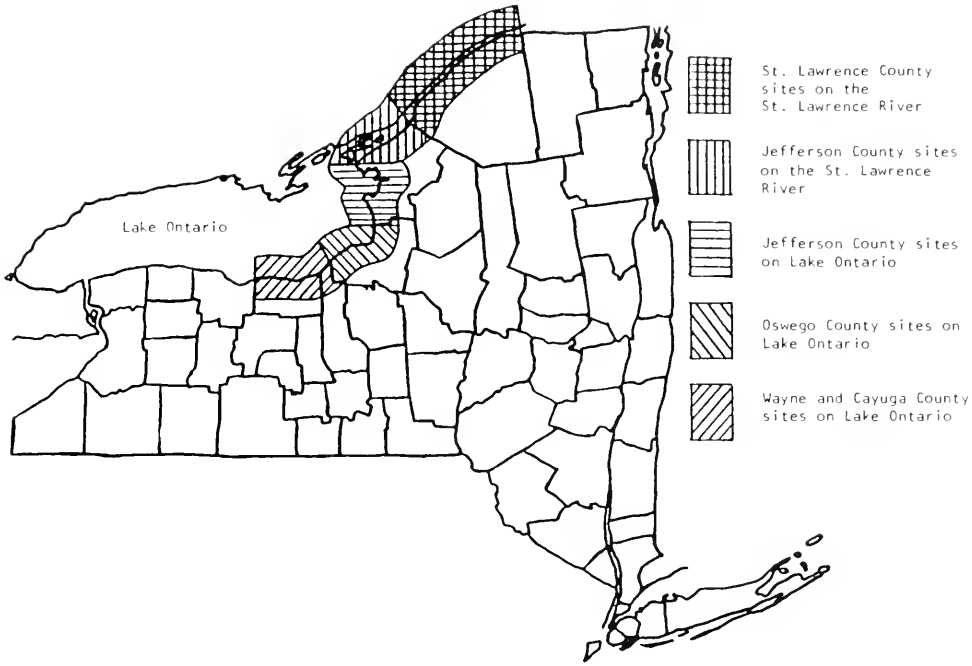

FIGURE 1.—Map of St. Lawrence River-eastern Lake Ontario bass fishery.

counties) who spent >5% of their time fishing for either smallmouth or largemouth bass at one of the designated sites. The study area comprised five sites chosen on the basis of geography, availability of data, and observed visitation. Two sites were on the St. Lawrence River and three were on eastern Lake Ontario.

The participation equation is equivalent to an ordinary demand function for a marketed commodity where quantity (visits to a site) is a function of prices (travel costs), income, and qualitative characteristics. The participation equation for the bass fishery was:

$$D_{ij} = f(TC_{ij}, I_i, PF_i, S_i, A_j, TC_{ik}) \qquad (1)$$

where D_{ij} = total days angling at site j by respondents from county of origin i for the 1976-77 fishing season

f = a symbol representing an explicit functional relationship between D_{ij} and the explanatory variables

TC_{ij} = travel costs from county of origin i to site j; calculated by measuring road distance from the midpoint of each county to the midpoint of each site and multiplying the measured distance by an estimate of the cost per mile

I_i = average annual income of anglers from county of origin i

PF_i = average preference level for bass of anglers from county of origin i; preference level represents the percentage of total angling time spent fishing for the species of interest

S_i = number of anglers to whom the questionnaire was sent in county of origin i; a constant percentage of the angler population across all counties

A_j = relative attractiveness of site j; the amount of shoreline miles at site j relative to the total miles available at all sites

TC_{ik} = an index of travel costs from county of origin i to substitute angling sites in the study area.

This demand function relates participation at sites not only to their own prices and quality, but also to the attributes of comparable substitute

sites. Travel costs were assumed to be a function of both monetary expenditures and the cost of travel time.[2] Ignoring time costs will cause biased estimates of demand and economic value (Cesario and Knetsch 1970). Cost of travel time was calculated by multiplying estimated travel time en route to the site by an hourly wage rate (Knetsch et al. 1976). Sample size was included as an independent variable in the participation equation because others have found that visitation increases at a nonlinear rate with increases in population (Cesario and Knetsch 1976; Grubb and Goodwin 1968). Travel costs to substitute sites, TC_{ik}, were represented in an index of travel costs reflecting the availability of substitute angling opportunities.[3] The attractiveness of available recreation sites can also be an important determinant of visitation patterns. The decision to visit a particular site depends, in part, on the attractiveness of that site compared with other available sites. Site attractiveness measures used by others have included angling success rates (Stevens 1966), size of the recreation area (Ravenscraft and Dwyer 1978), congestion at the site (McConnell 1977), and accessibility (Cesario and Knetsch 1976). Data limitations reduced the possible choices for attractiveness variables in this study to fishing success rates and shoreline distance.

Site Demand and Economic Value

The second step of the travel cost method derives the demand for and economic value of the recreation site from the participation equation. The usual procedure is to derive a demand curve for a specific site by estimating demand from each origin and aggregating over all origins for each increment of a hypothetical fee until aggregate demand for the resource is reduced to zero (Grubb and Goodwin 1968; Cesario and Knetsch 1976; Knetsch et al. 1976). This study estimated NEV for each origin using a separate site-specific demand curve. Then the site's total NEV was found by numerical aggregation across all origins. This procedure estimates NEV more accurately than the usual procedure because there is less aggregation in deriving the site demand curve (McConnell and Norton 1976; Menz and Wilton 1982).[4] Demand was estimated from the participation equation for each site with the following:

$$D_{ij} = C_{ij} + \beta_1 (TC_{ij} + p) + \epsilon \qquad (2)$$

where D_{ij} = the observed days of participation when the fee is zero[5]
TC_{ij} = travel costs from county of origin i to site j
C_{ij} = the composite of all other variables
p = the hypothetical fee charged for use of the site
ϵ = an error term.

The site's NEV to anglers in each origin was obtained by integrating the demand equation between the limits of current travel costs and the cost at which D_{ij} would become zero.

Results

Some anglers may fish exclusively for smallmouth bass, others for largemouth bass, and some may be unconcerned about the specific type of bass caught. Therefore, three separate analyses were conducted: one each for the smallmouth and largemouth bass fisheries and one for the "combined" bass fishery. The value of the combined fishery was determined in a separate analysis because addition of the smallmouth and largemouth bass results would double-count anglers who fish for both species. The same fishing sites were used for each analysis.

Characteristics of anglers and sites are presented in Tables 1 and 2. Smallmouth and large-

[2]Travel costs were converted to price per angler day by taking into account travel distance and whether lodging expenditures were reported by anglers. Analysis of the survey data indicated that anglers who resided at a (one-way) distance between 125 and 175 mi from the site generally incurred lodging expenditures, indicating an overnight stay at the site. Accordingly, price per angler day was assumed to equal one-half the estimated travel costs for anglers residing more than 150 mi from a site. For anglers closer to the site, price per angler day was assumed to equal estimated travel costs. Monetary costs were assumed to be 10¢/mile. Travel time costs were calculated by multiplying estimated travel time at 50 mph by a value equal to 35% of the wage rate in the angler's county of origin. Hotel costs were not included in the cost estimates since they could not be determined on a per angler day basis.

[3]Use of an index reflects the overall availability of substitutes. Dividing the index by four would give the average price of a substitute site in this fishery. A generalized approach to the treatment of substitute sites is preferable to a specific substitute site in a regional travel cost model (Cesario and Knetsch 1976; Dwyer et al. 1977; Ravenscraft and Dwyer 1978).

[4]This method will be more accurate than if an aggregate demand curve were used, but it will not provide as accurate an estimate of economic value as aggregation of individual economic values (Brown et al. 1965; Smith 1975a).

[5]The value of D_{ij} was set equal to zero whenever a negative quantity resulted from the calculation.

TABLE 1.—Characteristics of New York resident anglers in the St. Lawrence River-eastern Lake Ontario bass fishery, 1976.

	Combined bass		Smallmouth bass		Largemouth bass	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
Preference (%)	37 8	23 7	30 6	14 5	27.8	13 3
Experience (No. of years)	29 7	14 3	31 8	23.9	22 9	15 3
Education (No. of years)	13 3	2.9	13 3	2 9	13 2	2 9
Annual income ($)	18,100	9,500	18,600	9,900	16,900	8,500

TABLE 2.—Characteristics of sites and angler participation in St. Lawrence River-eastern Lake Ontario bass fishery, 1976.

		Angler participation				
		Distance traveled (mi)		Success rate (fish per angler day)		
Site	Shoreline (mi)	Mean	Standard deviation	Smallmouth	Largemouth	Combined
St Lawrence River						
St Lawrence County (Site 1)	64	171	93.3	0 85	0 20	0 84
Jefferson County (Site 2)	48	149	69 8	0 88	0 31	1 03
Lake Ontario:						
Jefferson County (Site 3)	63	99	63.8	1 30	0 31	1.39
Oswego County (Site 4)	24	62	57 5	0 64	0 26	0.71
Wayne & Cayuga Counties (Site 5)	32	35	29 7	0.73	0 25	0 80
Entire fishery	231	110	82.0	0 94	0 27	1.02

mouth bass anglers were similar in socioeconomic characteristics, but the average smallmouth bass angler had more angling experience. Average one-way distance traveled by anglers to the sites varied from 35 mi for the Wayne and Cayuga County sites on Lake Ontario to 171 mi for the St. Lawrence County sites on the St. Lawrence River. Angling success rates were highest at the Jefferson County sites on Lake Ontario.

The Participation Equation

There does not appear to be any theoretical justification for a particular functional form of the relationships for estimation (Smith 1975b). Various functional forms of the participation equation (Equation (1)) were estimated. The final form was as follows:

$$\log (D_{ij} + 0.8) = \beta_0 + \beta_1 \log TC_{ij} + \beta_2 \log I_i + \beta_3 \log PF_i + \beta_4 \log S_i + \beta_5 \log A_j + \beta_6 \log TC_{ik} + \epsilon \qquad (3)$$

where the β terms are parameters to be estimated and ϵ is the random component.[6] The double logarithmic model produced more significant parameter estimates and also exhibited greater explanatory power than linear and semilogarithmic forms, so it was used to derive the estimates for this part of the analysis.[7]

The results for the participation equation (Equation (3)) are presented in Table 3. Because assumptions about monetary and time costs of travel could influence the results, alternative participation equations were estimated using different values for these cost components. The results are also shown in Table 3. The effect and significance of the explanatory variables remained virtually unchanged, suggesting that confidence can be placed in the results from this stage of the analysis.

The estimates are consistent with theoretical expectations and are similar for the three fishery specifications. Most of the estimated coefficients were statistically significant at the 1% level and

[6]The quantity, 0.8, in Equation (3) is added to the fee to prevent the use of the logarithm of zero. All logarithms are natural logarithms.

[7]The objective in specifying the participation equation was to obtain reliable estimates of parameters rather than a high R^2 (Gum and Martin 1975). Other studies that have used the double log format are Grubb and Goodwin (1968), Smith (1975b), and Smith and Kopp (1980).

TABLE 3.—Estimated parameter values for participation equations for days of angling for St. Lawrence River-eastern Lake Ontario bass fishery.[1]

Parameter	Assumption for cost of travel and time[2]								
	10¢/mi and 35% of wage rate			15¢/mi and 35% of wage rate			10¢/mi and 50% of wage rate		
	Smallmouth	Largemouth	Combined	Smallmouth	Largemouth	Combined	Smallmouth	Largemouth	Combined
Travel cost to site (TC_{ij})	−1 452	−1 426	−1 487	−1 455	−1 428	−1 488	−1 448	−1 424	1 486
	(4 97)	(4 98)	(5 07)	(4 98)	(−4 79)	(5 08)	(4 95)	(4 97)	(5 07)
Income (I_i)	0 851	1 494	0 935	0 665	1 294	0 730	1 025	1 686	1 127
	(2 55)	(4 17)	(2 80)	(2 05)	(3 72)	(2 25)	(2 98)	(4 57)	(3 27)
Preference (PF_i)	0 447	0 337	0 470	0 446	0 334	0 471	0 447	0 332	0 470
	(1 99)	[3](1 39)	[3](1 95)	(1 99)	[3](1 38)	[3](1 96)	(1 99)	[3](1 37)	[3](1 95)
Sample size (S_i)	1 162	1 078	1 159	1 166	1 081	1 162	1 159	1 075	1 158
	(8 25)	(7 86)	(8 48)	(8 28)	(7 88)	(8 50)	(8 23)	(7 84)	(8 47)
Site attractiveness (A_j)	1 444	0 814	1 458	1 444	0 815	1 458	1 444	0 813	1 458
	(5 53)	(3 12)	(5 78)	(5 54)	(3 72)	(5 78)	(5 53)	(3 12)	(5 78)
Substitute travel costs (TC_{ik})	−0 598	−0 853	−0 799	−0 599	−0 857	−0 802	−0 599	−0 851	0 798
	(2 27)	(3 27)	(3 10)	(2 27)	(3 28)	(3 11)	(2 28)	(3 27)	(3 10)
Intercept	−4 243	−9 667	−3 839	1 881	−7 092	1 217	−5 622	11 199	5 368
	(−1 33)	(−3 06)	(1 23)	(0 60)	(−2 28)	(0 39)	(−1 75)	(−3 51)	(1 70)
F	33 10	27 21	36 76	33 20	27 29	36 82	32 99	27 12	36 70
R^2	0 455	0 434	0 471	0 456	0 435	0 471	0 454	0 433	0 470

[1]Each equation has the form of Equation (3); dependent variable is days of angling for bass anglers
[2]Figures in parentheses are t-values.
[3]Not significant at the 5% level.

all except those noted as such in Table 3 were significant at the 5% level. Travel costs from origin i to site j (TC_{ij}) and the measure of site attractiveness (A_j) were found to be highly significant determinants of participation. The effect of substitutes on site visitation depends on their location and attractiveness relative to the site being studied (Burt and Brewer 1971; Cicchetti et al. 1976; Dwyer et al. 1977). The negative and statistically significant coefficient for TC_{ik} suggests that the sites in this fishery serve as complements for one another and that anglers are drawn to the fishery as a whole instead of to a particular site.

Economic Value of the Fishery

Table 4 presents the estimated net economic benefits to New York resident bass anglers for the fishery. Values were estimated for each site and for each species of bass on a per angler day basis and as an annual total. The annual total for each site was calculated by multiplying the value per angler day by the estimated number of angling days as given in Table 5. B and C of Table 4 show the effect of alternative assumptions about distance and time costs.

It can be seen that the results vary widely from site to site and with different assumptions concerning the monetary component of travel costs. Variation among sites is due to the relative attractiveness of the sites, size of population in nearby counties, and other factors affecting visitation patterns. These factors affect the willingness of anglers to pay for the sites' services and the number of anglers attracted. Highest values per angler day were estimated for St. Lawrence County sites on the St. Lawrence River. At two sites the NEV per angler day for largemouth bass exceeded the NEV per angler day for smallmouth bass. However, due to a greater number of estimated angling days for smallmouth bass at these two sites, the total NEV of the smallmouth bass fishery exceeded that of the largemouth bass fishery for every site.[8] The value of the combined bass fishery at each site is less than the total of the individual smallmouth and largemouth bass values because the fisheries for

[8]It should be emphasized that the total value of the fishery equals the estimated number of angling days at each site times the per angler day value. This assumes that the angler day is entirely attributable to the site's bass fishery. To reduce possible bias from this assumption, the sample population was limited to anglers who fished at one of the five sites and indicated that they had spent more than 5% of their time fishing for bass.

TABLE 4.—Net economic value of the St. Lawrence River-eastern Lake Ontario bass fishery to New York resident anglers, 1976.

Type of fishery		Location					Total
		Site 1	Site 2	Site 3	Site 4	Site 5	
A. Estimates using travel costs of 10¢/mile and a time cost of 35% of the wage rate:							
Smallmouth	Per day ($)	36.46	27.23	26.53	15.53	19.13	
	Total ($)	2,916,800	5,702,000	4,795,500	1,026,500	2,280,300	16,721,000
Largemouth	Per day ($)	33.24	25.28	24.32	15.67	19.29	
	Total ($)	1,652,000	2,818,700	1,459,200	659,700	2,044,700	8,634,300
Combined	Per day ($)	35.22	25.99	24.64	15.43	18.55	
	Total ($)	3,610,100	5,889,300	4,854,100	1,263,700	2,769,500	18,386,700
B. Estimates using travel costs of 15¢/mile and a time cost of 35% of the wage rate							
Smallmouth	Per day ($)	47.36	35.40	34.46	20.07	24.69	
	Total ($)	3,788,800	7,412,800	6,182,100	1,326,600	2,943,000	21,653,300
Largemouth	Per day ($)	43.53	33.08	31.81	20.45	25.06	
	Total ($)	2,163,400	3,688,400	1,908,600	860,900	2,656,400	11,277,700
Combined	Per day ($)	46.03	33.94	32.18	20.14	24.06	
	Total ($)	4,718,100	7,690,800	6,341,400	1,649,500	3,592,200	23,992,000
C. Estimates using travel costs of 10¢/mile and a time cost of 50% of the wage rate:							
Smallmouth	Per day ($)	42.72	31.88	31.07	18.30	22.56	
	Total ($)	3,417,600	6,675,700	5,574,000	1,209,600	2,689,200	19,566,100
Largemouth	Per day ($)	38.69	29.42	28.31	18.30	22.64	
	Total ($)	1,922,900	3,280,300	1,698,600	770,400	2,399,800	10,072,000
Combined	Per day ($)	40.99	30.25	28.65	18.00	21.76	
	Total ($)	4,201,500	6,854,700	5,644,100	1,474,200	3,248,800	21,423,300

TABLE 5.—Visitation and expenditures by licensed New York resident bass anglers, 1976.[1]

	Site 1	Site 2	Site 3	Site 4	Site 5	Total
A. Smallmouth bass anglers:						
Number of anglers	6,700	16,000	10,800	5,100	8,000	46,600
Number of angler days	80,000	209,400	179,400	66,100	119,200	654,100
At-site expenditures per angler day ($)	6.05	10.14	8.20	3.62	3.35	7.21
Total expenditures per angler day ($)	9.46	13.39	12.17	6.01	4.68	10.24
B. Largemouth bass anglers:						
Number of anglers	4,100	8,700	4,100	3,400	6,400	26,800
Number of angler days	49,700	111,500	60,000	42,100	106,000	369,400
At-site expenditures per angler day ($)	6.95	9.04	6.85	3.78	2.04	5.79
Total expenditures per angler day ($)	11.64	12.37	10.38	5.02	3.17	8.47
C. Smallmouth and/or largemouth bass anglers:						
Number of anglers	8,400	18,200	12,400	6,900	9,900	55,800
Number of angler days	102,500	226,600	197,000	81,900	149,300	757,300
At-site expenditures per angler day ($)	6.18	10.10	8.47	3.93	2.95	7.07
Total expenditures per angler day ($)	10.83	13.38	12.41	6.15	4.41	10.10

[1]All values are based on the definition of bass angler for this study and are expanded from the survey sample to the angler population

the individual species are not mutually exclusive. Addition of the economic value across sites yields a total annual value for the five sites of $18,386,700 for the combined bass fishery in 1976. This amount represents the annual NEV to licensed New York resident bass anglers in 1976 for the five sites that make up the St. Lawrence River-eastern Lake Ontario bass fishery. The effect of changes in travel cost assumptions can be seen by comparison of A, B, and C of Table 4. Changes in per mile monetary costs influence NEV less than changes in time costs.

The results reported in Table 4 and discussed above relate to the fishery's economic value to licensed New York resident anglers in 1976. For policy purposes, the current value of the recreational fishery would be more appropriate. The most accurate way to estimate the current value of the fishery would be to use current angler visitation and travel cost data, which are unavailable. It would be inappropriate to use current travel cost information with visitation data from 1976 to estimate current demand for the fishery because visitation patterns may have significantly changed since the earlier time period. The value of the fishery can be stated in terms of 1982 dollars by multiplying the results in Table 4 by 1.5, which represents the ratio of 1982 to 1976

price levels (Federal Reserve Bank of St. Louis 1982). Consequently, the NEV for the combined bass fishery per angler day ranges from $23.14 at site 4 to $52.83 at site 1 in 1982 dollars, while NEV ranges from $1.9 million at site 4 to $8.8 million at site 2. The NEV of the combined bass fishery to licensed New York resident anglers would be approximately $27.6 million in 1982 dollars.

Conclusions

This paper has reported results of a study of the economic value of the St. Lawrence River-eastern Lake Ontario bass fishery to licensed New York resident anglers. A regional travel cost model was used to estimate demand and economic value for the sites that make up the fishery. The economic value of the fishery to anglers is considered to be the most appropriate measure of the fishery's contribution to economic welfare. Benefits to New York anglers are likely to be an important element of the fishery's recreational value.

The results of this study are important for policy concerning management of the fishery resource, but they should be interpreted cautiously for several reasons. First, there are benefits in addition to those considered here, including those to other anglers as well as to nonanglers. Second, there are possible errors in the benefit estimates either from misspecification of the underlying participation equation or from possible errors in the survey data. Third, an important issue in the valuation of recreational fisheries concerns the appropriate treatment of substitute sites. This study used an approach which considered substitution among a limited number of alternative bass fishing sites within the fishery, but did not consider all possible substitute sites or species because it would be impractical to do so. It should also be noted that the procedure used in this study allows the relative value of fish species to be compared (either within this study area or with bass fisheries elsewhere), but these results cannot be added to those for other species to determine their combined value. Despite these limitations, the results of this study of the St. Lawrence River-eastern Lake Ontario bass fishery should be useful for policy purposes. Many of the resource management options that are evaluated are likely to influence the quality of the fishery, and it is important that information on economic value be considered. Economic analysis is no panacea for resolving problems of alternative natural resource uses, but should play a part in informed policymaking.

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LIST OF FIGURES (Entire figure legends)
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(Continued on back cover)

Seattle, Washington

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ENERGY AND NITROGEN BUDGETS FOR THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS* (PISCES: CLUPEIDAE), A FILTER-FEEDING PLANKTIVORE

EDWARD G. DURBIN AND ANN G. DURBIN[1]

ABSTRACT

Experimentally derived energy and nitrogen budgets for the Atlantic menhaden permit a detailed investigation of the food consumption rate, energy expenditures, growth rate, and growth efficiency in this filter-feeding planktivore. The models were developed for adult fish (302 g wet weight, 26 cm fork length) at a temperature of 20° C. Three variables are shown to control the energy and nitrogen budgets: The swimming speed while the fish are feeding, the duration of the daily feeding period, and the concentration of plankton in the water.

Growth rate increased linearly, and growth efficiency increased asymptotically, with an increase in either plankton concentration or the duration of feeding, provided that swimming speed remained constant. However, with increasing swimming speed, growth curvilinearly increased from zero to a maximum value and then declined back to zero. Growth efficiency followed a similar pattern, but reached its maximum value at a slower swimming speed than that which maximized growth. The swimming speeds which maximized growth rate were dependent on plankton concentration, but were independent of the duration of feeding. Conversely, the swimming speeds which maximized gross growth efficiency depended on the duration of feeding, but were independent of food concentration. Laboratory studies demonstrated that menhaden regulate their swimming speeds according to the abundance of plankton in the water. Analysis of the energy budgets revealed that the voluntary swimming speeds of the menhaden were very close to those which maximize growth rate at different concentrations of plankton. We conclude that swimming speed in the menhaden has evolved over time towards maximizing growth rate rather than growth efficiency.

In most circumstances the growth efficiency for calories and nitrogen were significantly different. The observed swimming speeds in the menhaden resulted in higher growth efficiency for nitrogen at low plankton abundance, but higher efficiency for calories at moderate to high plankton abundance. This accounts for the seasonal increase in the fat content of the menhaden during the summer, yet indicates that protein will be conserved when food abundance is low.

The study of fish bioenergetics can provide considerable insight into how different biotic and abiotic factors interact to control food intake and growth in fishes. Here we describe energy and nitrogen budgets for adult Atlantic menhaden, *Brevoortia tyrannus*, a filter-feeding planktivore which ranges in inshore waters along the Atlantic coast from Florida to Maine (Nicholson 1978 and references therein). These budgets are based on experimental investigations of the physiological and behavioral responses of the adult Atlantic menhaden to differing food conditions (Durbin and Durbin 1975, 1981; Durbin et al. 1981).

In the energy budget, the sum of somatic and reproductive growth (G_K) equals the energy content of the ingested ration (R_K), minus the energy losses to respiration (T_K), excretion (E_K), and feces (F_K):

$$G_K = R_K - T_K - E_K - F_K. \quad (1)$$

We have attempted to incorporate into the energy budget the energetic gains and losses which occur during different phases of the normal daily activity of the fish. For example, the energetic expenditures during periods of feeding are considered separately from periods when the fish are not feeding. The energy budget is then used to predict food intake, growth rate, and growth efficiency of Atlantic menhaden under different feeding regimes.

In the nitrogen budget, growth in nitrogen (G_N) equals the nitrogen contained in the daily ration (R_N) minus the daily nitrogen losses to excretion (E_N) and in the feces (F_N):

$$G_N = R_N - E_N - F_N. \quad (2)$$

Food intake, growth rate, and growth efficiency are predicted.

The energy and nitrogen budgets measure different things; the nitrogen budget is mainly for a specific component (protein), while the energy (caloric) budget is more inclusive and attempts to account for

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all changes in body constituents. A comparison of the two budgets will enable us to determine the relative efficiency with which the Atlantic menhaden utilize the total energy content, as distinct from the nitrogen content, of their food for growth. Each of the budgets is presented in two forms, a general model (I) and a special case of this model (II) which incorporates additional details on the behavior of the fish in response to the abundance of food. Symbols used in the budgets are as follows:

R_K, R_N	Total daily food intake ("ration") (kcal/g dry weight per day; mg N/g dry weight per day)
T_K	Total daily oxygen consumption (kcal/g dry weight per day)
$T_{r,K}$	Total daily routine oxygen consumption (kcal/g dry weight per day)
$T_{f,K}$	Total daily oxygen consumption during feeding (kcal/g dry weight per day)
$T_{s,K}$	Oxygen consumption attributable to swimming activity (kcal/g dry weight per day)
$T_{SDA,K}$	Oxygen consumption due to the heat increment from food (kcal/g dry weight per day)
E_K, E_N	Total daily nitrogen excretion (kcal/g dry weight per day; mg N/g dry weight per day)
$E_{b,K}, E_{b,N}$	Total daily endogenous nitrogen excretion (kcal/g dry weight per day; mg N/g dry weight per day)
$E_{f,K}, E_{f,N}$	Total daily exogenous nitrogen excretion (kcal/g dry weight per day; mg N/g dry weight per day)
F_K, F_N	Total daily losses in the feces (kcal/g dry weight per day; mg N/g dry weight per day)
G_K, G_N	Total daily growth (kcal/g dry weight per day; mg N/g dry weight per day)
$K_{1,K}, K_{1,N}$	Gross growth efficiency $= \frac{G_K}{R_K}$ and $\frac{G_N}{R_N}$
p	Assimilation efficiency (dimensionless)
v	Volume searched during feeding (l/fish per hour)
F	Volume swept clear during feeding (l/fish per minute)
L	Food particle length (μm)
e	Filtration efficiency of the gill rakers (dimensionless)
s	Swimming speed during feeding ("foraging speed") (cm/second)
c,n	Concentration of plankton in the water (kcal/l; mg N/l)
h	Duration of the daily feeding period ("foraging time") (hours/day)
$s_{G,OPT}$	Foraging speed which maximizes growth rate at a given concentration of plankton
$s_{K,OPT}$	Foraging speed which maximizes gross growth efficiency for a given foraging time.

Atlantic menhaden are highly specialized planktivores which feed on suspended particulate material (phytoplankton, zooplankton, and detritus). During feeding, an Atlantic menhaden swims with its mouth open and gill opercula flared, causing the comblike gill rakers, which otherwise lie flat inside the mouth, to swing inward and form a fine-meshed screen across the throat (Peck 1894). Water entering the mouth is filtered through the rakers before exiting through the gill arches. Adult Atlantic menhaden do not pursue individual prey (Durbin and Durbin 1975). Instead they filter the column of water that lies directly ahead. Although the menhaden are size-selective, this merely reflects the mesh size of the gill rakers and does not represent active selection for specific types of prey.

Laboratory studies have shown that Atlantic menhaden change their swimming and feeding behavior according to the concentration of food in the water (Durbin et al. 1981). In the absence of food the fish swam at a characteristic speed of 0.47 body lengths/s, with a routine respiration rate of 0.1 mg O_2/g wet weight per h. The menhaden increased their swimming speed and respiration rate severalfold during feeding. Foraging speed increased asymptotically with increasing food concentration, while respiration rate increased exponentially with increasing foraging speed. The fish initiated and terminated feeding at distinct threshold concentrations of plankton that were inversely related to particle size. Exogenous nitrogen excretion in the Atlantic menhaden was proportional to the nitrogen content of the ration (Durbin and Durbin 1981). Digestion rates were rapid, and assimilation efficiency was high. The menhaden were evidently adapted for the efficient processing of large amounts of particulate material which is ingested during prolonged periods of continuous feeding.

These observations provide the basis for the development of the energy and nitrogen budgets and will be discussed in more detail below. In accordance

with the experimental data, the budgets are developed for the case of an adult Atlantic menhaden, 26 cm FL (fork length) and weighing 302 g wet and 101 g dry, which feeds upon the diatom *Ditylum brightwelli*. The temperature is 20°C.

DERIVATION OF ENERGY AND NITROGEN BUDGETS

Energy Budget (Model I)

The general equation for the energy budget is presented in Equation (1).

Energy Intake

TOTAL DAILY RATION, R_K (KCAL/G DRY WEIGHT PER DAY).—The daily ration, R_K (kcal/fish per d) which is obtained by an Atlantic menhaden will be equal to the volume searched (v, l/fish per h), times the efficiency (e, dimensionless) with which particles are removed from the volume searched, times the concentration (c, kcal/l) of food particles in the water, times the duration (h, h/d) of the feeding period.

$$R_K = v\ e\ c\ h \text{ (kcal/fish per d)}. \tag{3}$$

Volume searched (v).—During feeding, the mouth is held continuously open and the fish swim in school formation, travelling along a straight or curvilinear path without changing course to pursue individual prey. Thus each fish filters the column of water which lies directly ahead. The volume searched is equal for all prey types, and may be adequately described as a cylinder, or, more accurately, an ellipsoid, with a cross-sectional area equal to that of the fish's open mouth and a length equal to the distance covered by the fish per unit time, i.e., the foraging speed (s, cm/s). For an Atlantic menhaden averaging 26 cm FL, the gape was approximately elliptical, with major and minor axes of 3.91 and 2.90 cm, respectively; the total cross-sectional area of the mouth was therefore 8.93 cm² (Durbin and Durbin 1975). Thus

$$v = 32.148\ s \text{ (l/fish per h)}. \tag{4}$$

Filtration efficiency (e).—Filtration efficiency is the efficiency with which the Atlantic menhaden filters particles of a given size from the water and is equal to the observed removal rate or volume swept clear, F (l/fish per min), divided by the total volume searched, v (l/fish per min), i.e.,

$$e = \frac{F}{v}. \tag{5}$$

In feeding experiments (Durbin and Durbin 1975) the mean value of F for *Ditylum brightwelli* was 5.8 l/fish per min, while v was estimated to be 23.3 l/fish per min. This gives a value of $e = 0.25$ for *D. brightwelli*.

Filtration efficiencies for different-sized particles may be calculated from an equation describing the relationship between filtration efficiency and food particle length (Durbin and Durbin 1975):

$$F = 8.290 \log_{10} L - 9.733 \text{ (l/fish per min)}. \tag{6}$$

In the experiments the fish were unable to filter particles smaller than about 13 μm.

Incorporating the appropriate values for v and e into Equation (3), the ingested ration, R_K, for *D. brightwelli* would be given by

$$R_K = 8.037\ s\ c\ h \text{ (kcal/fish per d)}. \tag{7}$$

In the model the Atlantic menhaden weighed 302 g wet = 101 g dry (Durbin and Durbin 1981). Thus

$$R_K = 0.079574\ s\ c\ h \text{ (kcal/g dry weight per d)}. \tag{8}$$

ASSIMILATED RATION, pR_K (KCAL/G DRY WEIGHT PER DAY).—If the fecal losses, F_K, are subtracted from the ingested ration, R_K, a measure of the assimilated ration is obtained. The assimilated ration can also be determined by multiplying R_K by the assimilation efficiency, p, i.e., pR_K, where

$$p = \left(1 - \frac{F_K}{R_K}\right). \tag{9}$$

In our experiments with the Atlantic menhaden, we observed slight changes in the overall assimilation efficiency of a meal, depending on meal size (Durbin and Durbin 1981). However, because the observed differences in overall assimilation efficiency were small and because of the uncertainty about the significance of these differences, we assumed a constant assimilation efficiency for the model and took the means of the experimentally determined values. For Atlantic menhaden feeding on *D. brightwelli*, the mean assimilation efficiency, p, equalled 0.8636 for carbon, 0.9240 for nitrogen, and 0.8954 for calories (Durbin and Durbin 1981).

Substituting Equation (9) into Equation (1) we may rewrite the general equation for the energy budget:

$$G_K = pR_K - T_K - E_K \tag{10}$$

where the assimilated daily ration, pR_K, is given by

$$pR_K = 0.8954\ R_K \text{ (kcal/g dry weight per d)} \quad (11)$$

$$= 0.071250\ s\ c\ h \text{ (kcal/g dry weight per d)}. \quad (12)$$

Energy Output

RESPIRATION, T_K (KCAL/G DRY WEIGHT PER DAY).—In the absence of food, the Atlantic menhaden swam at a characteristic speed of 12.2 cm/s (0.47 body lengths/s), with a routine respiration rate of 0.10 mg O_2/g wet weight per h (Durbin et al. 1981).

During feeding the fish increased their swimming speed by a factor of 2.4- to 3.5-fold above the nonfeeding rate, depending on the plankton concentration in the water. Both swimming speed and respiration rate increased abruptly with the onset of feeding, and stabilized within a few minutes. One of the more interesting aspects of the Atlantic menhaden feeding behavior was that they would maintain a virtually constant swimming speed throughout the entire 7-h experimental feeding period, if the input of food remained constant. When the food input was stopped, the fish quickly consumed the remaining plankton in the tank, decreasing their swimming speed as the plankton concentration dropped. Thus the return to the routine swimming speed following feeding was quite rapid. In low-ration experiments, respiration rates declined to the routine, prefeeding rate almost immediately after feeding. In high-ration experiments, respiration rate remained slightly elevated above baseline for 2-5 h after feeding. The amount of energy expended above routine during the postfeeding period was small and did not show any clear relationship with food ration size. It has therefore been omitted for the purpose of the energy budget.

Based on these considerations, the respiratory costs for the energy budget are considered separately for periods of feeding and nonfeeding. Thus

$$T_K = T_{r,K} + T_{f,K} \text{ (kcal/g dry weight per d)} \quad (13)$$

where T_K = total daily expenditure for respiration
$T_{r,K}$ = routine respiration during the nonfeeding period
$T_{f,K}$ = respiration during feeding.

Oxygen consumption rates were converted to caloric equivalents by means of oxycalorific coefficients in Elliott and Davison (1975). The appropriate coefficients were determined from the ratios of oxygen consumed: nitrogen excreted by Atlantic menhaden before, during, and after feeding (Durbin and Durbin 1981). During feeding, Atlantic menhaden swimming at their preferred speed of about 41.3 cm/s appeared to be catabolizing protein. An oxycalorific coefficient of 3.20×10^{-3} kcal/mg O_2 was therefore used during periods when the fish were feeding. Nonfeeding menhaden catabolized about 28% protein and 72% fat (where $Q_{ox} = 3.28 \times 10^{-3}$ kcal/mg O_2), and the combined oxycalorific coefficient was 3.258×10^{-3} kcal/mg O_2.

Routine respiration rate, $T_{r,K}$.—The routine respiration rate of quietly swimming, nonfeeding Atlantic menhaden was 0.10 mg O_2/g wet weight per h = 0.299 mg O_2/g dry weight per h = 0.000974 kcal/g dry weight per h (Durbin et al. 1981). Thus the daily routine respiration during the nonfeeding period is given by

$$T_{r,K} = 0.000974\ (24\text{-}h) \text{ (kcal/g dry weight per d)} \quad (14)$$

where h is the duration of the feeding period (h/d).

Respiration during feeding, $T_{f,K}$.—The respiration rate increased significantly during feeding. This increase could be attributed to three sources: The higher voluntary swimming speed, the possible effect of excitement, and the specific dynamic effect of the food (SDA). The swimming speed was clearly the dominant factor, and accounted for 84.3% of the increased respiratory rate during feeding and 73.3% during the postfeeding period. Excitability was difficult to quantify, but our qualitative observations of the behavior of the fish indicated that they were least excitable during feeding and most excitable during the postfeeding period when they continued to hunt for food after the input to the tank had been stopped. SDA is considered to represent mainly the loss of energy during the deamination of protein, and it appears to constitute a fixed proportion of the energy content of a particular type of food (Muir and Niimi 1972). The energy cost of SDA is usually determined by monitoring the metabolic rate of the fish following a meal. Unfortunately in the present study we were unable to measure SDA separately because of the prolonged feeding period, during which ingestion and digestion occurred simultaneously. However, since about 80% of the ration was digested and assimilated during the 7-h feeding period (Durbin and Durbin 1981), most of the respiratory cost of SDA was included in the measurement of the total respiration rate during feeding.

The total respiration rate during feeding increased exponentially with increasing foraging speed (s, cm/s), where

$$T_{f,K} = 10^{0.02948\,s-1.5342} \text{ (mg } O_2\text{/g wet weight per h)} \quad (15)$$

$$T_{f,K} = 2.994 \quad (10^{0.02948\,s-1.5342}) \quad \text{(mg } O_2\text{/g dry weight per h).} \quad (16)$$

Converting to calories

$$T_{f,K} = 0.00958 \quad (10^{0.02948\,s-1.5342}) \text{ (kcal/g dry weight per h).} \quad (17)$$

The daily energy expenditure for respiration during feeding is therefore

$$T_{f,K} = 0.00958 \quad h \quad 10^{0.02948\,s-1.5342}) \text{ (kcal/g dry weight per d).} \quad (18)$$

Total daily respiration, T_K.—Combining Equations (14) and (18) we obtain an expression for the total respiratory expenditure per day as a function of the foraging speed (s, cm/s) and the foraging time (h, h/d):

$$T_K = h\,[0.00958\ (10^{0.02948\,s-1.5342}) - 0.000974] + 0.02338 \text{ (kcal/g dry weight per d).} \quad (19)$$

NITROGEN EXCRETION, E_K (KCAL/G DRY WEIGHT PER DAY).—Energy is lost through the excretion of nitrogenous compounds. In the absence of food the fish excreted nitrogen at a low rate (basal or endogenous excretion, $E_{b,N}$). Nitrogen excretion increased as a result of feeding (exogenous excretion, $E_{f,N}$). The total daily nitrogen excretion (E_N) is thus:

$$E_N = E_{b,N} + E_{f,N} \text{ (mg N/g dry weight per d).} \quad (20)$$

The energy equivalent of the excreted nitrogen was determined as follows: Of the total nitrogen excreted by menhaden, 69.6% was in the form of ammonia and 30.4% was in the form of dissolved organic nitrogen (DON) (Durbin and Durbin 1981). The caloric equivalent of ammonia nitrogen is 5.94×10^{-3} kcal/mg NH_3– N (Elliott and Davison 1975). The individual compounds comprising the DON excreted by Atlantic menhaden were not determined. For the purpose of the energy budget, the DON was assumed to consist of equal parts of urea, creatine, and trimethylamine, the major organic nitrogen compounds which are known to be excreted by teleosts (Watts and Watts 1974). The caloric equivalents of these compounds are: 5.51×10^{-3} kcal/mg urea-N (Elliott and Davison 1975), 13.32×10^{-3} kcal/mg creatine-N, and 41.3×10^{-3} kcal/mg trimethylamine-N (Weast 1977). The mean value for these compounds was 20.04×10^{-3} kcal/mg DON.

Endogenous nitrogen excretion, $E_{b,K}$.—The endogenous excretion rate equals 10.72 μg N/g dry weight per h (Durbin and Durbin 1981). The daily endogenous nitrogen excretion was therefore

$$E_{b,N} = 0.257 \text{ (mg N/g dry weight per d).} \quad (21)$$

Converting to calories

$$E_{b,K} = 0.0026282 \text{ (kcal/g dry weight per d).} \quad (22)$$

Exogenous nitrogen excretion, $E_{f,K}$.—The exogenous nitrogen excretion of menhaden fed *D. brightwelli* was directly proportional to the total nitrogen content of the ration, R_N (mg N/g dry weight per d) (Durbin and Durbin 1981):

$$E_{f,N} = 0.616\ R_N - 0.020 \text{ (mg N/g dry weight per d).} \quad (23)$$

Converting to calories

$$E_{f,K} = 0.006299\ R_N - 0.0002045 \text{ (kcal/g dry weight per d).} \quad (24)$$

The nitrogen content of a ration of *D. brightwelli*, R_N (mg), may be converted to kilocalories, R_K (kcal), according to the following relationship

$$R_K = 0.06158\ R_N \quad (25)$$

(Durbin and Durbin 1981). Thus if the daily ration is expressed in kilocalories rather than nitrogen, the daily exogenous nitrogen excretion becomes

$$E_{f,K} = 0.1023\ R_K - 0.0002045 \text{ (kcal/g dry weight per d).} \quad (26)$$

Total daily nitrogen excretion, E_K.—Combining Equations (21) and (23) we obtain an expression for the total daily nitrogen excretion rate

$$E_N = 0.616\ R_N + 0.237 \text{ (mg N/g dry weight per d).} \quad (27)$$

Combining Equations (22) and (26), the daily nitrogen excretion rate is expressed in calories

$$E_K = 0.1023\ R_K + 0.002423 \text{ (kcal/g dry weight per d).} \quad (28)$$

Since the total daily ration is given by $R_K = 0.079574\ s\ c\ h$ (kcal/g dry weight per d), we can substitute and obtain an expression for the total energy lost per day through nitrogen excretion, as a function of the foraging speed (s, cm/s) of the Atlantic menhaden, the concentration of food (c, kcal/l) and the foraging time (h, h/d):

$$E_K = 0.008140\ s\ c\ h + 0.002423 \text{ (kcal/g dry weight per d).} \quad (29)$$

Growth Rate, G_K and Gross Growth Efficiency, $K_{1,K}$

Equations (12), (19), and (29) may be combined to provide an estimate of the daily growth rate, G_K (kcal/g dry weight per d), as a function of menhaden foraging speed (s, cm/s), the concentration of plankton in the water (c, kcal/l), and the foraging time (h, h/d), since

$$G_K = pR_K - T_K - E_K \text{ (kcal/g dry weight per d)}$$

$$G_K = h\ [0.06311\ s\ c - 0.00958\ (10^{0.02948\ s - 1.5342}) + 0.000974] - 0.025803 \text{ (kcal/g dry weight per d).} \quad (30)$$

The gross growth efficiency, K_1 is calculated according to

$$K_1 = \frac{G}{R}. \quad (31)$$

Thus K_1 in calories is equal to

$$K_{1,K} = \frac{\text{Equation (30)}}{\text{Equation (8)}}. \quad (32)$$

From Equation (30) we can also determine the foraging speed which maximizes growth rate ($s_{G,\mathrm{OPT}}$), for any given values of c and h. First restating Equation (30) in a more general form, replacing the constants by A, B, C, D, E, J, and M,

$$G_K = h\ [A\ sc - B(10^{(Ds-E)}) + J] - M \text{ (kcal/g dry weight per d).} \quad (33)$$

We then differentiate Equation (30) with respect to s, i.e., set $\frac{dG}{ds} = 0$, and we find

$$s_{G,\mathrm{OPT}} = \frac{\log_{10}K + E}{D} + \frac{1}{D}\log_{10}c \quad (34)$$

where $K = \frac{A}{B(\log_e 10)\ I)}$. (35)

In the present study where *D. brightwelli* is the food,

$$s_{G,\mathrm{OPT}} = 119.4433 + 33.9213\ \log_{10}c. \quad (36)$$

To determine the equation for the swimming speed which maximizes gross growth efficiency ($s_{K,\mathrm{OPT}}$), i.e., when $\frac{dK_1}{ds} = 0$, we use the following general equation:

$$K_1 = \frac{\text{Equation (30)}}{\text{Equation (8)}} = \frac{h\ [A\ s\ c - B(10^{(Ds-E)}) + J]}{P\ s\ c\ h} - M \quad (37)$$

where P is the constant in Equation (8), i.e., in the present example, $P = 0.079574$. We next define the new constants

$$A' = \frac{A}{P} \quad (38)$$

$$B' = \frac{B}{P} \quad (39)$$

$$B'' = B'\ (\log_e 10)D \quad (40)$$

$$J' = \frac{J}{P} \quad (41)$$

$$M' = \frac{M}{P}. \quad (42)$$

And thus

$$K_1 = A' - \frac{B'\ 10^{(Ds-E)} - J'}{sc} - \frac{M'}{sc}. \quad (43)$$

For $\frac{dK_1}{ds} = 0$, we find the following identity

$$\frac{M'}{h} - J' = (B''\ s - B')\ 10^{(Ds-E)}. \quad (44)$$

This identity must be solved iteratively for $s_{K,\mathrm{OPT}}$ by using a given value of h and trial values of s.

In the present example using *D. brightwelli*, we find

$$\frac{0.32426}{h} - 0.01224 = (0.0081722\ s - 0.12039) \times 10^{(0.02948\ s - 1.5342)}. \quad (45)$$

Each term in the energy budget has now been defined in the same three variables: The foraging speed (s), the food concentration (c), and the foraging

time (h). Model I describes the potential interactions among these three variables, and their effects on menhaden energy intake, energy expenditure, growth, and growth efficiency.

Energy Budget (Model II)

Model II is a special case of Model I which incorporates information on the swimming and feeding behavior of the Atlantic menhaden in response to plankton concentration. Laboratory observations have shown that Atlantic menhaden adjust their foraging speed according to the concentration of food in the water. When *D. brightwelli* was the food, the threshold concentration for the onset of feeding was about 1 μg chlorophyll a/l. Between about 1 and 4 μg chlorophyll a/l, the menhaden increased their foraging speed roughly in proportion to increasing plankton concentration. Above 4 μg chlorophyll a/l, however, swimming speed remained nearly constant at about 41.3 cm/s (1.6 body lengths/s), independent of further increases in plankton concentration. Thus the relationship between the Atlantic menhaden foraging speed and *Ditylum* chlorophyll a (a, μg/l) was approximately asymptotic, where

$$s = \frac{29.62\ (a - 1)}{0.396 + (a - 1)} + 12.2 \text{ (cm/s)} \quad (46)$$

(Durbin et al. 1981). The equation includes the feeding threshold for *Ditylum* (1 μg chlorophyll a/l) and the routine (nonfeeding) swimming speed of the fish (12.2 cm/s), which represents the lower limit of the foraging speed.

The chlorophyll a content of *D. brightwelli* may be converted to kilocalories according to the following relationship:

$$1\ \mu\text{g chlorophyll a} = 6.06 \times 10^{-4}\ \text{kcal}. \quad (47)$$

Thus Equation (46) becomes

$$s = \frac{48{,}873\ c - 29.62}{1{,}650\ c - 0.604} + 12.2 \text{ (cm/s)} \quad (48)$$

where c (kcal/l) is the plankton concentration.

By substituting Equation (48) for s in Equations (8), (12), (19), (29), (30), and (32) for R_K, pR_K, T_K, E_K, G_K, and $K_{1,K}$, respectively, we are able to eliminate as a variable and rewrite the menhaden energy budget solely in terms of food concentration (c, kcal/l) and foraging time (h, h/d). This is Model II.

Nitrogen Budget (Model I)

The general equation for the nitrogen budget presented in Equation (2) may be rewritten:

$$G_N = pR_N - E_N \quad (49)$$

where p is the assimilation efficiency for nitrogen = 0.9240 (Durbin and Durbin 1981). The nitrogen budget is controlled by the same three variables as the energy budget: The foraging speed (s), the food concentrations (c or n), and the foraging time (h).

The total dialy ration, R_N (mg N/g dry weight per d), equals

$$R_N = 0.79574\ s\ n\ h \text{ (mg N/g dry weight per d)} \quad (50)$$

where n is the plankton concentration (mg N/l).

The assimilated daily nitrogen ration, pR_N, equals

$$pR_N = 0.073526\ s\ n\ h \text{ (mg N/g dry weight per d)}. \quad (51)$$

The endogenous, exogenous, and total daily nitrogen excretion rates, $E_{b,N}$, $E_{f,N}$, and E_N (mg N/g dry weight per d) are presented in Equations (21), (23), and (27), respectively.

Substituting Equation (27) into Equation (49), we obtain the following expression for the daily growth rate, G_N:

$$G_N = 0.308\ R_N - 0.237 \text{ (mg N/g dry weight per d)}. \quad (52)$$

Gross growth efficiency, $K_{1,N}$, equals

$$K_{1,N} = \frac{0.308\ R_N - 0.237}{R_N} \text{ (mg N/g dry weight per d)} \quad (53)$$

where R_N is calculated according to Equation (50).

If the ration is converted from units of nitrogen to kilocalories (Equation (25)), then Equations (52) and (53) become

$$G_N = 5.0016\ R_K - 0.237 \text{ (mg N/g dry weight per d)} \quad (54)$$

$$K_{1,N} = \frac{5.0016\ R_K - 0.237}{16.239\ R_K} \quad (55)$$

where R_K is calculated according to Equation (8).

Nitrogen Budget (Model II)

The empirical relationship between foraging speed, s (cm/s), and plankton concentration, a(μg/l) (Equa-

tion (46)), is expressed in units of nitrogen through the following relationship:

$$1\,\mu g \text{ chlorophyll a} = 0.00984 \text{ mg N.} \quad (56)$$

$$\text{Thus } s = \frac{3{,}010.2\,n - 29.62}{101.63\,n - 0.604} + 12.2 \text{ cm/s} \quad (57)$$

where n is the plankton concentration in mg N/l.

The nitrogen budget can then be expressed solely in terms of plankton concentration, n (mg N/l), and foraging time, h (h/d), by substituting Equation (57) into Equations (50), (51), (27), (52), and (53) to compute R_N, pR_N, E_N, G_N, and $K_{1,N}$ (mg N/g dry weight per d), respectively

If the food ration or the plankton concentration is expressed in kilocalories rather than units of nitrogen, Equation (48) is substituted into Equation (8), and then Equation (8) into Equations (54) and (55) for the calculations of G_N and $K_{1,N}$, respectively.

The Model II nitrogen budget, like energy budget II, is thus controlled by only two variables, c and h.

RESULTS

Energy Budget

The energy budget is presented in two forms, a general model (Model I) and a special case of this model which incorporates information on the swimming and feeding behavior of the fish in response to plankton concentration (Model II). Model I, which defines the range of values which the energy budget could theoretically assume, is a function of the foraging speed (s), the concentration of plankton in the water (c), and the foraging time (h). In Model II, foraging speed is a dependent function of plankton concentration, and the energy budget is defined simply in terms of the variables c and h. Thus the two models describe the potential, and the actual, bioenergetic ranges within which the menhaden operate.

In the following examples to illustrate the models, the variables s, c, and h assume values from 0 to 50 cm/s, 0 to 0.0090 kcal/l, and 0 to 24 h/d, respectively, which should encompass the range of these variables in nature. In examples where s is assumed to be constant, a value of 41.3 cm/s was selected, because in the experiments this was the average foraging speed of the Atlantic menhaden at moderate to high plankton concentrations, where s was nearly independent of food level. Where c = constant, a value of 0.0030 kcal/l was used, which is slightly above the threshold value of c at which s becomes food-concentration independent. We lack information on the foraging time of adult Atlantic menhaden in the wild. However, since they feed continuously in the laboratory when food is present, when h = constant, we assigned it a value of 14 h, which is approximately equal to the number of daylight hours during the summer at the latitude of Narragansett Bay.

In the experimental studies from which the budgets were derived, the variables s, c, and h took the following values: h = 7 h, c = 0.0010 to 0.0065 kcal/l, and s = 29.3 to 43.3 cm/s (1.1 to 1.7 body lengths/s). Within this relatively narrow range in foraging speed, the respiration rate increased from 2.2- to 5.4-fold over the routine rate. Slower foraging speeds (<29 cm/s) were observed during the transition period of declining phytoplankton concentration, after the input of food was terminated. The minimum foraging speed was greater than the routine swimming speed (12.2 cm/s), but was not closely determined in this study. The total ration ranged from 0.015 to 0.147 kcal/g dry weight, which corresponded to a feeding rate of 0.00217 to 0.02065 kcal/g dry weight per h.

Using Model I we have described how foraging speed, food concentration, and the duration of feeding affect the menhaden energy budget (Fig. 1).

In Figure 1, A1-A4, s increases, while c and h remain constant. The total and the assimilated daily food intake (R_K and pR_K) increase linearly with increasing values of s (Fig. 1, A1). Among the energy expenditure terms, the exogenous nitrogen excretion ($E_{f,K}$) increases linearly, the endogenous nitrogen excretion ($E_{b,K}$) and the routine metabolic rate ($T_{r,K}$) remain constant, and the respiration during feeding ($T_{f,K}$) increases exponentially with increasing s (Fig. 1, A2). Thus the assimilated daily ration increases linearly, whereas the total energy expended increases curvilinearly. If these two curves are drawn on the same axes, we find that they intersect twice, at a low and a high foraging speed (here, about 7 and 51 cm/s) (Fig. 1, A3). These intersections, where the energy intake is balanced by the output and $G = 0$, define a range of foraging speeds within which the energy intake exceeds expenditure, and positive growth takes place. At foraging speeds outside this range, the energy expenditures exceed the energy intake and the fish must draw upon stored energy reserves, thus undergoing negative growth. Within the defined range of foraging speeds, the growth curve (G_K) is convex upwards, increasing curvilinearly from zero to reach a maximum value at an intermediate swimming speed, then declining back to zero (Fig. 1, A4). The growth efficiency curve ($K_{1,K}$) shows a similar pattern, but reaches its maximum value at a different foraging speed than that for maximum growth.

In Figure 1, B1-B4, c increases, while s and h remain constant. The energy intake (R and pR) increases

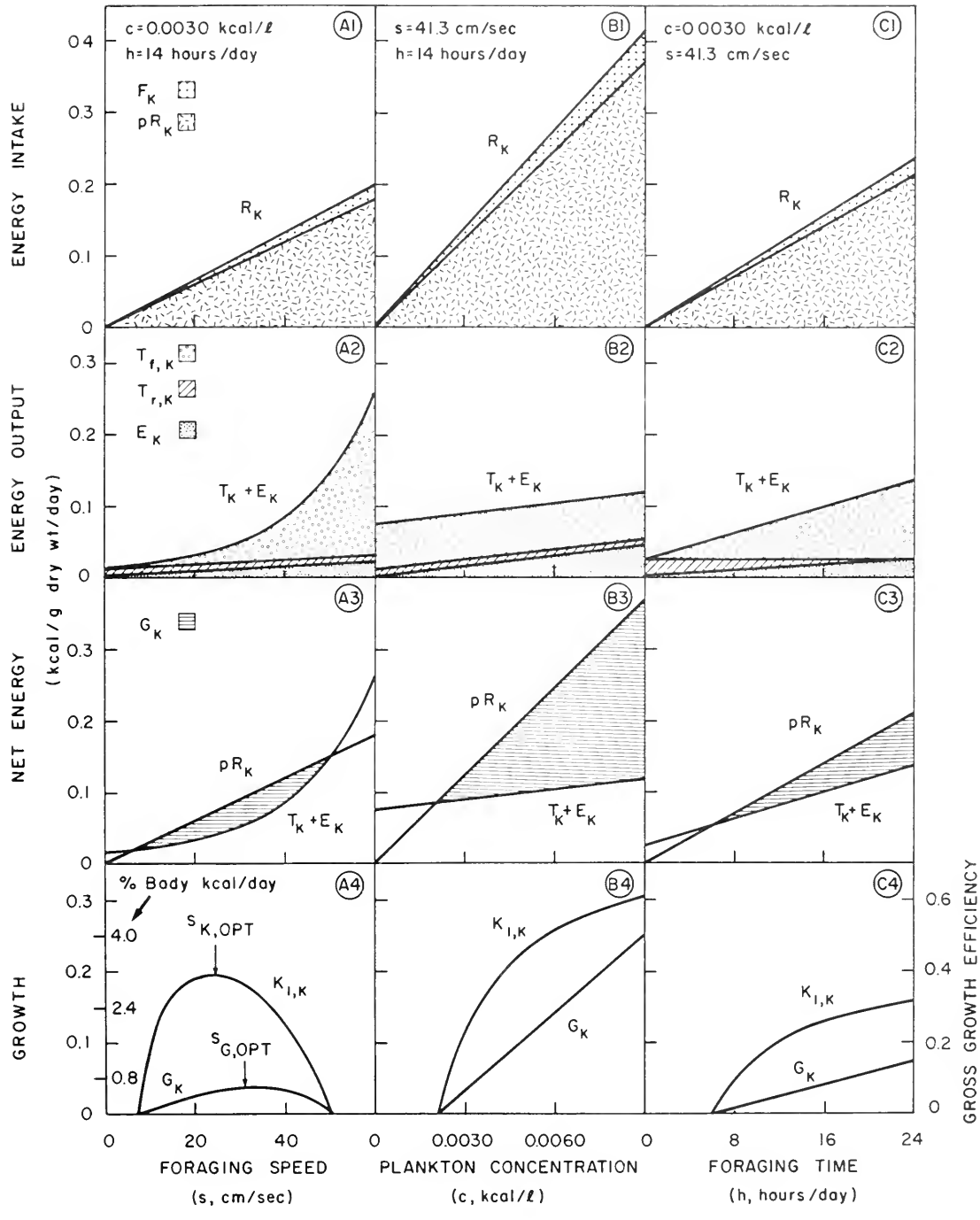

FIGURE 1.—Model I energy budget for the Atlantic menhaden at 20° C, where: A, foraging speed(s) increases, while plankton concentration (c) and foraging time (h) remain constant; B, plankton concentration increases, while foraging speed and foraging time remain constant; and C, foraging time increases, while foraging speed and plankton concentration remain constant. A1, B1, and C1 represent energy intake (R_K and pR_K); A2, B2, and C2, the energy output ($T_{r,K}$, $T_{f,K}$, E_K); A3, B3, and C3 compare the intake and output of energy and show the surplus energy which is available for growth; A4, B4, and C4 illustrate growth and gross growth efficiency.

linearly with increasing c (Fig. 1, B1). The energy expenditure to exogenous nitrogen excretion ($E_{f,K}$) also increases linearly, whereas $E_{b,N}$ and respiration ($T_{r,K}$ and $T_{f,K}$) are constant (Fig. 1, B2). The curves representing energy intake and expenditure both increase linearly with increasing values of c (Fig. 1, B3), and thus growth (G_K) increases linearly and gross growth efficiency increases asymptotically (Fig. 1, B4).

In Figure 1, C1-C4, h increases, while s and c remain constant. Here, also, the energy intake (R and pR) increases linearly with increasing h (Fig. 1, C1). The energy expenditure to endogenous nitrogen excretion ($E_{b,K}$) remains constant, while exogenous nitrogen excretion ($E_{f,K}$) and the respiration during feeding ($T_{f,K}$) increase linearly, and the routine respiration ($T_{r,K}$) declines linearly (Fig. 1, C2). The curves describing the energy intake and expenditure increase linearly with increasing values of h, (Fig. 1, C3), and again we find that growth (G_K) increases linearly and gross growth efficiency ($K_{1,K}$) increases asymptotically (Fig. 1, C4)

These examples demonstrate that in order for an Atlantic menhaden, which forages at s cm/s for h h/d, to obtain a maintenance ration, the concentration of food must equal a minimum threshold value, c_{min} (i.e., 0.0021 kcal/l in Fig. 1, B3-B4). Similarly, a menhaden foraging at s cm/s when the plankton concentration = c kcal/l, must feed for some minimum period h_{min} (in Fig. 1, C3 and C4; 6.2 h/d) in order to obtain a maintenance ration. There will also be a minimum foraging speed, s_{min}, required to obtain a maintenance ration for each combination of c and h (in Fig. 1, A3 and A4; 7.0 cm/s). If growth is to occur, s, c, and h must exceed s_{min}, c_{min}, and h_{min}. The general rule is that for any swimming speed (s), the more abundant the food, the smaller the maintenance ration, and the shorter the feeding time required to obtain the ration (Fig. 2, A, B). If an Atlantic menhaden forages at 41.3 cm/s, for example, the lowest concentration of *Ditylum* at which it could obtain a maintenance ration would be about 0.0018 kcal/l, assuming that it fed for 24 h/d. The maintenance ration would be about 0.143 kcal/g dry weight per d. With an increase in plankton concentration, the required feeding time and the maintenance ration decline very rapidly, reaching 4 h/d and 0.051 kcal/g dry weight per d at c = 0.0039 kcal/l, and declining more slowly thereafter to 1.3 h/d and 0.038 kcal/g dry weight per d at c = 0.009 kcal/l.

An interesting feature of the energy budget is that for any combination of c and h, there is a single foraging speed which will maximize the growth rate ($s_{G,OPT}$) (Fig. 1, A4). Similarly, growth efficiency reaches its maximum value at a unique foraging speed ($s_{K,OPT}$), which is always less than $s_{G,OPT}$. $s_{G,OPT}$ increases curvilinearly with increasing food concentration (Fig. 3), but is independent of the duration of feeding (Fig. 4, Equation (36)). In contrast, $s_{K,OPT}$ declines as the duration of feeding increases (Fig. 4), but is independent of food concentration (Fig. 3, Equation (45)). It should be remembered however that the values of G_K and $K_{1,K}$ when the fish swim at $s_{G,OPT}$ and $s_{K,OPT}$ are determined by both c and h. For example, if c = 0.0030 kcal/l, a fish will maximize its growth rate if it swims at 33.9 cm/s although the actual rate of growth

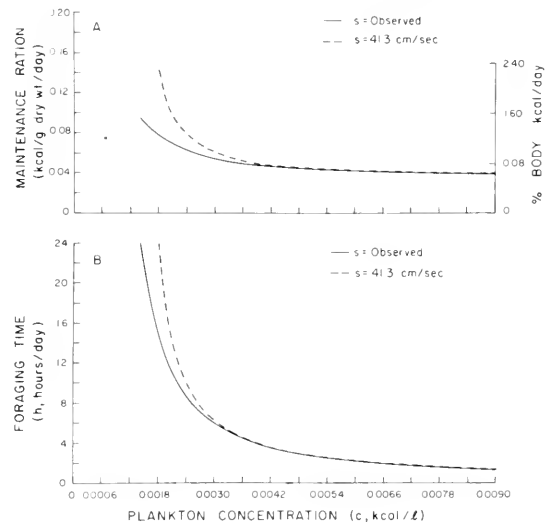

FIGURE 2.—A, relationship between the concentration of plankton and the maintenance ration of Atlantic menhaden which are assumed to swim at a constant speed of 41.3 cm/s (Model I) and at their actual speeds in response to plankton concentration (Model II). B, the foraging time required for the Atlantic menhaden to obtain a maintenance ration at different concentrations of plankton, assuming that they swim at 41.3 cm/s (Model I) or at the actual speed which has been observed in the laboratory (Model II).

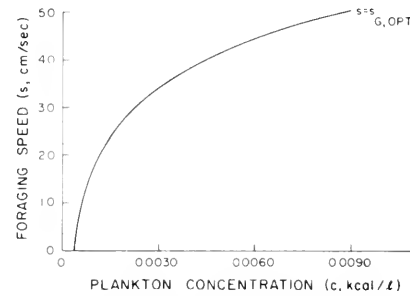

FIGURE 3.—The relationship between plankton concentration and the foraging speed which maximizes the Atlantic menhaden's growth rate ($s_{G,OPT}$). $s_{G,OPT}$ is independent of foraging time (h).

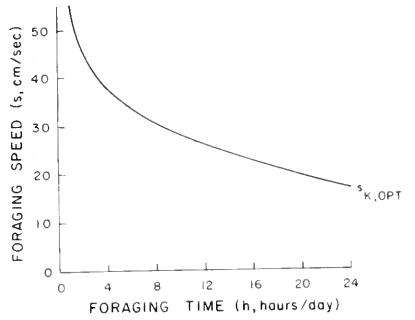

FIGURE 4.—The relationship between foraging time and the foraging speed which maximizes the Atlantic menhaden's gross growth efficiency ($s_{K,OPT}$). $s(s_{K,OPT})$ is independent of plankton concentration (c).

depends on h. Similarly, a fish feeding for 14 h/d will maximize its growth efficiency if it swims at 23.8 cm/s; however the resulting values of K_1 will depend on c.

The foregoing examples demonstrate that the relative size of each component in the energy budget (R_K, pR_K, T_K, E_K, and G_K) will vary according to the values of s, c, and h. Since the different elements retain no fixed proportions within the overall energy balance, there is no single "standard" energy budget which can be described for the Atlantic menhaden.

It can also be seen that in Model I, a change in either food concentration or the duration of feeding has a direct, proportional effect on the growth rate, because total energy intake and expenditure are linear functions of c and h, when s = constant. However, a change in s has a nonlinear impact on the growth rate. This is because the respiration rate is an exponential function of swimming speed, and thus a change in swimming speed causes a proportional change in energy intake but a more-than-proportional change in total energy output.

In the Model II energy budget, s is no longer an independent variable, but is a dependent function of food concentration c, according to the experimentally derived relationship in Equation (48). The foraging speed is nearly constant at moderate to high concentrations, but is reduced at low plankton abundance. The threshold concentration (0.0006 kcal/l) at which the fish stop feeding on *Ditylum* is also included in this model. The effect of reducing the foraging speed, when plankton concentration is low, is illustrated in Figure 5, which provides a comparison of Model II with Model I, where s = constant = 41.3 cm/s. (This foraging speed was chosen for the Model I example because it provides the best overall fit to Model II, facilitating the comparison between the two. The choice of another value for s would cause Model I to depart further from the actual behavior of the fish and would increase the difference between the two models.)

In Model I, we found that when s and h were constant, the curves describing R_K, pR_K, T_K, E_K, and G_K as a function of increasing c were all linear or constant (Fig. 1, B1-B4; Fig. 5, A1-A4). In Model II, these curves are nearly linear or constant at moderate to high plankton concentrations, where $s \sim$ constant. However, they become increasingly curvilinear at lower concentrations, when s is changing rapidly (Fig. 5, B1-B4). Thus we find that Model II is quite similar to Model I where s = 41.3 cm/s, when the food concentration is above c_{min} in the Model I example ($\sim$0.0021 kcal/l for h = 14 h/d). The models diverge significantly as c declines below c_{min}. If the Atlantic menhaden were to continue to swim at their "preferred" speed when the plankton concentration is low, a significant deficit in the energy budget would result (Fig. 5, A3). However, Model II shows that by reducing their foraging speed when food concentration is low, the Atlantic menhaden act to regulate their energy expenditure to remain close to their rate of energy uptake (Fig. 5, B3). Reducing the foraging speed has this effect, because of the exponential relationship between respiration and swimming speed. A reduction in foraging speed causes the respiration term to decline more rapidly than the ingestion term. The resulting change in the energy balance enables the fish to obtain a maintenance ration in less time, and at a lower concentration of food, than would have been possible had they continued to forage at the higher speed. The growth rate and growth efficiency are thereby enhanced at low concentrations (compare Fig. 5, A4 and B4). This effect can also be seen in Figure 2.

At the threshold concentration (0.0006 kcal/l) where Atlantic menhaden cease feeding on *Ditylum*, it can be seen (Fig. 5, B1 and B2) that the routine metabolic costs alone are greater than the energy which could be derived from feeding. The behavior of the fish apparently reflects the fact that it is not bioenergetically profitable to feed at such a low plankton density.

Nitrogen Budget

In the nitrogen budget there are three loss terms: The endogenous excretion, which is a constant, and the exogenous excretion and the fecal losses, which are proportional to the nitrogen content of the daily ration. The remaining nitrogen from the ration is retained as growth. Thus we find that the nitrogen

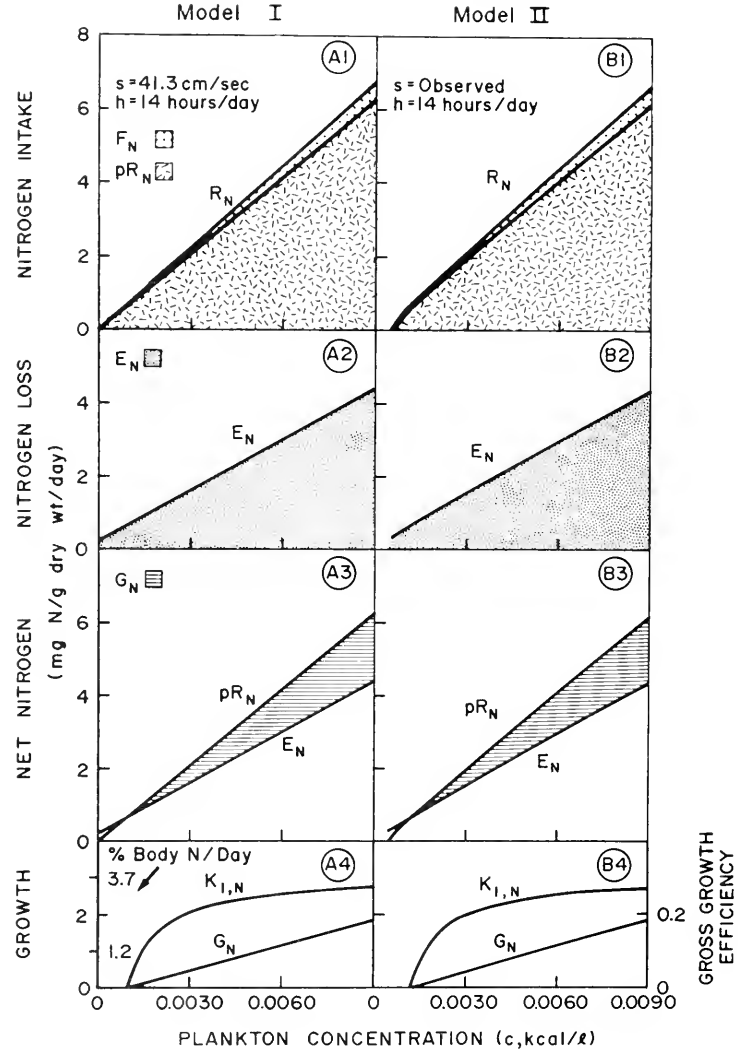

FIGURE 5.—A comparison of the Model I energy budget, where foraging speed and foraging time are constant while plankton concentration increases, with the Model II budget incorporating the actual voluntary swimming speed of the Atlantic menhaden at each concentration of plankton. Panels numbered 1, 2, 3, 4 are as in Figure 1.

budget, though functionally simpler than the energy budget, is controlled by the same three variables: The foraging speed (s, cm/s), the concentration of food (c, kcal or mg N/l), and the foraging time (h, h/d). In the Model I nitrogen budget, R_N, pR_N, $E_{f,N}$, and G_N all increase linearly, $E_{b,N}$ remains constant, and $K_{1,N}$ increases asymptotically with increasing values of s, c, and h (Fig. 6). However, as we found in the energy budget, these curves in the Model II nitrogen budget are nearly linear at plankton concentrations sufficiently high that $s \sim$ constant, but become increasingly curvilinear at low plankton concentrations because of the decline in the foraging speed (Fig. 7). Here, also, the reduction in foraging speed enables the Atlantic menhaden to obtain a maintenance ration in less time and at a lower concentration of plankton, and to increase their growth rate and growth efficiency, relative to the case in Model I where foraging speed was assumed to remain constant at 41.3 cm/s.

The nitrogen and energy budgets differ in some important ways. First, we have seen that in the energy budget, with an increase in swimming speed (s), the growth rate and growth efficiency increase from zero, reach a maximum, then decline back to zero (Fig. 1, A4). However, in the nitrogen budget, growth in nitrogen increases linearly (i.e., indefinitely), and growth efficiency increases asymptotically (Fig. 6, A4) with increasing swimming speed. Second, for any given s, c, and h, the predicted growth efficiency in calories is usually significantly different from that in nitrogen (Fig. 8). Figure 8 shows that differences ex-

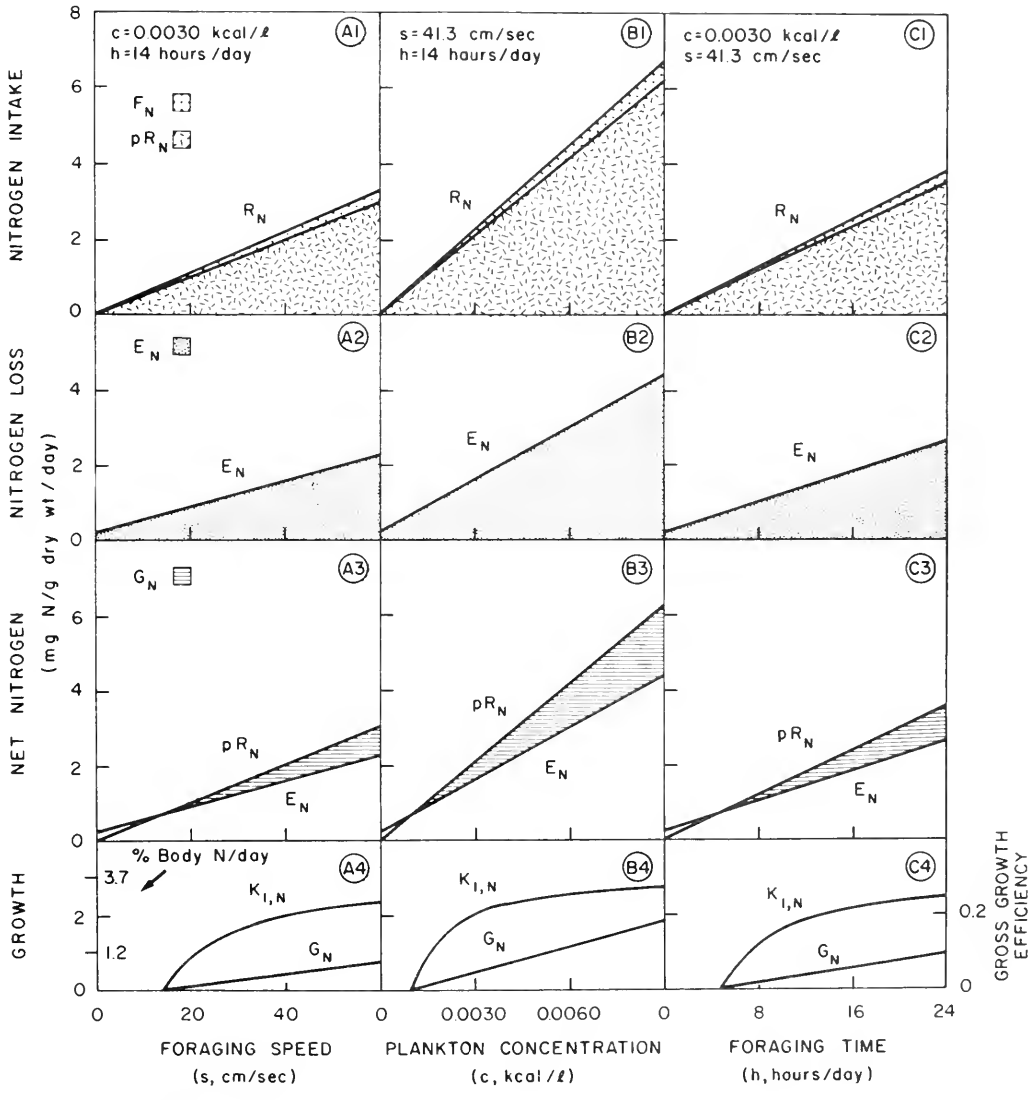

FIGURE 6.—Model I nitrogen budget for the Atlantic menhaden. Panels are as in Figure 1.

ist not only in the maximum or asymptotic values of the two growth efficiencies, but in the x-intercepts of the curves as well. The x-intercepts are of particular interest since they define the minimum requirements (s_{min}, c_{min}, h_{min}) for the fish to obtain a maintenance ration in nitrogen or calories. In Figure 8A, for instance, where c = 0.0030 kcal/l and h = 14 h/d, $s_{min,K}$ is $<s_{min,N}$. The Atlantic menhaden would be able to show positive growth in calories at a foraging speed of about 7 cm/s, whereas positive growth in nitrogen would require a higher foraging speed of about 14 cm/s. However, in Figure 8B, C, $c_{min,N}$ is $<c_{min,K}$ and $h_{min,N}$ is $<h_{min,K}$, respectively. Thus in these examples the menhaden would show positive growth in nitrogen at a lower food concentration, and with a shorter foraging time, than they would in calories.

Atlantic menhaden can exercise direct control over the variables s and h, but they may or may not have any impact on the environmental variable c. Thus it is of interest to consider how a change in the values of s and h will affect the minimum plankton concentration required for the Atlantic menhaden to obtain a maintenance ration in calories and nitrogen. The curve in Figure 9, calculated from the Model I budget, shows the combinations of s and h at which $c_{min,K} = c_{min,N}$. For all combinations of s and h, which fall below

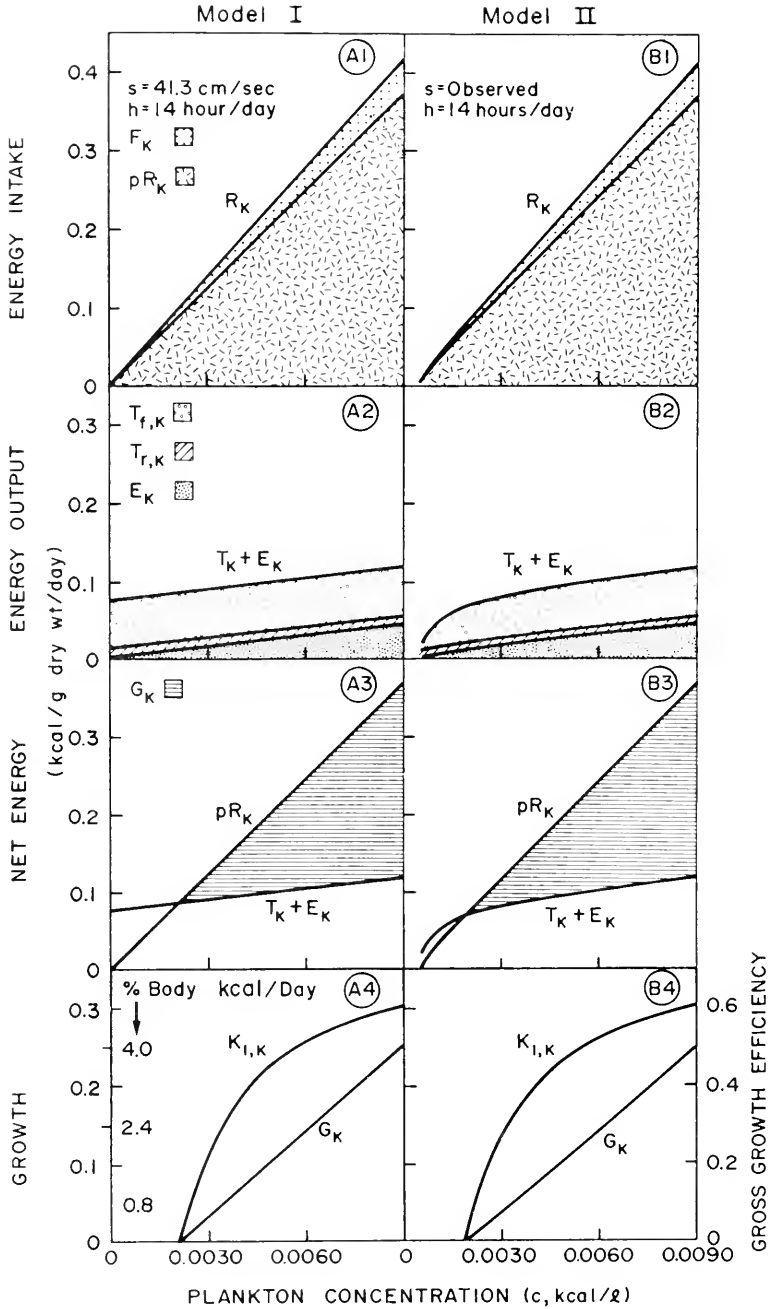

FIGURE 7.—Comparison of the Model I nitrogen budget where foraging speed and foraging time remain constant while plankton concentration increases, with the Model II budget incorporating the observed swimming speeds of the Atlantic menhaden at each plankton concentration.

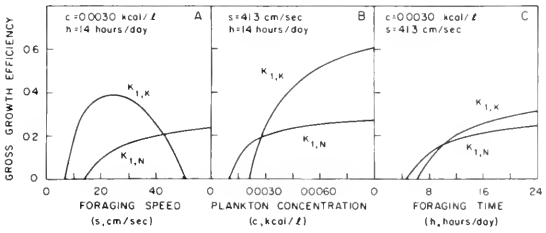

FIGURE 8.—Comparison of the gross growth efficiency of the Atlantic menhaden in calories ($K_{1,K}$) and nitrogen ($K_{1,N}$) where A, foraging speed(s) increases while plankton concentration (c) and foraging time (h) remain constant; B, plankton concentration increases while s and h are constant; and C, foraging time increases while s and c are constant.

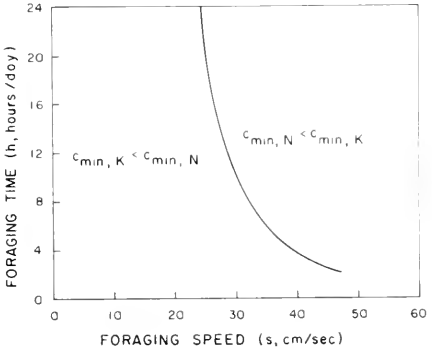

FIGURE 9.—Boundary curve defining the combinations of foraging time and foraging speed at which the minimum plankton concentration required for the Atlantic menhaden's growth in calories ($c_{min,K}$) is less than, and greater than, that required for growth in nitrogen ($c_{min,N}$).

this boundary, $c_{min,K}$ will be lower than $c_{min,N}$. Atlantic menhaden will be able to grow in calories at a lower food concentration than they can in nitrogen. Conversely, where s and h are greater than the boundary values, $c_{min,N}$ will be lower than $c_{min,K}$. Atlantic menhaden can grow in nitrogen at a lower food concentration than they can in calories.

Next we consider how the actual foraging speeds of the Atlantic menhaden compare with the boundary curve in Figure 9. Figure 10A shows the foraging speed in relation to food concentration. Figure 10B shows that for all values of h up to 24 h/d, Atlantic menhaden forage at speeds such that their minimum food requirement for growth in nitrogen is lower than for calories, i.e., $c_{min,N}$ is $< c_{min,K}$. Thus at low plankton concentrations, the growth efficiency in nitrogen is greater than in calories. However, it can be seen from Figure 9 that $K_{1,N}$ remains $> K_{1,K}$ only over a narrow range of food concentrations immediately above $c_{min,N}$. $K_{1,K}$ increases very rapidly above $c_{min,K}$ and soon overtakes $K_{1,N}$. Thus in most circumstances where the fish are growing, growth efficiency in calories will be considerably higher than in nitrogen.

DISCUSSION

Functioning of the Energy and Nitrogen Budgets

These models permit a detailed analysis of the energetics of the Atlantic menhaden, by showing how energy intake (ingestion), as well as energy losses and expenditures (feces, excretion, respiration) vary with the concentration and size of the food particles, the foraging speed of the fish, and the duration of feeding. These different components of the model, and the predicted growth rate and growth efficiency, are discussed in more detail below.

Energy Intake

VOLUME SEARCHED.—The volume searched by the Atlantic menhaden can be described in very

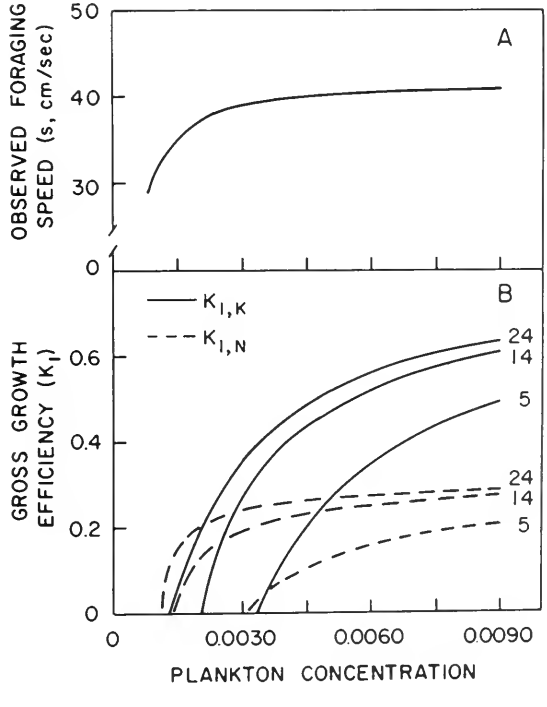

FIGURE 10.—A, laboratory defined relationship between Atlantic menhaden voluntary foraging speed and plankton concentration. B, gross growth efficiency of menhaden which forage at these swimming speeds for different periods of time.

simple terms, i.e., an ellipsoid with cross-sectional area equal to that of the fish's open mouth, and length equal to the distance travelled by the fish per unit time. The volume searched is equal for all types of prey. With other species of filter-feeding fishes, a slight modification of this basic formula may be necessary, according to the mode of feeding. For example, a number of species (northern anchovy, Leong and O'Connell 1969; alewife, Janssen 1978; gizzard shad, Drenner et al. 1978) are described as rhythmically opening and closing the mouth during feeding, apparently producing a suction which draws in particles located outside the perimeter of the mouth. Here, the cross-sectional area of the volume searched is somewhat larger than the mouth area; also, a correction factor is needed to account for the proportion of the time the fish's mouth is closed and not actually filtering. Nevertheless, the basic simplicity of the volume searched by a filter feeder is in marked contrast to the case of a predatory fish or particulate planktivore. Since these fishes visually locate and capture their prey, the volume searched is complex and depends on a variety of factors, including the visual capacity and adaptations of the fish, the inherent visibility and behavioral characteristics of the prey, and the nature of the underwater visual environment (quantity and quality of the illumination, clarity of the water). Thus the volume searched by a particulate feeder is different for different types of prey, and even if a fish were to swim at constant speed and feed on a single prey type, the volume searched will continually change according to variables such as the time of day, and the depth at which the fish swims (Durbin 1979).

FORAGING SPEED.—Foraging speed affects both the energy intake and expenditure terms in the energy budget, but only the energy intake in the nitrogen budget. Foraging speed is the principal determinant of the volume searched for food, since the cross-sectional area of the mouth in an Atlantic menhaden of a given size is constant. Foraging speed in the Atlantic menhaden increases asymptotically with increasing food concentration. Because of this there will be two critical levels of abundance for each prey species: c_t, the threshold concentration at which the menhaden are stimulated to feed, and c_i, the concentration at which foraging speed becomes approximately independent of food concentration. With *Ditylum*, the value of c_t was about 4.5 μg chlorophyll a/l (0.0027 kcal/l), and the fish swam at an average speed of 41.3 cm/s. From Figure 2 it is seen that when c = 0.0027 kcal/l, the fish swimming at 41.3 cm/s would obtain a maintenance ration in slightly more than 7 h. At higher food concentrations the required feeding time would be much less, generally <4 h. These results suggest that Atlantic menhaden feeding on *Ditylum* will swim at their "preferred" speed as long as the concentration is sufficiently high to enable the fish to meet their daily energy requirements in <8 h of feeding. At lower food concentrations the fish conserve energy by swimming more slowly during feeding. Whether these results are fortuitous and apply only to *Ditylum*, or instead imply a fundamental relationship between foraging speed and foraging time which is applicable to different food types, cannot be determined from present information.

FILTRATION EFFICIENCY.—The effective volume searched will be determined by the filtration efficiency (e). As described earlier (Equation (6)) filtration efficiency is fairly high for zooplankton-sized particles, but in the range of phytoplankton-sized particles declines sharply to a minimum size threshold of about 13 μm. This means that the Atlantic menhaden cannot directly exploit the <20 μm size fraction of phytoplankton, which forms the greater part of the total phytoplankton biomass on their summer feeding grounds (Durbin et al. 1975). Menhaden exploit this food resource indirectly, however, by feeding upon the zooplankton.

ASSIMILATION EFFICIENCY.—The efficiency with which food is assimilated further modifies the energy intake by the Atlantic menhaden and will affect the predicted growth rate and growth efficiency in the model. If assimilation changes with different meal sizes or rates of feeding, then the proportion of ingested energy which is available for metabolism and growth will also change. Most investigators have found that assimilation efficiency is independent of ration size (Gerking 1955; Menzel 1960; Pandian 1967; Birkett 1969; Iwata 1970; Beamish 1972; Kelso 1972; Staples and Nomura 1976). However, Elliott (1976) and Solomon and Brafield (1972) found a slight decrease in assimilation efficiency as meal size increased. (In the latter study the authors suggest that the change may have been an artifact arising from the incomplete recovery of a small amount of fecal material in the tank.) For the Atlantic menhaden we assumed a constant assimilation efficiency with different ration sizes.

The mean assimilation efficiencies observed for the Atlantic menhaden feeding on phytoplankton were quite high (86.4% for carbon, 92.4% for nitrogen, and 89.5% for calories). For Atlantic menhaden feeding on zooplankton the values were similarly high (86.7,

91.3, and 87.7%, respectively). The high values for zooplankton were consistent with results from other fishes (Gerking 1955; Pandian 1967; Beamish 1972; Kelso 1972). Few measurements of carbon, nitrogen, or caloric assimilation exist for marine herbivorous fishes. Menzel (1959) found that *Holacanthus* assimilated 85% of the nitrogen and 77.7% of the calories from two species of macroalgae. The lower assimilation in *Holacanthus* may have been related to the type of food. However, there do not appear to be any comparable studies with marine phytophageous fishes, which would indicate whether the high assimilation efficiency of the Atlantic menhaden is typical of this trophic group.

Energy Losses

RESPIRATION.—The major energy outputs by the Atlantic menhaden are respiration and excretion. Respiration by the menhaden was divided into feeding ($T_{f,K}$) and nonfeeding components ($T_{r,K}$). SDA was not included as a separate component, but for reasons discussed earlier was included as part of the feeding respiration rate. SDA is thought to be a fixed proportion of the energy content of the food ration, and in carnivorous fishes has been estimated at about 12.7-16% (Muir and Niimi 1972; Beamish 1974; Pierce and Wissing 1974; Schalles and Wissing 1976). Partitioning $T_{f,K}$ into its components, $T_{s,K}$ and $T_{\mathrm{SDA},K}$, would have caused some minor changes within the energy budget, but would not have significantly affected the predictions of growth rate and growth efficiency. The most important change would be in a case analagous to Figure 1B, where food concentration increases while s and h remain constant. Here, the ingested ration automatically increases in proportion to c because Atlantic menhaden filter a constant proportion of particles from the water. $T_{f,K}$ in this illustration is constant, which reflects the fact that its major component $T_{s,K}$ is constant. However, if SDA were included separately we would actually expect to see a small linear increase in $T_{f,K}$ because $T_{\mathrm{SDA},K}$ should presumably increase in proportion to the ration R_K.

For Atlantic menhaden, the metabolic cost of feeding appears to be high (Durbin et al. 1981). This is because of the very rapid increase in respiration rate per unit increase in foraging speed. This rate of increase was about 2.5 times greater than has been observed in other (nonfilter feeding) species during forced long-term swimming (Beamish 1978). Thus even minor changes in the foraging speed can have a significant impact on metabolic expenditures and the overall energy balance.

The energy budget demonstrates that for an active species such as the menhaden, it is not possible to use a constant multiplier of the standard metabolism, as recommended by Winberg (1956), to estimate metabolic expenditures in the field. Not only is the suggested multiplier of 2 times the standard rate too low (in our studies the routine rate was 3.4 times the estimated standard rate, and the average feeding rate 2.3-4.8 times routine, or about 8-17 times standard), but also the relative size of the respiration component within the overall energy budget is also a variable, changing according to the values of s, c, and h.

EXCRETION.—Excretion, the other major energy output, is similarly a variable. In contrast to respiration which depends on swimming speed and foraging time, excretion depends on the amount of food eaten. Excretion, therefore, will follow no constant relationship to respiration in the energy budget (Model I). The linear relationship between ration size and exogenous nitrogen excretion is similar to results in other studies (Gerking 1971; Savitz et al. 1977), although the proportion of nitrogen excreted will depend on the balance of amino acids in the food relative to the requirements of the fish.

Growth Rate and Growth Efficiency

The rates of energy intake and expenditure determine the amount of energy which is available for growth. Atlantic menhaden must invest considerable time and energy in feeding. The Model I energy and nitrogen budgets show that if foraging speed remains constant, then growth will increase linearly with increasing ration size, regardless of whether this is brought about by an increase in food concentration or foraging time. Consequently, gross growth efficiency increases asymptotically with increasing ration size. Model II demonstrates that given the actual swimming behavior of the menhaden, the relationship between ration size and growth is in fact very nearly linear at moderate-high plankton densities were s ~ constant, but becomes significantly curvilinear at lower plankton levels because of the decreasing foraging speed. With the reduction in foraging speed, the energy balance changes because proportionally less of the ingested ration is used to support metabolism, which leaves more energy available for growth.

Ivlev's (1960) bioenergetic model of the bleak, *Alburnus alburnus*, showed that in this particulate-feeding planktivore, growth increased asymptotically, rather than linearly, with increasing food concen-

tration. These results reflect basic differences in the ingestion process between filter- and particulate-feeding planktivores. Since a filter feeder like the Atlantic menhaden removes a constant proportion of the particles in the water per unit of time, without the necessity to capture and handle each item of prey individually, the ingestion rate increases linearly with increasing food concentration and swimming speed. In contrast, with the particulate planktivore, feeding is a series of discrete events and there will be a maximum ingestion rate set by the time required to capture and handle each prey. Thus, as Ivlev has shown experimentally (Ivlev 1960, 1961), ingestion rate increases asymptotically with increasing food concentration. This causes an asymptotic growth curve. There does not appear to be any information available to describe the ingestion pattern of a particulate feeder as a function of swimming speed. However, based on Holling's predation model (Holling 1966), an increase in the swimming speed of a particulate planktivore will increase the encounter frequency and hence the feeding rate. Based on this model we could expect that with increasing swimming speed, the ingestion rate will increase asymptotically towards a maximum rate set by the handling time.

In most laboratory studies of the relation between feeding and growth, the fish are given a fixed ration for a specified period, after which the amount of growth is determined. The food is made readily available to the fish, and hence the time and energy expended for feeding is presumably small. In the majority of these studies, growth was linearly related to ration size, which implies that assimilation efficiency and the increment in metabolism and growth per unit of ration remained constant at all ration levels (Pandian 1967; Birkett 1969; Gerking 1971; Jones and Hislop 1972, 1978; Niimi and Beamish 1974; Staples and Nomura 1976; Stirling 1977). Where reported, growth efficiency increased asymptotically with increasing ration size; this is a consequence of the observed linear growth-ration relation.

In several studies the relationship between growth and meal size appeared to be slightly curvilinear, however, with the growth rate somewhat depressed at high rations (Carline and Hall 1973; Elliott 1975; Wurtsbaugh and Davis 1977). Under these conditions, growth efficiency increased curvilinearly from zero at the maintenance ration to a maximum value, and thereafter declined curvilinearly. Warren and Doudoroff (1971) suggested that such a phenomenon could be caused either by a reduction in assimilation efficiency at high rations, or by a change in the energy balance within the fish, in which the metabolic component increased (higher SDA, or greater spontaneous activity) at the expense of the energy available for growth. Another possible cause of departure from linearity could arise from changes in the wet weight:dry weight ratios (Staples and Nomura 1976). These investigators found that fish at high ration levels increased in percent of dry weight relative to fish on low rations. Thus measurements of growth based on wet weight will overestimate the true growth of fish at low rations, and underestimate growth at high rations, which can lead to an apparent curvilinearity in the growth-ration relationship.

The growth of sockeye salmon on fixed rations increased nearly linearly with increasing ration size, in keeping with results from other similar studies (Brett et al. 1969; Brett and Shelbourn 1975). However the latter investigators found that if they included growth data from fish fed "excess rations," where voluntary food intake continually declined as the fish grew, the overall relationship between growth and increasing ration size was asymptotic, making the growth efficiency curve convex upwards.

The Model I prediction of a linear relation between ration size and growth in the Atlantic menhaden, when swimming speed is constant (i.e., activity = constant), and the slight departure from linearity by Model II, is therefore supported by most experimental studies of feeding and growth in other fish species. It should be noted that if assimilation efficiency in Atlantic menhaden were to decline at high feeding rates beyond the range of the experimental data, we would expect that growth rate will approach an asymptote, and growth efficiency will decline with further increases in ration size. However since the experiments covered the range of plankton concentrations which the fish might be expected to encounter in nature (Durbin and Durbin 1981), the possible decline in assimilation at very high feeding rates would not appear to be meaningful for Atlantic menhaden under most circumstances in the wild.

It should also be noted that since the foraging costs of obtaining a ration of a particular size will vary according to s, c, and h, there will not be a single (unique) relationship between ration size, growth rate, and growth efficiency in Atlantic menhaden.

The models predict that over most of the range of plankton concentrations where growth is possible, growth efficiency will be higher for calories than for nitrogen. These findings are consistent with field observations that the fat and caloric composition of the menhaden increases relative to protein during its season of growth (Dahlberg 1969; Dubrow et al. 1976). At low plankton concentrations the fish forage at speeds such that growth in nitrogen is possible even when there is an overall net energy deficit. This

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Optimal Foraging by Planktivores

In a landmark study, Ware (1975) combined Ivlev's (1960) data on *Alburnus* with Holling's (1966) predation model to develop a bioenergetic model of this particulate planktivore, which could be used to test different theories of optimal foraging. Ware was the first to demonstrate the existence of $s_{G,\mathrm{OPT}}$ and $s_{K,\mathrm{OPT}}$, and showed the importance of swimming speed in determining the energy balance within the fish. His analysis demonstrated that the swimming speeds of fish in nature can be extremely useful and sensitive indicators of how different species respond to and exploit changes in their food resource. An interesting feature of Ware's (1975) model of a particulate planktivore was that as c increased, $s_{G,\mathrm{OPT}}$ curvilinearly increased to a maximum at a single food concentration, and thereafter declined, whereas $s_{K,\mathrm{OPT}}$ declined monotonically with increasing values of c. These changes in $s_{G,\mathrm{OPT}}$ and $s_{K,\mathrm{OPT}}$ were due to the effect of handling time on the rate of ingestion in the Holling (1966) model. In contrast the present study, which extends Ware's concepts of $s_{G,\mathrm{OPT}}$ and $s_{K,\mathrm{OPT}}$ to a filter feeder, shows that since handling time is negligible in a filter feeder, $s_{G,\mathrm{OPT}}$ increases asymptotically with increasing values of c, whereas $s_{K,\mathrm{OPT}}$ is solely a function of h and independent of c. It is interesting that for both particulate and filter-feeding planktivores, distinct foraging strategies are required in order to achieve maximal growth rate or growth efficiency.

The experimental data from the Atlantic menhaden make it possible to determine whether the foraging behavior of this species is directed towards enhancing some measure of ecological fitness such as growth rate or growth efficiency. This may be done by comparing the growth rates and growth efficiencies calculated for the observed swimming speeds of the menhaden with those that would result if the fish were to swim at speeds equivalent to either $s_{G,\mathrm{OPT}}$ or $s_{K,\mathrm{OPT}}$. The comparison is made with $s_{G,\mathrm{OPT}}$ in Figure 11 for the case where $h = 14$ h/d and with $s_{K,\mathrm{OPT}}$ in Figure 12 for the case where $c = 0.0030$ kcal/l.

Figure 11 demonstrates that the growth of Atlantic menhaden which swim according to the laboratory derived relationship in Equation (48) is very close to the maximum possible growth at each concentration of plankton. This suggests that foraging speed in the adult Atlantic menhaden is a behavioral adaptation to maximize growth rate.

In contrast, at any given concentration of food the observed foraging speed was always $> s_{K,\mathrm{OPT}}$, which resulted in submaximal values of $K_{1,K}$ (Fig. 12). This is evidence that the fish were not acting to maximize growth efficiency. To maximize growth efficiency the fish would have had to regulate their foraging speed according to the duration of feeding. This was not observed in Atlantic menhaden in the laboratory, where foraging speed at a given concentration of food remained constant for periods of up to 7 h. Further, we have shown that foraging strategies which regulate swimming speed in order to maximize growth rate and growth efficiency are mutually exclusive.

Figures 4 and 11 provide an explanation for the hyperbolic nature of the plankton concentration-foraging speed relationships in Equation (48). $s_{G,\mathrm{OPT}}$ changes most rapidly at low concentrations of plankton, and it is in this region where Atlantic menhaden most strongly regulate their foraging speed, $s_{G,\mathrm{OPT}}$

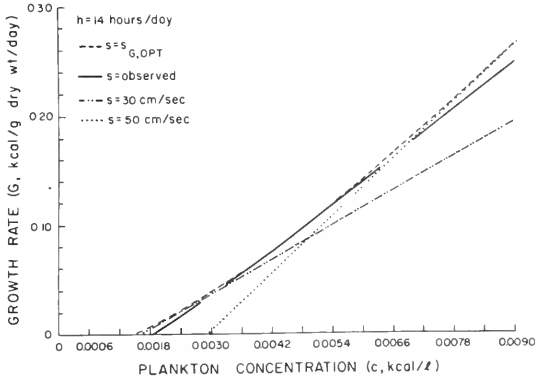

FIGURE 11.—A comparison of the growth of the Atlantic menhaden at different concentrations of plankton, when the fish swim according to $s_{G,\mathrm{OPT}}$; their actual voluntary speeds; and constant speeds of 30 and 50 cm/s. Foraging time is 14 h/d.

changes less rapidly at moderate-high plankton abundance, and in fact the constant preferred speed of the Atlantic menhaden (41.3 cm/s) is sufficiently close to $s_{G,\,OPT}$ that growth remains nearly maximal over a very broad range of plankton abundance. Thus there is no great "penalty" if the fish swim at constant speed rather than exactly at $s_{G,\,OPT}$ within this region of the curve. The choice of this preferred speed is fairly exacting, however. As can be seen in Figure 11, at speeds not greatly different from 41 cm/s (30 and 50 cm/s), growth will be suboptimal over much of the plankton concentration range.

How much of a sacrifice in growth efficiency is implied if the fish swim at $s_{G,OPT}$? Figure 12 indicates that $K_{1,\,K}$, though suboptimal, is still reasonably high when the fish swim at $s_{G,OPT}$. However, as the foraging speed increases above $s_{G,OPT}$, there is an increasingly rapid decline in $K_{1,\,K}$, as can be seen in Figure 12 where s = constant = 50 cm/s.

In conclusion, the present results, which demonstrate a very close agreement between the predicted relationship between $s_{G,OPT}$ and food concentration, and the observed relationship between foraging speed and c, indicate that the foraging speeds of the adult Atlantic menhaden have evolved over time towards maximizing growth rate. This optimization of growth rate has necessarily resulted in a submaximal growth efficiency. In his analysis of data for the bleak, Ware (1975) showed that the observed foraging speed when c ~ 0.000808 kcal/l was also quite close to the value of $s_{G,OPT}$ predicted from his model. However, there was insufficient information in Ivlev's (1960) original study to indicate whether the bleak adjusts its foraging speed to remain near $s_{G,OPT}$ at different plankton concentrations. Studies demonstrating selective feeding in planktivores (e.g., Brooks 1968; Leong and O'Connell 1969; O'Connell 1972; Werner 1974; Werner and Hall 1974; O'Brien et al. 1976; Eggers 1977; Confer et al. 1978) indicate that foraging strategies, which result in the maximization of energy intake, may be a more general phenomenon among these fishes. However, it should be pointed out that these feeding studies only consider energy intake and not energy expenditures, so that the extent to which these fishes are following optimal strategies for growth or growth efficiency cannot really be determined.

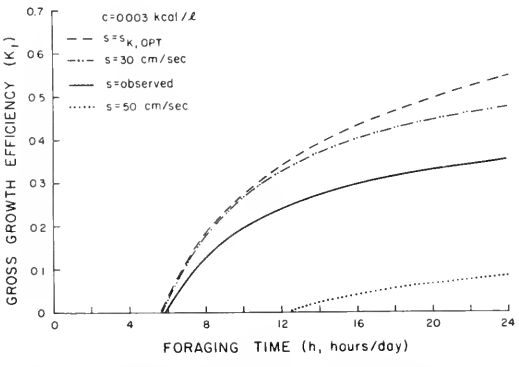

FIGURE 12.—A comparison of the gross growth efficiency of the Atlantic menhaden as a function of foraging time, when the fish swim according to $s_{K,OPT}$; their actual voluntary speeds; and constant speeds of 30 and 50 cm/s. Plankton concentration is 0.0030 kcal/l.

Extension of the Model to Particles of Different Size

Observations using several phytoplankton species as food (Durbin and Durbin 1975) indicated that the preferred (concentration independent) foraging speeds were similar for these species. However these estimates of swimming speed, made with a stopwatch, were not sufficiently accurate to distinguish the small changes in foraging speed that have been found to be significant in the energy budget. Thus it would be desirable to verify this observation using a more precise method, such as video or cinematography, to determine the swimming speeds.

In the same study it was, however, clear that the threshold concentration for the onset of feeding (c_t) and the concentration at which foraging speed became approximately independent of food concentration (c_i) were quite different for plankton particles of different size. The inverse nature of this relationship is consistent with the fact that when an Atlantic menhaden forages at a given speed, its energy expenditure is the same for all food types, yet its energy intake declines with decreasing food particle size because of the declining efficiency of the gill rakers. This means that a higher concentration of small particles is needed in order for a fish to satisfy its minimum energy requirement, and thus we would expect an increase in c_t and c_i as particle size declines.

The constants in the equations presented here have been specified for *Ditylum brightwelli*, which is about 80 μm long. A change in particle size will change the filtration efficiency (e), which will necessitate recalculation of some of the constants in the equations for $R, E, G, s_{G,OPT}$, and $s_{K,OPT}$. This is a simple matter except for the last two quantities, and for these we have presented the steps in the integration of the equations in sufficient detail (Equations (33) to (45)) to permit recomputation for different particle sizes.

It is of particular interest to consider how $s_{G,OPT}$ changes with a change in food particle size. It has

been shown (Fig. 4) that $s_{G,OPT}$ increases with increasing food concentration. This is because with increasing c, the rate of energy intake increases per unit of energy expenditure. An increase in food particle size affects the ingestion rate in a manner analagous to an increase in particle abundance, and thus we find that $s_{G,OPT}$ increases with increasing particle size as well (Fig. 13). $s_{G,OPT}$ is most strongly affected by food particle size in the range of 20-60 μm, moderately affected within the range of 60-300 μm, and relatively unaffected by further increases in particle size above about 300 μm. In other words, $s_{G,OPT}$ is strongly size-dependent in the range of phytoplankton particles, less so in the range of microzooplankton, and is for practical purposes independent of particle size in the range of copepodites and late-stage nauplii. This pattern, of course, reflects the filtration efficiency curve of the gill rakers (Equation (6)).

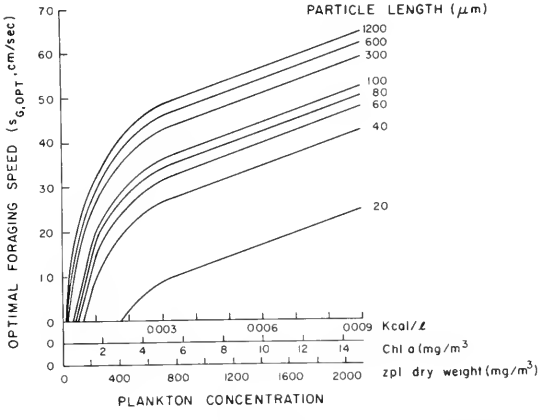

FIGURE 13.—The effect of particle size on the relationship between the foraging speed which maximizes the Atlantic menhaden's growth rate ($s_{G,OPT}$) and plankton concentration.

Figure 13 illustrates the need for information on how the Atlantic menhaden responds to mixtures of different-sized particles. For example, do the menhaden respond to the total biomass of particles, or do they key in on certain size classes, ignoring the remainder even though they may filter these particles simultaneously with the larger prey? We have seen that Atlantic menhaden feeding on a single food type will alter their energy expenditures according to the abundance of food, such that they maximize their growth rate at each level of food abundance. However there is a need for further investigation of their feeding behavior on different sizes and mixtures of particles to determine the degree to which they act as "optimal foragers" in a mixture of plankton species.

Application of the Atlantic Menhaden Models to the Field

The energy and nitrogen budgets have been derived in terms of three controlling variables, each of which can be determined from direct field measurements: The foraging speed (s), the concentration of plankton (c), and the foraging time (h). Foraging speed can be measured in the field using acoustic techniques, and this procedure can be used to verify our predictions of swimming speed based on laboratory investigations of the relationship between s and c. If confirmed in the field, these laboratory studies will enable us to eliminate s as an independent variable and define the budgets simply in terms of c and h. However, as mentioned previously, before we can use this approach in the field, where the fish feed on a variety of particle sizes, additional laboratory work is needed to quantify the foraging speed-food-concentration relationships for different types and sizes of plankton. The foraging time (h) could be determined from diel surveys of stomach contents to determine gut fullness and the state of digestion of the food (the latter is an indicator of how recently the food was ingested). If h proves to be relatively invariant, or under simple control of an external variable such as day length, it may ultimately become possible to describe the energy and nitrogen budgets of the Atlantic menhaden solely as a function of the average concentration of different-sized plankton in the water.

The effects of body size and temperature also need to be considered in applying the models to the field. Hettler (1976) has investigated the effects of body size, temperature, and salinity on routine metabolism in juvenile Atlantic menhaden. The influence of these variables on the swimming and feeding behavior of the Atlantic menhaden, and on the other components of the energy budget, must be investigated as well, before a general energy and nitrogen budget for the Atlantic menhaden can be described.

Another point to consider in applying the present energy budget to the field is that Atlantic menhaden in nature may have additional energy expenditures beyond those of the laboratory fish, principally the costs of predator avoidance, spawning activity, and the energy cost of migration. The first two activities would increase respiratory expenditure, and correspondingly reduce the amount of surplus energy that is available for growth. It is not clear to what extent seasonal migrations of the Atlantic menhaden (Nicholson 1971, 1978) represent an additional energy cost, however, since it is possible that the Atlantic menhaden continue feeding as they move along their migratory routes. In addition, the seasonal migration

does not require elevated swimming speed since Atlantic menhaden swimming at a routine speed of 12.2 cm/s could accomplish the distance between Rhode Island and Cape Hatteras, N.C., well within the 3-4 mo duration of the spring and fall migrations.

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REPRODUCTION AND EMBRYONIC DEVELOPMENT OF THE SAND TIGER SHARK, ODONTASPIS TAURUS (RAFINESQUE)[1]

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ABSTRACT

The capture of one ripe male, 191.5 cm TL, and 26 pregnant female, 236.6-274.3 cm TL, sand tiger sharks, *Odontaspis taurus*, from the east-central coast of Florida from 1946 to 1980 has permitted examination of early reproductive activity and embryonic development in this species.

Variations in ovulation rates and oviducal gland activity produce six distinct egg capsule types at varying times during gestation. Some egg capsules produced during early gestation contain only ovalbumin and/or mucus while others contain several fertilized ova. As gestation proceeds, more capsules contain unfertilized ova and ovulation rates increase. These latter capsules serve principally as food for the surviving embryo.

Sixty-two embryos, 13-1,060 mm TL, provided information on intrauterine development which allowed classification of seven developmental periods based on gestation time, embryonic anatomy, posture, activity, and source of nutrition. Initially, embryos 13-18.5 mm TL obtain nutrition from internal coelomic yolk supplies during a period of early tissue differentiation. In embryos between 18.5 and 51 mm TL, consumption of encapsulated yolk supplies occurs until hatching, between 49 and 63 mm TL. After hatching, the embryo absorbs yolk-sac nutritive supplies and may also consume uterine fluid. At about 100 mm TL, the embryo begins to hunt and consume other intrauterine embryos. Seven to nine months into gestation, ova are no longer fertilized. In each uterus, the single remaining embryo, 334-1,060 mm TL, consumes enlarged yolk capsules containing 7-23 unfertilized ova. Just prior to parturition the maternal ovary is greatly reduced in size, few egg capsules are found within the uteri, and in each uterus the remaining embryo exhibits reduced yolk consumption and an enlarged liver. Parturition observed in captivity typically takes place from December through March, after 9-12 months of gestation. Newborn juveniles are about 100 cm long.

The sand tiger shark, *Odontaspis taurus* (Rafinesque, 1810), is a cosmopolitan species distributed in subtropical and temperate waters at depths <60 m (Bass et al. 1975). In the western Atlantic, adult sand tiger sharks occur from the Gulf of Maine to Brazil (Bigelow and Schroeder 1948). Although sand tiger sharks have been captured on both coasts of Florida (Springer 1938, 1948, 1963; Clark and von Schmidt 1965), captures have been more common along the Florida east coast (Dodrill[4]).

Unlike the adults, free-swimming juvenile *O. taurus* in the western Atlantic are restricted only to temperate (Bigelow and Schroeder 1953) and warm-temperate waters, extending as far south as northern Florida. Juveniles 109.3-157.7 cm in total length (TL) have been recorded in neritic waters from the vicinity of Fernandina Beach (lat. 30°40′N, Nassau County) on the Florida Atlantic coast, from Cedar Key (lat. 29°15′N, Levy County) in the northeastern Gulf of Mexico (Don Hoyt[5]), and from the northern Gulf of Mexico (Branstetter 1981).

In the western Atlantic, females with near-term embryos have been captured off eastern Florida and in the northern Gulf of Mexico (Springer 1948; Hoyt footnote 5; Robert Jenkins[6]). At parturition, two young are born (95-110 cm TL), one developing in each uterus (Springer 1948; Cadenat 1956; Sadowsky 1970; Bass et al. 1975).

Published observations on the early intrauterine development of *O. taurus* are limited to the accounts of Coles (1915), Springer (1948), Cadenat (1956), and Bass et al. (1975). Springer (1948) was the first to observe embryonic oviphagy in *O. taurus*. He found large quantities of yolk in the stomachs of embryos dissected from females from the northern Gulf of Mexico and east-central Florida. Bass et al. (1975) described an intact 40 mm embryo found in the

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[4]Dodrill, J. W. 1977. A hook and line survey of the sharks found within five hundred meters off shore along Melbourne Beach, Brevard County, Florida. Unpubl. M.S. Thesis, 304 p. Fla. Inst. Technol., Melbourne, FL 32901.

[5]Don Hoyt, Florida Shark Club, Inc., Jacksonville, FL 32211, pers. commun. 1967-77.

[6]Robert Jenkins, Marineland Inc., St. Augustine, FL 32084, pers. commun. 1977.

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stomach of a 170 mm embryo dissected from a female from Natal, South Africa. These were the smallest embryos yet recorded from *O. taurus* and provided the first description of embryonic cannibalism in this species.

The capture of 28 pregnant *O. taurus* from various locations on the east coast of Florida (1946-80) provided 62 embryos, 13-1,060 mm TL (Table 1, Fig. 1). These specimens have allowed a more detailed description of early embryonic development in this species than was possible previously. This study describes the various developmental stages in *O. taurus* based principally on embryonic anatomical development and changes in maternal gonadal morphology.

METHODS

All adult *O. taurus* specimens examined were captured either on rod and reel sport fishing gear or on static 10-30 hook set lines. Fourteen specimens were captured 200 m to 19 km from shore in neritic waters off Melbourne Beach, Brevard County, Fla. (lat. 28°00'N, long. 80° 33'W). All specimens came from depths of 5-12 m. A 15th specimen was caught at lat. 27°25'N, long. 80°12'W, east of Fort Pierce Inlet, St. Lucie County, Fla. A 16th specimen, a 240 cm female, gave birth to two pups at Sea World of Orlando, Fla., and all three were examined. This latter adult female was captured on 21 August 1980 at Port Canaveral, Brevard County (lat. 28°24.5'N). Eleven other specimens were captured prior to our study; these data and, in some cases, embryos from these specimens were included (Table 1).

Embryos and adult reproductive tracts were preserved in 10% Formalin[7] and stored in 10% buffered Formalin or 70% ethanol, or were frozen. All of these specimens were entered and catalogued into the Indian River Coastal Zone Museum (IRCZM). Egg diameters and embryos <130 mm TL were measured using vernier calipers to the nearest 0.1 mm. All length measurements including total length (TL) follow Bass et al. (1975).

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

TABLE 1.—Uterine embryo and egg capsule data for *Odontaspis taurus*, from the Florida east coast, arranged chronologically by month of examination of embryos, 1947-81.

Date	Adult size (cm, TL)	No. of egg capsules in uteri		Encapsulated embryos (mm, TL)		Damaged (a) or consumed (b) embryos (mm, TL)		Hatched embryos (mm, TL)		Total no. of embryos
		Left	Right	Left	Right	Left	Right	Left	Right	
15 May 1977	254.5	20	20	0	0	0	0	0	0	0
16 May 1977	254.9	18	19	0	0	0	0	0	0	0
28 May 1977	260.3	26	27	0	0	0	0	0	0	0
5 June 1978	264.2	8	8	0	0	0	0	0	0	0
5 June 1976	258.1	35±2	34±2	41	42	0	0	57	?	3
5 June 1976	262.5	20±2	20±2	38*	38*	0	0	0	0	2+?
5 June 1976	263.2	20-35	20-35	38*	38*	0	0	0	0	2+?
6 June 1978	274.3	8	8	0	0	0	0	0	0	0
9 June 1976	249.5	29±4	29±4	27	31	0	0	0	0	2
28 June 1976	254.1	47	53	27, 34	27, 38, 46	0	0	63	62	7
8 July 1978	274.2	66**	69**	13, 18	?	49(a)	45(a), 49(a)	131	131	7
18 July 1976	271.5	78	81	34	0	0	51(a)	127	100	4
27 July 1975	263.0	?	?	?	?	0	0	317	317±10	2
29 July 1977	254.0	77**	77**	0	0	0	0	271	227	2
5 Aug. 1976	236.6	68	65	0	0	9(b), 22(b), 30(b) 35(a), 36(b), 41(a)	41(b)	334	320	9
4 Sept 1970	282.5			17.5	18.5	?	?	?	?	2+?
4 Sept 1970	269.2	?	?	?	?	?	?	330±10	330±10	2
3 Nov 1962[1]	?	?	?	?	?	?	?	?	650	1
8 Nov 1954[1]	?	?	?	?	?	?	?	830	890	2
24 Nov 1947[2]	273.0	0	0	0	0	0	0	970	960	2
24 Nov. 1947[2]	239.0	0	0	0	0	0	0	825	0	1
12 Dec. 1976[3]	266.7	?	?	?	?	?	?	1,000±10	1,000±10	2
30 Dec. 1958[1]	261.6	?	?	?	?	?	?	1,025	1,033	2
22 Jan. 1947[2]	?	?	?	?	?	?	?	1,000±10	1,000±10	2
22 Jan. 1947[2]	?	?	?	?	?	?	?	0	0	?
15 Feb. 1959[1]	261.5	?	?	?	?	?	?	1,060	>1,060	2
9 Mar. 1947[2,4]	272.0	?	?	?	?	?	?	1,050	1,030	2
22 Mar. 1981	[5]240.0	?	?	?	?	?	?	910	♀[5]	2

*Length given as 1.5 inches, therefore not accurately determined.
**Blastodiscs were observed on some eggs.
? Egg capsules and embryos could have been present but were not recorded.
[1]F. G. Wood, formerly of Marineland Inc., St. Augustine, FL 32084, pers. commun. 1976-77.
[2]Springer 1948.
[3]E. Herbert, Florida Shark Club, Jacksonville, FL 32211, pers. commun. 1976-77.
[4]A. McBride, Curator, Marineland Inc., St. Augustine, FL 32084, unpubl. data, 1947.
[5]Specimens were still living in captivity April 1983 at Sea World of Orlando, Fla.

The entire reproductive tract was removed and examined as fresh, frozen, or preserved material. Uterine fluid volume was determined by tying off both ends of the uterus in a fresh specimen, removing the uterus, making a small incision in the uterine wall, and allowing the contained fluid to drain into a graduated flask. Selected preserved ovaries were cut into sections which were weighed to the nearest 0.1 g. Ovarian egg counts were made by counting all macroscopic eggs in two preserved sections from an ovary of known weight. These ova counts were then multiplied by the ratio of total ovarian weight/section weight, to predict the total number of ova in the entire ovary.

A 13.0 mm TL embryo taken from an egg capsule from a shark caught on 8 July 1978 was embedded in paraffin, cut on a rotary microtome at 6 μm on a sagittal plane, and stained with a Cason modification of the Mallory-Heidenhain stain (Humason 1972).

Fresh sperm samples were fixed in 2.5% glutaraldehyde, prepared for scanning electron microscopy, and examined on a Zeiss Novascan. Several Polaroid electron micrographs were taken for sperm descriptions.

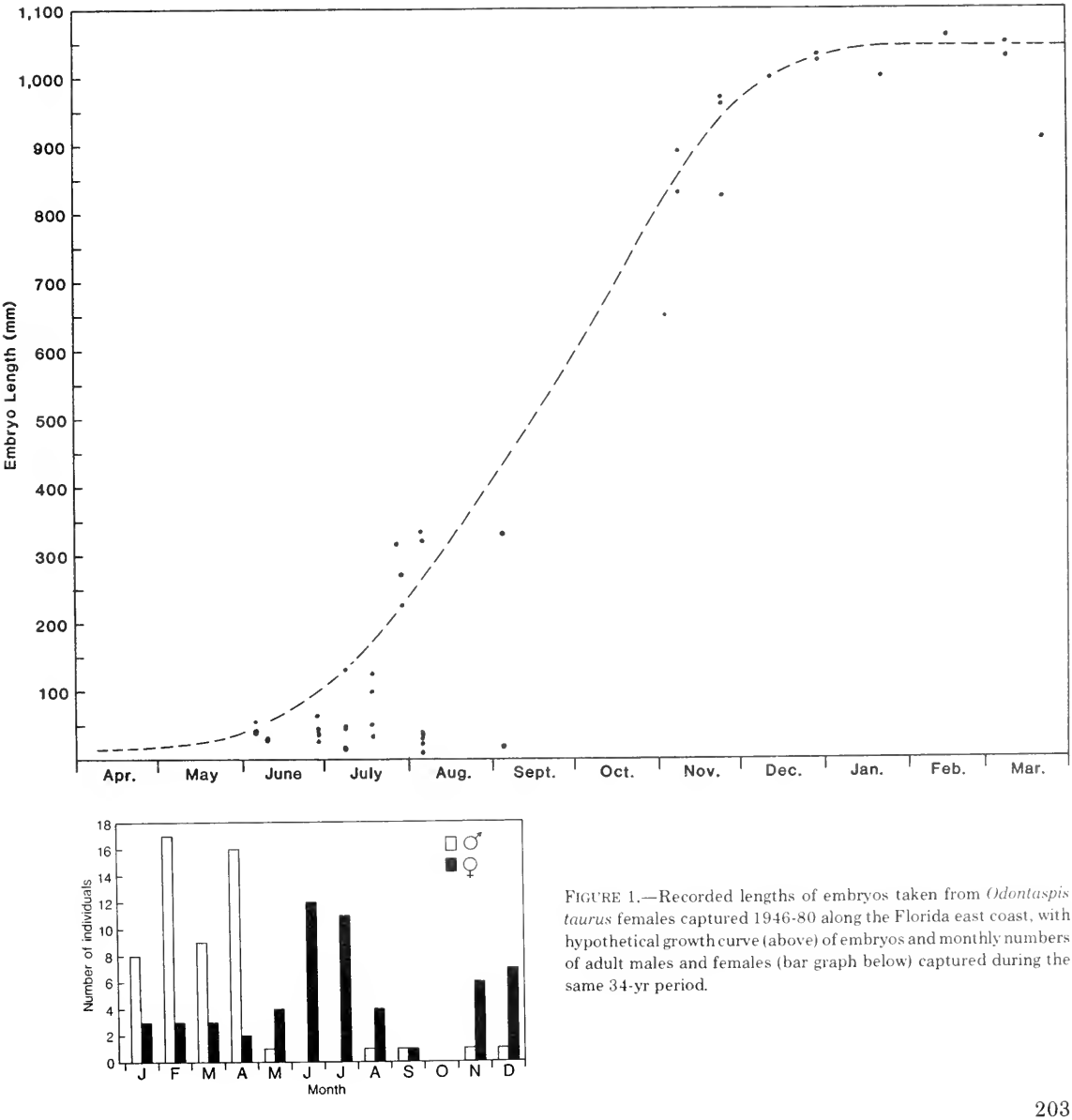

FIGURE 1.—Recorded lengths of embryos taken from *Odontaspis taurus* females captured 1946-80 along the Florida east coast, with hypothetical growth curve (above) of embryos and monthly numbers of adult males and females (bar graph below) captured during the same 34-yr period.

Drawings and Kodachrome transparencies were made of various embryos, egg capsules, and reproductive organs.

OBSERVATIONS AND DESCRIPTIONS

Mating Activity

(Mating Period, Location, and Spermatozoa)

The occurrence of similar-size males or females in unisexual groups has been documented on several occasions (records of the Florida Shark Club show 107 *O. taurus* landings, Burton 1932[8]; Sadowsky 1970; Bass et al. 1975; Hoyt 1976-77 see footnote 5; Wood 1976-77[9]). These observations show that female groups of *O. taurus* make coordinated seasonal coastal movements possibly for breeding, gestation, and eventually parturition (Fig. 1). Females captured at the same time and location tended to have embryos in the same state of development, suggesting coordinated breeding activity and postbreeding migrations. Observations of many annual cycles from 1947 to 1981 established winter-spring as a breeding period off the Florida east coast and provided comparisons of data on gestation (i.e., embryonic development rates and seasonality).

A 191.5 cm TL ripe male *O. taurus*, captured 8 February 1980 in shallow water (10 m depth) in the vicinity of Fort Pierce Inlet, St. Lucie County, Fla. (lat. 27°25.7'N, long. 80°12.5'W), showed evidence of recent mating activity. His claspers were turgid and hematose, with sperm and seminal fluid actively flowing from the clasper tip. The testes were also enlarged (22.5 × 3.5 cm, 0.68 kg). A larger 203 cm TL male examined from Fort Macon, 1.5 km west of Beaufort Inlet, N.C. (lat. 34°40'N, 10 January 1978), contained testes which were considerably smaller (8.0 × 5.0 cm, 0.064 kg). Several scanning electron micrographs were made of the sperm from the 8 February 1980 male specimen. A single sperm had a typical chondrichthian helical head structure 31 μm long and a tail 40.3 μm long (Fig. 2B). The entire length of the sperm was 69-71.5 μm. Living sperm were observed to rotate about their long axes, propelled by the circular motion of the extended tails.

Mating scars resulting from copulatory activity have been commonly observed in female "galeoid" sharks; however, it appears that courtship scars on males are rare (Springer 1967; Stevens 1974; Pratt 1979). Springer (1960) had noted the presence of fresh cuts on female *Eulamia milberti* (= *Carcharhinus plumgeus*) in correlation with the presence of early embryos. Springer (1963) found that most of the *O. taurus* taken in a shark fishery operating in the Atlantic off east-central Florida were females with a high incidence of courtship scars; but no dates were given for these observations. *Odontaspis taurus* females we captured on 9 June and 5 August 1976 (Table 1) had tooth puncture wounds between the 1st and 2d dorsal fins. The 191.5 cm male, taken on 8 February 1980 off Fort Pierce Inlet, had been recently raked by another shark along the upper left side of the body behind and above the gill openings (Fig. 2A). This wound consisted of eight incisions, created by a narrow, long tooth rather than a flat, wide blade tooth, typical of many carcharhinid sharks. As *O. taurus* has a long narrow tooth cusp, it is possible that the wound was the result of either an attack by, or copulation with, another sand tiger shark. These observations indicate that copulatory activity may take place off the Florida east coast and therefore account for the following observations of the earliest embryonic development in specimens from this geographical region.

Early Gonadal and Embryonic Developmental Period

(January-September; 0-60 mm TL)

General Female Anatomy

The female reproductive tract of *O. taurus* may be divided into the ovary, ostium, anterior oviduct, oviducal gland, isthmus, uterus, and vagina, typical of most galeoid sharks. Only the right ovary is functional and enlarged. Above the ovary and attached to it via membranous connective tissue (mesovarium) is the ostium which collects ovulated ova and distributes them to the oviducts. The two oviducts (paired, right and left) bifurcate from the ostium. The anterior oviducts are about 9 mm in diameter and 300 mm in length from ostium to oviducal glands in a 254 cm female. The heart-shaped oviducal glands (53 × 93 mm in the same female) function in egg capsule formation. Much larger than the anterior oviduct, the portion of the oviduct following the oviducal gland known as the isthmus is 20-34 mm in diameter, allowing for the passage of multiple encapsulated ova. The isthmus opens into

[8]E. M. Burton, The Charleston Museum, Charleston, S.C., pers. commun. 24 Oct. 1932 to J. T. Nichols, American Museum of Natural History, N.Y. (made available by Stewart Springer, Mote Marine Lab., Sarasota, FL 33577).

[9]F. G. Wood, Marineland Inc., St. Augustine, FL 32084, pers. commun. 1976-1977.

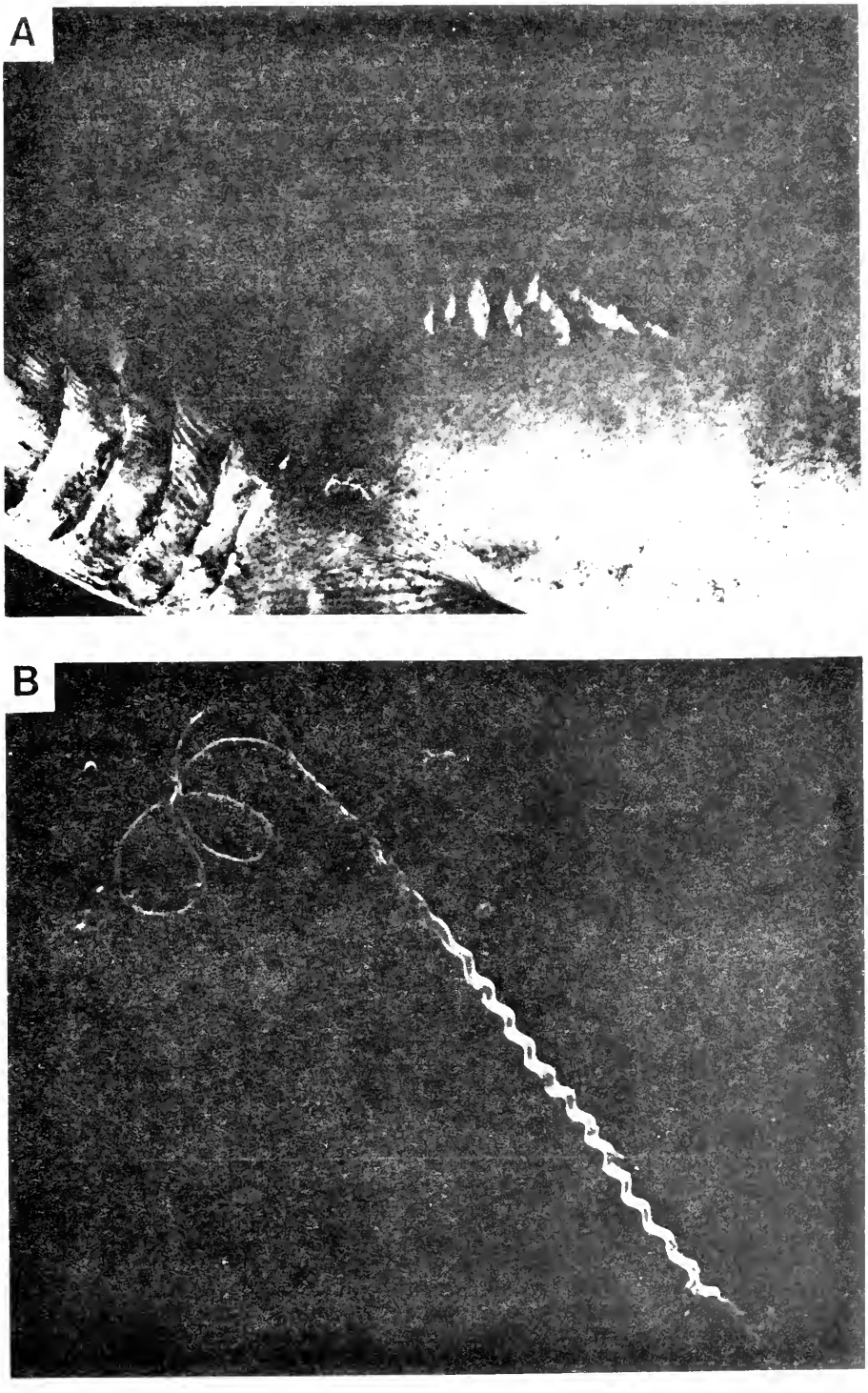

FIGURE 2.—A 191.5 cm TL ripe male *Odontaspis taurus* captured 8 February 1980 off Fort Pierce Inlet, Fla. (A) Tooth rake scars along upper left side of body behind and above gill openings. (B) Scanning electron micrograph of a 69-71.5 μm sperm, with head structure 31 μm long and tail 40.3 μm long (1,950× magnification).

the uterus which is heavily folded and vascularized near its opening. The 7-8 mm uterine wall in *O. taurus* does not function in placentation as in carcharhinid sharks. The paired uteri unite posteriorly to form a common vagina.

Ovarian Activity

This period begins from January to April with insemination of the female *O. taurus* and extends into the following September as exhibited by the prolonged fertilization of ova via stored sperm. Ova fertilization apparently occurs in the anterior oviduct or oviducal gland (Fig. 3Ba, b) prior to egg capsule formation. The oviducal gland then produces a variety of collagen egg capsules, some of which contain fertilized ova (Figs. 4, 5). Egg capsules are then deposited in the uterus. Although encapsulated embryos are present in the uterus for 5-6 mo, the development of a single embryo from fertilization to hatching in utero takes about 3-4 mo.

The number of ova and the general overall size of the ovary increased during early pregnancy. During this period, ova diameters ranged from 2.0 to 10.2 mm and weights ranged from 1.6 to 410 mg. A 254.5 cm TL female *O. taurus* captured 15 May 1977 contained a 4.6 kg ovary with 22,180 ova 1.3-10.0 mm in diameter (Table 2). Encapsulated fertilized ova (i.e., blastodiscs were evident) were present in the uterus, but no embryos. All 11 sand tiger sharks examined between June and August possessed greatly hypertrophied right ovaries (left ovaries are atrophic and nonfunctional) weighing between 3.7 and 8.5 kg and taking up considerable space (360-455 mm in length) in the body cavity (Fig. 3, Table 2). The largest ovary (8.5 kg) came from an 8 July 1978 sand tiger shark, which also had two embryos that were past the "early" uterine developmental stages and in the "post-hatch" cannibalistic stage during which consumption of ova would be their primary means of nutrition.

Oviducal Gland Activity

The paired oviducts of *O. taurus* may be divided into four basic sections (Fig. 3B). The anterior portion (a) is a narrow tube lined with ciliated columnar epithelial cells, extending between the ostium and the oviducal or nidamental gland. This anterior tube is 310 mm long in a 254 cm sand tiger shark and about 9 mm in diameter. The oviducal gland (b) secretes mucus, ovalbumin, and the major elasmobranch egg case component, collagen (Wourms 1977). Neither the anterior portion of the oviduct nor the oviducal glands were sectioned and examined in detail for sperm storage; therefore, the exact site of fertilization in *O. taurus* remains unknown. However, fertilization must occur prior to encapsulation of the ova in the shell membrane or collagen egg capsule. Encapsulation takes place within the oviducal gland.

TABLE 2.—Comparative reproductive data for female *Odontaspis taurus* arranged chronologically by month of capture, 1947-78.

Date	Location	Shark (cm, TL)	Ovary		Ova		Embryos in both uteri
			Weight (kg)	Length (cm)	No.	Size (mm)	
24 Feb 1960	Gulf of Mexico[1]	296	—	40	>1,000	>10	0
15 May 1977	West Atlantic Brevard Co., Fla. Melbourne Beach	254.5	4.6	36	22,180	1.3-10.0	0
9 June 1976	West Atlantic Brevard Co., Fla Melbourne Beach	249.5	3.7	—	13,200	>5-10	2
28 June 1976	West Atlantic Brevard Co., Fla Melbourne Beach	254.1	—	45.5	>1,000	—	7
8 July 1978	West Atlantic Brevard Co., Fla Melbourne Beach	274.2	8.5	41.4	24,290	2.5-10.2	7
27 July 1947	Gulf of Mexico[2] Chandleur Is., La	312.5	—	—	24,000	>1-10	2
29 July 1977	West Atlantic Brevard Co., Fla. Floridana Beach	254.0	—	45.7	>1,000	2-9.5	2
5 Aug. 1976	West Atlantic Brevard Co., Fla. Melbourne Beach	236.6	4.5	31.0	12,810	3-10	9
24 Nov. 1947	West Atlantic[1] Brevard Co., Fla. Off Cape Canaveral	273	—	—	>100	10	1

[1]Clark and Von Schmidt 1965.
[2]Springer 1948.

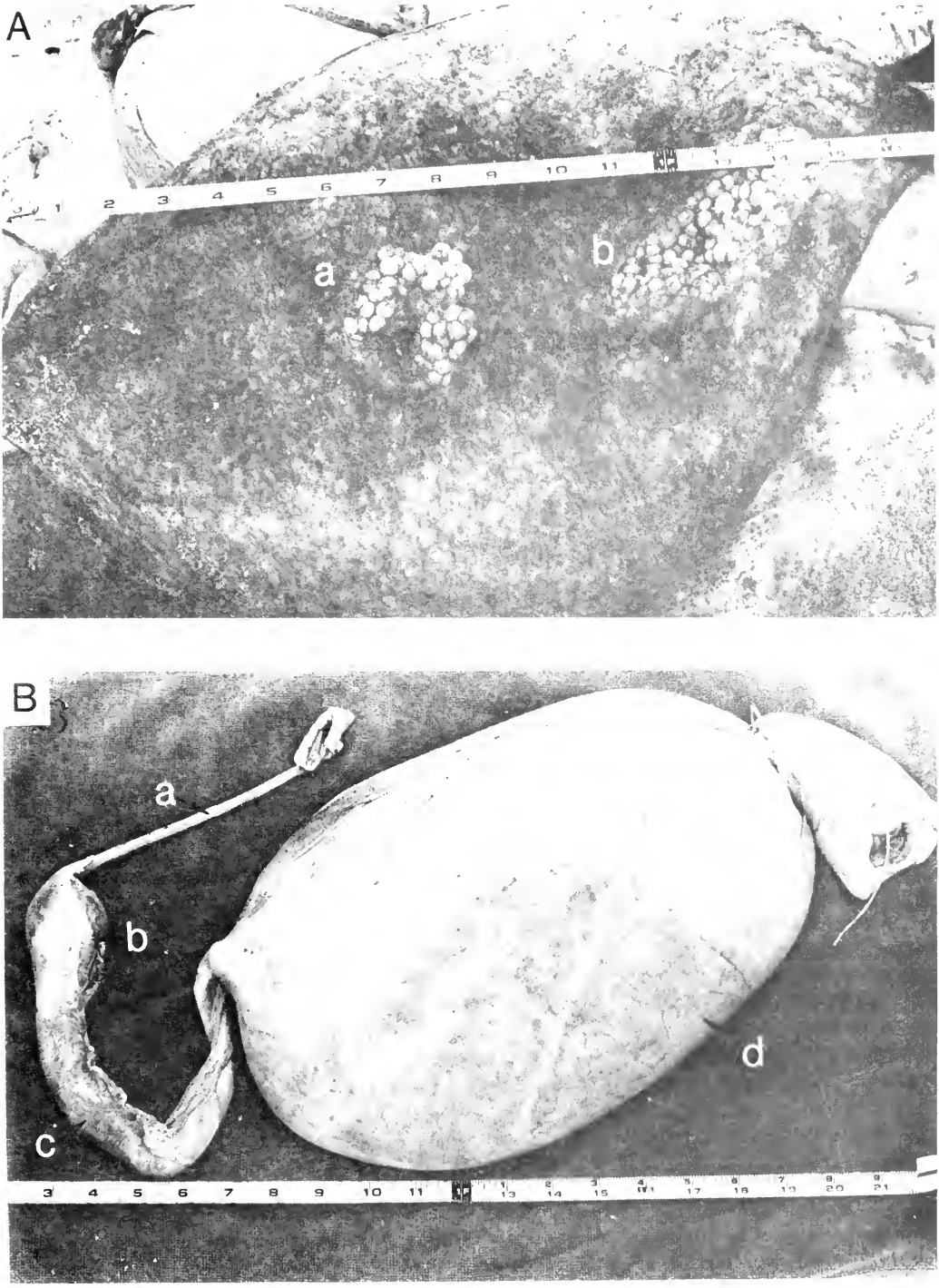

FIGURE 3.—A 254 cm female *Odontaspis taurus* captured 29 July 1976 at Melbourne Beach, Fla. (A) Enlarged ovary with ova (a and b) extending through damaged portions of ovarian membrane. (B) Oviduct consisting of (a) thin tube leading from ostium to (b) oviducal gland; (c) isthmus, and (d) uterus containing embryos and egg capsules.

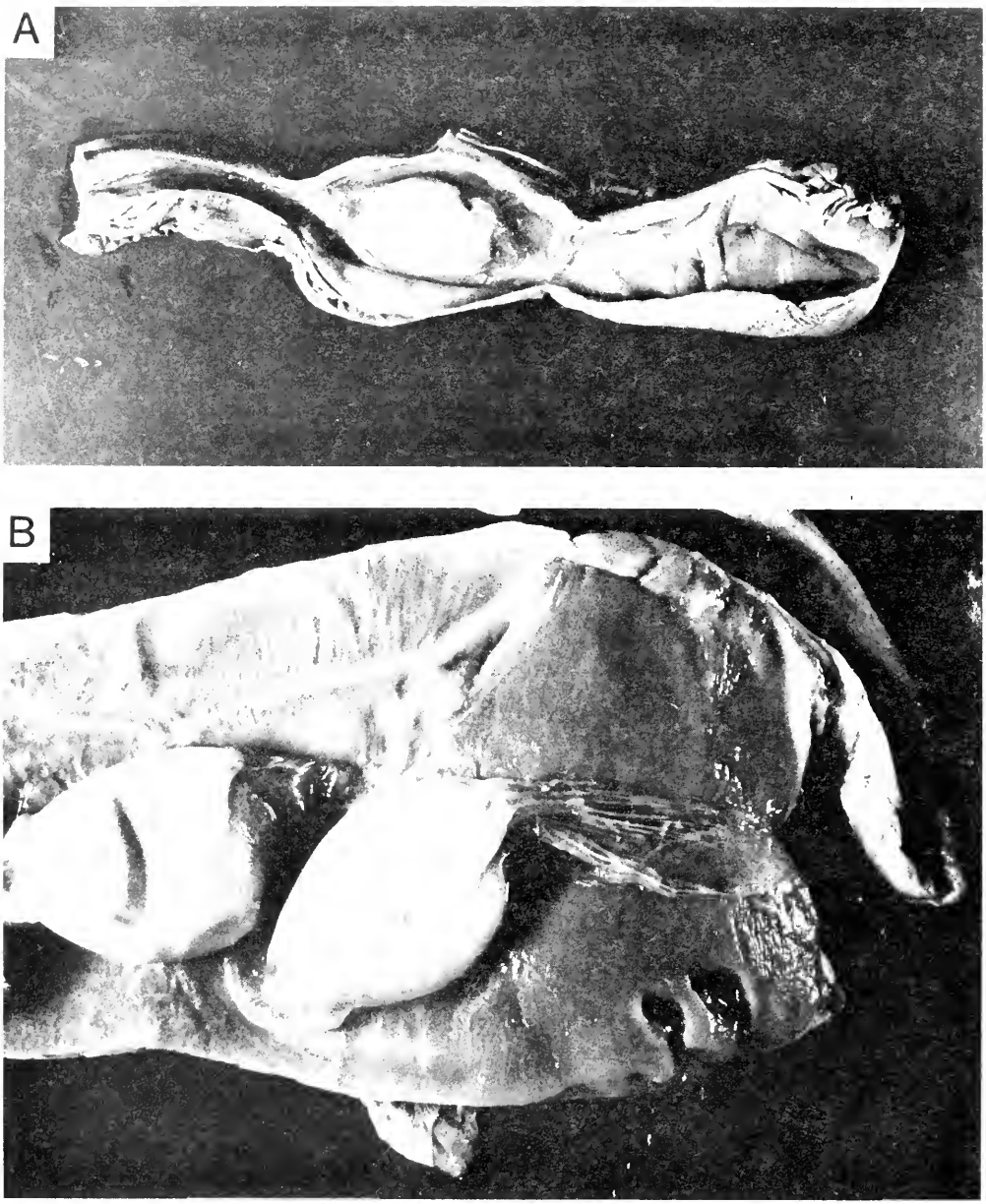

FIGURE 4.—Dissection from a female *Odontaspis taurus* of (A) oviducal gland (right) and isthmus containing a Type I egg capsule which had 16 ova; (B) two Type V "short tail" gel capsules leaving the oviducal gland.

This bulbous organ varies in size with reproductive activity and produces a wide variety of egg capsules (Figs. 4, 5). Egg capsules leave the oviducal gland and proceed down the elastic narrow isthmus (Fig. 3Bc), 250-350 mm in length, 20-34 mm in diameter, connecting the gland with the expanded uterus (Fig. 3Bd). There is an increase in vascularization and folding of the inner epithelial lining where the isthmus joins the enlarged uterus.

The size of the uterus, the volume of the uterine fluid, and the length of the isthmus increased during early gestation (June to July). The volume of fluid in a single uterus increased from 260 ml, to 325 ml, to 1,600 ml in specimens from 15 May, 28 May, and

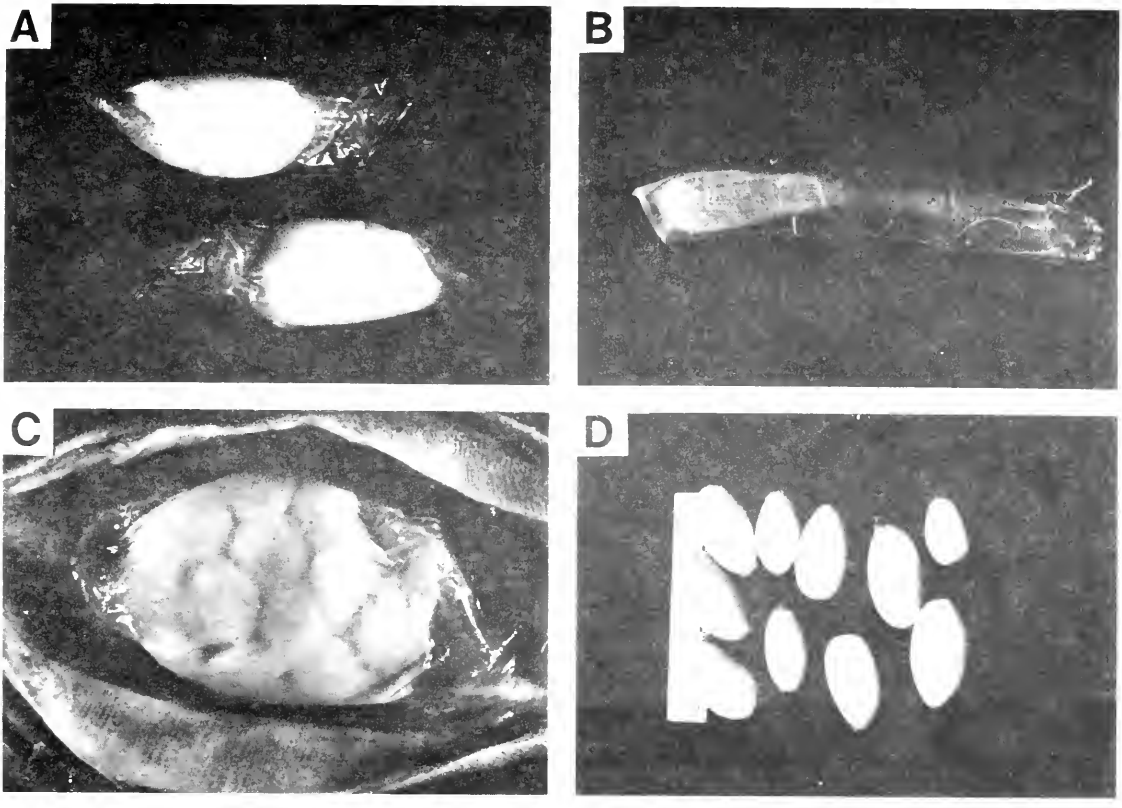

FIGURE 5.—(A) Type V "short tail" gel capsules from *Odontaspis taurus*, containing ovalbumin and/or mucus; (B) Type IV "long tail" gel capsules; (C) Type I blastodisc capsule, containing 16 ova; (D) Type II ovoid yolk capsules, containing 18 ova each. (Photo courtesy Marineland Inc., St. Augustine, Fla.)

29 July, respectively. The uterine fluid also increased in relative cloudiness and contained numerous ruptured egg capsules and yolk fragments.

During early gestation the oviducal gland produced at least six distinct types of egg capsules (Figs. 4, 5):

Type I blastodisc capsules (Figs. 4A, 5C)—contain 7-18 ova, 1-14 of which have visible blastodiscs. This capsule type was more prevalent during early gestation, as 83% of the intact capsules, examined in a 16 May 1977 specimen, contained blastodiscs, 25% in a 28 May 1977 specimen, 22% in a 28 June 1976 specimen, and none in a 5 August 1976 specimen. The overall capsule number was generally low, 15 or fewer per uterus.

Type II ovoid yolk capsules (Fig. 5D)—consist of a light amber shell membrane enclosing a rounded bulbous head containing the ova and a flattened transparent amber tail 40-58 mm long. We found these capsules to contain a large yolk volume consisting of 7-18 ova (mean = 11), 10 mm in diameter, with no sign of fertilization (i.e., no blastodisc). Springer (1948) found 16-23 ova (mean = 19) per capsule of this type in a female containing 260.4-266.7 mm embryos. Ovoid yolk capsules increased in numbers as Type I blastodisc capsules declined. Dimensions of Type II capsules ranged from 21 to 29 × 78 to 118 mm and weight from 8.6 to 19.4 g. Ova in the egg mass during the first 2-3 mo of pregnancy comprised only 60-80% of the capsule volume, while the remainder consisted of ovalbumin and/or mucus adjacent to the tail. A gelatinous ovalbumin/mucoid substance also lined the inner walls of the egg capsule.

Type III reduced yolk capsules—have the same dimensions as Type II ovoid yolk capsules but contain only 1-3 ova. Type III capsules were observed only during the first 3 mo of gestation.

Type IV "long tail" gel capsules—contain amber, green, or white gelatinous material, fluid, and no ova. Although not determined, the variably

colored gelatinous material probably contains ovalbumin and mucus, in different proportions. The dimensions are usually similar to those of the Type II capsules but may vary, as total lengths of up to 170 mm were observed in capsules with very long tails (Fig. 5B). These capsules were most common during the first 3 mo of gestation.

Type V "short tail" gel capsules (Figs. 4B, 5A)— are the smallest capsules, are generally flattened, and contain only gelatinous ovalbumin/mucoid material. These capsules were also most common during the first 3 mo of gestation.

Type VI embryo capsules—contain an embryo and a reduced volume of yolk. Despite the presence of multiple ova and several blastodiscs in embryo capsules, dissection of all Type VI capsules failed to show more than one embryo developing within a single capsule.

Prior to entering the uterus, egg capsules of the same type were found in similar positions in both oviducts of a particular adult. No matter how many eggs were ovulated, encapsulation of albumin would occur synchronously in each oviducal gland, thus producing egg capsules of the same type at the same time. Calculation of egg capsule production rates, based on changes in uterine capsule numbers, indicates that capsule formation takes place at 24-36 h intervals. Initial egg capsules contain ovalbumin and/or mucus derived from the oviducal gland. As the ovulation rate and the number and volume of ova increased during later stages of gestation, more ova were present in the oviducal gland when encapsulation occurred. At this time only ovoid yolk capsules, Type II, were found in the oviduct and uterus.

Embryonic Development

Multiple embryos from *O. taurus* develop in each uterus during the early stages of gestation. However, the maximum number of capsules containing macroscopic embryos is low (no more than 9% or 2-7 of all capsules in both uteri combined at any given time). Encapsulated embryos were found from June to September. The maximum number of embryos in a single uterus was seven, ranging in size from 19 to 334 mm TL. Four of these seven were found in the mouth and stomach of the largest embryo. After June, the number of undamaged encapsulated embryos and the percentage of capsules with blastodiscs declined.

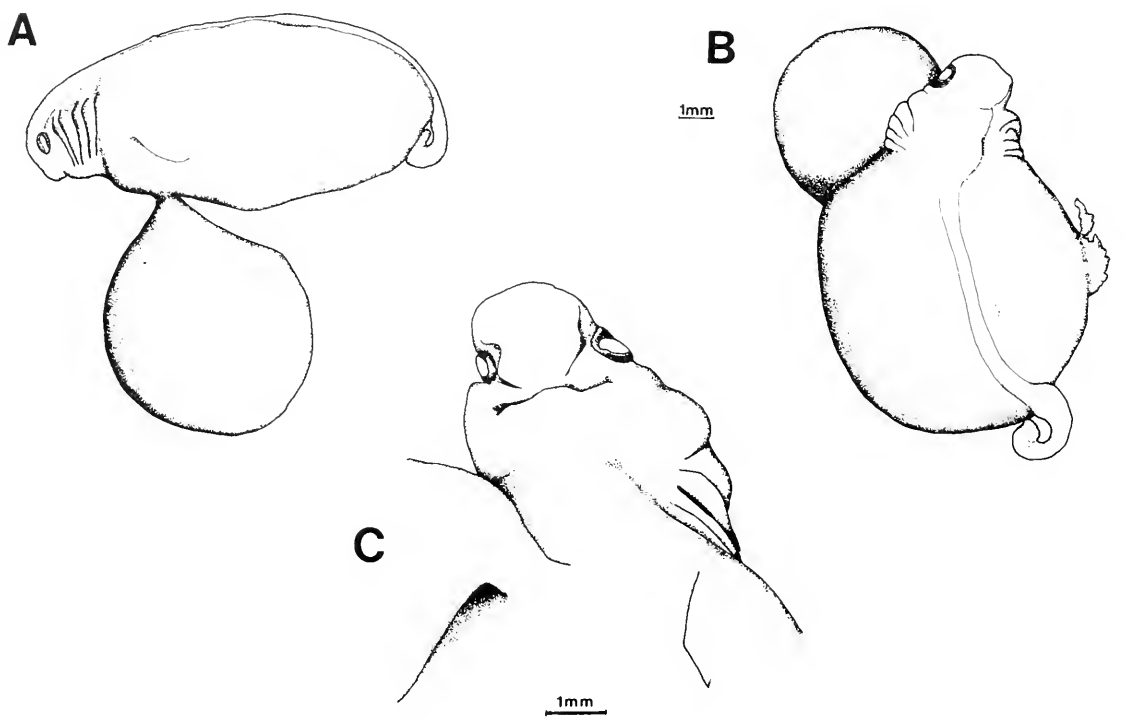

FIGURE 6.—Three views of a 13 mm embryo (IRCZM 103179) taken from an adult *Odontaspis taurus*, 274.2 cm long, captured 8 July 1978. (A) Left side; (B) dorsal; (C) ventral.

13 MM EMBRYO (IRCZM 103179, Figs. 6-8).—The 13 mm embryo is described from one of four embryos, 13-131 mm, taken from the left uterus of a 274.2 cm sand tiger shark caught 8 July 1978 (Table 1). This and an 18 mm embryo were undamaged and encapsulated, while three other embryos partially encapsulated or free within the same sand tiger shark were damaged by attacks from two larger 131 mm embryos, one in each uterus. The 13 mm embryo was the smallest examined. It contained yolk both internally and in a yolk sac. The embryo was obviously restricted in mobility appearing as little more than a yolk mass with a head, notochord, and minute pectoral fin buds. The 13 mm embryo resembles an amphibian embryo after gastrulation and formation of primary organ rudiments. It does not resemble the early embryos described for other elasmobranchs [e.g., *Heterodontus japonicus* (Smith 1942); *Chlamydoselachus anguineus* (Gudger 1940); *Mustelus canis* (TeWinkel 1950, 1963)]. Histological sections showed an incomplete connection between internal yolk supplies and an external yolk sac (Fig. 8A). A membrane at the junction of the yolk stalk and the yolk sac appears to isolate the yolk-sac yolk from the yolk stalk and coelomic yolk supplies in the 13 mm embryo. The coelomic cavity, cardiac stomach, valvular intestine, and pericardial cavity all contained yolk. The maximum horizontal diameter of the embryo was 9 mm, due principally to the contained yolk. This diameter was greater than that of the yolk sac (6.0 mm). The gill arches and mouth cavity were open, but the latter was lacking dentition. No retinal tissue was seen and gonadal tissue was undifferentiated.

18.5 MM EMBRYO (IRCZM 103134, Fig. 9).—The 18.5 mm embryo was from the right uterus of a 282.5 cm TL female *O. taurus* captured 4 September 1970. Although encapsulated, the embryo and the capsule had been greatly damaged. This embryo was similar to the 13 mm embryo but differed in having less internal yolk and greater differentiation of external features. A spiracle was present as were first and second dorsal, caudal, anal, and pelvic fin buds in addition to the pectoral fin buds which had developed earlier. The yolk sac was 6.0 mm in diameter as in the 13 mm embryo.

FIGURE 7.—Angle horizontal sagittal view of a 13 mm *Odontaspis taurus* embryo (IRCZM 103179), head and branchial region: (b) brain; (o) orbit; (ga) gill arches; (ysy) yolk sac yolk.

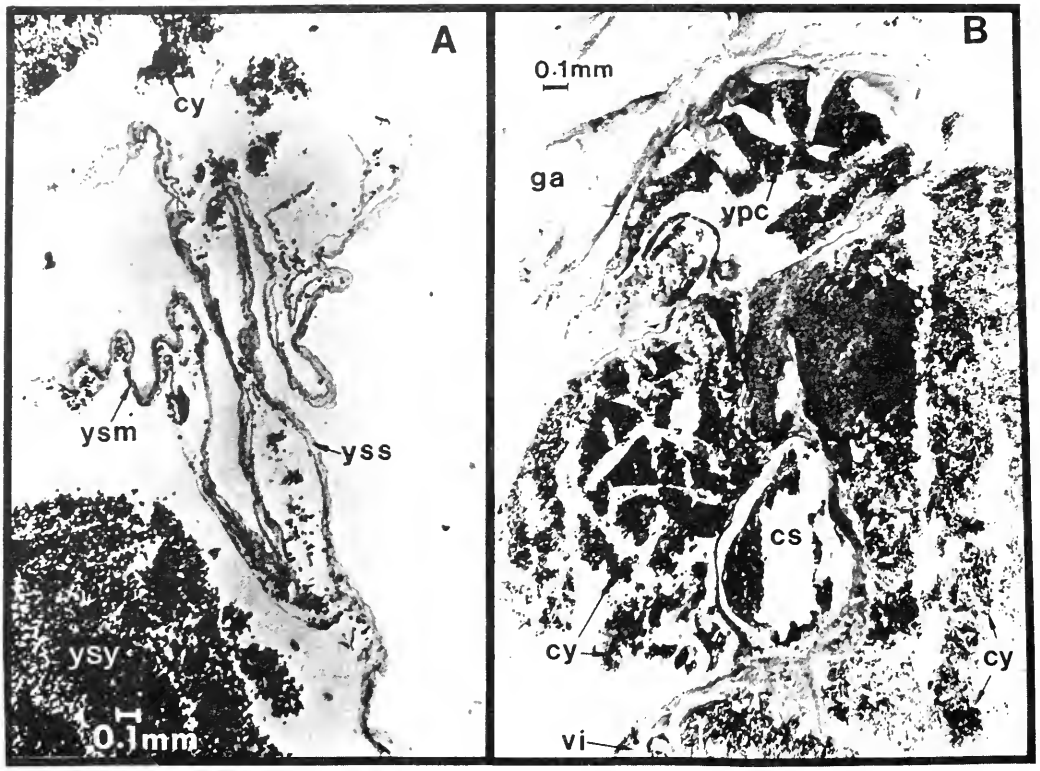

FIGURE 8.—Angle horizontal sagittal view of head section of a 13 mm *Odontaspis taurus* embryo (IRCZM 103179). (A) Pericardial and anterior coelomic cavities: (cy) coelomic yolk; (yss) yolk-sac stalk; (ysy) yolk-sac yolk; (ysm) yolk-sac membrane. (B) Yolk stalk, yolk sac, and lower coelomic cavity: (ypc) yolk in pericardial cavity; (cs) cardiac stomach; (cy) coelomic yolk; (vi) valvular intestine; (ga) gill arches.

31.0 MM EMBRYO (IRCZM 103139, Fig. 10).—This encapsulated embryo was the only one present in the right uterus of a 249.5 cm female *O. taurus* captured 9 June 1976. The 7.5 mm diameter yolk sac was slightly larger than that of smaller embryos examined. All fin buds had developed further. External gill filaments were present.

49.0 MM EMBRYO (IRCZM 103102, Fig. 11).—The 49.0 mm embryo was found free in the uterus of a 274.2 cm TL female *O. taurus* caught 8 July 1978. The emaciated condition, numerous small puncture wounds, and absence of large numbers of branchial filaments on this embryo indicated that it had been attacked by the larger 131 mm embryo also present in the uterus. Although the 49 mm embryo is near the size range of other recently hatched embryos (i.e., 51-63 mm) from *O. taurus* females caught during June, it also could have been torn from its egg capsule by the larger embryo. Apparently also damaged by attacks from the larger embryo, the yolk sac of this embryo was only 4 mm in diameter. Erect wide triangular teeth lacking basal denticles were clearly visible. The stiff, sharp structure of these teeth indicated that they were functional and could have enabled the embryo to hatch from the egg capsule. Gill filaments extended from the gill arches, although many were damaged and probably removed when the embryo was attacked.

57 MM EMBRYO (IRCZM 103145, Fig. 12).—The 57 mm embryo was found free along with an unhatched 41 mm embryo in the left uterus of a 258.1 cm TL female *O. taurus* captured 5 June 1976. This embryo revealed maximum development in external branchial filaments. Numerous long filaments extended from both the gill openings and spiracle (Fig. 12A). A single 3.7 mm filament extended from the cornea at the dorsal edge of the iris (Fig. 12B). Rudimentary claspers were evident on the inner margin of the pelvic fins, indicating secondary sex characteristics were developing.

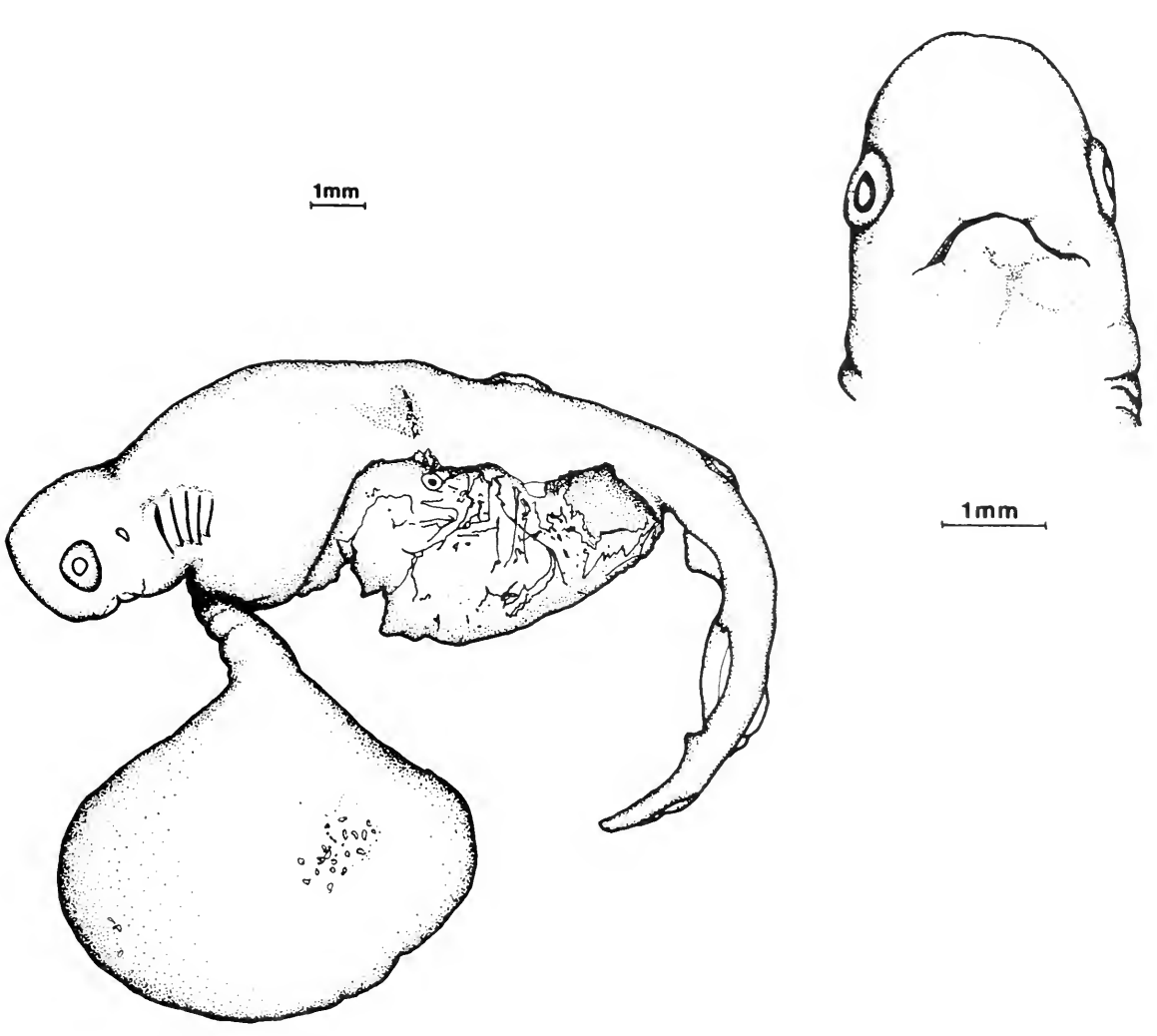

FIGURE 9.—Two views of an 18.5 mm *Odontaspis taurus* embryo (IRCZM 103134) taken from the right uterus of a 282.5 mm TL female captured 4 September 1970, showing damage by intrauterine attacks from larger embryo.

Posthatch and Intrauterine Cannibalistic Period

(June-September; 60-334 mm)

This period is characterized by hatching of the largest encapsulated embryos, consumption of yolk-sac yolk supplies, and active cannibalism by the largest hatched embryo upon other intrauterine encapsulated or small hatched embryos until only one embryo remains. These events occur simultaneously in each uterus. From June to September this developmental period overlaps the latter part of the early gestation phases of other sibling embryos.

Two hatched embryos, 62 and 63 mm, (Fig. 13) from each uterus of a late June sand tiger shark were noticably more robust than five 27-46 mm embryos still encapsulated in these uteri. However, there was no evidence that the larger embryos had begun to feed upon other egg capsules, encapsulated embryos, or other free embryos. The 62 and 63 mm specimens still possessed 5.5-6.0 mm diameter yolk sacs and branchial filaments.

At about 100 mm, the embryo has consumed the contents of the yolk sac and begins obtaining nourishment through adelphophagy and oophagy. Evidence of intrauterine cannibalism was found in the uterus of a 271.5 cm female *O. taurus*, caught 18 July 1976, which contained a large hatched embryo (100 mm) that had attacked and badly damaged

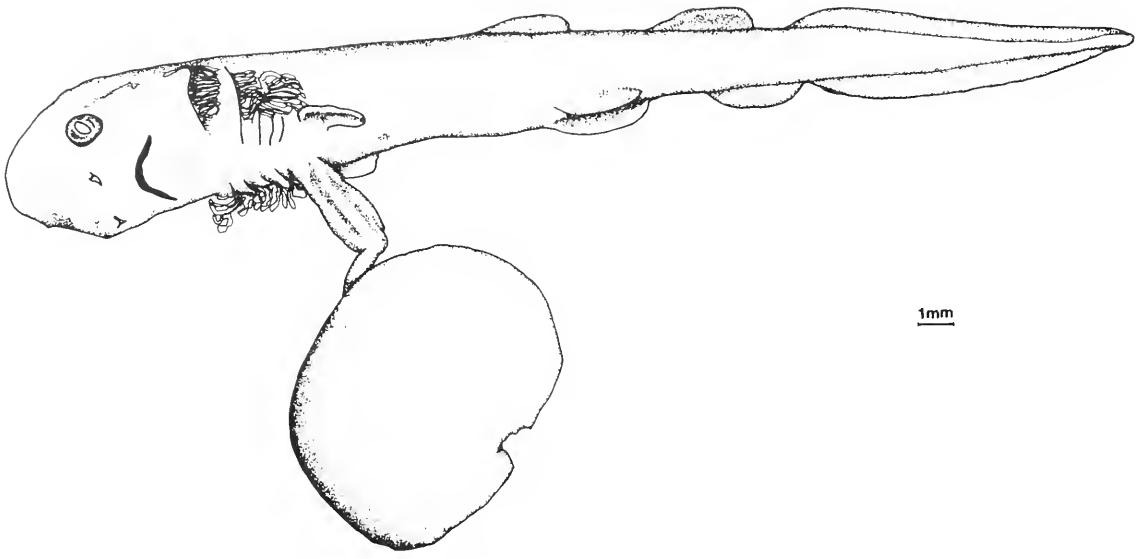

FIGURE 10.—View of a 31.0 mm *Odontaspis taurus* embryo (IRCZM 103139) taken from the right uterus of a 249.5 cm female captured 9 June 1976.

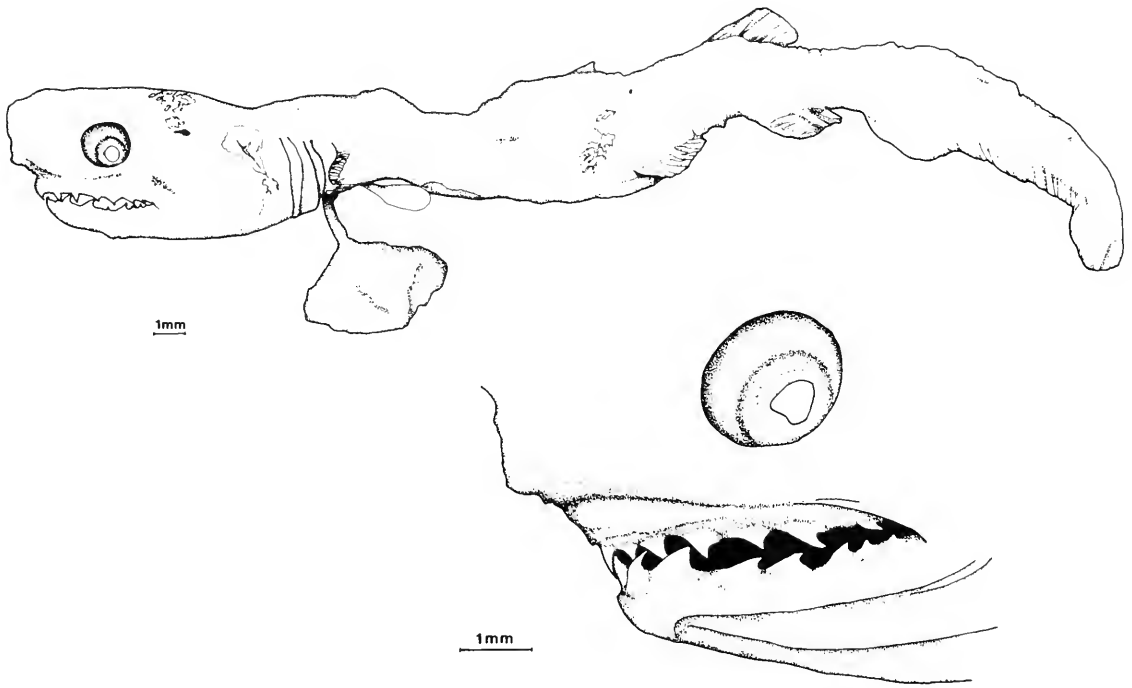

FIGURE 11.—Two views of a 49 mm *Odontaspis taurus* embryo (IRCZM 103102) taken from a 274.2 cm TL female captured 8 July 1978, showing emaciation and injuries from intrauterine attacks by a larger 131 mm embryo.

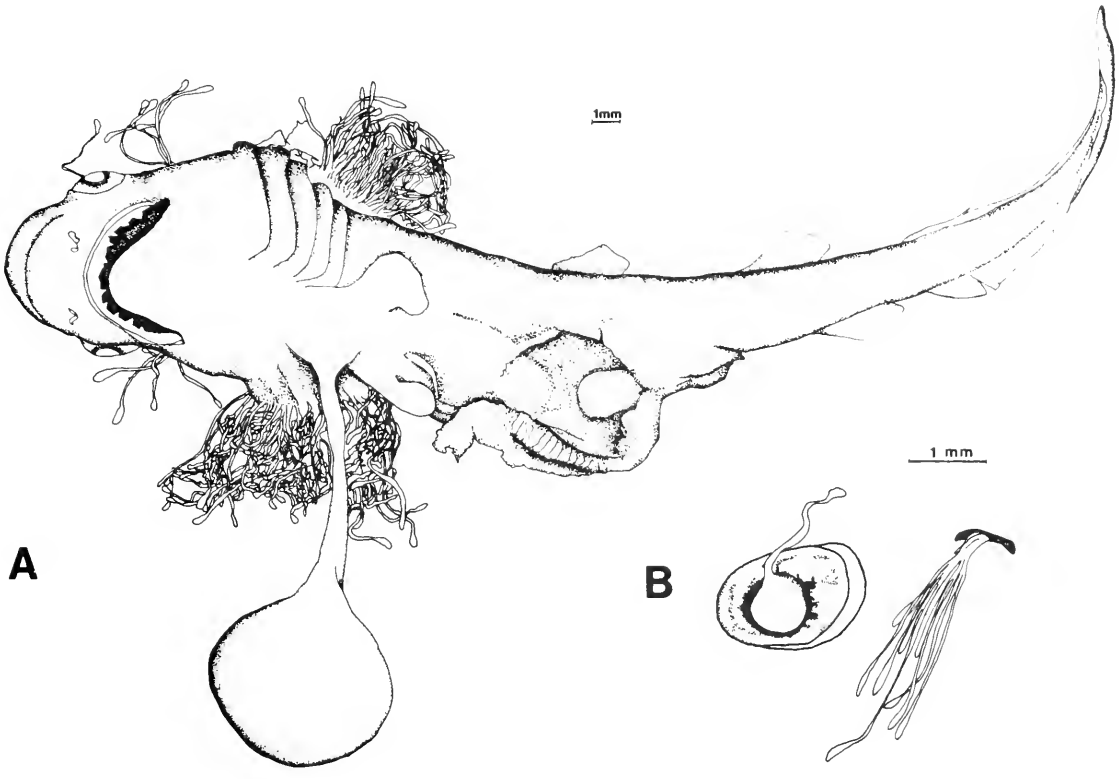

FIGURE 12.—(A) A 57 mm *Odontaspis taurus* embryo (IRCZM 103145) taken from a 258.1 cm TL female captured 5 June 1976; (B) enlargement of orbit and spiracle showing associated filaments.

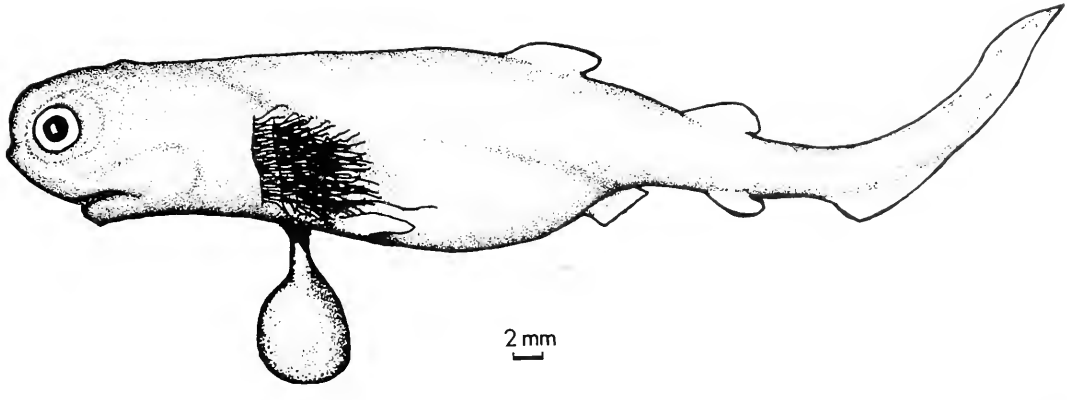

FIGURE 13.—Hatched 62 mm *Odontaspis taurus* embryo with 6 mm yolk sac taken from right uterus of a female caught 28 June 1976, Melbourne Beach, Fla.

(puncture wounds and torn gut) a 51 mm embryo (drawn to scale; Fig. 14A). Having already developed teeth, the 51 mm embryo (see Figure 11 of a 49 mm embryo) had a potential for competitive interaction with the larger 100 mm embryo, although at a decided size disadvantage. It is possible that the 51 mm embryo had not hatched prior to the attack. However, empty and broken egg capsules were not found in the uterus. There is no evidence that the 100 mm embryo had tried to consume any of the other 81 egg capsules in the uterus, nor were there broken or damaged capsules in the opposite uterus which contained a 127 mm hatched embryo.

We obtained further evidence that hatched embryos and/or encapsulated embryos are selectively preyed upon by their larger siblings within the uterus. Two embryos (45 and 49 mm) in the right uterus of an 8 July 1978 female *O. taurus* were badly damaged by the attack of a 131 mm male embryo. Six empty egg capsules were found within the same uterus. None of the other 63 egg capsules were damaged (some of which contained fertilized ova). In the left uterus, a 49 mm embryo had been mutilated by a 131 mm embryo and two of the 66 egg capsules were empty. A 334 mm embryo from the left uterus of a 5 August 1976 adult *O. taurus* had four embryos 9-36 mm TL within its pharynx. Two damaged capsules still contained two embryos (35 and 41 mm), both of which had been punctured numerous times through the capsule membrane. Sixty-eight undamaged capsules did not contain embryos. None of the 65 undamaged capsules in the right uterus contained embryos. However, this uterus contained an intact 41 mm embryo with an egg capsule fragment within the stomach of the largest embryo (320 mm).

100 MM EMBRYO (IRCZM 103137, Fig. 14B).—This male embryo was found in the right uterus of a 271.5 cm adult *O. taurus* captured 18 July 1976. It had well-developed fin rudiments and a particularly well-developed caudal fin. The gill slits were large and without external filaments. Both upper and lower labial furrows were prominent. The yolk sac was absent although an attachment scar was present. Erect teeth, more slender than in previous embryos, were present in multiple rows. The teeth lacked lateral secondary basal cusps (basal denticles) typical of adult *O. taurus*. The teeth of this embryo were obviously functional because punctured and torn egg capsules and a damaged (tooth-marked) 51 mm embryo were found in the same uterus.

131 MM EMBRYO (IRCZM 103103, Fig. 14C).—A male embryo, from an 8 July 1978 sand tiger shark,

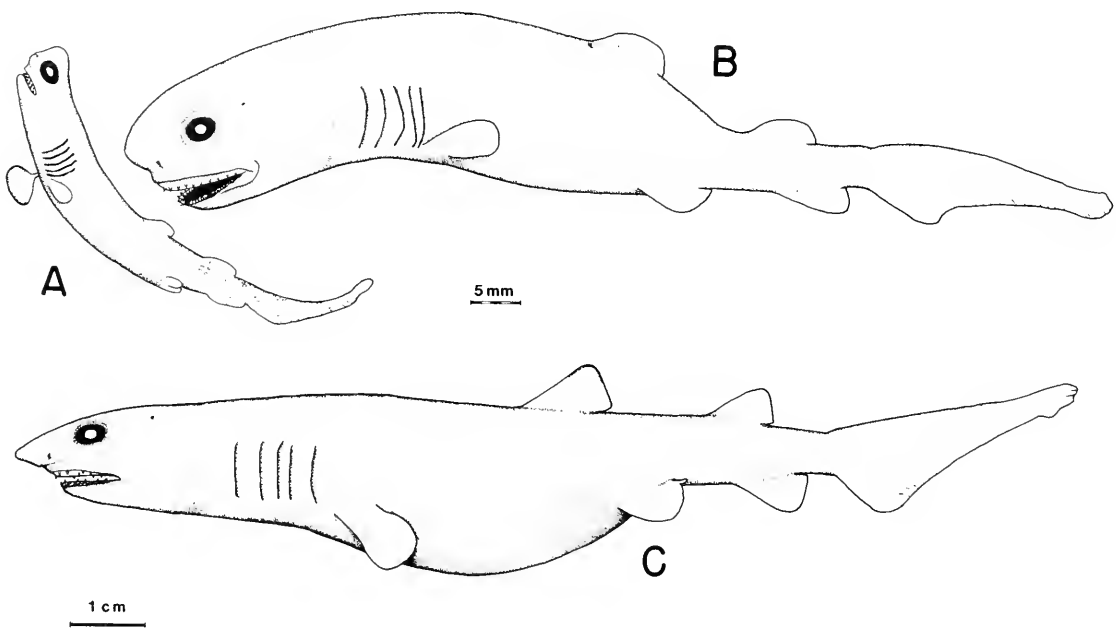

FIGURE 14.—(A) A 51 mm *Odontaspis taurus* embryo attacked and damaged by (B) a 100 mm male embryo inside the uterus of a 271.5 cm female captured 18 July 1976 (both IRCZM 103137). (C) A 131 mm male embryo (IRCZM 103103) taken from the uterus of a female captured 8 July 1978. This embryo had attacked and damaged the 49 mm embryo shown in Figure 11.

resembled the 100 mm embryo, except that all fins but the pectorals were similar to those of the adult and the gut was more distended with yolk. This embryo had attacked the 49 mm (Fig. 11) and 45 mm embryos present in the same uterus.

227 AND 271 MM EMBRYOS (IRCZM 103101, Fig. 15A, B).—The 227 mm female and larger 271 mm male embryo came from a 29 July 1977 sand tiger shark. The snout was narrow and had lengthened, resembling that of the adult as did other anatomical features, including the fins. In both embryos the entire digestive tract and abdominal wall were distended from the consumption of yolk. Many broken egg capsules were also found within the uteri.

334 MM EMBRYO (IRCZM 103135, Fig. 15C).—This was a female embryo from a 5 August 1976 sand tiger shark. The stomach was distended with yolk. Many "adultlike" features were apparent. This embryo contained four smaller embryos (9-36 mm) in its pharynx.

Late Gestation, Postcannibalistic, Oophagous, Preparturition Period

(September-March; 334-1,000 mm)

After fertilization of *O. taurus* ova has ceased and all other developing embryos have been consumed by the surviving embryo, unfertilized ova become the primary source of nutrition. This transitional period begins in August-September when embryo lengths reach 330-340 mm.

Embryonic growth and development rates are rapid during this period (Fig. 15C, Table 3). A 330 mm embryo in September may attain 650-890 mm by late October or early November and 830-970 mm by late November. During this period the embryo consumes large quantities of yolk and a length of 1.0 m may be reached in December (Figs. 15D, 16). Embryos reaching 1.0 m are near parturition which may take place between December and March, after a gestation period of 9-12 mo. A maximum size of 1.2 m TL may be reached before birth (Cadenat 1956). A 272

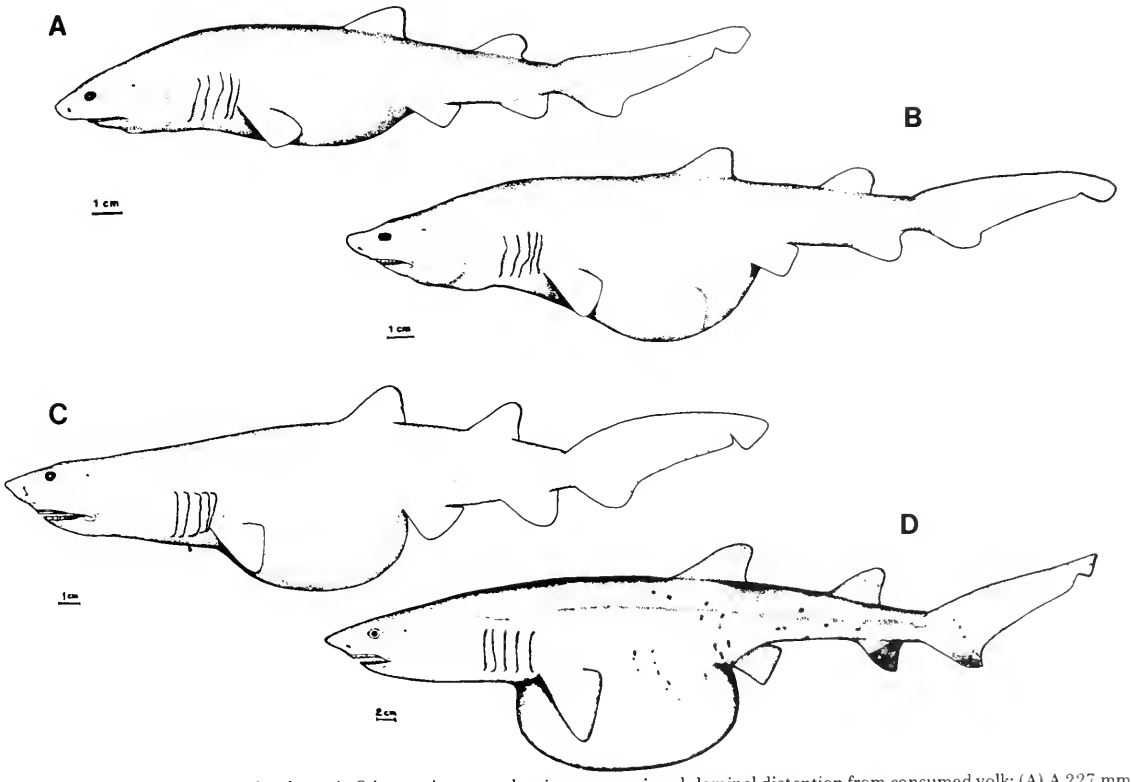

FIGURE 15.—Four specimens of embryonic *Odontaspis taurus* showing progressive abdominal distention from consumed yolk: (A) A 227 mm female embryo (IRCZM 103101) from the right uterus and (B) a 271 mm male embryo (IRCZM 103101) from the left uterus, of a female captured 29 July 1977; (C) a 334 mm female embryo (IRCZM 103135) taken from a female captured 5 August 1976; and (D) an 80-100 cm embryo.

TABLE 3.—Postparturition growth [total length (TL) and total weight] of two captive juvenile *Odontaspis taurus* from observations made by F. G. Wood at Marineland Inc., St. Augustine, Fla. NR = not recorded.

	Male		Female	
Date	TL (cm)	Weight (kg)	TL (cm)	Weight (kg)
Born 15 Feb. 1959	NR	NR	NR	NR
17 Feb.	106	6.2	NR	NR
9 Oct.	126	12.6	NR	NR
29 Dec.	137.5	19.1	139	19.1
30 Aug. 1960	NR	NR	145	NR
12 Dec.	NR	NR	NR	37.5
28 Dec.	NR	NR	167	NR
16 June 1961	NR	NR	175.5	40.7 died
17 Mar. 1962	167.5	NR died[1]		
Mean growth rate (TL)	1.62 cm/mo 19.44 cm/yr		2.03 cm/mo 24.36 cm/yr	

[1]37 mo old, claspers extended 7.5 cm past pelvic fin tip.

cm *O. taurus* female was captured 10 April 1946 and kept in an aquarium for 11 mo; it died on 9 March 1947. Her autopsy revealed two decomposing near-term embryos 103-105 cm TL (6.1 and 6.4 kg) (McBride 1947[10]; Springer 1948).

The oophagous stage in development is preceded by an increase in ovary size, ovulation rate, number of ova per capsule, and number of Type II capsules produced. The number of ova per capsule increased to a maximum of 23 ova/capsule during the fall and winter (Fig. 5D). During late gestation the embryos swallowed such great quantities of yolk that their stomachs became greatly distended. Cadenat (1956) found 1.5 kg of yolk (18.8% total body weight) in a near-term *O. taurus* embryo weighing 8 kg. This distention of the abdomen has precipitated the term "yolk stomach" used by earlier authors, particularly for the oophagous embryos of *Lamna nasus* ("Dottermagen" of Lohberger 1910).

The distention of the embryonic stomach declines in the final days near parturition. At birth the young *O. taurus* do not have excessive amounts of yolk within the digestive tract. We examined a 91.0 cm, 3.75 kg dead female pup (Fig. 17) from a 240 cm female *O. taurus* held captive since 21 August 1980, in a display tank ("Shark Encounter") at Sea World of Orlando. The pup died immediately after birth on 22 March 1981. The stomach and intestine of the newborn shark were not distended with yolk, although yolk was present. Another pup, born simultaneously with the other uterus, lived and is presently on display (April 1983).

Simultaneous to the decline in yolk consumption is an increase in the size of the embryo's liver. The left and right lobes of the liver of the specimen from Sea World of Orlando measured 20.3 and 23.7 cm, respectively, with a total liver weight of 372 g (9.9% of total body weight). Cadenat (1956) found the liver of a near-term embryo to be relatively large, contributing 6.43% of the total body weight, in a 110 cm specimen. The large liver in the near-term embryo compares favorably with the largest liver recorded in adults at 7.54% total body weight (Cadenat 1956). A similar condition of large liver size and reduced yolk consumption has been observed in a near-term oophagous embryo (97 cm TL) of *Isurus paucus* (Gilmore in press).

The increase in size of the embryo's liver corresponds to an observed decline in maternal ovarian activity and ovary size near the end of gestation (Springer 1948). The liver of the pregnant near-term female sand tiger shark also reaches a minimum size at this time (2.88% total body weight, Cadenat 1956), revealing the maximum uilization of the adult's nutritive materials to support the two large, ravenous embryos.

Nutritional supplies stored within the embryo's liver can then be utilized during the last few days of gestation and after birth preceding the first capture of prey. The surviving newborn female *O. taurus* from Sea World of Orlando did not eat until 25 d after birth. She first ate (two pieces of clam) a day after she attacked and killed another small shark (*Triakis semifasciata*, Frank Murru[11]). After the initial feeding the young sand tiger shark ate dead clams, squid, and fish (blue runner, *Caranx crysos*, sardines, herrings, "smelt", and mackerel) during daily feeding periods.

Fortunately *O. taurus* has been kept in captivity for extended periods (up to 10 yr, 2 mo; R. van der Elst[12]). Several births have taken place both in a South African aquarium (van der Elst footnote 12) and American aquaria (Wood footnote 9; Murru footnote 11). Wood (footnote 9) made the following observations of the birth of *O. taurus* pups in an aquarium at Marineland, St. Augustine, Fla., on 15 February 1959 from a female captured 11 November 1958 (Fig. 18):

> "The head of the first pup was first observed about 0945 extending 3 to 4 inches [7.6 to 10.2 cm] from the cloaca. The head came out a little further during the next 30 minutes. The pup was born c. 1015.

[10]A. F. McBride, formerly with Marineland Inc., St. Augustine, Fla., pers. commun, 8 Nov. 1947 to Stewart Springer, Mote Marine Lab., Sarasota, FL 33577.

[11]F. Murru, Curator of Fishes, Sea World of Orlando, FL 32809, pers. commun. 1981.

[12]R. van der Elst, S. Afr. Assoc. Mar. Biol. Res., Durban, South Africa, pers. commun. 1977.

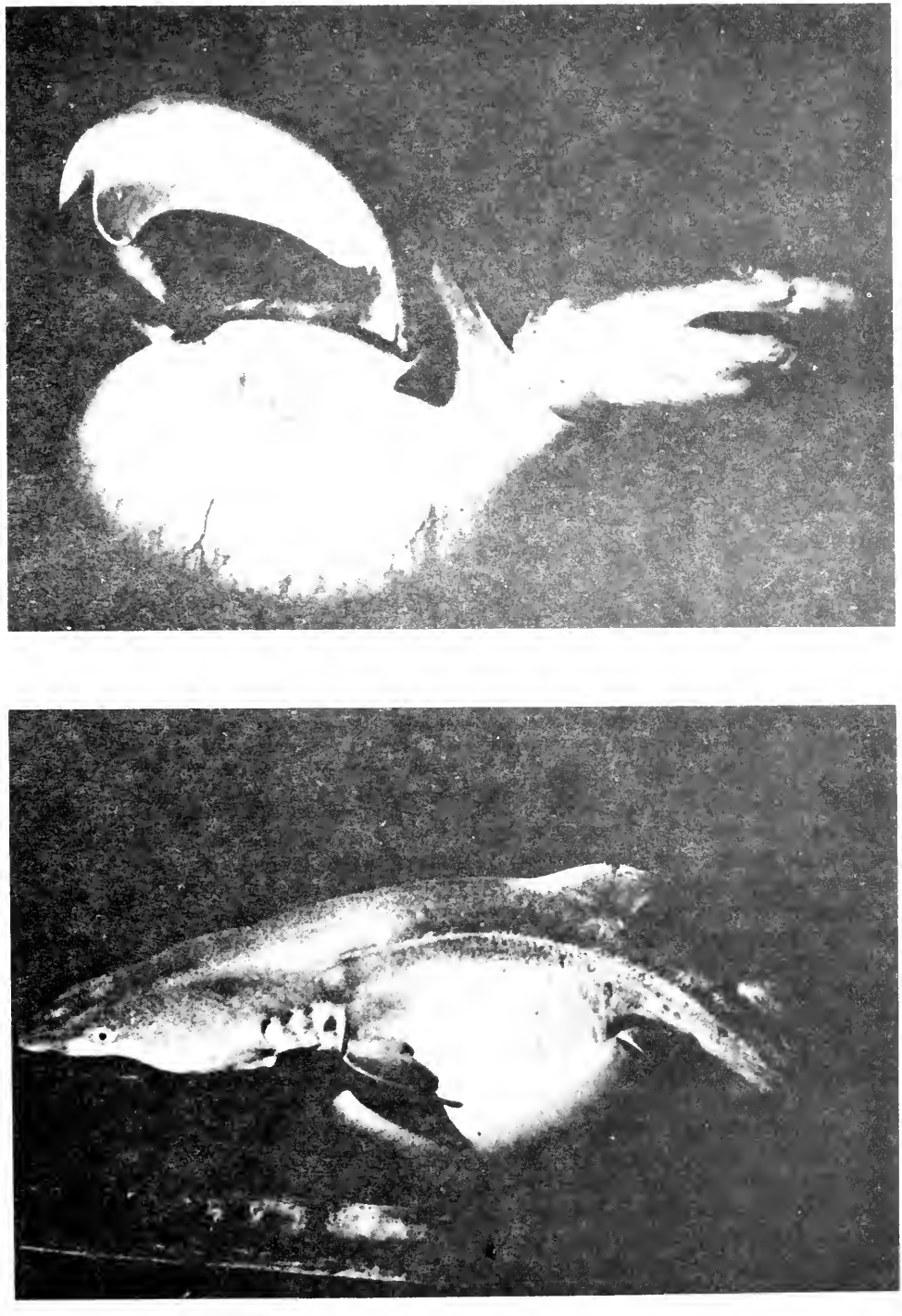

FIGURE 16.—Two views of an *Odontaspis taurus* embryo (80-100 cm) dissected from a dead female, showing extent of preparturition yolk consumption. Note adultlike color pattern on embryo. Measurements not taken. (Photos courtesy of Marineland Inc., St. Augustine, Fla.)

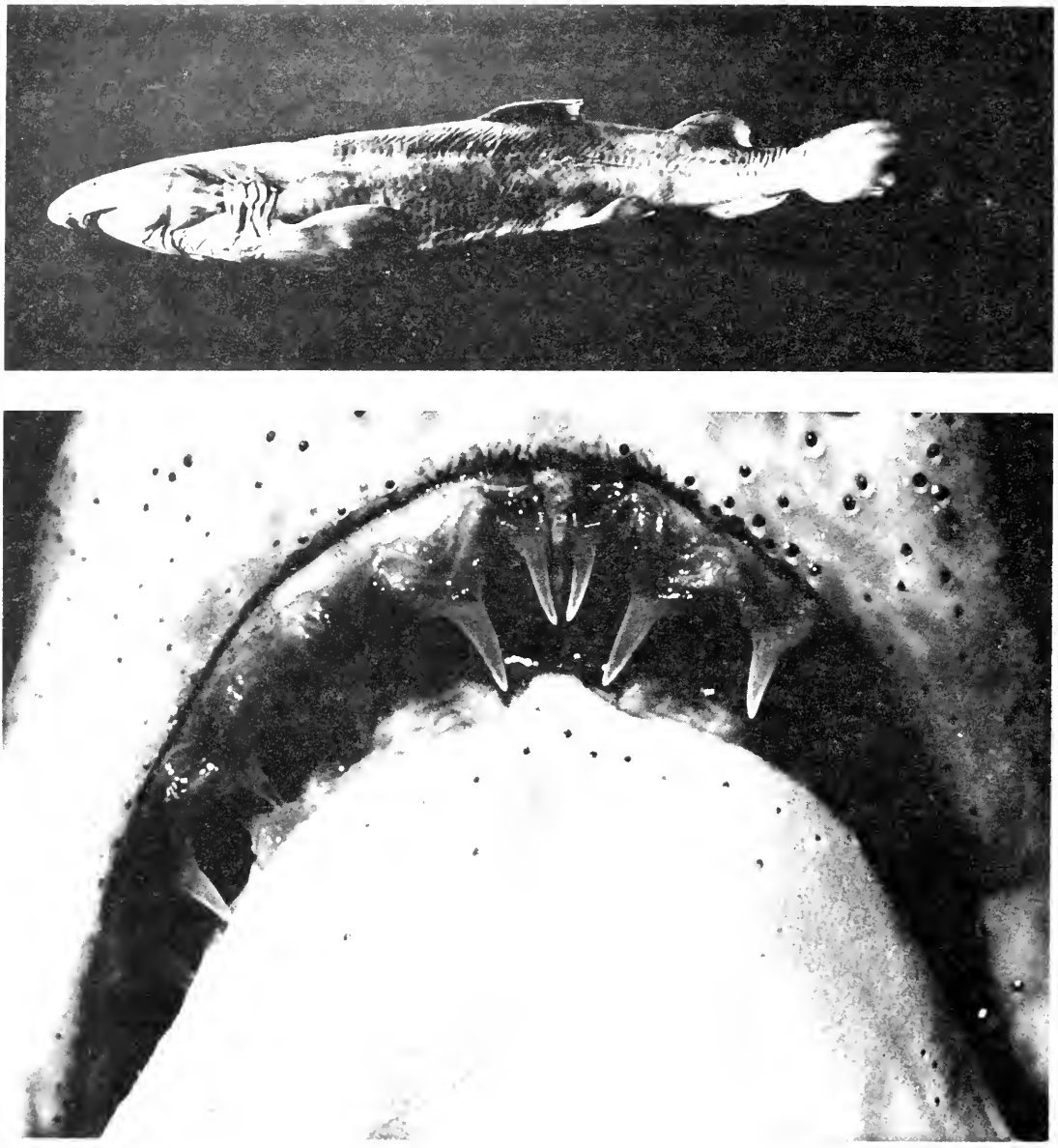

FIGURE 17.—(Upper) Lateral view of a 91.0 cm female *Odontaspis taurus* (IRCZM 103182) born 22 March 1981 at Sea World of Orlando, Fla.; (lower) view of dentition of same empryo.

"The female had been swimming between 5 and 8 feet [1.5 to 2.4 m] off the bottom in the center section. The pup was born c. 6 ft [1.8 m] above the bottom. It immediately swam off. The mother shark did not alter course or speed at the time the pup fell free.

"Within less than a minute after the first pup was born, about 3 inches [7.6 cm] of tail appeared. The end of the tail disappeared 10 to 12 minutes later. Approximately 10 minutes later the tip of the second pup's snout emerged following 3 to 4 inches [7.6 to 10.2 cm] of the head. The head disappeared a few minutes later. It appeared from this and the distortions of the female shark's belly that the pup turned several times inside of her in the course of half an hour or so.

"The tip of the tail appeared and disappeared again, then the snout began to emerge about an hour after the first pup had been born. This was followed by gradual emergence to [of] the head to

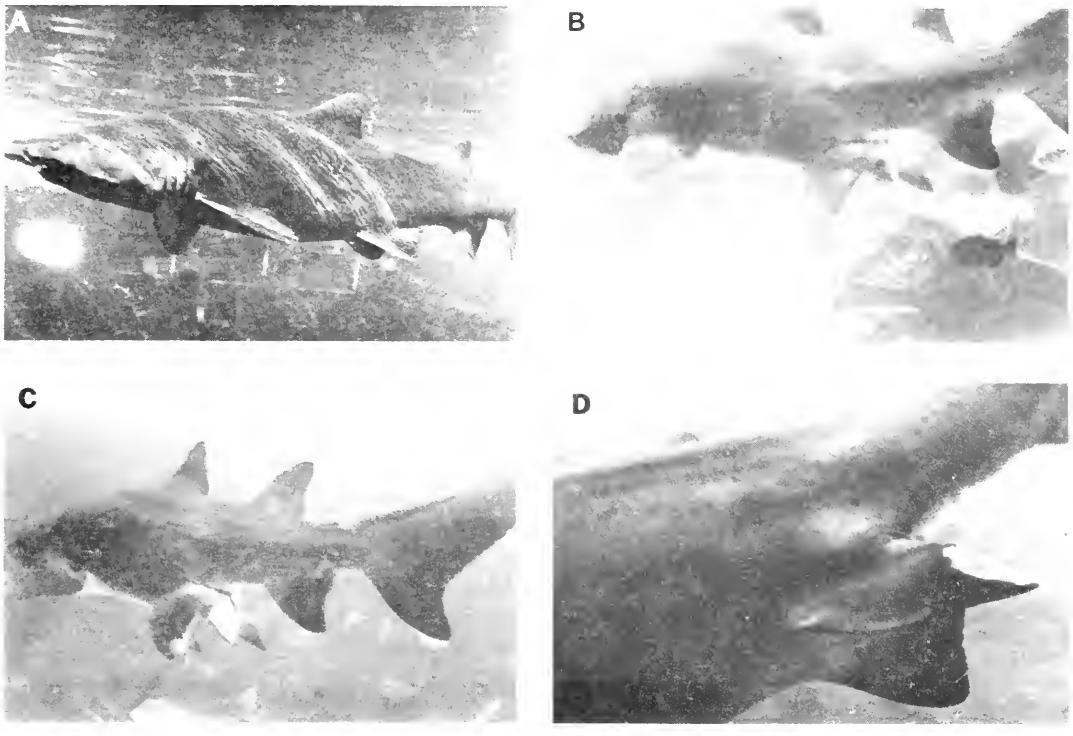

FIGURE 18.—Aquarium birth of *Odontaspis taurus* embryo, 15 February 1959, at Marineland Inc., St. Augustine, Fla. (A) Adult female with distended abdomen; (B) initial emergence of embryo snout; (C, D) inverted emergence of head to gill openings prior to completing birth. (Photos courtesy of Marineland Inc., St. Augustine, Fla.)

about the second gill slit. For about 40 minutes the pup came no farther, then it gradually moved out to the origin of its pectorals. Five to 8 minutes later the mother abruptly speeded up and banked in the water with her belly outward. The pup popped out at 1233, rose to the surface, then came back to the bottom.

"Both pups swam rapidly and rather erratically until caught . . . ."

Other births observed by Wood (footnote 9) were not so prolonged and were more difficult to analyze, e.g., a birth occurred on 30 December 1958, within 7 min following a cloacal discharge. Complete emergence of the embryo took 2-3 s. Regardless of the length of birthing time, embryos have been consistently observed to emerge headfirst. This is in contrast to recent observations of tail-first births of carcharhinoids [e.g., *Carcharhinus milberti* (Wass 1973); *Sphyrna mokarran* (Mooney 1975); *Galeocerdo cuvieri* (Bravo 1980)].

Increase in length and weight after birth in captivity can be seen in Table 3. Newborn *O. taurus* gain considerable weight during the first few months. A 106 cm, 6.2 kg pup born on 15 February 1959 was 137.5 cm and 19.1 kg by 29 December 1959. This same pup survived in captivity until 17 March 1962. Notes taken by Wood (footnote 9) point out that this specimen, a male, appeared to be nearing sexual maturation. At an age of 37 mo and length of 167.5 cm (Table 3) the shark's claspers extended 75 mm past the pelvic tips and the "general appearance" of the testes indicated the shark was becoming sexually mature. Our observations indicate males are mature when at least 191.5 cm (see Observations and Descriptions section). These data indicate that western Atlantic *O. taurus* may mature earlier than South African specimens which were found to first mature at lengths of 220 cm (Bass et al. 1975). South African observations of captive *O. taurus* indicate that "maturity is attained after about 8 years in the females . . . although the five year old male that we have is not far from maturity" (van der Elst footnote 12). Our pregnant females from the east coast of Florida ranged in size between 236.6 and 274.3 cm TL. These sizes are within the range of 240-272 cm for pregnant South African female *O. taurus* (Bass et al. 1975).

DISCUSSION AND SUMMARY

Reproduction in *Odontaspis taurus* is typified by the occurrence of both synchronous group and synchronous individual physiological activities. Unisexual male and female groups converge on a mating ground, and intersexual behavioral activities such as biting (i.e., typically male biting female) may serve as a precopulatory release mechanism (Springer 1967; Stevens 1974). Over several years some variation is apparent, but the simultaneous presence of several females in a similar reproductive state off the Florida east coast indicates a definite seasonality for reproductive activity.

After mating, the oviducal glands produce six basic types of egg capsules. Capsules without ova are produced initially, suggesting that oviducal gland activity precedes ovulation. Ova-laden egg capsules are produced during the latter half of gestation, principally as a food source for the remaining embryo in each uterus.

The synchronous occurrence of egg capsules of the same type in the oviduct and the variation in ova numbers per capsule could be partially explained by three hypothetical physiological mechanisms, portions of which have been documented in various elasmobranchs:

1) Extrinsic stimuli may cause the pituitary gland to secrete hormones which eventually cause ovarian ova to maturate. (Removal of the pituitary in *Scliorhinus caniculus* prevents ovulation, Dodd et al. 1960.) During the period of ova maturation, luteal tissue may form (TeWinkel 1950; Chieffi 1967) and could possibly secrete hormones which initiate oviducal gland activity preceding ovulation. Egg capsules would then be produced initially without ova. TeWinkel (1950) similarly deduced that in *Mustelus canis*, "... it is not unlikely, therefore, that ovarian hormones present at the time of ovulation or slightly preceding it, stimulate the secretion of a single egg-case by each oviducal gland irrespective of the number of ova discharged." Sperm would have to be stored if mating activity were the extrinsic stimuli affecting the pituitary and if ova maturation took some time. Although we have not documented if or where sperm is stored in *O. taurus*, the most likely location would be the oviducal gland which has been shown to be the site for sperm storage in other elasmobranchs (Metten 1939; Prasad 1945; Pratt 1979).

2) Extrinsic stimuli may cause the pituitary to secrete hormones which eventually cause ovarian ova to maturate and, in addition, directly affect oviducal gland activity. Steroid sex hormones (e.g., estrogen) have been shown to directly affect the secretory activity of the oviduct in *Squalus caniculus* (Hisaw and Abramowitz 1938; Dodd et al. 1960; Simpson et al. 1963). Mobilization of egg capsule production in the oviducal gland may take less time than ova maturation, therefore producing egg capsules without ova.

3) Sperm arriving at the oviducal gland may stimulate the gland to secrete ovalbumin and collagen capsules preceding pituitary hormone release. However, pituitary hormones and/or luteal hormones may maintain ovarian and oviducal gland activity through gestation.

The staggered development of the *O. taurus* embryos indicates that sperm had been stored for 2-4 mo, and either fertilization of some ova took place as late as July and August or development of fertilized capsules was somehow delayed.

Embryonic development may be divided into several phases within the developmental periods already discussed, based on anatomical characteristics and nutritive strategies (Fig. 19) Encapsulated early embryos derive nutrition from internal coelomic yolk supplies, although a yolk sac and stalk are present. The presence of yolk sacs 6.0 mm in diameter or larger in embryos 13-57 mm demonstrates little apparent change in the external yolk supply during a period of extensive growth and differentiation within the egg capsule. In the 13 mm embryo, external consumption of other encapsulated ova is improbable,

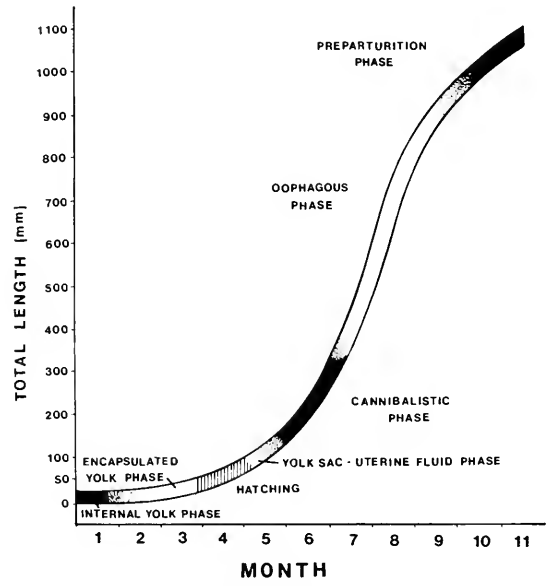

FIGURE 19.—Embryonic growth curve and nutritional phases in development of *Odontaspis taurus*.

because cellular differentiation and organ formation were still in a primitive phase of development. When they have developed sufficiently to consume external food, larger early embryos (20-63 mm) may consume other ova contained within their own capsule. Therefore, following the consumption of internal, endocoelomic yolk, the embryo may enter another nutritional phase while still encapsulated. These observations suggest that initial internal coelomic yolk supplies and other encapsulated ova and albumin contribute more to initial embryonic growth and differentiation in embryos 49-57 mm TL than does the yolk of their own yolk sac. Although several blastodiscs and ova are observed in a single capsule, only one embryo develops indicating that the activity of one blastodisc somehow reduces or arrests the activity of other blastodiscs.

After developing functional teeth and hatching at 49-63 mm, the embryo may utilize a variety of nutritive sources. It is possible that intrauterine fluid, as well as the yolk remaining in the yolk sac, may be a food source. The 62 and 63 mm specimens still possessed a 5.5 mm diameter yolk sac and well-developed branchial filaments. Uterine fluid was found to increase in volume after hatched embryos were found. It is possible that this fluid may be absorbed through the extensive branchial filaments found in these embryos. However, these filaments also may have a respiratory function. Of the many anatomical features observed in the developing embryos, the presence of a filament attached to the cornea of the 57 mm embryo was among the most interesting. Its presence on the cornea suggests a respiratory rather than a nutritive function. The normally high metabolic demand of retinal tissue suggests that there may be a need for such a filament.

After the embryo hatches, the yolk sac eventually declines in size demonstrating the utilization of this nutritive source. Uterine fluids were observed to increase in volume when newly hatched embryos were present. This fluid could also be consumed by the embryo. Activity of the hatched embryo within the uterus may cause uterine hormones to induce increased ovarian activity, since ovulation rates and uterine yolk capsules increase after the first embryo hatches. Other embryos also developing in some of these capsules were not attacked when hatched embryos were only 17-40 mm larger than encapsulated embryos. The size advantage of a hatched 63 mm embryo over a 46 mm encapsulated embryo may not be great enough for an active attack, even though the potential prey is restricted in movement due to its encapsulation. The first embryo to hatch apparently does not begin to hunt for and detect other encapsulated embryos until it reaches about 100 mm in length. Initially only those capsules containing embryos are attacked, while up to 81 capsules without embryos are undamaged. Attacks are made by puncturing and cutting the capsule membrane with teeth. These attacks may also puncture and tear the embryo within the capsule, as we found punctured, dead embryos still encapsulated. The encapsulated embryo that was attacked is probably consumed later after the capsule is eventually opened by repeated attacks from the larger embryo.

It is apparent from these data that the first embryo to hatch and reach a length approximating 100 mm would be most likely to survive. By the time the embryo reaches a length of 227-340 mm, during August and September, it will have consumed its intrauterine competitors. If the embryo first to develop dies in utero before consuming all other embryos, the next largest embryo will probably become the dominant predator and continue the developmental pattern. The two 320 and 334 mm embryos from 5 August 1976 had consumed other embryos and also contained 7.5-9.0 g of yolk in their stomachs. After reaching 300-400 mm and having consumed all smaller embryos, the embryo begins attacking egg capsules which contain 7-23 unfertilized ova. In most cases the capsules were not consumed but were torn open near the posterior portion of the capsule and the ova or gelatinous material had been removed. Embryos 131 mm or greater in length were found to contain varying quantities of yolk in both their stomachs and valvular intestines.

The embryo increases significantly in size (i.e., from 334 to 1,060 mm) by consuming uterine yolk supplies and uterine fluid. After the embryos reach a length of about 1.0 m and weights of 3.8-10.0 kg, parental ovarian activity is reduced, stomach yolk content of the embryo declines, and its liver increases in size. After 9-12 mo of gestation, birth occurs.

Teeth in the newborn *O. taurus* are well developed, extending beyond the gums (Fig. 17B). The teeth in the newborn 91 cm female pup we examined had well-developed lateral tooth denticles typical of adult specimens. However, Taniuchi (1970) reported no *O. taurus* <100 cm with lateral tooth denticles.

Although only two young are produced at the end of a lengthy gestation period, they have several selective advantages as top predators in marine food webs. The newborn sand tiger sharks are large at birth and are comparable in size to many common adult neritic predators (e.g., scombrids and carangids). They are also larger than the young of most other galeoid sharks (45-60 cm, Wourms 1977). Their larger size as a top predator also allows a

greater range of available prey for consumption. The predation rate on young *O. taurus* will be lower as few fish are larger. A similar argument has been made by Wourms (1977) for the selective advantages of viviparity in chondrichthyan fishes in general. However in *O. taurus*, not only is the near-term embryo quite large but also it is conditioned in utero to hunt, attack, and consume prey. At birth they are "experienced young" (Springer 1948). The young sand tiger sharks, one from each uterus, having already killed for survival before birth, may have a selective advantage during competitive interactions with other interspecific predators of similar age or size (except possibly other lamnoid and some galeoid sharks). The advantage in interspecific competition may have been demonstrated, although under captive conditions, in the lethal attack of a 25 d-old *O. taurus* pup on *Triakis semifasciata*.

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COPEPODS AND SCOMBRID FISHES: A STUDY IN HOST-PARASITE RELATIONSHIPS

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ABSTRACT

Host specificity of the copepods parasitic on scombrid fishes is the basis for an analysis of the host-parasite relationship. A total of 46 different species of parasitic copepods were collected from 47 species of Scombrinae (the monotypic Gasterochismatinae is excluded). A revised host-parasite list is presented, including new data by R. F. Cressey and H. B. Cressey. Those copepod species present on more than one host species have preferred hosts, and indicate tendencies to being host specific. The copepods present an American species of *Scomberomorus* suggest evolutionary trends in that group. Two species (ancestral *S. cavalla* and ancestral *S. sierra*) were probably present prior to the separation of the Atlantic and Pacific Oceans. The present Atlantic *S. maculatus* and *S. brasiliensis* arose from a *S. sierra* ancestor. Copepod data suggest that the Indo-West Pacific *S. commerson* is the most primitive extant species, while *S. multiradiatus* is the most advanced. The copepods parasitic on *Sarda* species indicate the origin of that genus in Australasia, with the Atlantic *S. sarda* being the most advanced species. The genus *Allothunnus*, previously regarded as a member of the tribe Sardini, is shown to have affinities with the Thunnini and may be the most primitive member of that tribe. A cladistic analysis of the copepod genus *Unicolax* correlates well with current hypotheses of the phylogeny of scombrid genera. Host-parasite relationships of the Scombrinae are compared with those found in a previous study of host-parasite relationships in needlefishes (Belonidae). Parasite-based host phylogenies follow the methods of Brooks.

In this paper we test the validity and application of several parasitological theories regarding host-parasite relationships of copepods parasitic on scombrid fishes. As in our earlier joint effort (Cressey and Collette 1970), in which we treated the relationships of parasitic copepods and needlefishes, the analyses are enhanced by the collaboration of specialists representing each animal group (Cressey—parasitic copepods, Collette and Russo—scombrid fishes). Parasite taxonomy on which the present paper is based has been published separately (Cressey and Cressey 1980). Additional material collected since that publication and an updated list of hosts and copepods, because over 200 additional scombrids have been examined, are included in this paper. Examples of 10 genera of copepods are illustrated (Fig. 1) to indicate the kinds of copepods that parasitize scombrids.

Because many earlier reports on parasitic copepods contain misidentifications of both host and parasite, we rely on our own collections or direct examination of specimens used in published accounts.

The often repeated "Fahrenholz rule" (Noble and Noble 1973:548) suggests that related parasites are found on related hosts, thus indicating host phylogeny. This generalization we now know is an oversimplification.

Hennig (1966:109-110) illustrated how it is possible to have the same parasite species on hosts of polyphyletic origin through incomplete parallelism. Cautions on the use of parasites as indicators of host phylogeny, echoed by Mayr (1957), Hennig (1966), Noble and Noble (1973), and others, are well-founded. We feel, however, that these problems can be minimized by studying comprehensive collections of both hosts and parasites, using the maximum number of parasite groups on the hosts. Presence of parasites on any host may reflect host ecology, chorology, or phylogeny. We believe that information on host-parasite phylogeny has increased validity as sample size, and the numbers of parasite species from different parasite groups (Crustacea, Trematoda, Protozoa, etc.) available for study increases.

When a parasite group is taxonomically well understood, it can be treated as a host character with as much validity as host morphology, serology, and ecology.

Objections or reservations regarding the parasite approach to host phylogeny raised by Mayr (1957) and Hennig (1966) are based on studies or examples, using a relatively small number of parasite species, usually within one parasite taxon (genus or family). If, however, one repeats the analysis of the same hosts

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using numerous parasite groups, the parasite taxa that do not parallel the host phylogeny are likely to become apparent.

Another parasitological theory we have tested is "Szidat's rule," which suggests that primitive (generalized) parasites are found on primitive hosts and that advanced (specialized) parasites are found on advanced hosts. We provide an example supporting this concept when we consider the scombrid host preferences of the copepod genus *Unicolax* on scombrid hosts (p. 254).

SAMPLING ADEQUACY AND HOST SIZE

Before considering host specificity, it is necessary to know whether enough hosts were examined to provide samples of all species of the usual parasite fauna. Individual collections of copepods from each scombrid species were recorded on cards sequentially, enabling us to consider the question: "How many specimens of a host species should be examined before all parasitic copepod species are likely to have been collected?" Examples are given in Table 1.

TABLE 1.—Number of specimens that had to be examined in order to find all known copepod species.

Species	Totel specimens examined	Specimens examined until all collected	No. of copepod spp.
Scomberomorus commerson	130	53	9
Scomberomorus sierra	116	12	3
Sarda sarda	106	35	4
Euthynnus affinis	74	44	8
Auxis spp.	68	60	6
Scomberomorus concolor	47	2	3

Of the six species presented in Table 1, the two species of *Scomberomorus* endemic to the eastern Pacific (*S. sierra* and *S. concolor*) required a relatively small number of individuals to be examined (2-12 specimens), until all parasitic copepods were collected. Wider ranging species (*S. commerson, Sarda sarda, Euthynnus affinis,* and *Auxis* spp.) required examination of a greater number of specimens (35-60) before we collected all of their copepod species. The two endemic species have fewer species of parasitic copepods than the nonendemic species. Other scombrids with restricted distributions (*Scomberomorus multiradiatus*, *S. sinensis*, and *S. munroi*) also have fewer parasitic copepod species than related species with wider distributions.

When collecting parasitic copepods from hosts with wide distributions, specimens must be examined from throughout the range. We found that the number of parasite species is usually less at the periphery of the host's range, so that conclusions relative to total parasite fauna for a species cannot be based on geographically limited collections.

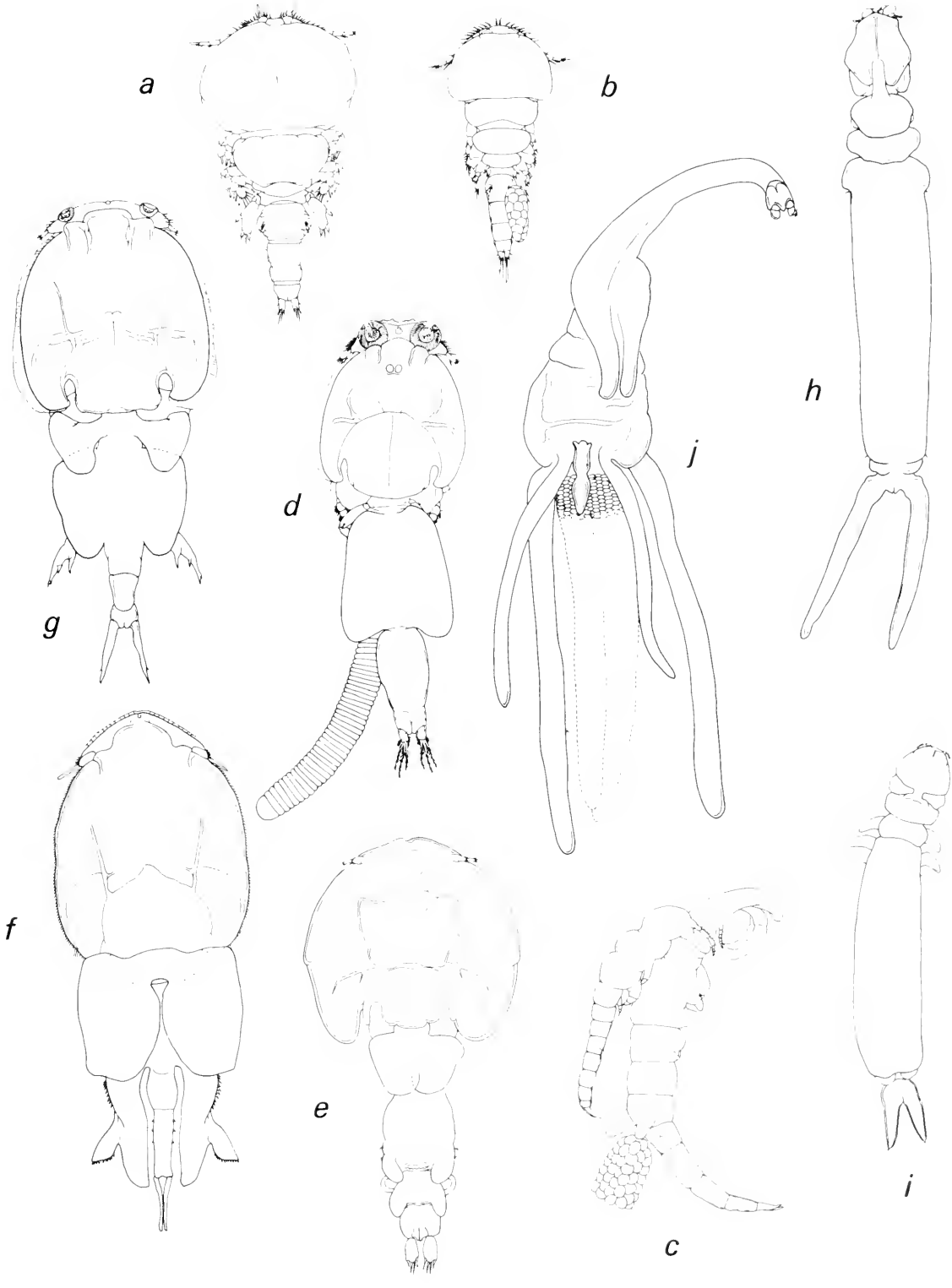
We also examined the relationship between host size and infestation density in order to determine its importance in sampling adequacy. It is generally accepted that larger individuals of host species usually support a greater parasite fauna, both in number of species and individuals. Although little work has been done on the ectoparasite fauna in relation to host size (age), Dogiel et al. (1961:9) noted an increase in the numbers of *Ergasilus* sp. on the gills of *Esox lucius* on larger fish. Cressey and Collette (1970) found that specialized copepods (those possessing holdfasts or that are very host specific) are found mainly on larger needlefish, while generalized copepods (less host specific and not highly modified) are found most often on smaller needlefish individuals.

In the present study, copepods of the families Pseudocycnidae, Bomolochidae, and Shiinoidae parasitic on three species of *Scomberomorus* were considered (Table 2). We chose these copepod species for the study because they remain attached in preserved specimens. Pseudocycnids (Fig. 1h, i) are firmly attached to gill filaments; bomolochids (Fig.

FIGURE 1.—Examples of copepods parasitic on scombrids: a) *Unicolax anonymous*, female; b) *Holobomolochus asperatus*, female; c) *Shiinoa inauris*, female and males; d)*Caligus bonito*, female; e) *Elytrophora brachyptera*, female; f) *Gloiopotes hygomianus*, female; g) *Tuxophorus cybii*, female; h) *Pseudocycnus appendiculatus*, female; i) *Pseudocycnoides armatus*, female; j) *Brachiella thynni*, female and dwarf male attached.

TABLE 2.—Infestation densities of *Scomberomorus commerson*, *S. maculatus*, and *S. brasiliensis* for three copepod groups, *Pseudocycnoides*, Bomolochidae, and *Shiinoa*.

Range of hosts (mm FL)	No. of hosts	*Pseudocycnoides* No. of parasites	*Pseudocycnoides* % density	Bomolochidae No. of parasites	Bomolochidae % density	*Shiinoa* No. of parasites	*Shiinoa* % density
100-200	32	64	2.0	31	1.0	0	0
201-300	47	202	4.3	89	1.9	1	0.02
301-400	17	35	2.1	11	0.7	5	0.3
401+	16	34	2.1	8	0.5	25	1.6


a
b
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i

1a, b) are in the nasal sinuses and can only be collected by cutting open the nares; shiinoids (Fig. 1c) are firmly attached to lamellae of the nasal rosettes. Other copepods, such as caligids, are not as firmly attached, and many specimens are undoubtedly lost during handling and preservation of the hosts. The *Scomberomorus* species were represented by a reasonable number of specimens with adequate size-range coverage.

The apparent optimum size for infestation by the two species of pseudocycnids and the two bomolochids is between 201 and 300 mm FL (fork length). Infestations of *Pseudocycnoides armatus* and *P. buccata* seem to remain at the same levels (about 2 per fish) in groups with smaller and larger size individuals with about twice that infestation rate in the optimum size range. Infestations of the bomolochids *Unicolax ciliatus* (from *S. commerson*) and *Holobomolochus divaricatus* (from *S. maculatus* and *S. brasiliensis*) apparently decrease with increased host size after 300 mm FL; no *Scomberomorus* over 500 mm FL examined was parasitized by bomolochids. The two species of *Shiinoa* (*S. inauris* from *Scomberomorus brasiliensis* and *S. maculatus* and *Shiinoa occlusa* from *Scomberomorus commerson*), on the other hand, are not found on smaller fish, and the greatest infestation rate occurs on fish over 400 mm FL.

The change in infestation rate with host size in some of these parasite species may be due primarily to mechanical factors. In order for female pseudocycnids to remain attached to the gill filaments, the lateral lobes of the cephalon must partially encircle the filament. Until a prospective host reaches an optimum size, the filament may be too small for the adult copepod to secure itself. As the host fish grows, the filaments may become too large for the parasite to remain attached. Two very large *S. commerson* (1,115 and 1,150 mm FL) from New South Wales, Australia, were parasitized by several *P. armatus*. These copepods were considerably longer than average for the species (8.1 vs. 4.9 mm), which may account for their ability to infest a larger size host. *Shiinoa* attaches to its host by piercing a nasal lamella with its recurved second antennae which are opposed by an elongate and recurved rostrum. The combination results in a ring through the lamella, with the rest of the parasite hanging free. It may be necessary for the host to attain a minimum size (275 mm FL in our data) before the lamella is large enough to accommodate the parasite. (*Shiinoa* males attach to female copepods rather than the host.)

The presence of bomolochid species on 100-200 mm hosts cannot be as easily correlated with mechanical factors. Bomolochids are not firmly attached to their hosts. Those species considered here are found loose within the nasal sinuses and are capable of moving about possibly as scavengers more than as true parasites. Possibly the reduction in infestation of bomolochids in larger fish is associated with the increased presence of *Shiinoa* in the nasal sinuses of hosts larger than 300 mm.

ECOLOGICAL RELATIONSHIPS

To determine the influence of ecological relationships as opposed to phylogenetic host specificity of parasitic copepods found on scombrids, we examined the literature records of parasitic copepods from fishes with habits similar to those of scombrids (large size, open ocean, fast swimming, predatory, etc.). We compiled data for the following fish groups: Billfishes (Istiophoridae and Xiphiidae), sharks, *Alepisaurus, Lampris, Coryphaena,* several genera of Carangidae, *Rachycentron, Pomatomus,* and the gempylids, *Ruvettus* and *Thyrsites.*

We have tried to use discretion in evaluating the reliability of literature records. For example, Bere (1936) reported *Caligus bonito* from *Pomatomus saltatrix, Lutjanus griseus, Mugil cephalus, Oligoplites saurus, Scomberomorus maculatus,* and *S. cavalla.* She indicated in her report that the copepod material was identified by C. B. Wilson. The first author of this paper examined the specimens, deposited in the Smithsonian (USNM 79090), in order to verify the *Pomatomus* record. Bere presumably sent Wilson the material separated by host. Wilson apparently put together all specimens that he identified as a single species. The collection contains about 15 *Caligus* specimens with no host names and represents three species—*Caligus bonito, C. mutabilis,* and males of a third species. It is impossible to verify the occurrence of *C. bonito* on *Pomatomus,* and the record must be ignored. Another record (Capart 1959) of *C. pelamydis* from *Pomatomus* is questionable because Capart's illustration does not appear to be of *C. pelamydis.* Eliminating unreliable reports leaves *C. coryphaenae,* a relatively distinct species, as the only copepod common on scombrids which also occurs on many ecologically similar species. It has been recorded from the following nonscombrid genera: *Caranx, Elagatis, Coryphaena, Xiphias, Squalus, Seriola, Isurus, Echeneis,* and *Sphaeroides.* There have been a few reports of *Caligus productus* and *C. pelamydis* from nonscombrid hosts, but both of these copepods have been often confused with closely related species. Rohde (1980) reported *C. pelamydis* from 3 of 88 specimens of *Trachurus trachurus* and 22 of 122

specimens of *Scomber scombrus* with *C. pelamydis* from Helgoland (these copepod identifications were verified by G. Boxshall of the British Museum (Natural History)).

As the record shows, most species of copepods common on scombrid hosts are restricted to scombrids. *Caligus coryphaenae* apparently is the only common scombrid parasitic copepod whose host choice is influenced by ecological rather than phylogenetic factors.

There is evidence that in some cases the presence of a species of parasitic copepod on two or more host species which are not closely related may be the result of an association between the hosts. The parasitic copepod *Pumiliopes jonesi* (= *P. capitulatus*) is common on the eyes of scombrids of the tribe Scombrini (*Rastrelliger* and *Scomber*) and on the clupeids *Clupanodon punctatus* and *Herklotsichthys dis-plonotus*. Both groups are filter-feeding schooling fishes.

Another example is *Caligus macarovi* (= *C. fulvipurpureus*) common on the Pacific saury, *Cololabis saira* (Hotta 1962), but reported on *Auxis* as well by Gussev (1951). *Cololabis* feeds primarily on planktonic crustaceans with eggs and larvae of fishes forming secondary diet items (Hotta and Odate 1956; Taka et al. 1980). *Auxis* feeds on a wide variety of small fishes, cephalopods, and planktonic crustaceans (Uchida 1981). We are unaware of any records of *Auxis* preying on *Cololabis,* but sauries are common food items of billfishes.

HOST SPECIFICITY

Host specificity is concerned with the predilection of a parasite species for one or a few species of host or hosts. The comprehensive data on which this study is based demonstrate host specificity.

The occurrence of a species of parasite in a variety of host species does not necessarily imply a lack of host specificity. Careful analysis of collection data with reference to percent of host individuals parasitized by a particular parasite species will usually show that one or a few host species are heavily infested, some occasionally infested, and some rarely infested with the parasite species. Dogiel et al. (1961) referred to these groups as main, secondary, and accidental hosts. Holmes (1979) referred to the three groups as required hosts, suitable hosts, and unsuitable hosts. Holmes considered required and suitable hosts as those with which the parasite can develop to maturity (or to an infective stage in intermediate hosts), and unsuitable hosts as those with which the parasite cannot develop, but may be transported to a suitable or required host. Not enough is known of the life histories of most parasitic copepods to evaluate their state of "well being" on respective hosts. Collection data, however, indicate that species found on several host species vary in infestation rate in ways suggesting the host categories of Dogiel et al. and Holmes. In addition, unpublished data based on parasitic copepod collections by the first author from fishes of the Gulf of Mexico indicate the same categories of infestation.

The recently published revised data on the parasitic copepods of scombrids (Cressey and Cressey 1980) enable us to compare data based on a synoptic review of literature records of copepods parasitic on scombrids (Silas and Ummerkutty 1967) with a survey based solely on verified host and parasite identifications (Cressey and Cressey 1980). We have used the same format as that of Holmes and Price (1980) except we have considered specificity at the generic level rather than the family level (our data are based only on the Scombridae).

Comparisons of the two analyses (Tables 3, 4) point out the inadequacies of an unverified data base. Data based on the literature survey of Silas and Ummerkutty (1967) indicate that 60% of the copepod species parasitic on scombrids are specific to 1 genus, 5% to 2 genera, 11% to 3 or 4 genera, 2% to 5 or more genera, and 23% were also recorded from nonscombrid hosts. The data based on Cressey and Cressey (1980) and additional records in this paper indicate 54% specific to 1 genus, 18% to 2 genera, 9% to 3 or 4 genera, 9% to 5 or more genera, and only 9% are also found on nonscombrids. Clearly, the latter is a better

TABLE 3.—Host specificity of scombrid copepods based on data from Silas and Ummerkutty (1967).

	Number of host species infested				
No. of genera infested	1	2	3-4	5-8	Scombrid and nonscombrid
1	28	3	3		
2		2	1		
3-4			3	3	
5+				1	
Nonscombrids					13

TABLE 4.—Host specificity of scombrid copepods based on data from Cressey and Cressey (1980) and later.

	Number of host species infested					
No. of genera infested	1	2	3-4	5-8	9+	Scombrid and nonscombrid
1	11	6	2	4	1	
2		3	2	3		
3-4			2	1	1	
5+					4	
Nonscombrids						4

index to host specificity at the generic level than that based solely on literature. The Silas and Ummerkutty data indicate a higher specificity at the level of 1 genus of host; they also indicate a higher percentage of "generalists" (36% with 3 or more genera plus nonscombrids). Furthermore, the Cressey and Cressey and later data indicate a gradual transition from greater to lesser host specificity, whereas the data based on Silas and Ummerkutty do not.

Comparison of percent specificity (percent species with only one host, see Price 1980:123) shows a wide range of specificity per genus of scombrid copepod parasites (Table 5). Specificity to a genus of hosts seems more meaningful to us, so we have also calculated these figures. Six of the seven families that contain scombrid copepod parasites show relatively high percent specificity at the generic level (50-75%) while the Caligidae is distinctly lower (35%).

TABLE 5.—Percent specificity (percent species with only one host) and percent generic specificity (percent species with hosts only in one genus) in genera of copepod parasites of scombrid fishes.

Copepod genus	No. of species	Percent specificity	Percent generic specificity
Bomolochidae	(12)	(33)	(58)
Holobomolochus	3	33	100
Unicolax	5	20	75
Ceratocolax	1	0	0
Nothobomolochus	1	0	100
Orbitocolax	1	100	100
Pumiliopes	1	0	0
Shiinoidae	(2)	(0)	(50)
Shiinoa	2	0	50
Caligidae	(12)	(17)	(35)
Caligus	12	17	35
Eurypharidae	(4)	(75)	(75)
Elytrophora	2	50	50
Gloiopotes	1	100	100
Caligulus	1	100	100
Tuxophoridae	(3)	(67)	(67)
Tuxophorus	3	67	67
Pseudocycnidae	(4)	(25)	(75)
Pseudocycnus	1	0	0
Pseudocycnoides	3	33	100
Lerneopodidae	(4)	(25)	(75)
Brachiella	2	0	0
Clavellisa	1	100	100
Clavellopsis	1	100	100

Scombrinae

The subfamily Scombrinae is composed of two groups of two tribes. The more primitive mackerels (Scombrini) and Spanish mackerels (Scomberomorini) have a distinct notch in the hypural plate, lack any bony support for the median fleshy caudal peduncle keels, and do not have the penultimate vertebral centra greatly shortened.

Scombrini

The tribe Scombrini contains the two genera of mackerels, *Scomber* and *Rastrelliger*. Mackerels have small conical teeth and a large number of gill rakers. Characters differentiating the two genera have been given by Matsui (1967:table 4).

Copepod fauna: 9 species in 7 genera. Bomolochid copepods can be separated into two subgroups based on the presence of one or two major setae (in addition to the remainder of the normal complement) on each caudal ramus. The genera found on *Scomber* and *R. brachysoma* (*Pumilopes, Orbitacolax,* and *Nothobomolochus*) are members of the group with one major terminal seta. Although members of this same copepod subgroup are found on other fish families, none are found on other scombrids. This host specificity of some members of that subgroup to the Scombrini distinguishes the true mackerels from the other scombrid tribes. *Pumiliopes jonesi* is the only copepod found in both genera of Scombrini and nowhere else, occurring in the orbits of two species of each genus. The infestation rate in *Rastrelliger* was 13%, in *Scomber* only 2%.

Scomber Linnaeus

We follow most recent authors (Fraser-Brunner 1950; Collette and Gibbs 1963; Matsui 1967) in considering *Pneumatophorus* a synonym of *Scomber*. *Scomber* differs from *Rastrelliger* in a number of anatomical characters which have been summarized by Matsui (1967:table 4). Copepod fauna: 5 species in 4 genera. Only the lerneopodid *Clavellisa scombri* is restricted to *Scomber*, occurring on gills of *Scomber japonicus* and *S. australasicus* in our material. It was originally described from a host identified as *S. scombrus* from Trieste, but we failed to find it in 97 specimens of that species.

Matsui (1967) recognized three species of *Scomber*: *S. scombrus* Linnaeus in the North Atlantic and Mediterranean; *S. australasicus* Cuvier in the western Pacific from Japan to southern Australia east to the Hawaiian Islands, and across the eastern Pacific barrier to Socorro Island off Mexico; and *S. japonicus* Houttuyn, a worldwide antitropical species. All the copepod species known from the three species have been found on *S. japonicus*, of which we have examined about 500 specimens.

Rastrelliger Jordan and Starks

Matsui (1967:table 4) summarized the diagnostic characters of *Rastrelliger*. Copepod fauna: 5 species in 5 genera. *Pumiliopes jonesi* and two other bomo-

lochids were found in two species of *Rastrelliger, O. aculeatus* in the orbits, and *N. kanagurta* on the gills.

Matsui (1967) recognized three species of *Rastrelliger*: *R. faughni* Matsui from Taiwan, the Philippine Islands, Indonesia, and western India; *R. brachysoma* (Bleeker) in the same general area of the western Pacific as *R. faughni* but extending east to Fiji; and *R. kanagurta* (Cuvier) which is widespread throughout the Indo-West Pacific from Taiwan, the Philippines, Samoa, and Australia east throughout the Indian Ocean to Madagascar and the Red Sea. At least one individual has gone through the Suez Canal into the eastern Mediterranean Sea (Collette 1970). All but one of our copepod records are from *R. kanagurta* and *R. faughni.* Our only lernanthropid was a female *Lernanthropus kanagurta* from a Bornean specimen of *R. brachysoma.* This is probably not a usual scombrid parasite (Cressey and Cressey 1980:45).

Scomberomorini

This is the most speciose tribe in the family, containing 20 of the 48 species. Most of these (18 species) belong to *Scomberomorus*, the Spanish mackerels and seerfishes; the other 2 species belong to the monotypic genera *Acanthocybium* and *Grammatorcynus*. Copepod fauna: 25 species in 8 genera. The copepod genus most characteristic of the Scomberomorini is *Shiinoa*, found attached to the nasal rosettes of *Acathocybium*, *Grammatorcynus*, and 10 species of *Scomberomorus*. (*Shiinoa* was also found on one specimen of *Gymnosarda,* but we do not believe *Gymnosarda* is a usual host for this copepod.)

Scomberomorus Lacepède

Scomberomorus differs from the other two genera in the tribe, *Acanthocybium* and *Grammatorcynus,* by usually lacking a swim bladder. The genus is composed of 18 species (Collette and Russo 1980). There is one species in the Gulf of Guinea and Mediterranean Sea—*S. tritor* (Cuvier); four in the western Atlantic—*cavalla* (Cuvier), *regalis* (Bloch), *maculatus* (Mitchill), and *brasiliensis* Collette, Russo, and Zavalla-Camin; and two in the eastern Pacific—*concolor* Lockington and *sierra* Jordan and Starks. The remaining 11 species are in the Indo-West Pacific: *guttatus* (Bloch and Schneider); *koreanus* (Kishinouye); *lineolatus* (Cuvier); *plurilineatus* Fourmanoir; *commerson* (Lacepède); *sinesis* (Lacepède); *semifasciatus* (Macleay); *queenslandicus* Munro; *niphonius* (Cuvier); *munroi* Collette and Russo; and *multiradiatus* Munro. Copepod fauna: 23 species in 7 genera. In addition to two species of *Shiinoa, Scomberomorus* is commonly parasitized by the pseudocycnid genus *Pseudocycnoides* (*buccata, armatus, scomberomori*), the bomolochid genera *Holobomolochus* (*divaricatus, asperatus, nudiusculus*), and *Unicolax* (*U. ciliatus*), and several species of *Caligus* (especially *C. biseriodentatus, C. infestans,* and *C. cybii* in the Indo-West Pacific, *C. mutabilis* and *C. productus* in the western Atlantic, and *C. omissus* in the eastern Pacific). The speciose nature of *Scomberomorus* and its copepod parasites requires further discussion, by regions.

ORIGINS AND EVOLUTION OF AMERICAN *SCOMBEROMORUS*.—Six species of *Scomberomorus* occur in American waters. (Figs. 2, 3). Two of these, *S. sierra* and *S. concolor*, are restricted to the eastern Pacific from about lat. 10° to 40°N. *Scomberomorus concolor* presently occurs only in the Gulf of California. The four Atlantic species are *S. cavalla*, found from about lat. 30°S to 45°N; *S. brasiliensis*, a southern coastal species (Belize to southern Brazil); *S. maculatus,* a northern coastal species (Yucatan to Massachusetts); and *S. regalis*, a largely insular species (most abundant in the Bahamas and West Indies).

The six species of American *Scomberomorus* are parasitized as a group by the following species of copepods: *H. asperatus* (*S. cavalla*), *H. nudiusculus* (*S. sierra, S. concolor*), *H. divaricatus* (*S. brasiliensis, S. maculatus, S. regalis*), *Shiinoa inauris* (*Scomberomorus maculatus, S. brasiliensis, S. regalis*), *C. mutabilis* (*S. cavalla, S. brasiliensis, S. maculatus*), *C. omissus* (*S. sierra, S. concolor*), and *P. buccata* (all species mentioned in this paragraph).

To use parasitic copepods as indicators of host phylogeny we determined the pleisiomorphy-apomorphy of certain taxonomic characters. This is possible within a closely related group of parasites based on reduction and modification of characters for parasitism. It seems reasonable to assume that, as species of a parasite group evolve, the later (more recent) species are more specialized or reduced than the older species. If we assume that hosts and parasites evolve together, the information on the evolution of one group should provide evolutionary information about the other group. Four genera of copepods parasitic on *Scomberomorus* lend themselves to analysis and are discussed below.

Three species of *Holobomolochus* parasitic on American species of *Scomberomorus* and a fourth species from *Caranx hippos* form a subgroup of the genus (see Cressey and Cressey 1980:8). In these species,

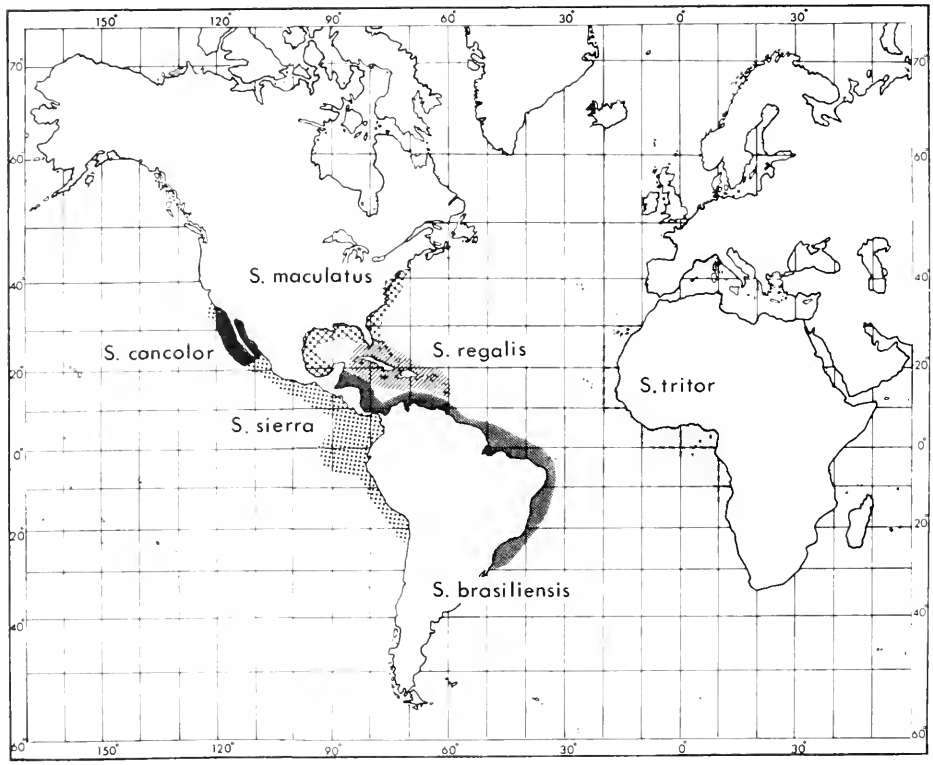

FIGURE 2.—Distribution of Atlantic and eastern Pacific species of *Scomberomorus*.

the last exopod segments of legs 2-4 bear a number of plumose setae, heavily sclerotized spines, and shorter nonplumose setae with armature intermediate to that on spines and setae. Long plumose setae (adaptations for free swimming) are primitive, whereas heavily sclerotized spines (adaptations for attachment) are advanced characters. The three *Holobomolochus* from *Scomberomorus* show a transition in the numbers of each of these character states. *Holobomolochus asperatus* (parasite of *S. cavalla*) bears 18 long plumose setae and 7 sclerotized spines on the last exopod segments of legs 2-4. The same appendages of *H. nudiusculus* (on eastern Pacific *Scomberomorus*) bear 16 plumose setae, 2 intermediate setae/spines, and 7 spines. The same appendages of *H. divaricatus* (on all western Atlantic *Scomberomorus* except *cavalla*) bear 14 setae, 4 intermediate setae/spines, and 7 spines. This transition in decreased numbers of long plumose setae and increase in intermediate setae/spines within these three parasite species suggests *H. asperatus* to be the most primitive, *H. nudiusculus* intermediate, and *H. divaricatus* to be most advanced. If the hosts reflect the phylogeny of the parasites, then this suggests that *S. cavalla* is the most primitive; the two eastern Pacific species—*S. sierra* and *S. concolor*—are intermediate; and the three western Atlantic species—*S. regalis, S. maculatus,* and *S. brasiliensis*—are the most advanced of the American species of *Scomberomorus*.

Holobomolochus has 23 currently recognized species in the western Atlantic and eastern Pacific and 1 species from the eastern Atlantic (a species from India is not a *Holobomolochus*, as reported by Pillai 1973). *Unicolax ciliatus*, a species of another bomolochid genus, is found on 9 species of *Scomberomorus* in the Indo-West Pacific and on *S. tritor* in the eastern Atlantic. Four remaining species of *Unicolax,* including Atlantic and eastern Pacific species, are found only on non-*Scomberomorus* scombrids. This parasite distribution and host affiliation suggest that *Holobomolochus* was already well established on American *Scomberomorus* before the appearance of *Unicolax* in this area. Based on the evidence that *U. ciliatus* has not undergone further speciation on 10 *Scomberomorus* species despite the geographic isolation of one of those species (*S. tritor* from the eastern Atlantic) and the presence of *Holobomolochus* on the American *Scomberomorus,* it can be assumed that *Holobomolochus* is older than *Unicolax.*

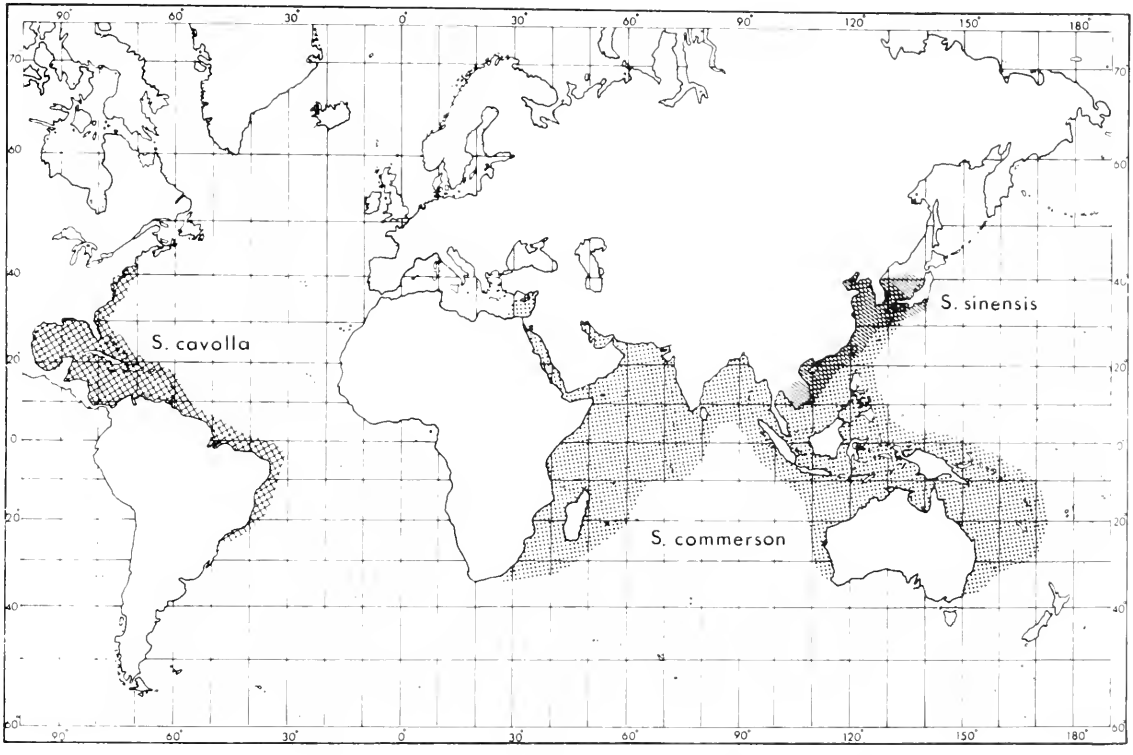

FIGURE 3.—Distribution of *Scomberomorus cavalla, S. commerson,* and *S. sinensis.*

Unicolax appears to be more advanced than *Holobomolochus* by possessing a heavily sclerotized modified seta on the first antenna and having 1 seta rather than 2 setae on the mid-endopod segment of leg 3.

The highly modified copepod genus *Shiinoa* (Shiinoidae) is comprised of three species: *Shiinoa occlusa* from Indo-West Pacific *Acanthocybium, Grammatorcynus, Scomberomorus,* and *Gymnosarda* and the eastern Atlantic *S. tritor*; *Shiinoa inauris* from western Atlantic *Scomberomorus* (except *S. cavalla*); and *Shiinoa elagatis* from Indo-Pacific *Elagatis* (Carangidae). The first author is describing a fourth species from the Indian Ocean jack, *Caranx malabaricus.* Of the three described species *S. elagatis* with 3-segmented rami of legs 1 and 2 is the most primitive. *Shiinoa occlusa* from Indo-West Pacific scombrids is intermediate with 3-segmented rami of legs 2 and 3 but with fewer spines and setae and reduced body segmentation compared with *S. elagatis. Shiinoa inauris* from three of the four western Atlantic *Scomberomorus* (all except *S. cavalla*) is most advanced with only 2 segments in the exopods of legs 2 and 3 of the females and 2 segments in both rami of legs 2 and 3 of the males.

Infestations by the western Atlantic *S. inauris* and its speciation probably did not occur until after the last geologic separation of the eastern Pacific. On scombrids, *Shiinoa* has differentiated into only two species. Although this genus is recorded from 10 species of *Scomberomorus,* the highest rates of infestation among scombrid hosts are in *Grammatorcynus* and *Gymnosarda. Shiinoa occlusa,* from Indo-West Pacific scombrids, is more primitive than the western Atlantic *S. inauris,* indicating the latter's probable derivation from Indo-Pacific stock.

The presence of the highly specialized siphonostome copepod parasite, *P. buccata,* on all species of American *Scomberomorus* with relatively high infestation rates (30-63%) indicates that this parasite was present before the separation of Atlantic and eastern Pacific Oceans, but, in spite of the present isolation, the two populations have not differentiated (unlike the three *Holobomolochus* species).

From this it appears that dispersal and some speciation of American *Scomberomorus* occurred prior to their being parasitized by bomolochid and shiinoid copepods.

The evidence derived from an analysis of the copepods parasitic on the six American *Scomberomorus* species suggests the following sequence of events:

1. During the period when the eastern Pacific and Atlantic Oceans were continuous, two species of *Scomberomorus* were probably present, an ancestral *S. cavalla* and an ancestral *S. sierra.* Both of these were infested with species of *Holobomolochus* and *P. buccata.*

2. As the land mass of Central America separated the Atlantic from the Pacific, the two ancestral forms were divided into four populations. The Atlantic population of *S. cavalla* persisted while the Pacific population disappeared. The Pacific *S. sierra* population persisted and gave rise to *S. concolor,* while the Atlantic population subsequently divided into a southern species, *S. brasiliensis,* and a northern species, *S. maculatus.* The derivation of *S. regalis* was also probably from a *sierra* ancestor. The origin of pre-*cavalla* and pre-*sierra* populations was probably derived from the Indo-Pacific *S. commerson* line and the *S. tritor* line, respectively (Fig. 4).

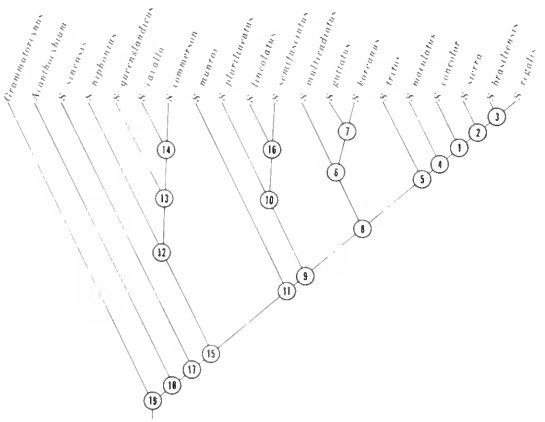

FIGURE 4.—Tentative cladogram of the Scomberomorini. Numbers refer to morphological characters from Collette and Russo (text footnote 3).

3. The population of ancestral *S. sierra* in the Atlantic differentiated to produce ultimately the northern coastal species *S. maculatus* and the southern coastal species *S. brasiliensis* and insular *S. regalis.*

4. Some species of copepods differentiated as either new host species were formed, or populations of related hosts were isolated.

5. An additional genus (*Shiinoa*) of parasitic copepod became established on three of the Atlantic species of *Scomberomorus* (*brasiliensis*, *maculatus*, and *regalis*) after the formation of a land barrier separating the eastern Pacific from the Atlantic. The absence of *Shiinoa* on *Scomberomorus cavalla* may indicate that *S. cavalla,* derived from the *S. commerson* line, may have occupied the Atlantic prior to the parasitization of scombrids by *Shiinoa.* The later infestations of *Shiinoa* in the western Atlantic may have been derived from *Scomberomorus tritor* and consequently occur only on the three western Atlantic species of *Scomberomorus* derived from the *tritor* line.

Based on the anatomy of *Scomberomorus,* the American species belong to different species groups. *Scomberomorus cavalla* is the western Atlantic replacement for *S. commerson,* which is widespread in the Indo-West Pacific. The other five American species, plus *S. tritor* from the eastern Atlantic, form the *S. regalis* species group (Fig. 4), defined by the presence of nasal denticles (Collette and Russo manuscr. in prep.[3]). These five American species share a unique specialization of the fourth left epibranchial artery (Collette and Russo footnote 3), which indicates that these species were derived from an *S. tritor* ancestor. This pattern of relationships is fully compatible with that derived from the copepod data.

INDO-WEST PACIFIC *SCOMBEROMORUS.*—There are 11 recognized species of Indo-West Pacific *Scomberomorus* (Collette and Russo 1980; Figs. 3, 5, 6). Four genera of parasitic copepods are common on Indo-West Pacific species of *Scomberomorus* (Table 6): *Unicolax*, parasitic in the nasal sinuses; *Shiinoa*, attached to the nasal lamellae; *Pseudocycnoides*, at-

[3]Bruce C. Collette and Joseph L. Russo. Systematics and morphology of the Spanish mackerels (*Scomberomorus*). Manuscr. in prep., 400 p. Systematics Laboratory, National Marine Fisheries Service, NOAA, Smithsonian Institution, Washington, DC 20560.

TABLE 6.—Infestation of Indo-West Pacific species of *Scomberomorus* with parasitic copepods. Host species arranged from most infested (most primitive?) to least infested (most specialized?). The eastern Atlantic *S. tritor* is included for comparison.

Species	*n*	Total copepod species	Total genera	Common genera[1]
commerson	130	9	6	4
semifasciatus	26	5	4	4
queenslandicus	39	5	4	4
guttatus	58	4	4	4
plurilineatus	14	5	5	4
niphonius	19	4	4	4
munroi	19	3	3	3
koreanus	6	4	2	2
lineolatus	14	3	3	3
sinensis	10	3	2	1
multiradiatus	29	2	2	2
tritor	21	4	3	3

[1] *Unicolax, Pseudocycnoides, Shiinoa, Caligus.*

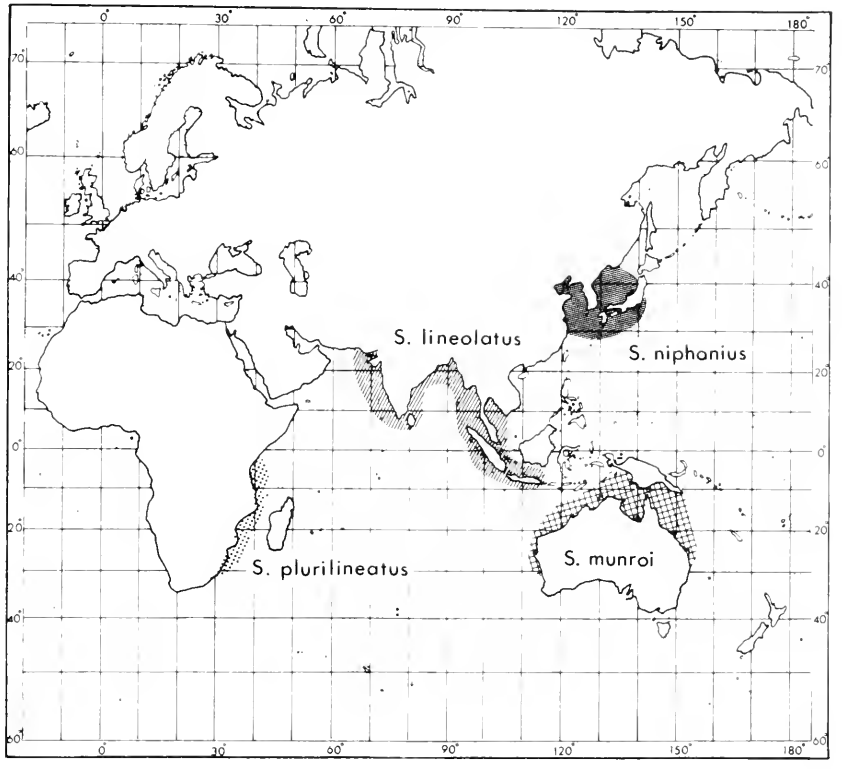

FIGURE 5.—Distribution of *Scomberomorus lineolatus*, *S. plurilineatus*, *S. munroi*, and *S. niphonius*.

tached to the gill filaments; and several species of *Caligus*, found in the gill area, mouth, and on the body surface.

The generally accepted theory that the more primitive members of a host group usually harbor more species of parasites than those that evolved later indicates the following. *Scomberomorus commerson* is the most widespread species occurring from the eastern Mediterranean (recent Suez migrant) eastward throughout the Indian Ocean into the western Pacific Ocean (see Figure 3). Nine species of copepods, from four genera cited above plus two additional genera (*Tuxophorus* and *Brachiella*), have been collected from *S. commerson*. No other species of *Scomberomorus* harbors more than seven species and six genera of copepods. Thus, the parasite data indicate *S. commerson* to be the most primitive member of the Indo-West Pacific *Scomberomorus*. If the converse is true, the data suggest that *S. multiradiatus* with only two copepod species is the most advanced (specialized).

The data further suggest that the origin of *S. commerson* was in the Indo-Australian Archipelago, because all nine species of copepods are reported from specimens in that area with a decrease in the number of parasite species to the north and west (Fig. 7).

Scomberomorus niphonius is unusual among the Indo-West Pacific members of the genus in its copepod parasites. Most Indo-West Pacific *Scomberomorus* are parasitized by *P. armatus*. *Scomberomorus niphonius* is commonly parasitized by a closely related species, *P. scomberomori*, which has more primitive characters than *P. armatus*, and is apparently specific to *S. niphonius*. This suggests that *S. niphonius* may be primitive compared with the other Indo-West Pacific species. *Scomberomorus niphonius* might also be considered primitive based on one of its morphological characters (Fig. 4). It is the only species in the genus to have a straight intestine. Most other species of *Scomberomorus* have two bends (and three sections) to the intestine. One species, *S. koreanus*, has three bends (and five sections), presumably a specialized condition.

Two of the 19 specimens of *S. niphonius* were parasitized by *C. pelamydis* (the only *Caligus* so far reported from it) which is found on several other scombrids, most commonly on species of *Sarda*. *Caligus cybii*, closely related to *C. pelamydis*, has been reported from six Indo-West Pacific species of

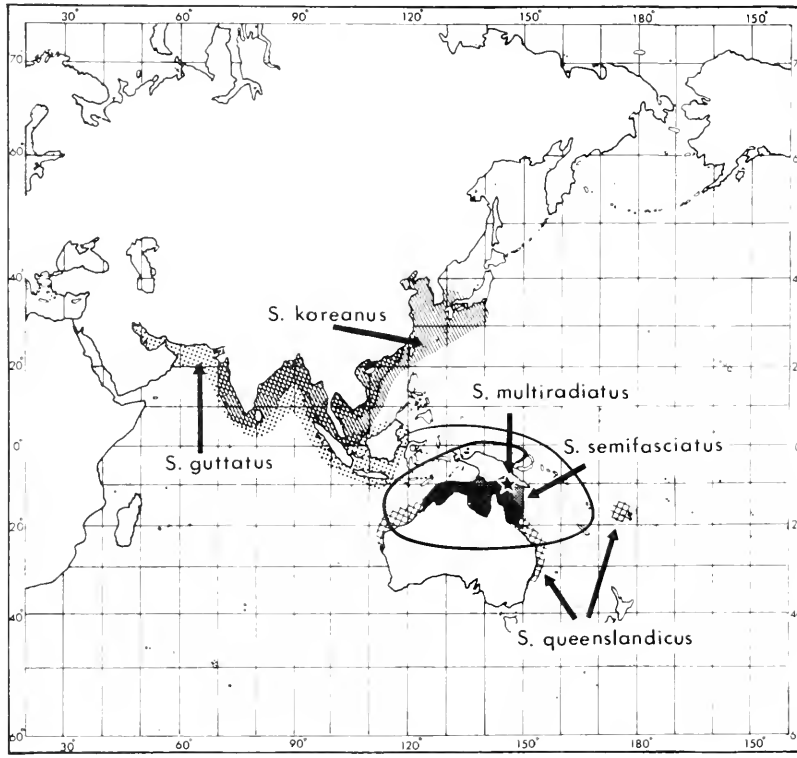

FIGURE 6.—Distribution of *Scomberomorus guttatus*, *S. koreanus*, *S. multiradiatus*, *S. semifasciatus*, and *S. queenslandicus*.

Scomberomorus, including species whose ranges overlap those of *S. niphonius*, *S. koreanus*, and *S. sinensis*. The first author cannot ascertain with certainty which of these two copepods, based on their morphology, may be the more primitive, but the reduced specificity of *C. pelamydis* and the apparent restriction of *C. cybii* to Indo-West Pacific *Scomberomorus* suggest *C. pelamydis* to be more primitive. If true, this supports the indication of the primitive nature of *S. niphonius* provided by the two species of *Pseudocycnoides*.

A single specimen of *C. pelamydis* has also been collected by us from *S. sinensis*. This might be used to argue that *S. commerson* and *S. niphonius* arose from a common ancestor, with *S. niphonius* now restricted to the northwest Pacific (colder water) and *S. commerson*, together with other species, occupying the more temperate and tropical waters. *Scomberomorus commerson* and *S. sinensis* both have prominent dips in the lateral line, but the dip is under the second dorsal finlets in the former species and under the first dorsal fin in the latter species; this similarity may be due to convergence rather than close relationships. These three species (*S. commerson*, *S. niphonius*, and *S. sinesis*), *S. cavalla*, and *S. queenslandicus* all appear to be relatively primitive (Fig. 4).

Grammatorcynus Gill

Although included in the Scomberomorini by recent works such as Collette (1979), the exact systematic position of this monotypic genus is in doubt (Collette and Russo 1979), because it also shares some characters with the Scombrini. It has the same number of vertebrae as do the Scombrini (31), usually 13 precaudal plus 18 caudal. Its possession of an extra, ventral lateral line is unique in the family. The double-lined mackeral, *G. bicarinatus* (Quoy and Gaimard) is known from much of the tropical Indo-West Pacific, particularly near coral reefs from the Marshalls and Carolines, Philippine Islands, Australia, and the East Indies east to the Red Sea. Copepod fauna: 5 species in 2 genera, *Shiinoa* and *Caligus*. Only one species of *Caligus*, *C. asymmetricus*, is at all common on *Grammatorcynus* (14.9%). This copepod has been found on nine scombrids in the Indo-West Pacific and is perhaps more characteristic of the Sardini (*Cybiosarda elegans*, *Sarda*

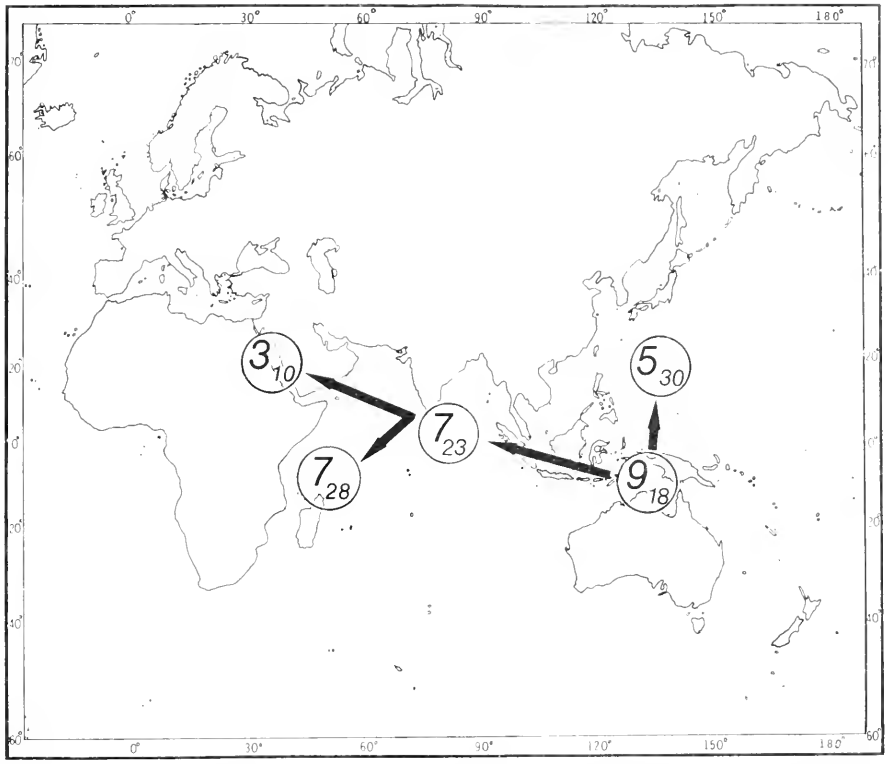

FIGURE 7.—Numbers of copepod species on *Scomberomorus commerson* in different areas of its distribution (large numbers represent number of copepod species; small numbers represent number of hosts examined).

orientalis, S. australis) with infestations of 8-12%.

Acanthocybium Gill

This monotypic genus appears to be a specialized offshoot of *Scomberomorus* and does not merit placement in its own subfamily or tribe as has been advocated by some previous authors (e.g., Starks 1910). It is closest to the *Cybium* group of *Scomberomorus* (*S. cavalla* and *S. commerson*), according to Conrad (1938) and Mago Leccia (1958). The wahoo, *A. solandri* (Cuvier), is a large species (reaching over 1,500 mm SL) and has a well-developed swim bladder. It is a high-seas epipelagic species found round the world in tropical and subtropical waters. Copepod fauna: 6 species in 5 genera. *Acanthocybium* is similar to the other Scomberomorini in being parasitized by *Shiinoa* and *Tuxophorus,* but the rate of infestation is very low. The most common two copepods are the euryphorid *Gloiopotes hygomianus* (infestation rate of 42% of our 64 specimens, 54% of the 100 fish from the Line Islands examined by Iverson and Yoshida 1957) and the lerneopodid *Brachiella thynni* (61% of our specimens, 98% of those examined by Iverson and Yoshida). The other four species of *Gloiopotes* are parasites of billfishes (Istiophoridae).

Some workers in the past (e.g., Lütken 1880) and the present (G. David Johnson, pers. commun.[4]) believe that *Acanthocybium* is closely related to the billfishes. We feel that the parasite data are best interpreted as evidence of ecological similarity between the groups (fast swimming, high-seas species) rather than as evidence of phylogenetic relationships. *Brachiella thynni* was also found on three species of *Thunnus* (*T. obesus, T. albacares,* and *T. thynnus*) and two of *Scomberomorus* (*S. regalis* and *S. plurilineatus*). This species has been reported from a variety of hosts, usually attached in the axil of the pectoral fin. A second species of *Brachiella* is known only from two western Pacific species of *Scomberomorus*. There seems little ecological or phylogenetic information that can be drawn from parasitism by *Brachiella.*

Parasitic copepods of the genera *Tuxophorus* and *Gloiopotes* suggest relationships between *Scomberomorus* and *Acanthocybium* of the Scomberomorini

[4]G. David Johnson, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412.

and the Istiophoridae (Table 7). Three species of the copepod genus *Tuxophorus* are parasitic on the body surface of species of *Scomberomorus* and *Acanthocybium* in the Atlantic and Indo-West Pacific Oceans. When the paper by Cressey and Cressey (1980) went to press, these three species, *T. cybii, T. cervicornis,* and *T. collettei,* were retained in *Tuxophorus* because they conformed to the diagnosis of that genus. Subsequent considerations by the first author lead to the conclusion that they are not members of *Tuxophorus* but represent a new genus closely related to *Gloiopotes* or are possibly members of *Gloiopotes.* The presence of frontal lunules on these three species is the only character separating them from *Gloiopotes,* as it is presently defined. An earlier work on the parasitic copepods of lizardfishes (Cressey and Cressey 1979) gave an example of a caligid genus (*Abasia*), which showed a transition series of six species with a gradual reduction in the frontal lunule from well developed to absent. This indicates the possibility that the presence or absence of the frontal lunule is not always a valid generic character. The genus *Tuxophorus* was described by Wilson (1908) for *T. caligodes,* based on material collected from Atlantic *Rachycentron canadus* and *Echeneis naucrates.* The second species, *T. wilsoni,* was described by Kirtisinghe (1937) from the carangid, *Chorinemus,* from Sri Lanka.

Four of the five species of *Gloiopotes* are found on the body surface of various species of istiophorids; the fifth, *G. hygomianus,* is restricted to *A. solandri.* The occurrence of *Gloiopotes* on *Acanthocybium* and istiophorids might be used as evidence to support relationships between the two groups. The question is: "Are these relationships ecological or phylogenetic?" The morphological similarities between *Acanthocybium* and the Istiophoridae seem best explained as convergences; those between *Acanthocybium* and *Scomberomorus* indicate that *Acanthocybium* is the specialized sister-group of *Scomberomorus* (Fig. 4). Thus, we argue that the presence of *Gloiopotes* on *Acanthocybium* and istiophorids is an ecological relationship, but that the occurrence of three species of *Tuxophorus* on *Acanthocybium* and *Scomberomorus* reflects shared phylogeny. Support for this argument could come from the presence of *Gloiopotes* on some open ocean, fast-swimming host but we have no such data. The explanation for the occurrence of species of *Gloiopotes* only on *Acanthocybium* and istiophorids must remain uncertain for the present.

TABLE 7.—Host-parasite records for *Tuxophorus cybii, T. collettei, T. cervicornis,* and *Gloiopotes* spp.

Host-parasite	Area
Tuxophorus cybii	
Acanthocybium solandri	Indian Ocean
Tuxophorus cervicornis	
Scomberomorus commerson	Indo-Pacific
Tuxophorus collettei	
Scomberomorus regalis	Atlantic
Gloiopotes hygomianus	
Acanthocybium solandri	Cosmopolitan
Gloiopotes americanus	
Istiophorus americanus	Atlantic
Gloiopotes ornatus	
Tetrapturus albidus	Atlantic
Makaira nigricans	Atlantic
Gloiopotes huttoni	
Tetrapterus audax	Indo-Pacific
Makaira indicus	Indo-Pacific
Istiophorus platypterus	Indo-Pacific
Gloiopotes watsoni	
Tetrapterus audax	Indian Ocean
Makaira nigricans	Indo-Pacific
Makaira indicus	Indian Ocean
Istiophorus platypterus	Indo-Pacific

Sardini

The bonitos consist of eight species placed in five genera (Collette and Chao 1975). Except for *Allothunnus*, the Sardini differ from the Thunnini in lacking prominent prootic pits on the ventral surface of the cranium. Collette and Chao (1975:table 14) summarized the characters distinguishing the five genera of Sardini. Copepod fauna: 11 species in 5 genera. *Caligus bonito* has been found on all. *Unicolax collateralis* was found in *Orcynopsis*, Cybiosarda, and two species of *Sarda.*

Orcynopsis Gill

The monotypic *Orcynopsis* and *Cybiosarda* show several characters that distinguish them from *Sarda* and *Gymnosarda* (Collette and Chao 1975). *Orcynopsis* is a short-bodied and short-headed bonito. *Orcynopsis unicolor* (Geoffrey St. Hilaire) is an eastern Atlantic endemic whose range is centered in the Mediterranean Sea but extends south to Dakar, Senegal, and north to Oslo, Norway (Collette and Chao 1975: fig. 69). Copepod fauna: 1 specimen of *U. collateralis* and 1 specimen of *Caligus bonito.*

Cybiosarda Whitley

As noted above, the monotypic genera *Cybiosarda* and *Orcynopsis* share a suite of characters that differentiate them from *Sarda* and *Gymnosarda* (Collette and Chao 1975). *Cybiosarda elegans* (Whitley) is virtually an Australian endemic; is found along the northern three-quarters of the continent from Perth, Western Australia, to Sydney, New South Wales (Collette and Chao 1975:fig. 69); and occurs along the south coast of Papua New Guinea (Collette

1979). Copepod fauna: 3 species in 2 genera, the same species as in *Orcynopsis* plus *Caligus asymmetricus*, which is found on various species in three of the four tribes.

Sarda Cuvier

The four species of *Sarda* all have several dorsal stripes, ranging from horizontal to oblique in orientation. *Sarda* and *Gymnosarda* share a number of characters that distinguish them from *Orcynopsis* and *Cybiosarda* (Collette and Chao 1975).

Collette and Chao (1975) recognized four species of *Sarda* (Fig. 8): *Sarda australis* (Macleay) is restricted to the east coast of Australia, Norfolk Island, and New Zealand; *S. chiliensis* inhabits the eastern Pacific where it is divisible into two subspecies, *S. c. chiliensis* (Cuvier) from Peru and Chile and *S. c. lineolata* (Girard) from Alaska to Baja California; *S. orientalis* (Temminck and Schlegel) is widespread in the Indo-Pacific from South Africa and the Red Sea east to Japan, China, the Philippine Islands, the Hawaiian Islands, and across into the eastern Pacific from Baja California to Peru; and *S. sarda* (Bloch) is found throughout tropical and temperate waters of the Atlantic Ocean including the Gulf of Mexico and the Mediterranean and Black Seas (Collette and Chao 1975; Fig. 8).

A summary of the 26 most important characters used in distinguishing the species of *Sarda* was presented by Collette and Chao (1975:table 17).

Copepod fauna: 9 species in 3 genera. In addition to the two widespread bonito parasites, *U. collateralis* and *Caligus bonito,* three other copepods are common on species of *Sarda*; *Ceratocolax euthynni*, *Caligus pelamydis,* and *C. asymmetricus.* The presence of five common copepods on species of *Sarda* presents an opportunity for further analysis.

Over 200 specimens of the four species of *Sarda* were examined with an overall infestation rate of 75% (156 of 206 specimens examined). It is thought that as a host species or related group of host species disperses from its place of origin it loses parasites in the process (see discussion of *Scomberomorus commerson* above). When one examines the infestation rates of the individual *Sarda* species, first with all of its copepod parasites and secondly each species with its individual parasite species, the change in infestation rates from one *Sarda* species to another may reflect the speciation of *Sarda* species away from the center of origin of the genus.

An analysis of these data (Table 8) indicates an origin of the genus in Australasia (*S. australis, S. orientalis,* or an ancestor of theirs) with the eastern Pacific *S. chiliensis* derived from *S. australis* and the Atlantic *S. sarda* from *S. chiliensis.* The infestation rates of *C. bonito, C. asymmetricus,* and *U. collateralis* suggest that the copepod parasites of *S. sarda* could have been derived from those of *S. orientalis.* The occurrence of *C. pelamydis* on *S. sarda,* however, and its absence on *S. orientalis* reinforce the idea that *S. sarda* may have been derived, along with its parasites, from *S. australis* or *S. chiliensis* but not from *S. orientalis. Sarda sarda* has the lowest overall infestation rate (68%) and has lost one *Caligus* species (*asymmetricus*) and replaced *U. collateralis* with the Atlantic scombrid bomolochid copepod *Ceratocolax euthynni.*

The overall infestation rates of the four species of *Sarda* are *S. australis*, 90%; *S. orientalis*, 82%; *S. chiliensis*, 76%; and *S. sarda*, 68%. These data support the proposal that species radiation progressed from Indo-West Pacific to eastern Pacific to Atlantic within the genus.

The 26 morphological characters used by Collette and Chao (1975:table 14) to distinguish the species of *Sarda* tend to support the evolutionary hypothesis deduced from the copepod data. *Sarda sarda* is the most specialized of the four species in its increased numbers of vertebrae and other correlated meristic characters. *Sarda australis* appears most primitive in such characters as number of dorsal and anal finlets. It shares some primitive characters, such as the occasional presence of vomerine teeth, with *S. sarda.* If other similarities between these two species (location of first closed haemal arch, length of haemal pre- and postzygapophyses, shape of vertical wing of pelvic girdle, etc.) can also be considered primitive, then *S. chiliensis* and *S. orientalis* are in a relatively intermediate evolutionary position. In some cases,

TABLE 8.—Infestation rates by four species of copepods on the four species of *Sarda* (arrows indicate direction of decrease).

Copepod species	*Sarda* species							
	orientalis		*australis*		*chiliensis*		*sarda*	
Caligus bonito	36.4	←	59.1	→	55.6	→	31.1	
Caligus pelamydis	—	←	50.0	→	8.9	→	7.5	
Caligus asymmetricus	12.1	→	9.1	→	—	→	—	
Unicolax collateralis	36.4	→	9.1		—		—	

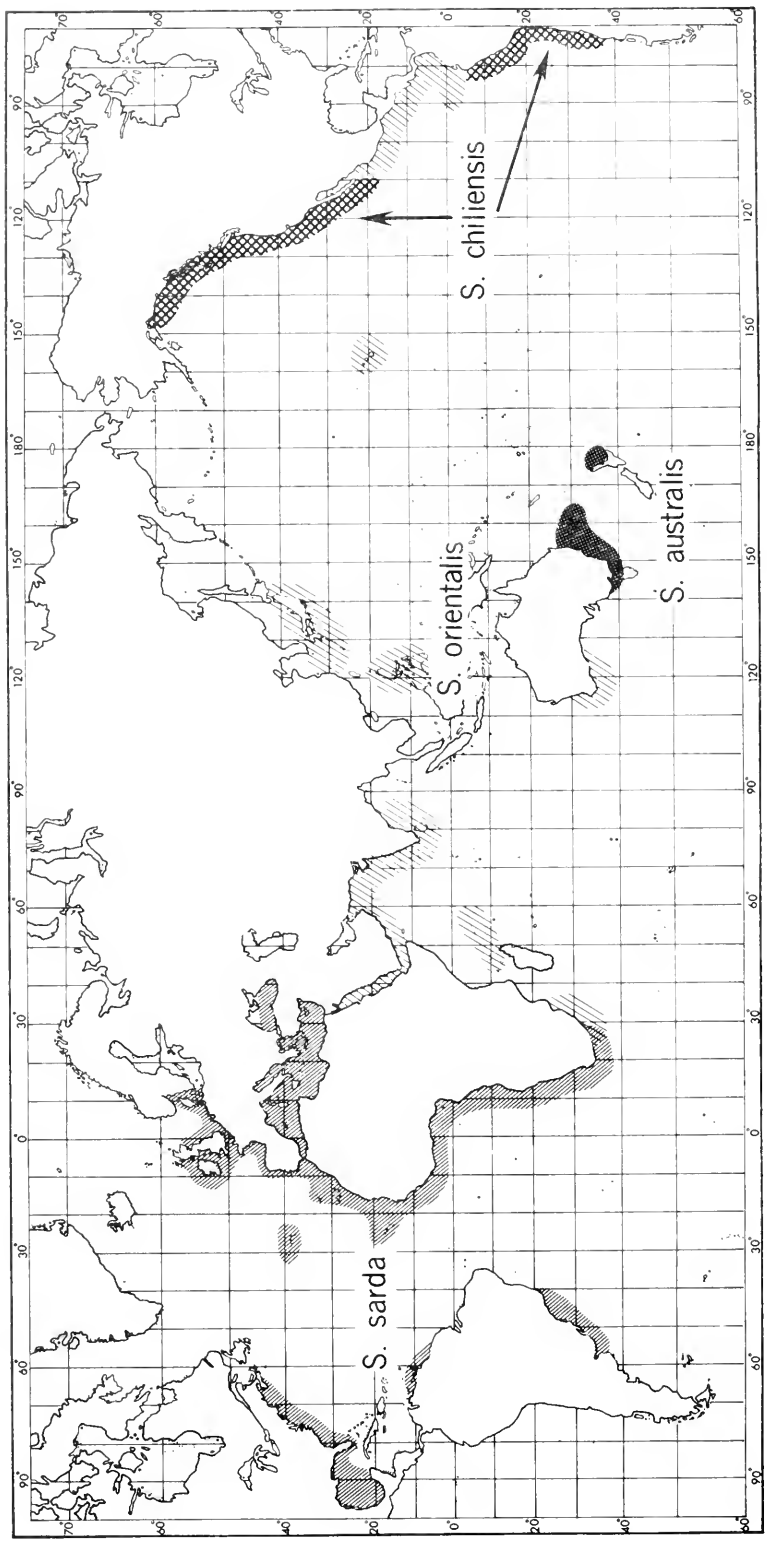

FIGURE 8.—Distribution of the four species of *Sarda*.

such as complete loss of vomerine teeth, these species have diverged from the primitive condition.

Gymnosarda Gill

The monotypic genus *Gymnosarda* differs from other bonitos in a series of characters (Collette and Chao 1975). The dogtooth tuna, *G. unicolor* (Rüppell), is a coral reef species of the tropical Indo-West Pacific (Collette and Chao 1975:fig. 69). Its large eyes and teeth, numerous olfactory lamellae, and well-developed swim bladder indicate that it is more of a lurking predator on larger fishes than are the other bonitos. Copepod fauna: 3 species in 2 genera. Each copepod species was found only once, so it is difficult to draw any conclusions from the data. One species, *C. bonito,* is characteristic of the Sardini. *Caligus productus* is known from a wide variety of hosts, both scombrid (14 species from all tribes except Scombrini) and nonscombrid. *Shiinoa occlusa* is otherwise restricted to Indo-West Pacific species of Scomberomorini.

Allothunnus Serventy

The systematic position of this monotypic genus is still in some doubt. It was included in the Sardini by Collette and Chao (1975) because it lacked the specializations considered diagnostic of the Thunnini and showed similarities to the bonitos in characters such as the otoliths. It differs from all other scombrids in having the prootic bones remarkably extended laterally as wings that frame the posterior margin of the orbit and in having a very large number of gill rakers. *Allothunnus* resembles the Thunnini and differs from other Sardini in having a prootic pit in the ventral surface of the skull. The pineal window is large and oval in *Allothunnus,* elongate and slit-shaped in the Thunnini and all other Sardini. The liver has three subequal lobes as in the bluefin tuna species group of *Thunnus*. *Allothunnus fallai* Serventy is found around the world in the Southern Ocean south of lat. 35°S (Collette and Chao 1975:fig. 69) with one highly unusual record from the Los Angeles-Long Beach harbor complex (Fitch and Craig 1964).

Copepod fauna: *Elytrophora brachyptera* was present in all 5 Pacific specimens that we examined and was also reported by Webb (1976) in 45 of 47 specimens that they examined from Tasmania. This copepod is otherwise known only from the tuna genus *Thunnus* where we have found it in six of seven species (all but *T. tonggol*). These copepod data support a closer phylogenetic relationship between *Allothunnus* and *Thunnus* than was indicated by Collette and Chao (1975). Two specimens from off the tip of South Africa, however, carried the copepod *C. bonito,* a common parasite of Sardini species. Infestation by *C. bonito* can be viewed as primitive in *Allothunnus;* infestation by *Elytrophora* advanced. Sharing specialized morphological characters and copepod parasites suggests that serious consideration must be given to transferring *Allothunnus* from the Sardini to a position as the most primitive member of the Thunnini. This issue will be considered further by Collette.

Thunnini

The four genera of tunas are unique among bony fishes in having countercurrent heat exchanger systems of rete mirabilia in the circulatory system. These systems allow tunas to retain metabolic heat so that the fish is warmer than the surrounding water. The three more primitive genera (*Auxis*, *Euthynnus*, and *Katsuwonus*) and the yellowfin tuna group of *Thunnus* have central and lateral heat exchangers; the specialized bluefin tuna group of *Thunnus* has lost the central heat exchanger and has evolved well-developed lateral heat exchangers (Carey et al. 1971; Graham 1973, 1975). Copepod fauna: 17 species in 7 genera. *Caligus coryphaenae, C. asymmetricus,* and *C. productus* were found on species in all four genera of Thunnini. *Caligus coryphaenae* is common on the body surface of seven species of *Euthynnus, Katsuwonus,* and *Thunnus,* and we have one record from *Auxis* sp. (and one record from *Acanthocybium*). It is also common on species of the dolphin genus *Coryphaena,* a similarity we believe due to similarity of epipelagic habits. *Caligus productus* was found on 20 species of scombrids, from all tribes except the Scombrini. It occurred on 9 of the 13 species of Thunnini but was common (infestation 28-92%) on *Katsuwonus* and 3 species of *Thunnus. Caligus asymmetricus* was also found on scombrids from all tribes except the Scombrini, on a total of nine host species. It appears to be more characteristic of the Sardini, occurring commonly (infestation 8-12%) in *Cybiosarda* and two species of *Sarda,* than of the Thunnini (found in four species, infestation 1-7%). One additional copepod, *Pseudocycnus appendiculatus*, is characteristic of Thunnini and occurs on 9 of 13 species, in all genera except *Auxis*. However, it is common (infestation 14-27%) in only three species of *Thunnus*: *T. tonggol*, *T. albacares*, and *T. maccoyii*.

Auxis Cuvier

This is the most primitive genus of the Thunnini.

Differences from the more advanced three genera of Thunnini were summarized by Collette (1979). Copepod fauna: 6 species in 2 genera, *Unicolax* and *Caligus*. The two species of *Unicolax* are shared with several species of Sardini and with species of *Euthynnus* in the Thunnini. *Euthynnus* is the genus most closely related to *Auxis*. Three of the species of *Caligus* are also found in the other three genera of Thunnini. The fourth, *C. pelamydis*, is shared only with *Euthynnus* among the Thunnini, but parasitizes scombrids in the other three tribes, particularly the Sardini. We have not found *P. appendiculatus* on *Auxis*, but it is known from species in the other three genera of Thunnini. Thus, infestation of copepods clearly relates *Auxis* to the other Thunnini, particularly *Euthynnus*.

There are two species of frigate mackerels (Fitch and Roedel 1963): The narrow-corseleted *A. thazard* (Lacepède) and the wide-corseleted *A. rochei* (Risso). The two species have been clearly distinguished in the Pacific by Kishinouye (1923), Wade (1949), and Matsumoto (1960) under a variety of names. Both species are widely distributed in tropical and subtropical waters of the Indo-Pacific, and both species apparently also occur in the Atlantic (Richards and Randall 1967). Confusion in identification of many specimens dictates that we refer all our copepod records for the genus to *Auxis* sp. Frigate mackerels are the smallest of the tunas, *A. rochei* reaching 600 mm FL and *A. thazard* at least 420 mm.

Euthynnus Lütken in Jordan and Gilbert

Euthynnus is closely related to both the more primitive *Auxis* and the more advanced *Katsuwonus*. Some workers (Fraser-Brunner 1950; Collette and Gibbs 1963) have placed the monotypic *Katsuwonus* in synonymy with *Euthynnus*, but this obscures the relationships of *Euthynnus* sensu stricto with *Auxis* and of *Katsuwonus* with *Thunnus*. *Euthynnus* differs from *Auxis* in having a common trunk for the dorsal and ventral branches of the cutaneous artery. It is less advanced than *Katsuwonus* because the ventral branch of the cutaneous artery is short and dendritic (Godsil 1954), much less developed than the dorsal branch. The dorsal cutaneous artery lies dorsal to the corresponding vein in *Euthynnus*, not ventral as in *Auxis*. Collette (1979) has summarized the generic differences along the genera of Thunnini. Copepod fauna: 11 species in 4 genera. Three species of *Caligus* (*asymmetricus*, *pelamydis*, *productus*) and *P. appendiculatus* are widespread among the Thunnini. Two species of *Unicolax* (*collateralis* and *mycterobius*) are shared only with *Auxis* in the Thunnini but also with species of Sardini. *Caligus bonito* was found on all three species of *Euthynnus* but is most commonly found on members of the tribe Sardini.

There are three allopatric species of *Euthynnus*: *E. alletteratus* (Rafinesque) in the Atlantic; *E. affinis* (Cantor) throughout the Indo-West Pacific; and *E. lineatus* Kishinouye in the eastern Pacific. There is a valid record of *E. affinis* from the eastern Pacific (Godsil 1954:139) and two of *E. lineatus* from the Hawaiian Islands (Matsumoto and Kang 1967; Matsumoto 1967). Godsil (1954: table 17) has summarized the characters that differentiate the species (with *E. affinis* as *E. yaito*). Two bomolochid and one caligid copepod parasites of *Euthynnus* apparently show host specificity within the genus. *Unicolax anonymous* is known only from the nasal sinuses of *E. alletteratus* in both the eastern and western Atlantic. *Ceratocolax euthynni* is also restricted to the Atlantic, but occurs on *Sarda sarda* as well. *Caligus regalis* is restricted to *E. affinis* (and *Grammatorcynus* in the Scomberomorini) and may replace the closely related, more widespread *C. coryphaenae* on this host.

Katsuwonus Kishinouye

This monotypic genus is related to both *Euthynnus* and *Thunnus*, and is more advanced than *Euthynnus*. The generic characters of *Katsuwonus* are summarized by Collette (1979). The skipjack tuna, *Katsuwonus pelamis* (Linnaeus), is a moderate-sized tuna, about a meter long and weighs 18 kg, rarely more than 23 kg. It has the highest number of gill rakers of any of the Thunnini, 53-63 on the first arch. It is cosmopolitan in tropical and subtropical seas. Copepod fauna: 6 species in 3 genera. The three species of *Caligus* and *P. appendiculatus* are widespread among species of Thunnini. The fifth copepod, *U. reductus*, is a highly specialized species restricted to *Katsuwonus*. It appears to replace the more primitive *U. collateralis*, *U. mycterobius*, and *U. anonymous*, which are common in the nasal sinuses of the two more primitive genera of *Thunnini*, *Auxis* and *Euthynnus*. This copepod evidence tends to support recognition of *Katsuwonus* as a separate genus.

Thunnus South

This, the most advanced genus of Scombridae, contains seven species. Posterior to the corselet, the body is covered with small scales but is naked in other genera of Thunnini. A swim bladder is present in all the species except *T. tonggol*. Vertebral trellis-

work (containing the central heat exchanger; Graham 1975, 1979) is present in *Euthynnus* and *Katsuwonus,* and is reduced (yellowfin tuna species group) or absent (bluefin tuna group) in *Thunnus.* Collette (1979) concluded that it was useful to utilize subgenera in *Thunnus* to reflect the adaptive significance of the difference in heat exchangers between the two groups of species, the subgenus *Thunnus* for the bluefin tuna group of species including *T. obesus, Neothunnus* for the yellowfin tuna group. Copepod fauna: 10 species in 5 genera. Three species of *Caligus* and *P. appendiculatus* are widespread among species of Thunnini. The lerneopodid *Brachiella thynni* occurs, usually in the axil of the pectoral fin, on a wide variety of hosts both scombrid and nonscombrid. In the Scombridae, it is most common on *Acanthocybium* and was also present on three species of *Thunnus* (*T. obesus*, 24%; *T. albacares*, 7%; *T. thynnus,* 4%). Occurrence of the euryphorid *Elytrophora* is of particular interest. Six species of *Thunnus* (all but *T. tonggol*) share *E. brachyptera* with *Allothunnus fallai.* As noted under the discussion of the latter, this indicates that the systematic position of *Allothunnus* within the tribe Sardini needs to be reconsidered.

Subgenus *Neothunnus* Kishinouye

This subgenus contains the three tropical species of *Thunnus* which have central heat exchangers, as do the three less advanced genera of Thunnini. Gibbs and Collette (1967:99) found that these three species were similar to each other in 15 or 16 of 18 characters. The three species are the blackfin tuna, *Thunnus atlanticus* (Lesson), of the western Atlantic, Martha's Vineyard, Mass., to Rio de Janeiro; the longtail tuna, *T. tonggol* (Bleeker), of the Indo-West Pacific, Japan to Australia west through the Indo-Australian Archipelago to Somalia and the Red Sea; and the yellowfin tuna, *T. albacares* (Bonnaterre), a pantropical species. Differences between the species were treated in detail by Gibbs and Collette (1967).

Copepod fauna: 7 species in 4 genera. Differences in copepod infestation in *Thunnus* appear to reflect species differences rather than subgeneric differences. *Caligus asymmetricus,* a copepod common on the three more primitive genera of Thunnini, was found on *T. albacares,* which tends to confirm closer relationships between the three primitive genera and *Neothunnus* than with *Thunnus.* However, the copepod was found only on one specimen of *T. albacares,* so this is only weak confirmatory evidence. We found the most common copepods on *T. albacares* worldwide to be *C. productus* (46%), *E. brachyptera* (35%), *C. coryphaenae* (29%), *P. appendiculatus* (19%), and *B. thynni* (7%). In an intensive study of 200 *T. albacares* from the Gulf of Guinea, Baudin Laurencin (1971) found three of the five copepods in similar rates of infestation: *Caligus productus,* 64%; *P. appendiculatus,* 27%; and *B. thynni,* 7%. He did not report either *E. brachyptera* or *C. coryphaenae,* although both occur in the eastern Atlantic, and we have the latter from *T. albacares* in the Gulf of Guinea.

Subgenus *Thunnus* South

This subgenus contains the four larger species of tunas which have invaded cooler waters owing to their possession of effective lateral heat exchangers. Gibbs and Collette (1967:99) showed that three species of this group resembled each other in 14-16 of 18 characters. Striations caused by blood vessels are present on the ventral surface of the liver, and vascular cones are associated with the dorsal surface of the liver, indicating the presence of a visceral heat exchanger. Three species clearly belong to this subgenus: the Atlantic and Pacific bluefin tunas, *Thunnus thunnus thynnus* (Linnaeus) and *T. t. orientalis* (Temminck and Schlegel); the southern bluefin tuna, *T. maccoyii* (Castelnau); and the albacore, *T. alalunga* (Bonnaterre). The fourth species, the bigeye tuna, *T. obesus* (Lowe), is intermediate between the subgenera, sharing 12 characters with *T. maccoyii* and 10 with *T. albacares* (Gibbs and Collette 1967:99). Because it has lost the central heat exchanger, Collette (1979) believed that it belongs to the subgenus *Thunnus,* although it is the most different of the four species in the subgenus. The characters that distinguish the species of the subgenus *Thunnus* and the distributions of the species are treated in detail by Gibbs and Collette. All four species are found worldwide. The bluefin tuna extend into temperate waters of the North Atlantic (*T. t. thynnus*) and the North Pacific (*T. t. orientalis*). The southern bluefin, *T. maccoyii,* has a distribution pattern similar to those of *Gasterochisma* and *Allothunnus* in the Southern Ocean. *Thunnus alalunga* is found from lat. 42°N to 32°S in the Atlantic, lat. 10°N to 30°S in the Indian Ocean, and lat. 50°N to 45°S in the Pacific; however, most of the albacore fisheries are concentrated in temperate waters. *Thunnus obesus* has much the same latitudinal distribution as *T. albacares,* but it is usually found in deeper and cooler waters than *T. albacares.*

Copepod fauna: 8 species in 5 genera. *Thunnus obesus* differs in infestation from the other three species of the subgenus in lacking *C. productus,* in

having the highest infestation by *B. thynni* (24%), and in having a second species of *Elytrophora, E. indica,* which was found only on Indo-Pacific specimens of *T. obesus. Elytrophora indica* frequently occurs with *E. brachyptera*, but we lack data on possible microhabitat differences between the two copepods.

HOST SPECIFICITY AND TAXONOMIC RELATIONSHIPS OF *CALIGUS* PARASITIC ON SCOMBRIDS

The genus *Caligus,* with over 200 recognized species, has been reported from species of marine fishes of several diverse higher taxa. Most species do not exhibit strict host specificity; those which have been commonly reported are known from more than one host species. Adults of *Caligus* species are occasionally found in plankton samples, indicating that species of *Caligus* may easily transfer from one host individual to another. Many, however, seem to be restricted to a genus or family of fishes. Furthermore, if one analyzes the data from comprehensive collections, it becomes clear that although a parasite may be present on several host species, it is consistently more common on some than others, which we interpret as a trend toward specificity. The first author has never found an equal rate of infestation of any *Caligus* species among its hosts in any large collections examined. There have always been one or two host species with significantly higher infestation rates, when as many as 10 host species are involved (unpubl. data). We have analyzed the data for *Caligus* most common on scombrids, and the results are consistent with this concept.

Ten most common of the 16 species of *Caligus* reported by Cressey and Cressey (1980) were chosen for study. These 10 *Caligus* species can be divided into 5 subgroups, based on the segmentation and number of setae on the fourth leg exopod, the presence or absence of a posterior process on the base of the second antenna, and the presence or absence of the postantennal spine. These groups are 1) *productus, asymmetricus*; 2) *bonito, omissus, mutabilis*; 3) *infestans*; 4) *pelamydis, cybii*; and 5) *coryphaenae, regalis.* All of the 10 species are found on more than one species of host (scombrid or otherwise). Frequency of their occurrences, however, indicates definite host preferences.

The distribution of infestation rates and host specificity indices (based on Rohde 1980) for *C. productus* and *C. asymmetricus* are given in Table 9. Neither of these two species are found on species of Scombrini. *Caligus productus* is most common on the closely related genera *Katsuwonus* and *Thunnus* and to a lesser extent on *Scomberomorus, Acanthocybium,* and *Gymnosarda.* Five of the six records of *C. productus* on species of *Scomberomorus* are from the Atlantic. *Caligus asymmetricus* complements *C. productus* in host distribution. It is common on hosts where *C. productus* is absent or rare, and uncommon or absent on those where *C. productus* is most common. The only genera of the three tribes infested, which so far are negative for either of these two copepods, are *Orcynopsis* and *Allothunnus.* This is due probably to the few specimens (seven) of each that we have examined.

Two species of *Caligus* (*cybii* and *infestans*) are apparently specific to Indo-West Pacific *Scomberomorus,* whereas there is apparently no *Caligus* species-specific to Atlantic *Scomberomorus.*

The next group of *Caligus* species are *bonito, mutabilis,* and *omissus. Caligus bonito* is circumglobal whereas *C. mutabilis* is restricted to the western Atlantic and *C. omissus* is, so far, only known from the eastern Pacific. The latter two species are very similar. In 1960, Causey reported *C. mutabilis* from several species of fishes, including *Scomberomorus sierra* from the Gulf of California and the Pacific coast of Mexico. The material from *S. sierra* was undoubtedly *C. omissus*, and it is likely that the rest was also. Wilson (1937) also reported *C. mutabilis* from *S. maculatus* (presumably *sierra*) from Pacific Mexico, which was probably *C. omissus.* None of these collections are available for verification, but we feel that these Pacific records of *C. mutabilis* should be discounted. The first author has collected *C. mutabilis* from two species of *Lutjanus* from the west coast of Florida, and it is apparent from the literature that all three of these

TABLE 9.—Infestation rates and host specificity indices of *Caligus productus* and *C. asymmetricus* on genera of Scombrinae (specificity indices in parentheses).

	C. productus	*C. asymmetricus*
Scombrini	—	—
Rastrelliger		
Scomber	—	—
Scomberomorini		
Grammatorcynus	2 (0.14)	14.9 (1.0)
Scomberomorus	1 (0.11)	1 (0.33)
Acanthocybium	17 (0.34)	—
Sardini		
Orcynopsis	—	—
Cybiosarda	—	8 (0.5)
Sarda	1.5 (0.32)	2.8 (0.2)
Gymnosarda	14.3 (0.26)	—
Allothunnus	—	—
Thunnini	3 (0.17)	1.3 (0.16)
Auxis		
Euthynnus	1.3 (0.2)	3.3 (0.25)
Katsuwonus	38.6 (0.5)	1 (0.16)
Thunnus	41.4 (1.0)	1 (0.12)

copepod species are occasional parasites of non-scombrid hosts.

The distribution of infestation rates on scombrid hosts for these three species is summarized below. *Caligus bonito* is apparently most common on species of Sardini and is only an occasional parasite of Atlantic *Scomberomorus* and *Grammatorcynus* and with scattered records from Thunnini (mostly western Atlantic and eastern Pacific).

Caligus mutabilis is apparently restricted to the western Atlantic, and its most common scombrid hosts are species of *Scomberomorus*. As in the case of *C. productus* in the Atlantic, this copepod probably replaces the Indo-Pacific species of *Caligus*, more host-specific to Indo-Pacific *Scomberomorus*.

Caligus infestans has been recorded primarily from *S. commerson* from the Indian Ocean and eastward as far as Indonesia. Although its preferred host ranges north to Japan and east to Fiji, *C. infestans* apparently is replaced in these areas by *C. cybii*, host-specific to Indo-West Pacific *Scomberomorus*. Kabata (1965) reported *C. infestans* from *Euthynnus alletteratus* (= *affinis*) from queensland, and Heller (1865) originally described this species from *Scomber* from Java. The second author believes the latter host to be incorrect and the host was probably *Rastrelliger*. Four literature records and five additional collections reported by Cressey and Cressey (1980) indicate that *S. commerson* is undoubtedly its preferred scombrid host.

Caligus pelamydis and *C. cybii* are, together with *C. coryphaenae* and *C. regalis*, the most primitive of the 10 species considered here (assuming a 3-segmented fourth leg exopod is primitive to a 2-segmented one). *Caligus pelamydis* has been reported many times (Margolis et al. 1975; Cressey and Cressey 1980) primarily from *Sarda sarda* (usually reported as *Pelamys sarda* or *Gymnosarda pelamys*) and *Scomber scombrus*. Although our recent collections indicate *Sarda* species as a frequent host, several other literature records from *Scomber scombrus* may indicate that this fish is a more common host than our collections indicate. Most literature records are from European waters, whereas most of the *S. scombrus* we examined were from the western Atlantic. Possibly this copepod is more common on European *S. scombrus* than on American specimens. In addition, *C. pelamydis* has been reported from *Euthynnus*, *Auxis*, and *Scomberomorus niphonius*.

It is interesting to note that *C. pelamydis* is a common parasite of *S. niphonius*, whereas its close relative, *C. cybii*, is reported from six other Indo-West Pacific species of *Scomberomorus*. It seems likely that *C. pelamydis* is more primitive than *C. cybii*. This suggests that *S. niphonius* is the most primitive species of Indo-West Pacific *Scomberomorus*. The ranges of both *C. cybii* and *C. pelamydis* overlap in Japan (*C. cybii* from *S. koreanus*, 11 of 19 fish infested). *Caligus cybii* apparently evolved parasitizing species of Indo-West Pacific *Scomberomorus* other than *S. niphonius*.

The closely related *C. coryphaenae* and *C. regalis* are both found on the body surface of their hosts. Consequently, the data may be biased because much of the host material used for this study is preserved in museum collections, and body-surface copepods, for the most part, are no longer present. Most of the specimens of Thunnini, however, were examined in the field, and infestation rate data are more reliable. Because *C. coryphaenae* is ubiquitous (circumglobal distribution and on many different species of hosts), it can be presumed to be more primitive than *C. regalis* (restricted to the Indian Ocean and southwestern Pacific and found only on *E. affinis* and *Grammatorcynus*). *Caligus coryphaenae* is also common on *Coryphaena hippurus* and *C. equiselis*. Within the Scombridae, both species are primarily parasites of the Thunnini with scattered records on Scomberomorini (*Acanthocybium* and *Grammatorcynus*). *Caligus regalis*, previously known only from *E. affinis*, has recently been collected by the first author from three specimens of *G. bicarinatus* from Australia. This is within the known geographic range of the parasite, but is another example of copepod parasites shared by the Scomberomorini and the Thunnini.

Within each of the four groups of *Caligus* with more than one species discussed here, one species of *Caligus* is widely distributed (circumglobal in three cases) and the remaining species are much more restricted in distribution (Figs. 9-12).

In conclusion, analysis of the collection data for the 10 species of *Caligus* considered here suggest the following:

1. Although *Caligus* species are generally not restricted to one host, they are often confined to a genus, tribe, or family and, in all cases considered here, they show strong host preferences at a generic or specific level. For example, although *C. productus* is found on three of the four tribes of Scombridae, it has significantly higher rates of infestation on *Katsuwonus* and *Thunnus* within the Thunnini. *Caligus bonito* is recorded from three tribes of scombrids but is much more common on the tribe Sardini.

2. Within each group of related *Caligus* parasitic on scombrids, one species is either circumglobal or is significantly more widespread than any others.

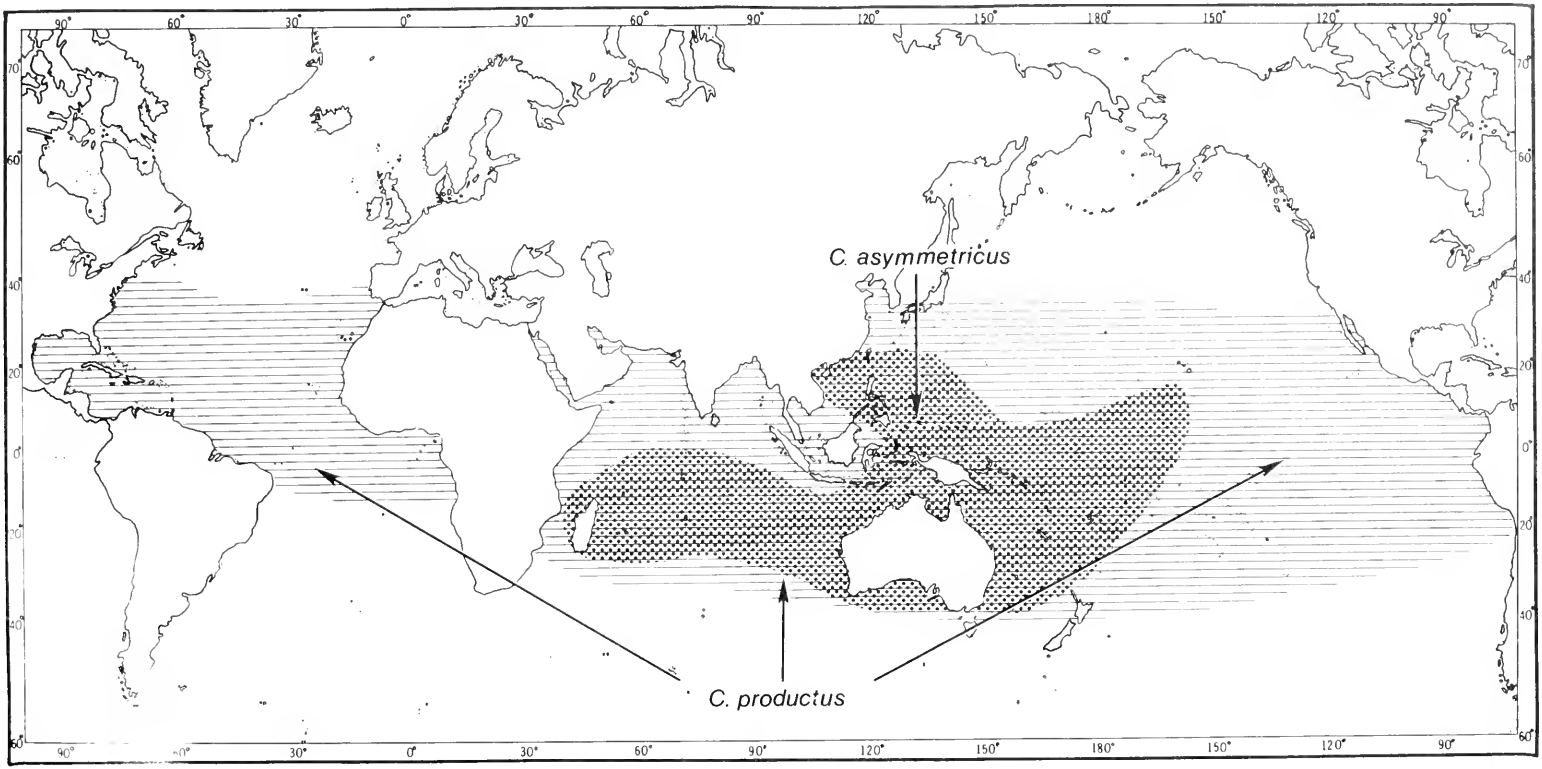

FIGURE 9—Distribution of *Caligus productus* and *C. asymmetricus*.

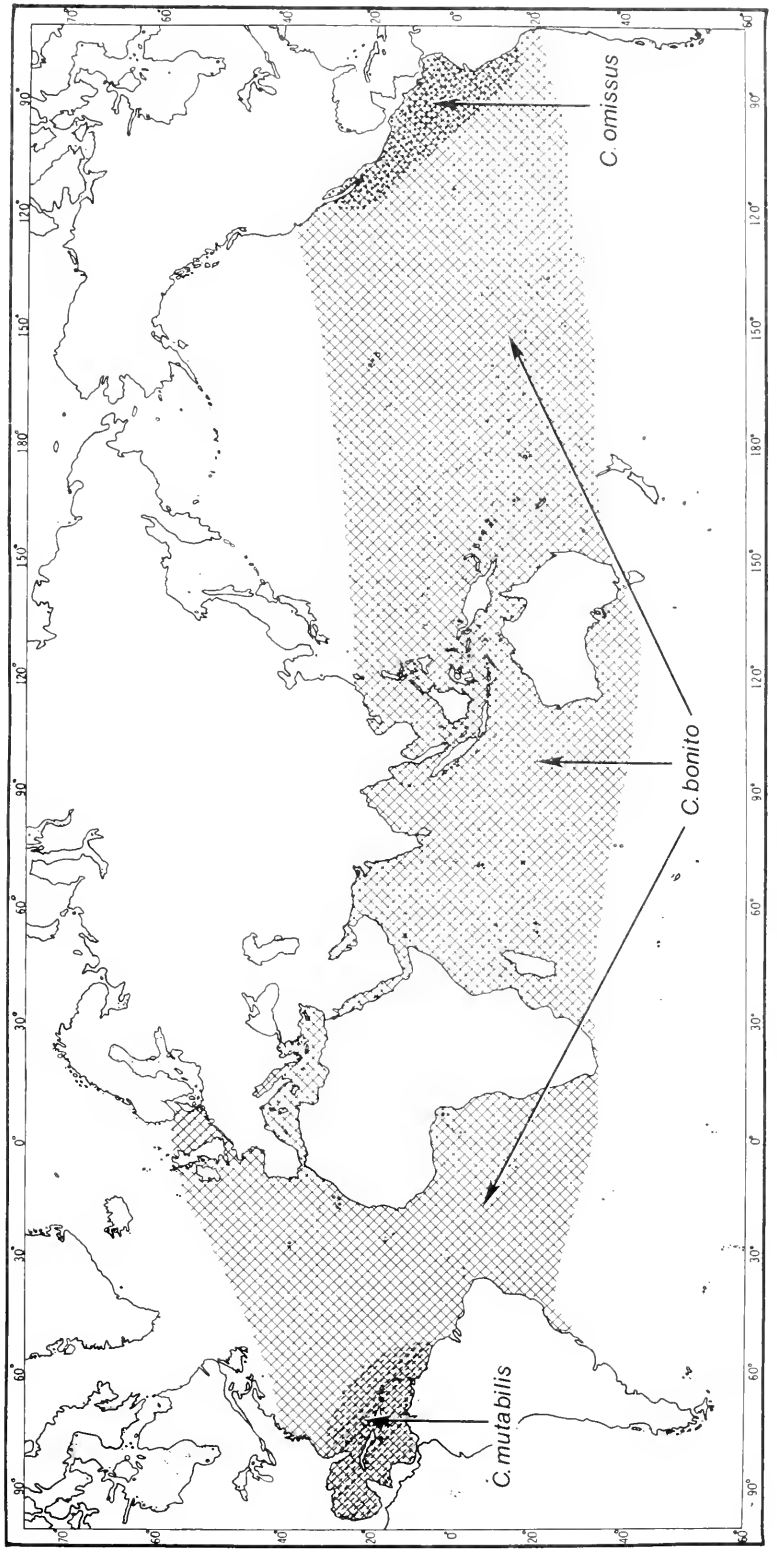

FIGURE 10.—Distribution of *Caligus mutabilis*, *C. bonito*, and *C. omissus*.

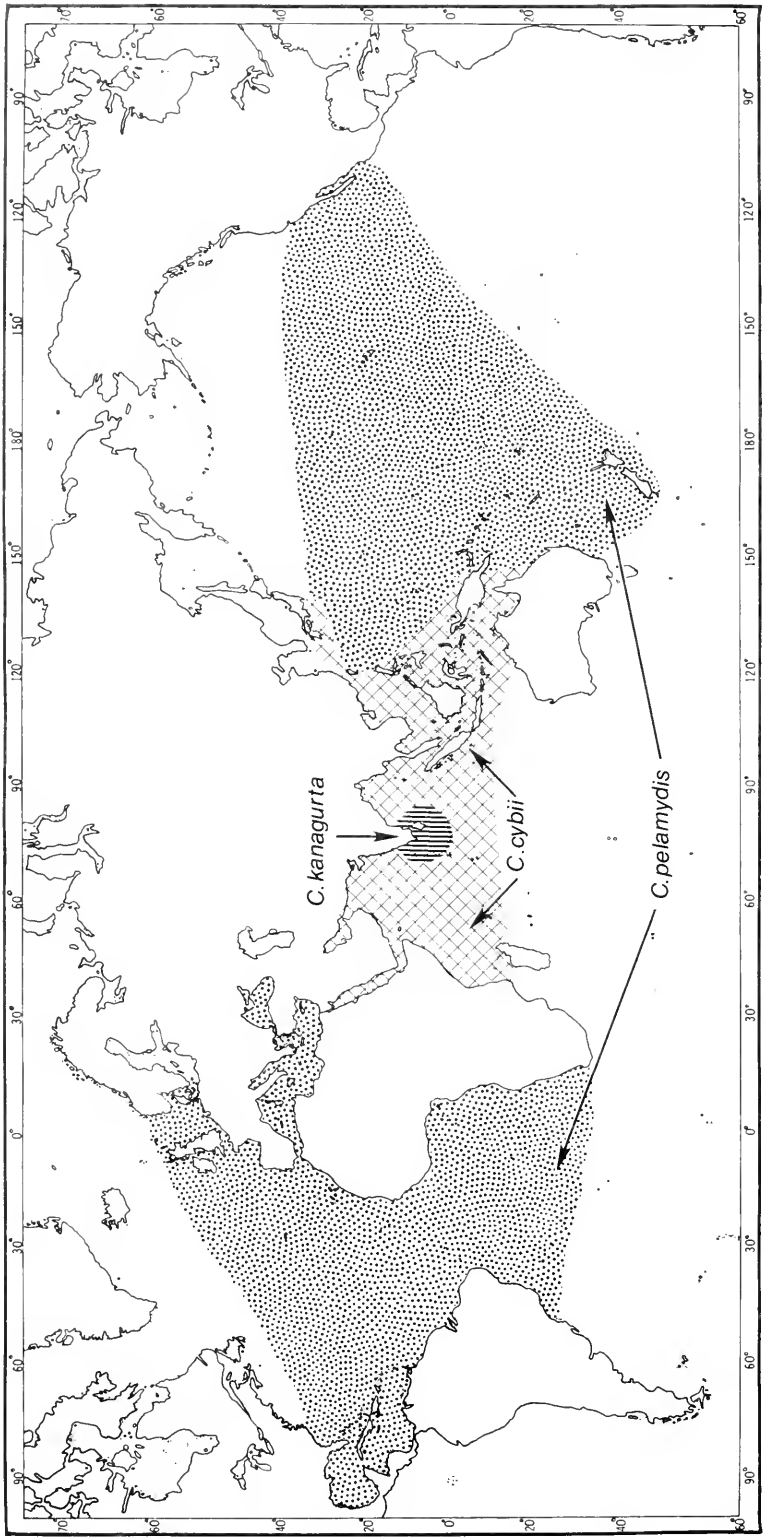

FIGURE 11.—Distribution of *Caligus pelamydis*, *C. cybii*, and *C. kanagurta*.

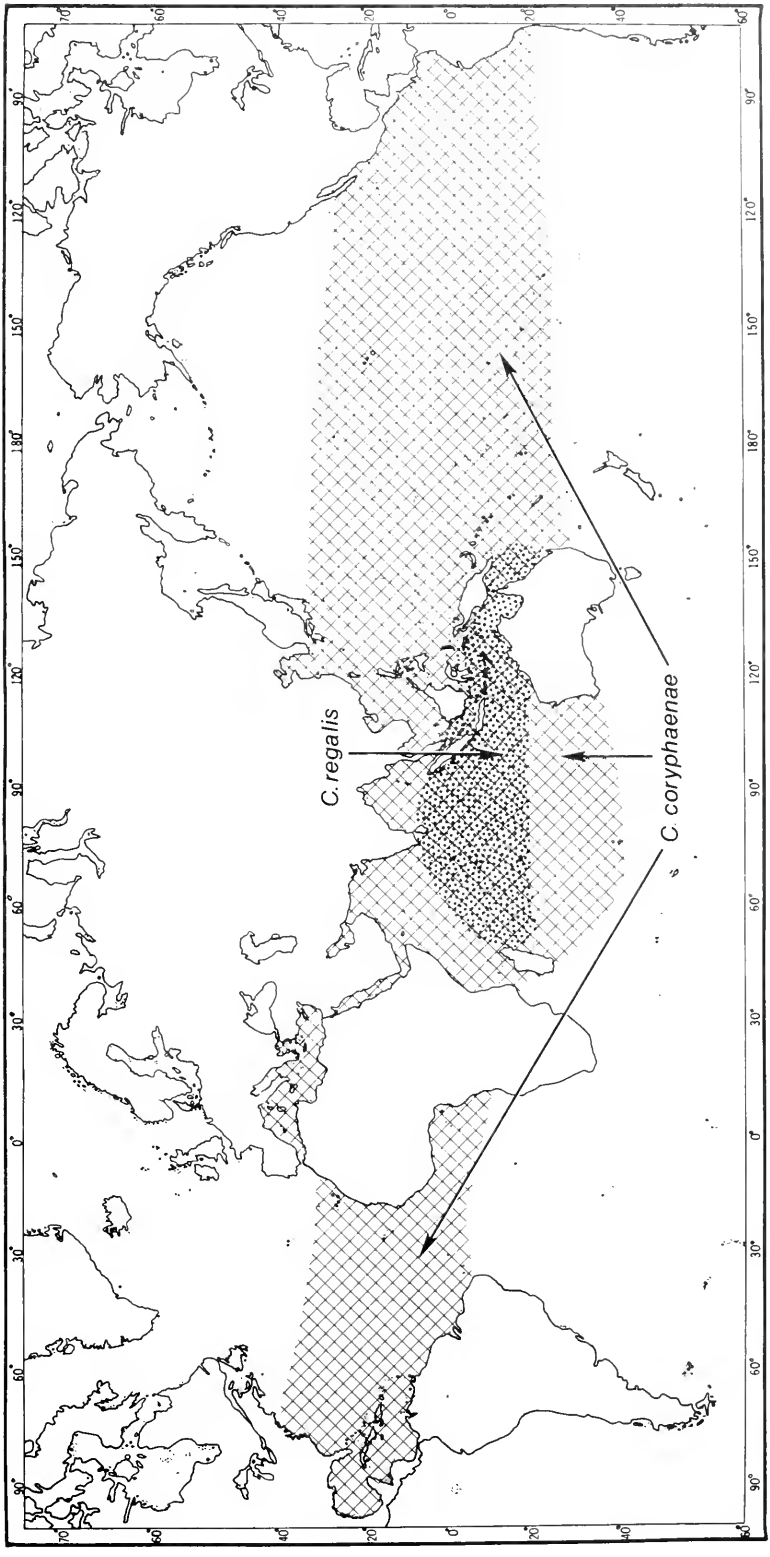

FIGURE 12.—Distribution of *Caligus coryphaenae* and *C. regalis*.

3. *Scomberomorus niphonius* is possibly the most primitive species of the genus based on *Caligus* and other copepod parasites (*Pseudocycnoides scomberomori*, a copepod specific to *S. niphonius*, is more primitive than *P. armatus* found on several other Indo-West Pacific *Scomberomorus*).

Scombrid Phylogeny

Historic

Many workers have arranged the scombrids according to their ideas of relationships within the group. In this section we present a brief history of scombrid classifications, culminating in the most recently published article by Collette and Russo (1979). Then we present a classification derived from infestation by parasitic copepods and discuss differences between the two classifications.

Modern attempts at classification of the scombrid fishes date from Regan (1909), who placed the family Scombridae as the sole member of a division Scombriformes in the suborder Scombroidei of the order Percomorphi. Starks (1910) was the first to define subdivisions within the family recognizing five subfamilies: Scombrinae, Scomberomorinae, Acanthocybinae, Sardinae, and Thunninae (Fig. 13). Starks based his classification on osteology. Characters from soft anatomy, particularly the viscera and the circulatory system, were added by Kishinouye (in particular, his classic 1923 monograph). Kishinouye was so impressed by the differences that he separated the most advanced scombrids as a separate order, Plecostei, with two families, the Thunidae (*Thunnus*) and the Katsuwonidae (*Auxis, Euthynnus,* and *Katsuwonus*). Rather illogically, he left the other scombrids as two families, Scombridae (*Scomber* and *Rastrelliger*) and Cybiidae (all the bonitos and seerfishes) of the Teleostei, suborder Acanthopterygii (Fig. 14). The next revisor of the family, Fraser-Brunner (1950) overreacted to this splitting of the scombrids into four families in two orders by ignoring the anatomical data in constructing his classification (Fig. 15). The most recent classification of the scombrids (Collette and Russo 1979) has been slightly revised for presentation here (Fig. 16).

Parasite Based

Once a host-parasite relationship has been established, several events can occur with respect to the evolution of this relationship. Assuming the host will evolve and allowing for speciation, the parasite may gradually change maintaining compatability with its changing host or the parasite may be divided into separate populations because of a speciation event in the host. In the former case, there is no speciation event in the host, thus a single parasite population would remain sympatric. In the latter case, the speciation event in the host would divide the parasite population into two allopatric populations and act as a vicariant event with respect to the parasites. The

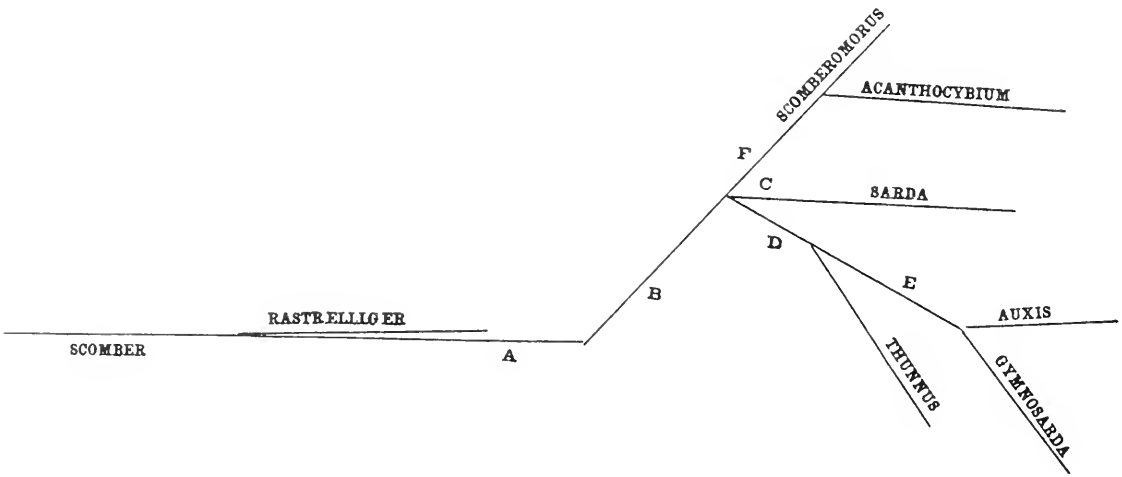

FIGURE 13.—Diagram of relationships of the Scombridae from Starks (1910). A) Characters of *Scomber*. B) Acquirement of interposed opisthotics. C) *Thunnus* type of cranial crests, and the inferior cranial pit indicated, with the *Scomberomorus* type of ethmoid and nasals. D) The inferior cranial pit excluding the pterotic from the brain cavity, and the condition of the ethmoid and nasals of *Scomber*. E) The condition of the infravertebral processes from which *Auxis* and *Euthynnus* (given as *Gymnosarda* by Starks 1910) have diverged. F) The *Scomberomorus* type of cranial crests, elongate form, concave ethmoid, and nonprojecting nasals.

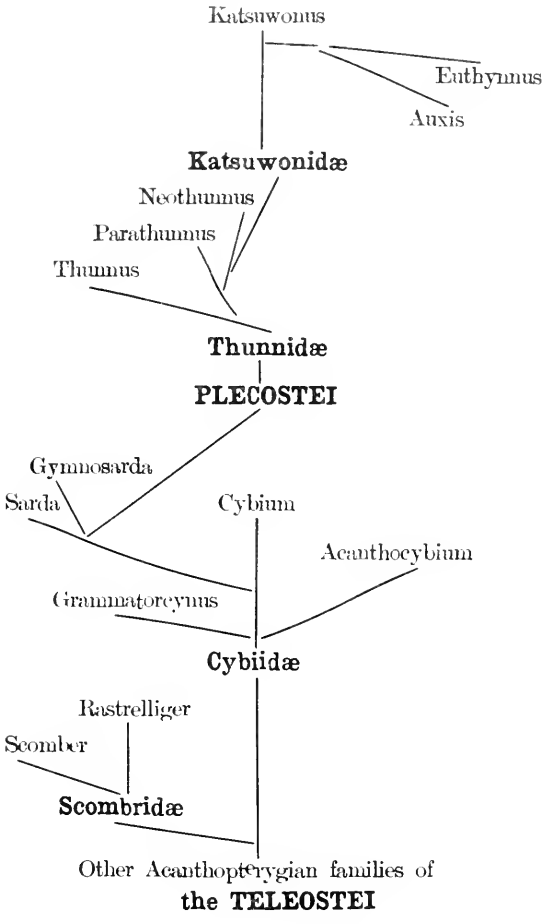

FIGURE 14.—Diagram showing classification of scombrid fishes adopted by Kishinouye (1923).

isolated parasite populations may remain the same, speciate, or one or both may become extinct. Morphological data from hosts or parasites may be used to reconstruct or estimate phylogenetic relationships. If questions regarding coevolutionary events are asked, however, information concerning the phylogeny of both hosts and parasites is necessary. Brooks (1979) discussed types of host-parasite relationships and outlined parasitic distributions on hosts and the coevolutionary implications of such distributions. Brooks (1981) provided a method for testing coevolutionary hypotheses.

Cladistic analysis of hosts and parasites, using morphological characters, will provide information concerning the phylogeny of both hosts and parasites. If host and parasite phylogenies are concordant, the distribution of parasites on hosts can be explained by cospeciation events. If, on the other hand, host-parasite relationships are convergent, they indicate host transfer or broadening coaccommodation (Brooks 1981). Using the additive binary coding method presented by Brooks to generate character state trees for host or parasite phyletic relationships, it is possible through character analysis to generate host trees based on parasite phyletic relationships and parasite trees based on host phyletic relationships. By direct comparison of these trees with each other it is possible to test hypotheses of coevolution.

In an attempt to utilize parasite data and to objectively resolve the problem of phyletic relationships among the genera of Scombridae, the first author coded our copepod infestation data and the third author subjected the data to a cladistic analysis, using a computer program (WAGNER 78) written by J.

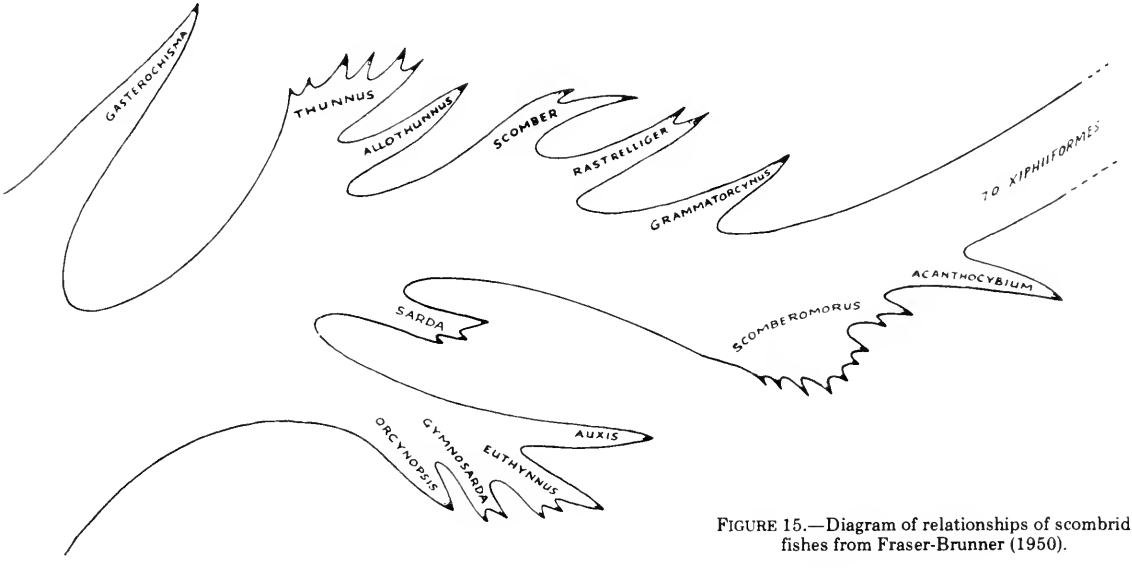

FIGURE 15.—Diagram of relationships of scombrid fishes from Fraser-Brunner (1950).

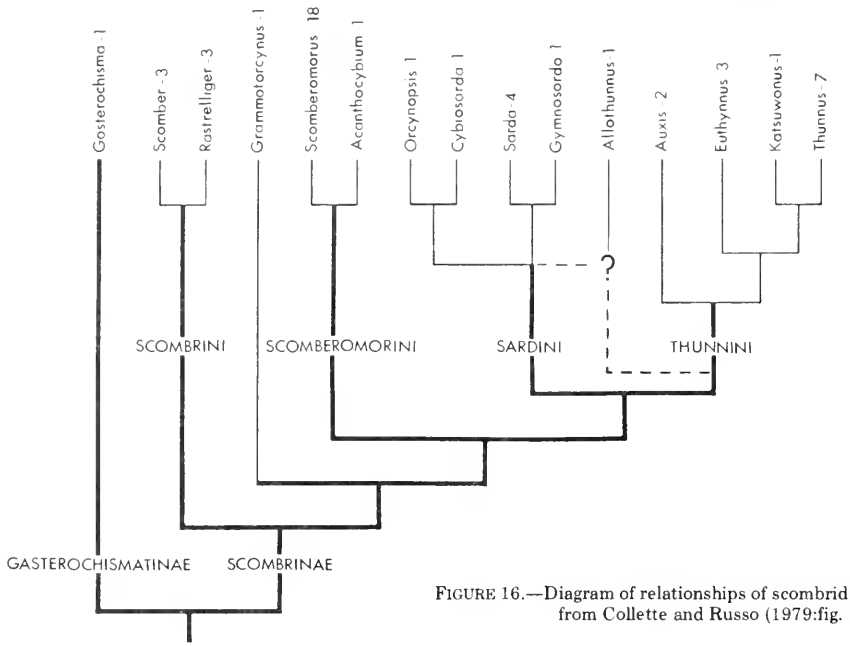

FIGURE 16.—Diagram of relationships of scombrid fishes modified from Collette and Russo (1979:fig. 1).

S. Farris (following Farris 1970 and Farris et al. 1970). Infestation by a given copepod species was, somewhat arbitrarily, considered primitive; absence, specialized. A transformation series was used to indicate decreasing amounts of parasitism by a given copepod species across a matrix of scombrid genera. The Wagner tree was rooted at *Rastrelliger,* one of the most primitive members of the Scombrinae. The resulting Wagner tree (Fig. 17) shows major differences from the diagram of relationships based on host morphology (Fig. 16). The only concordant sister groups produced in this tree are *Acanthocybium* and *Scomberomorus.*

There are at least two problems with coding the infestation data in this manner. Use of copepod species ignores information concerning the relationships of the species. Another difficulty is coding copepod infestation as a two-state character (present or absent in a host species), when *Caligus* infestation data can only be interpreted as host preference (relative percent of infestation) rather than as host specificity (see previous section on *Caligus*). The program was rerun using infestation by genera of copepods and defining *Caligus* presence as more than 5% infestation to correct for this problem. This Wagner tree (Fig. 18) is much closer to the diagram based on host morphology. Several concordant sister groups are present: *Scomberomorus-Acanthocybium* defined by the acquisition of *Tuxophorus* at node (5), *Grammatorcynus-Scomberomorus* + *Acanthocybium* defined by the acquisition of *Caligus* at node (4); *Katsuwonus-Thunnus*, loss of *Ceratocolax* at node (9); and *Euthynnus-Katsuwonus* + *Thunnus*, acquisition of *Pseudocycnus* at node (8).

There are also several differences between this Wagner tree and the diagram of relationships based on host morphology. *Gymnosarda* is associated with *Grammatorcynus-Acanthocybium* group based on the presence of *Shiinoa* in all four genera. However, we found *Shiinoa* in only one specimen of *Gymnosarda*, so not much reliance can be placed on this association. We found only two other copepods on *Gymnosarda,* single occurrences of *C. bonito* and *C. productus,* which were omitted in this run of the program. There was only one common copepod on *Allothunnus* (*Elytrophora*), but there were also records of the same two species of *Caligus* as in *Gymnosarda.* Perhaps examining more specimens of *Gymnosarda* and *Allothunnus* (we examined only seven of each) would yield more copepods that would cluster these two genera with the natural group of the Sardini plus Thunnini.

We turned from attempts at producing a cladistic classification of all scombrids, using the infestation data, and decided to use only a portion of the data, infestation by the nasal bomolochids of the genus *Unicolax.* The five known species of *Unicolax* are all parasites in the nasal sinuses of scombrid fishes. The first author compared characters within the species of *Unicolax* with those in the related outgroup genus

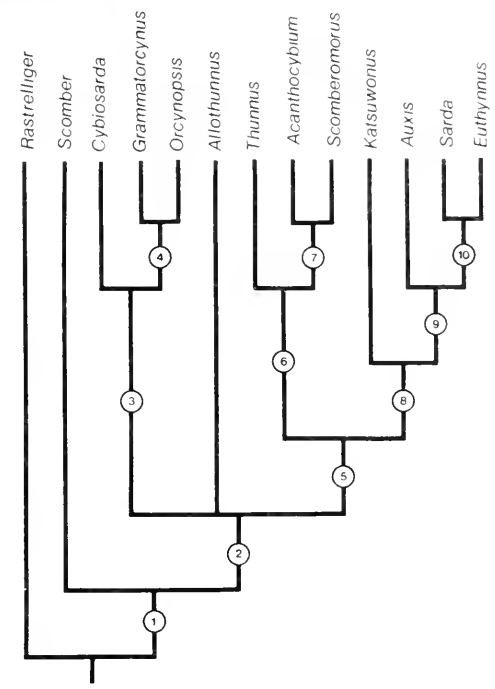

FIGURE 17.—Wagner tree of scombrid hosts based on infestation by copepod species. Synapomorphies (gain, loss, or reduction in infestation rate of copepod species) occurred at the following nodes: 1) loss of *Lernanthropus kanagurta, Orbitacolax aculeatus,* and *Nothobomolochus kanagurta*; 2) loss of *Pumiliopes jonesi*; 3) gain of *Caligus asymmetricus* and *Unicolax collateralis*; 4) gain of *Caligus bonito*; 5) gain of *Caligus productus* and *C. coryphaenae*; 6) gain of *Brachiella thynni*; 7) gain of *Shiinoa occlusa* and reduction of infestation of *Caligus productus*; 8) reduction of infestation of *Caligus asymmetricus*; 9) gain of *Caligus pelamydis, Unicolax mycterobius, U. collateralis*, and reduction of infestation of *C. productus* and *C. coryphaenae*; 10) gain of *Caligus bonito, Ceratocolax euthynni*, and reduction of infestation of *Unicolax mycterobius*.

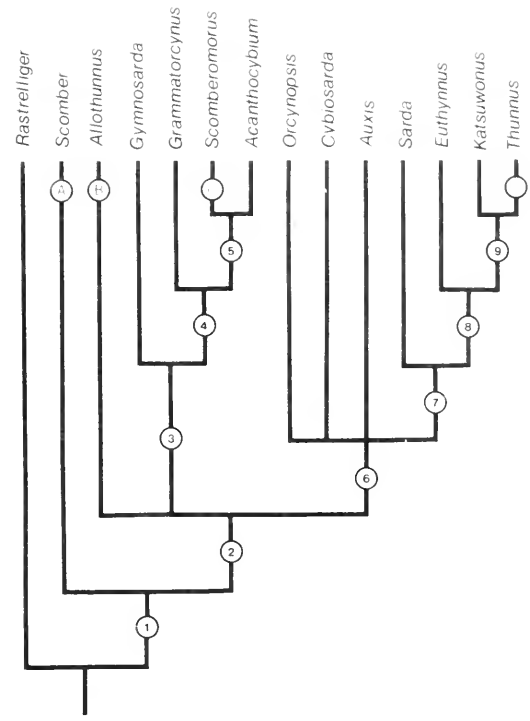

FIGURE 18.—Wagner tree of scombrid hosts based on infestation by copepod genera. Synapomorphies (gain or loss of copepod genera) occurred at the following nodes: 1) *Orbitocolax, Nothobomolochus,* and *Lernanthropus*; 2) loss of *Pumilopes*; 3) gain of *Shiinoa*; 4) gain of *Caligus*; 5) gain of *Tuxophorus*; 6) gain of *Unicolax*; 7) gain of *Ceratocolax* and *Caligus*; 8) gain of *Pseudocycnoides*; 9) loss of *Ceratocolax*. Autapomorphies are A) gain of *Clavellisa*; B) gain of *Elytrophora*; C) gain of *Homobomolochus, Unicolax,* and *Pseudocycnoides*; D) loss of *Unicolax* and gain of *Elytrophora*.

Bomolochus. The eight characters used are as follows: Number of setae on the exopod of leg 4 (many = plesiomorphic, few = apomorphic); presence or absence of surface ornamentation on the abdomen and caudal rami (presence = plesiomorphic, absence = apomorphic); first exopod segment of leg 2 with long hairs or short spinules (hairs = plesiomorphic, spinules = apomorphic); number of setae on the first maxilla (4 = plesiomorphic, 3 = apomorphic); number of setae on exopod last segment of leg 2 (5 = plesiomorphic, 4 = apomorphic); number of segments in first antenna (7 = plesiomorphic, 6 = apomorphic); endopod segments with a row of short hairs (plesiomorphic) or patch of fine spinules (apomorphic); exopod spines of leg 2 with fine hairs (plesiomorphic) or mostly toothed (apomorphic).

Phylogenetic relationships of the copepod parasites of the genus *Unicolax* are represented in the branching diagram (Fig. 19), generated with the

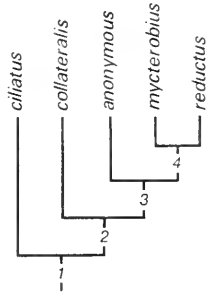

FIGURE 19.—Cladogram showing relationships of *Unicolax* species. The nodes (*1-4*) represent the following: *1* = species of *Unicolax*; *2* = teeth on leg 2 exopod spines; *3* = endopod segments with patches of spinules; *4* = fewer than 5 setae on fourth leg exopod.

WAGNER 78 program using characters of copepod morphology. The additive binary matrix of this tree is presented in Figure 20. Phylogenetic relationships of the scombrid hosts (Fig. 21) are adapted from Collette and Russo (1979) and represent a monophyletic sub-

	1	2	3	4	5	6	7	8	9
1									
2									
3									
4									
5									
6									
7									
8									
9									

FIGURE 20.—Additive binary matrix based on relationships of *Unicolax* parasites.

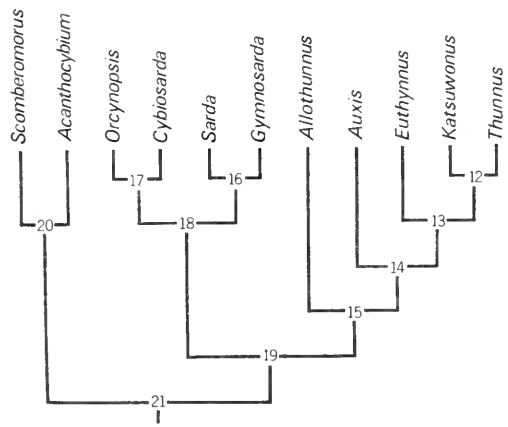

FIGURE 21.—Cladogram of scombrid hosts based on host morphology. Nodes 12-21 represent hypothetical ancestors.

set of the Scombridae. The additive binary matrix of this tree is presented in Figure 22.

In Figure 23 we have indicated the scombrid genera in the tribes Scomberomorini, Sardini, and Thunnini parasitized by *Unicolax,* based on the phylogeny of the Scombrinae proposed by Collette and Russo (1979). The copepod species are ranked from the most plesiomorphic (generalized) to the most apomorphic (specialized), based on the Wagner tree of *Unicolax* (Fig. 19).

As stated earlier, parasite phylogenies can be coded as characters and used to generate host trees; conversely, host phylogenies can be coded as characters and used to generate parasite trees (Brooks 1981). In cases where a host has more than one parasite or a parasite has more than one host the character states for the two series are inclusively OR'd (Copi 1972) and a single series is used. By logically OR'ing two characters, a character state is said to be present in the union of two groups, if and only if it is present in one or both groups. For example, in Figure 20, *Auxis* harbors *U. collateralis* (2) and *U. mycterobius* (4). The character states for a host bearing *U. collateralis* can be determined by reading across line 2 of the additive character matrix, that is a one or logical true for states 2, 8, and 9 and not true for the others. The character states for a host bearing *U. mycterobius* can be determined by reading across line 4, that is a one or logical true for states 4, 6, 7, 8, and 9 and not true for the others. Logically OR'ing the two rows of the matrix results in the character states 2, 4, 6, 7, 8, and 9 being true and the others being not true. Referring to the parasite tree (Fig. 19), these character states represent the host, *Auxis*, as having or having had during the course of its evolution (sensu lato) parasitic taxa (2) *U. collateralis*, (4) *U. mycterobius*, and hypothetical ancestors (1), (2), (3), and (4).

Proceeding in this manner for each host, a parasite (parasite ancestor) by host matrix is constructed. This matrix was subjected to cladistic character analysis using the WAGNER 78 program for optimization. The resulting Wagner tree (Fig. 24) is rooted at a hypothetical host ancestor without *Unicolax* parasites. According to Brooks' (1981) methodology, this tree is an estimate of host phylogeny in lieu of host morphological data. It estimates host phylogeny based on phylogenetic events of their parasites. Because we have a host phylogeny based on morphological data, a direct comparison between the two trees is possible. We attempt to explain the source of differences between the estimate of host phylogeny based on parasites and a cladogram based on host morphology.

The most notable difference is that the base, node (5) of the host by parasite tree (Fig. 24), is formed by an unresolved multicotomy. This has resulted because it is more parsimonious to assume that the four scombrid taxa, which lack *Unicolax,* never had them than to assume they were first acquired then lost. Node (4) is a subset of node (21) on the host phylogeny (Fig. 21) and is based on a common *Unicolax* ancestor [node 1, (Fig. 19)]. Node (3) is a subset of node (19) on the host phylogeny and is based on the presence of ancestor (2) and parasite (2), *U. collateralis.* An unresolved tricotomy is present at node (3) because the only parasite shared by the hosts *Cybiosarda* and *Orcynopsis* is *U. collateralis,* which is present below node (3) and is therefore treated as

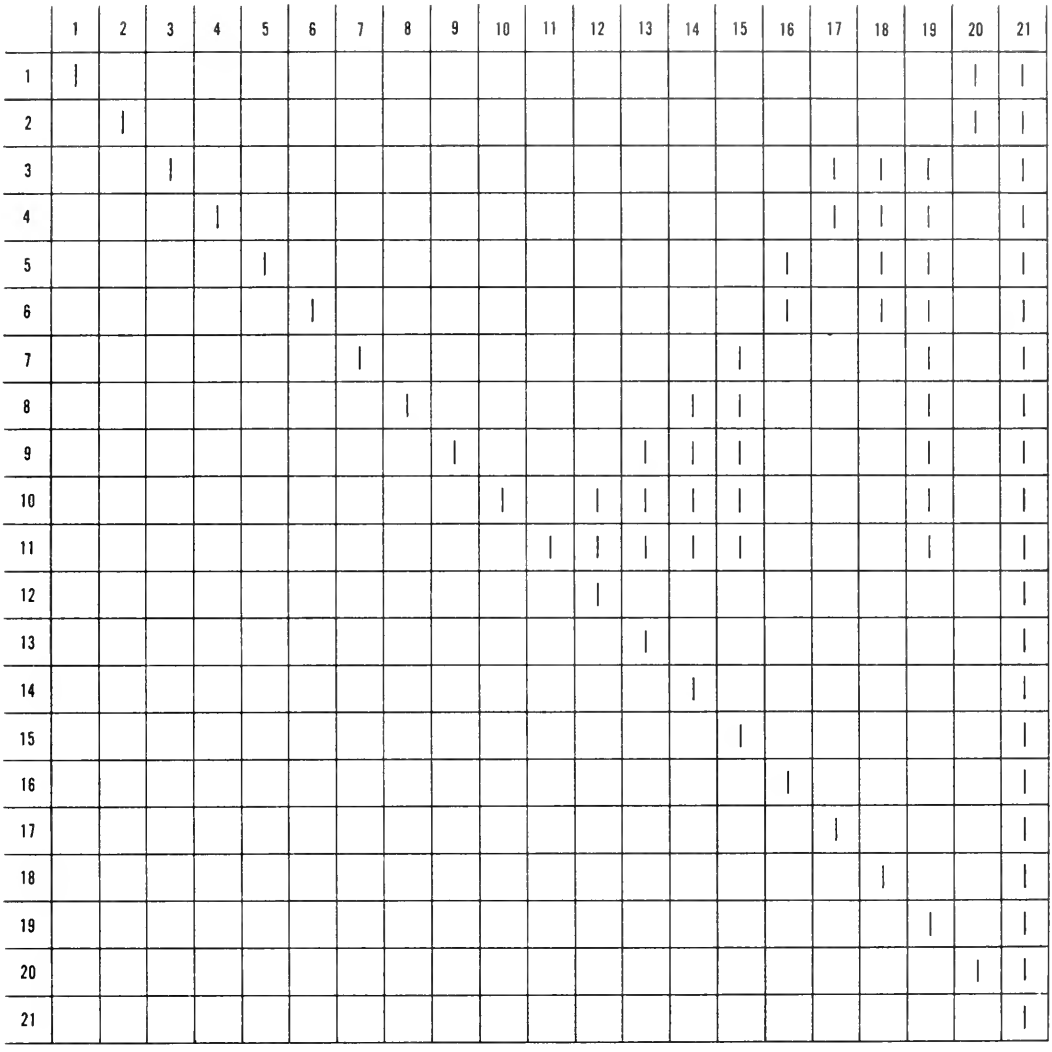

FIGURE 22.—Additive binary matrix based on scombrid relationships. Numbers 1-11 are host taxa and 12-21 are hypothetical ancestors represented in Figure 21.

synplesiomorphous. Node (2) is based on ancestors (2) and (4). Node (1) is an unresolved tricotomy and does not represent a subset of the host phylogeny because it includes *Sarda*. This node is based on the presence of parasite (4), *U. mycterobius*. Events which are not shared (autopomorphous) include the acquisition of (1), *Unicolax ciliatus* in *Scomberomorus*; the acquisition of (5), *U. reductus* and the loss of (2); *U. collateralis*, in *Katsuwonus*; and the acquisition of (3), *U. anonymous*, in *Euthynnus*. The loss of the parasite *U. collateralis* in *Katsuwanus* is the only homoplasy in the host by parasite tree.

The above procedure can also be used to generate a parasite phylogeny by using a data matrix constructed from information concerning host phylogeny. The parasite host tree (Fig. 25) is rooted at a nonscombrid ancestor based on the assumption that the common ancestor of *Unicolax* was from a nonscombrid. This tree (Fig. 25) can be compared with the tree representing parasite phylogeny, which is based on an analysis of parasite morphological characters (Fig. 19). Node (4) on the parasite by host tree (Fig. 25) is comparable with node (1) on the parasite phylogeny (Fig. 19). *Unicolax ciliatus* is the sister group of all other parasitic taxa in both trees. Node (3) of the parasite by host tree contains all elements of node (2) on the parasite phylogeny; however, *U. reductus* is removed as the sister group of other taxa on the

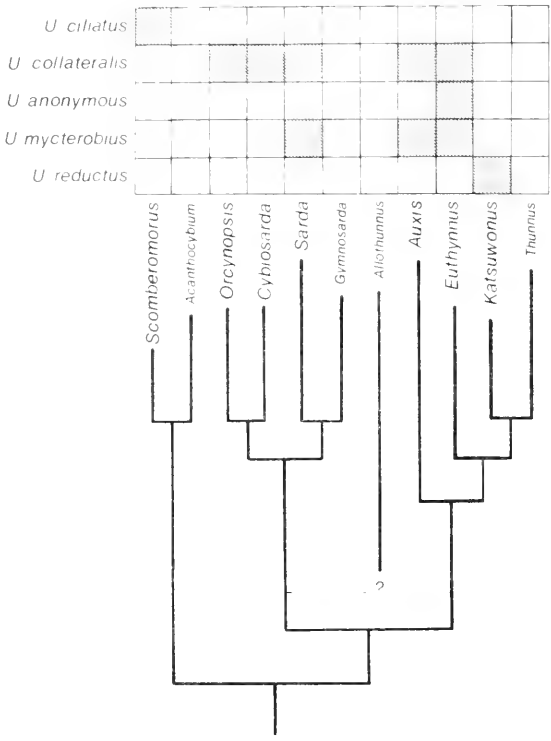

FIGURE 23.—Occurrence of species of *Unicolax* on scombrids in the tribes Scomberomorini, Sardini, and Thunnini. Copepods are ranked from most plesiomorphic (top) to most apomorphic (bottom). Scombrids are arranged to depict hypothesized phylogenetic relationships.

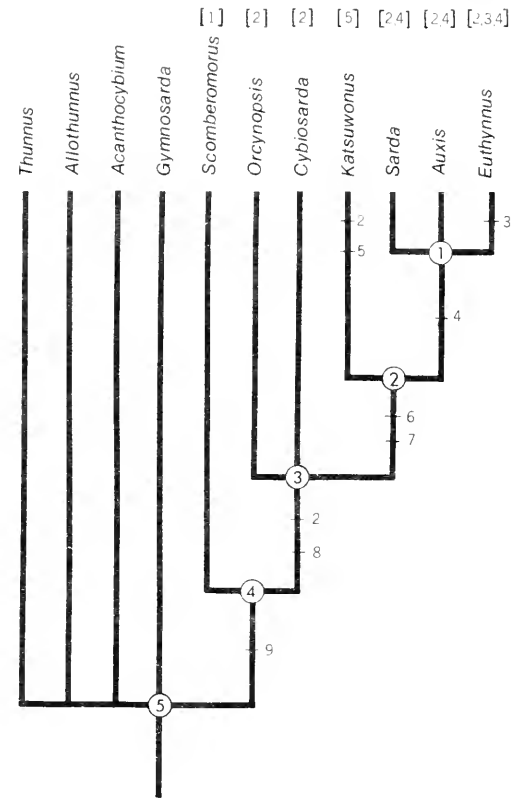

FIGURE 24.—Host tree based on parasitic phylogenetic information. Numbers in brackets at top of figure represent infestation by 1) *Unicolax ciliatus*, 2) *U. collateralis*, 3) *U. anonymous*, 4) *U. mycterobius*, and 5) *U. reductus*. Numbers crossing branches on tree represent acquisitions of parasites or parasite ancestors, except for number 2 leading to *Katsuwonus* which indicates a loss.

parasite by host tree whereas *U. collateralis* occupies this position on the parasite phylogeny. This discrepancy occurs because parasites *U. anonymous, U. collateralis,* and *U. mycterobius* are all found on the host *Euthynnus* (9), at node (2) on the parasite by host tree (Fig. 25). *Unicolax collateralis* and *U. mycterobius* are then grouped because they co-occur on host taxa 5 (*Sarda*) and 8 (*Auxis*) as well as nodes (16) and (18) of the host phylogeny (Fig. 21). Hypothesized hosts, which are not shared (autapomorphies), include *Scomberomorus* and host node (20) for *U. ciliatus, Katsuwonus* and host node (12) for *U. reductus,* and *Orcynopsis, Cybiosarda,* and host node (17) for *U. collateralis.* The parasite by host tree (Fig. 25) presents no homoplasy.

If we make the assumption that the host and parasite phylogenies, which are based on morphological data, are both true, how do we explain the current distribution of parasites on hosts? This question is analogous to questions of biogeography. We know by generating a host tree from parasitic phylogenetic information and by generating a parasite tree from host phylogenetic information that the two data sets are

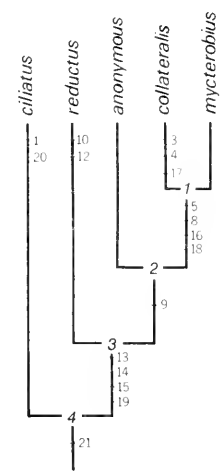

FIGURE 25.—Parasite tree of *Unicolax* species based on host phylogenetic information. Numbers crossing branches on tree represent historic infestations of hosts or host ancestors by parasites or parasite ancestors.

not concordant. We also know that several parts of these data sets are in agreement, that is to say, some evolutionary events in *Unicolax* are correlated with speciation (vicariant) events in the Scombridae. These events are easily explained by models of allopatric speciation and hypotheses of dispersal are unnecessary. Before we can suggest a dispersal event, we must first factor out host-parasite relationships which are due to cospeciation events. They may be done by overlaying parasitic phylogenetic data in the form of a character state tree on the host phylogeny. This procedure is similar to the generation of the host by parasite tree (Fig. 24), with the exception that the parasite phylogenetic information is forced onto the host cladogram.

In our example the scombrid host tree was coded as a character state tree. A character by scombrid taxon matrix was constructed so that each character was repeated a number of times. To this we added the characters from the parasite phylogeny by host data matrix used to generate the host by parasite tree. The repetition of the character by scombrid taxa matrix has the effect of forcing the tree into a particular shape, in our case, the original host cladogram. The number of replicates is large enough so the parasite phylogeny data does not alter the outcome of the tree. This combined data matrix was submitted to the WAGNER 78 program and a most parsimonious tree was generated. This tree (Fig. 26) is the same shape as the original host phylogeny, and characters relating to historical events of the parasites are overlayed or forced onto the tree in a parsimonious configuration.

The overlay presented in Figure 26 indicates that parasite evolutionary events (−2), (17), (−8), and (−9) (indicated as characters circled in broken lines) were reversed or lost in several host taxa or lineages. This indicates the loss of a parasite or a hypothetical ancestral parasite. The only independent acquisition of parasites or hypothetical ancestral parasites occurred between *Sarda*, node (8), and *Auxis* on the cladogram. In both cases parasite 4, *U. mycterobius*, and its hypothetical ancestors (6) and (7) not only were independently acquired but also must have been independently evolved. In this case it is more reasonable to invoke an hypothesis of dispersal and to explain the infestation of *Sarda* by *U. mycterobius* by dispersal from another scombrid host. This hypothesis is more parsimonious than the coevolutionary hypothesis in that it requires one dispersal event rather than a series of independent identical evolutionary events (having serious taxonomic implications for parasitic taxa, i.e., if two taxa evolve in independent lineages they must be considered separate, possibly sibling species). It must be noted that an hypothesis of independent evolutionary events leading to the establishment of *U. mycterobius* on *Sarda* may in itself require a dispersal event earlier in its evolutionary history.

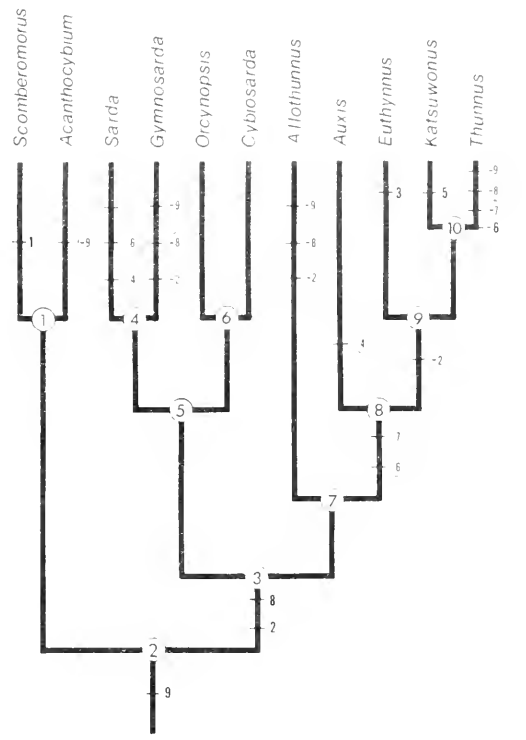

FIGURE 26.—Overlay of historical parasite information on host phylogeny. Negative numbers indicate losses and numbers circled in broken lines indicate independent acquisitions or losses of parasites or parasite ancestors.

The coevolution of *Unicolax* and its scombrid hosts can be reconstructed as follows. The three higher tribes of the Scombrinae (Scomberomorini, Sardini, and Thunnini) share *Unicolax,* indicating that this genus arose from a more primitive bomolochid after the ancestors of these three tribes evolved from the Scombrini. *Unicolax ciliatus,* the most primitive species of *Unicolax,* is present only in the most primitive of the three tribes, the Scomberomorini. *Unicolax collateralis* is found on members of the tribes Sardini and Thunnini. Infestation by *U. anonymous* yields little information because it is restricted to *Euthynnus alletteratus* from both sides of the Atlantic. It is apparently a more recently derived species that has not spread far geographically or host-wise. *Unicolax mycterobius* is restricted to the two most primitive genera of the Thunnini (*Auxis* and *Euthynnus*) except for its presence on two specimens of *Sarda orientalis* from Japan. This seems best explained as

dispersal from its usual host. It may be an example of a parasite species utilizing an alternate host in the absence of its preferred host. Finally, *U. reductus*, the most specialized species of *Unicolax*, has been found only on a highly specialized host, *Katsuwonus*. This indicates that *Katsuwonus* evolved from the *Euthynnus* stock, and *U. reductus* evolved from the ancestor of *U. mycterobius*.

It should be noted that, in each of the three tribes, *Unicolax* was not found in the most specialized scombrid genus. In *Thunnus* this may be the result of competition resulting from heavy infestations of the monogenetic trematode, *Nasicola klawei* (Stunkard), in the nasal sinuses of the host fish. There is no evidence, however, that parasite competition is a factor in *Acanthocybium*, *Gymnosarda*, and *Allothunnus*. It may be that as each of the tribes evolve, the most specialized members lose parasites. This concept is consistent with other data presented elsewhere in this paper (see *Scomberomorus* infestation data in Table 6 and *Sarda* parasite discussions).

COMPARISON OF COPEPOD PARASITES IN SCOMBRIDAE AND BELONIDAE

After completing the analysis of the parasitic copepods of the Scombridae, it seemed instructive to make comparisons with those of the Belonidae, the only other family of fishes that has been studied in a similar manner (Cressey and Collette 1970). The Scombridae (48 species) is a larger family than the Belonidae (32 species). All scombrids are marine species, although several enter estuaries and only *Scomberomorus sinensis* is found far up the Mekong River. Four genera of Belonidae (*Belonion*, *Potomorrhaphis*, *Pseudotylosurus*, and *Xenentodon*) plus three species of *Strongylura* are restricted to freshwater, and populations of several other species of *Strongylura* invade freshwater long enough to acquire freshwater parasites. Thus, parasites of the family Ergasilidae (nine species) must be omitted in any comparisons because they are restricted to hosts in freshwater. Several other families of copepods cannot be used because their habitat does not occur in the host group. Species of Shiinoidae live inside the nasal cavities of their host, attached to the lamellae of the nasal rosettes. Belonidae have an open nasal pit with no place for a *Shiinoa* to attach. Scombrid species breathe largely by ram-jet ventilation of the gills and so have small oral valves in the upper and lower jaws, apparently too small to house the caligid copepod *Caligodes* which was found on seven species of Belonidae. Several species of the caligid genus *Caligus* were found on needlefishes but all in small numbers, partially because Cressey and Collette's study used mostly preserved specimens that were prone to lose parasites like *Caligus*, which are mostly external.

Two ecological habitats, parasitized by three families of copepods in the two families of fishes, seem comparable—gills and oropharyngeal cavity. Bomolochid copepods are found in the oropharyngeal cavity of both host families (and also in the nasal cavities of the Scombridae). Species of the closely related families Lernanthropidae and Pseudocycnidae attach permanently to the gills of belonids and scombrids, respectively (Table 10).

Comparison of the parasitic copepod fauna of the most speciose genera of each family, *Strongylura* and *Scomberomorus*, reveals some interesting distributional patterns. *Bomolochus bellones*, the common bomolochid of *Strongylura*, extends from the

TABLE 10.—Comparison of parasitic copepod fauna on gills (Lernanthropidae and Pseudocycnidae) and oropharyngeal cavities (Bomolochidae) in genera from the Belonidae (*Strongylura*) and Scombridae (*Scomberomorus*).

Strongylura		*Scomberomorus*
5 species	Indo-West Pacific	10 species
Bomolochus bellones (5/5)		*Unicolax ciliatus* (9/10)
Bomolochus sinensis (1/5)		*Pseudocycnoides armatus* (8/10)
Nothobomolochus digitatus (1/5)		*Pseudocycnoides scomberomori* (1/10)
Lernanthropus belones (3/5)		
Lernanthropus tylosuri (5/5)		
S. senegalensis	Eastern Atlantic	*S. tritor*
Bomolochus bellones		*Unicolax ciliatus*
3 species	Western Atlantic	4 species
Bomolochus bellones (3/3)		*Holobomolochus divaricatus* (3/4)
Lernanthropus belones (3/3)		*Holobomolochus asperatus* (1/4)
Lernanthropus tylosuri (2/3)		*Pseudocycnoides buccata* (4/4)
2 species	Eastern Pacific	2 species
Bomolochus constrictus (2/2)		*Holobomolochus nudiusculus* (2/2)
Bomolochus ensiculus (2/2)		*Pseudocycnoides buccata* (2/2)
Lernanthropus belones (2/2)		
Lernanthropus tylosuri (1/2)		

Indo-West Pacific through the eastern Atlantic to the western Atlantic Ocean. It is replaced by two species of bomolochids in the eastern Pacific—*B. constrictus* and *B. ensiculus*. *Unicolax ciliatus*, the common bomolochid of *Scomberomorus*, extends from the Indo-West Pacific to the eastern Atlantic. It is replaced in the western Atlantic by *H. divaricatus* and *H. asperatus* and in the eastern Pacific by *H. nudiusculus*.

The gill parasites, *Lernanthropus* and *Pseudocycnoides*, show a similar pattern. The two species of *Lernanthropus*, being circumglobal, extend farther than *Bomolochus* does. *Pseudocycnoides armatus* is found on species of *Scomberomorus* in the Indo-West Pacific. It is replaced in the western Atlantic and eastern Pacific by *P. buccata*. No *Lernanthropus* or *Pseudocycnoides* were found on the single host species of *Strongylura* and *Scomberomorus* in the eastern Atlantic.

Host specificity at the generic level depends on factors such as the number of species in a given host genus, maximum body size of the host species, and distribution of the host species. The most speciose genera in each family (*Scomberomorus* with 18 of 47 species in the Scombrinae and *Strongylura* with 14 of 32 species in the Belonidae) have the most copepod species, 50 and 85%, respectively, of the total parasite fauna recorded for these two families (Table 11). However, if one calculates a mean number of copepod species per host species, a different picture emerges. In both fish families, monotypic genera, including large pantropical species, contain the most copepod species per host species, *Acanthocybium* and *Katsuwonus* in the Scombridae with 6 of 46 species of copepods and *Ablennes* in the Belonidae with 9 of 21.

The genera with the next highest number of copepod species per host species are moderate-sized species, *Euthynnus* (three species) with 3.7 copepod species per host species in the Scombridae and *Platybelone* (monotypic) with 7 of 21 in the Belonidae. The three genera with the lowest number of parasitic copepods per host species in the Belonidae (0-0.5) are a special case, without parallel in the Scombridae, small (4-28 cm body length) freshwater South American species. No copepods were found on the South African monotypic *Petalichthys* but only a few host specimens were examined.

ACKNOWLEDGMENTS

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TABLE 11.—Number of parasitic copepod species per genus and maximum size of Belonidae and Scombridae. (Maximum size of belonid species given in cm body length and of scombrid species in cm fork length.)

Belonidae					Scombridae				
Genus	No. spp.	Max. size (cm BL)	No. spp. copepods	x̄ no. copepod spp. /host spp.	Genus	No. spp	Max. size (cm FL)	No. spp. copepods	x̄ copepod spp. /host spp.
Ablennes	1	73	9	9	*Acanthocybium*	1	183	6	6
Belone	2	32-53	3	1.5	*Allothunnus*	1	96	3	3
Belonion	2	4	0	0	*Auxis*	2	40-50	6	3
Petalichthys	1	21	0	0	*Cybiosarda*	1	42	3	3
Platybelone	1	30	7	7	*Euthynnus*	3	64-100	11	3.7
Potamorrhaphis	3	10-16	1	0.5	*Grammatorcynus*	1	100	5	5
Pseudotylosurus	2	20-28	1	0.5	*Gymnosarda*	1	108	3	3
Strongylura	14	23-59	18	1.3	*Katsuwonus*	1	100	6	6
Tylosurus	5	39-130	11	2.2	*Orcynopsis*	1	130	2	2
Xenentodon	1	17	2	2.0	*Rastrelliger*	3	20-35	5	0.7
					Sarda	4	50-85	9	2.3
					Scomber	3	40-50	6	2.0
					Scomberomorus	18	30-220	23	1.3
					Thunnus	7	90-300	10	1.4
Totals	32		21	0.68		47		46	0.98

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APPPENDIX

Below is a list of scombrid hosts and their parasitic copepods. Numbers after fish names indicate the number of fish examined. Numbers after copepod names indicate number of fish infested. Asterisks indicate new record since Cressey and Cressey (1980).

SCOMBRINI

Rastrelliger brachysoma (33)
Lernanthropus kanagurta (1)
Rastrelliger faughni (14)
Pumiliopes jonesi (2)
Nothobomolochus kanagurta (2)
Orbitacolax aculeatus (2)
Rastrelliger kanagurta (124)
Pumiliopes jonesi (20)
Nothobomolochus kanagurta (7)
Caligus kanagurta (2)*
Orbitacolax aculeatus (2)*
Scomber australasicus (55)
Pumiliopes jonesi (5)*
Clavellisa scombri (4)
Scomber japonicus (500)
Clavellisa scombri (9)
Pumiliopes jonesi (8)
Caligus pelamydis (1)
Caligus mutabilis (1)
Clavelopsis saba (1)
Scomber scombrus (97)
Caligus pelamydis (1)

SCOMBEROMORINI

Acanthocybium solandri (64)
Brachiella thynni (39)
Gloiopotes hygomianus (27)
Caligus productus (11)
Shiinoa occlusa (2)
Caligus coryphaenae (1)
Pennella species (1)
Tuxophorus cybii (1)
Grammatorcynus bicarinatus (47)
Shiinoa occlusa (9)
Caligus asymmetricus (7)
Caligus regalis (4)*
Caligus bonito (1)*
Caligus pelamydis (1)*
Caligus productus (1)*
Scomberomorus brasiliensis (62)
Pseudocycnoides buccata (39)
Holobomolochus divaricatus (14)
Caligus mutabilis (4)
Shiinoa inauris (3)
Scomberomorus cavalla (36)
Pseudocycnoides buccata (18)
Holobomolochus asperatus (10)
Caligus mutabilis (2)
Caligus productus (1)
Scomberomorus commerson (130)
Pseudocycnoides armatus (25)
Unicolax ciliatus (23)
Caligus cybii (16)
Shiinoa occlusa (15)
Caligus biseriodentatus (12)
Caligus infestans (7)
Tuxophorus cervicornis (3)
Brachiella magna (2)
Caligus asymmetricus (2)
Tuxophorus cybii (1)
Scomberomorus concolor (47)
Pseudocycnoides buccata (14)
Holobomolochus nudiusculus (13)
Caligus omissus (7)
Scomberomorus guttatus (58)
Caligus biseriodentatus (17)
Unicolax ciliatus (14)
Pseudocycnoides armatus (3)
Shiinoa occlusa (1)
Scomberomorus koreanus (19)
Caligus cybii (11)
Pseudocycnoides armatus (4)
Unicolax ciliatus (1)*
Scomberomorus lineolatus (14)
Unicolax ciliatus (3)
Caligus biseriodentatus (1)
Pseudocycnoides armatus (1)
Scomberomorus maculatus (77)
Pseudocycnoides buccata (27)
Holobomolochus divaricatus (25)
Shiinoa inauris (7)
Caligus mutabilis (2)
Scomberomorus munroi (6)
Caligus cybii (3)
Unicolax ciliatus (2)
Caligus biseriodentatus (1)*
Caligus productus (1)
Scomberomorus multiradiatus (29)
Pseudocycnoides armatus (8)
Caligus biseriodentatus (7)*
Scomberomorus niphonius (19)
Pseudocycnoides scomberomori (6)
Unicolax ciliatus (3)
Caligus pelamydis (2)
Shiinoa occlusa (1)
Scomberomorus plurilineatus (14)
Pseudocycnoides armatus (12)
Unicolax ciliatus (4)*
Brachiella thynni (1)*
Caligus asymmetricus (1)*
Shiinoa occlusa (1)*
Scomberomorus queenslandicus (39)
Caligus biseriodentatus (12)
Unicolax ciliatus (3)
Pseudocycnoides armatus (2)
Caligus cybii (1)*
Shiinoa occlusa (1)
Scomberomorus regalis (38)
Pseudocycnoides buccata (12)
Holobomolochus divaricatus (11)
Shiinoa inauris (5)
Caligus productus (3)
Caligus bonito (1)
Brachiella thynni (1)
Tuxophorus collettei (1)
Scomberomorus semifasciatus (26)
Pseudocycnoides armatus (5)
Unicolax ciliatus (4)
Caligus cybii (3)
Shiinoa occlusa (2)*
Caligus biseriodentatus (1)*
Scomberomorus sierra (116)
Pseudocycnoides buccata (48)
Caligus omissus (39)
Holobomolochus nudiusculus (28)
Scomberomorus sinensis (10)
Caligus cybii (2)
Brachiella magna (1)
Caligus pelamydis (1)*
Scomberomorus tritor (21)
Unicolax ciliatus (4)
Shiinoa occlusa (1)
Caligus productus (1)
Caligus diaphanus (1)

SARDINI

Sarda sarda (106)
Caligus bonito (33)
Ceratocolax euthynni (21)
Caligus pelamydis (8)
Caligus productus (1)
Sarda australis (22)
Caligus bonito (13)
Caligus pelamydis (11)
Caligus asymmetricus (2)
Unicolax collateralis (2)
Sarda chiliensis (45)
Caligus bonito (25)
Caligus pelamydis (4)
Caligus productus (1)
Sarda orientalis (33)
Unicolax collateralis (12)
Caligus bonito (12)
Caligus asymmetricus (4)
Caligus kanagurta (2)*
Caligus productus (1)
Caligus coryphaenae (1)*
Unicolax mycterobius (1)*
Gymnosarda unicolor (7)
Caligus bonito (1)
Caligus productus (1)
Shiinoa occlusa (1)
Cybiosarda elegans (38)
Unicolax collateralis (16)
Caligus asymmetricus (3)
Caligus bonito (1)*
Orcynopsis unicolor (7)
Unicolax collateralis (1)
Caligus bonito (1)*
Allothunnus fallai (7)
Elytrophora brachyptera (5)
Caligus bonito (2)*
Caligus productus (1)*

THUNNINI

Auxis species (68)
Unicolax collateralis (19)
Unicolax mycterobius (9)
Caligus productus (2)
Caligus asymmetricus (1)
Caligus coryphaenae (1)
Caligus pelamydis (1)
Euthynnus affinis (74)
Unicolax collateralis (32)
Caligus asymmetricus (5)
Caligus regalis (5)
Pseudocycnus appendiculatus (4)
Unicolax mycterobius (3)
Caligus pelamydis (2)
Caligus productus (1)
Caligus bonito (1)
Euthynnus alletteratus (64)
Caligus coryphaenae (9)
Unicolax collateralis (8)
Ceratocolax euthynni (7)
Caligus productus (5)
Caligus bonito (4)
Pseudocycnus appendiculatus (3)
Unicolax mycterobius (3)
Unicolax anonymous (2)
Caligus pelamydis (1)
Euthynnus lineatus (15)
Unicolax collateralis (4)
Caligus bonito (3)
Katsuwonus pelamis (135)
Caligus productus (54)
Caligus coryphaenae (51)
Pseudocycnus appendiculatus (8)
Unicolax reductus (3)
Caligus bonito (2)*
Caligus asymmetricus (1)
Thunnus alalunga (13)
Elytrophora brachyptera (8)
Caligus coryphaenae (1)
Caligus productus (1)
Pseudocycnus appendiculatus (1)
Thunnus albacares (112)
Caligus productus (51)
Elytrophora brachyptera (39)
Caligus coryphaenae (32)
Pseudocycnus appendiculatus (21)
Brachiella thynni (8)
Caligus asymmetricus (1)
Thunnus atlanticus (76)
Caligus productus (70)
Caligus coryphaenae (9)
Elytrophora brachyptera (1)
Thunnus maccoyii (7)
Elytrophora brachyptera (5)
Caligus productus (1)*
Pseudocycnus appendiculatus (1)*
Thunnus obesus (42)
Elytrophora brachyptera (20)
Caligus coryphaenae (18)
Brachiella thynni (10)
Elytrophora indica (11)
Pseudocycnus appendiculatus (3)
Thunnus thynnus (57)
Caligus coryphaenae (16)
Caligus productus (16)
Elytrophora brachyptera (11)
Pennella species (3)
Brachiella thynni (2)
Caligus bonito (1)
Pseudocycnus appendiculatus (1)
Thunnus tonggol (29)
Pseudocycnus appendiculatus (7)
Caligus kanagurta (1)*

POPULATION ASSESSMENT OF THE GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*, FROM CALIFORNIA SHORE CENSUSES, 1967-80

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ABSTRACT

Estimates of abundance by year were developed for the California-Chukotski stock of gray whales, from a 13-year consecutive series of shore censuses, conducted near Monterey, Calif. Annual estimates of population size range from a low of 10,414 for 1971-72 to a high of 17,577 for 1979-80. Standard errors are about 10% of population estimates. During the 13 years censused, the population increased annually by 2.5%, concurrent with a 1.2% harvest in the Soviet subsistence fishery, indicating a 3.7% net annual productivity.

Seasonal migratory timing was relatively constant during the study period. Gamma probability density function models of the annual migrations past Monterey had an overall mean day of 9 January, with a range from 8 to 19 January. A slight depression in mean hourly count for 0070-0800 h, during 1978-79 and 1979-80, contrasted with a constant mean hourly count through 10 daylight hours during the previous 11 years. Aerial surveys of the offshore distribution of southward migrating whales during 1979-80 agreed closely with those reported for 1978-79, indicating that 40% pass within 1 mile (1.6 km) of shore and 90% within 2 miles (3.2 km). In the shore censuses, about 20% of the passing whales were missed due to their distance offshore.

The estimation of population size for large whales has traditionally been based upon information derived from exploitation, e.g., catch per unit effort, mark-recapture, or related data (Allen 1980). Because of the recent decline in exploitation of marine mammals, assessment techniques based upon sighting surveys are increasing in importance (Eberhardt et al. 1979). The annual migration of the California stock of gray whales, *Eschrichtius robustus* (Lilljeborg 1861), makes it especially well suited to assessment by means of sighting surveys. Assessment studies on this stock can potentially aid in the development of sighting survey field and analysis techniques, especially those in which the observer is stationary and the population mobile. This paper presents some recent developments in the use of shore-based census data for whale population assessment, and the results of the 1979-80 gray whale census. Revised population estimates for the previous 12 annual censuses are also reported, along with a consideration of change in population size during the period 1967-80.

Each year during the northern winter the California stock of gray whales migrates from feeding waters in the Bering and Chukchi Seas, south along the west coast of North America, to calving areas in Mexical waters (Fig. 1); the stock returns to the Arctic in the spring (Rice and Wolman 1971). In many places along the route, the whales pass very close to land (Gilmore 1960; Pike 1962; Rice and Wolman 1971; Rugh and Braham 1979). Consequently, it is feasible to census the migrating whales visually from strategic points along the shore.

Early shore-based censuses were summarized by Reilly et al. (1980). Systematic censuses of southward migrating gray whales were initiated during the winter of 1967-68 at both Point Loma (lat. 32°40'N; 130 m above sea level) in San Diego, Calif., and at Yankee Point (lat. 36°29'N; 23 m above sea level) near Monterey, Calif. The San Diego count was conducted intermittently until 1977-78, for a total of 5 yr. The San Diego data were not analyzed in this study because an unverified proportion of the population passes far offshore south of Point Conception (Rice 1965) and because the migration route may have been influenced by increased boat traffic (Rice 1965; Reeves 1977). The Monterey census was conducted each year for 13 yr up to and including 1979-80. Beginning in 1975-76 the counting station was moved 3.7 km south to Granite Canyon (21 m above sea level) due to real estate development of the Yankee Point site. The Monterey data were used as the basis for this study, because they form a continuous time series and are less complicated by coastal geography and boat traffic than the San Diego data.

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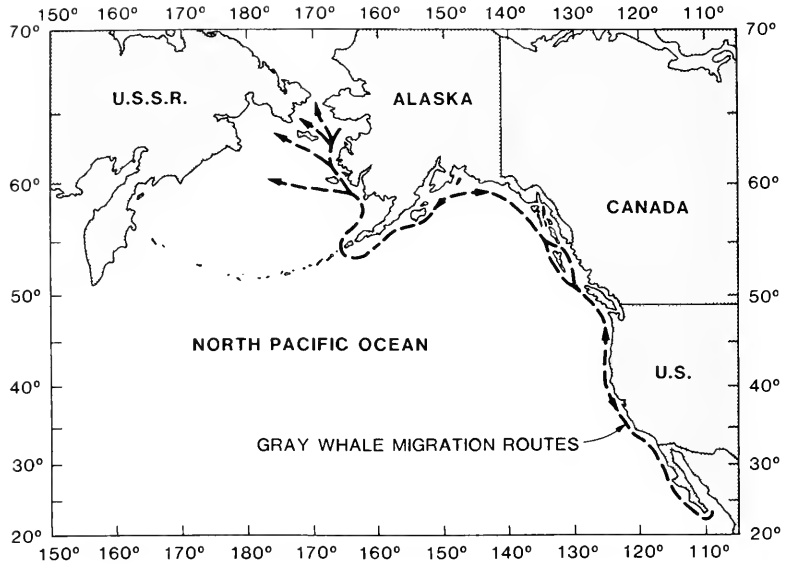

FIGURE 1.—The approximate migration route of the California stock of gray whales.

To estimate total abundance by extrapolating from recorded counts of passing whales one must determine the following:

1) What proportion of the population, if any, passes beyond sight of the observers? Does this change with time or experience? How does the observer's accuracy in estimating the distance to passing whales vary with distance?
2) Are there diel variations in migration rate? How can daylight counts be used to estimate the number of whales passing at night?
3) How do weather (visibility) conditions affect census results?
4) Does the observer's ability to count the number of individuals within a passing group vary with group size?
5) Are the initiation and termination of the migration fully represented in the data?

During the 1978-79 southward migration we conducted two types of verification experiments aimed at addressing the questions of points 1 and 4 above. These were reported in detail in Reilly et al. (1980). In one experiment we tested 12 observers simultaneously for accuracy in estimating distances to and numbers within 50 events in which whales passed the Granite Canyon station. The observers estimated the distance offshore to within one of seven predefined distance intervals, as during the actual annual censuses (see Methods). We found significant heterogeneity between observers for both distance and count estimates. Given this heterogeneity, there were also consistent biases recorded: In placing whales to within correct intervals out to 1 mi (1.6 km) and beyond 1.5 mi (2.4 km), and in estimating the true number of individuals present in groups of one whale, and four or more. Further analysis of this data (Reilly 1981) indicated that "experienced" observers were on average no more accurate than inexperienced observers, but somewhat more precise.

A second experiment was conducted during 1978-79 to characterize the width of the migration corridor offshore from the Monterey counting stations (Reilly et al. 1980). A small aircraft flew a series of transects perpendicular to the coast in the vicinity of the stations, recording locations of sighted whales (Fig. 2). The results indicated that, contrary to previous assumptions and characterizations of 95% of the population passing within 1.6 km (Rice and Wolman 1971; Sund and O'Connor 1974), we found only about 40% within 1.6 km, with significant numbers passing offshore between 1.6 and 4.5 km. This experiment was repeated during 1979-80, with results reported here.

Regarding night migration rate (point 2 above), after a review of all available information, we accepted an assumption of a constant 24-h rate. Contrary to the earlier report of Ramsey (1968), we found no evidence of a diurnal fluctuation from the shore census data. During the 1979-80 migration a new (prototype) infrared image sensor, supplied by the U.S. Department of Defense, was tested at Granite Canyon. As with previously tested night-vision devices (Reilly et al. 1980), it proved unsatisfactory.

The possible effect of visibility conditions on cen-

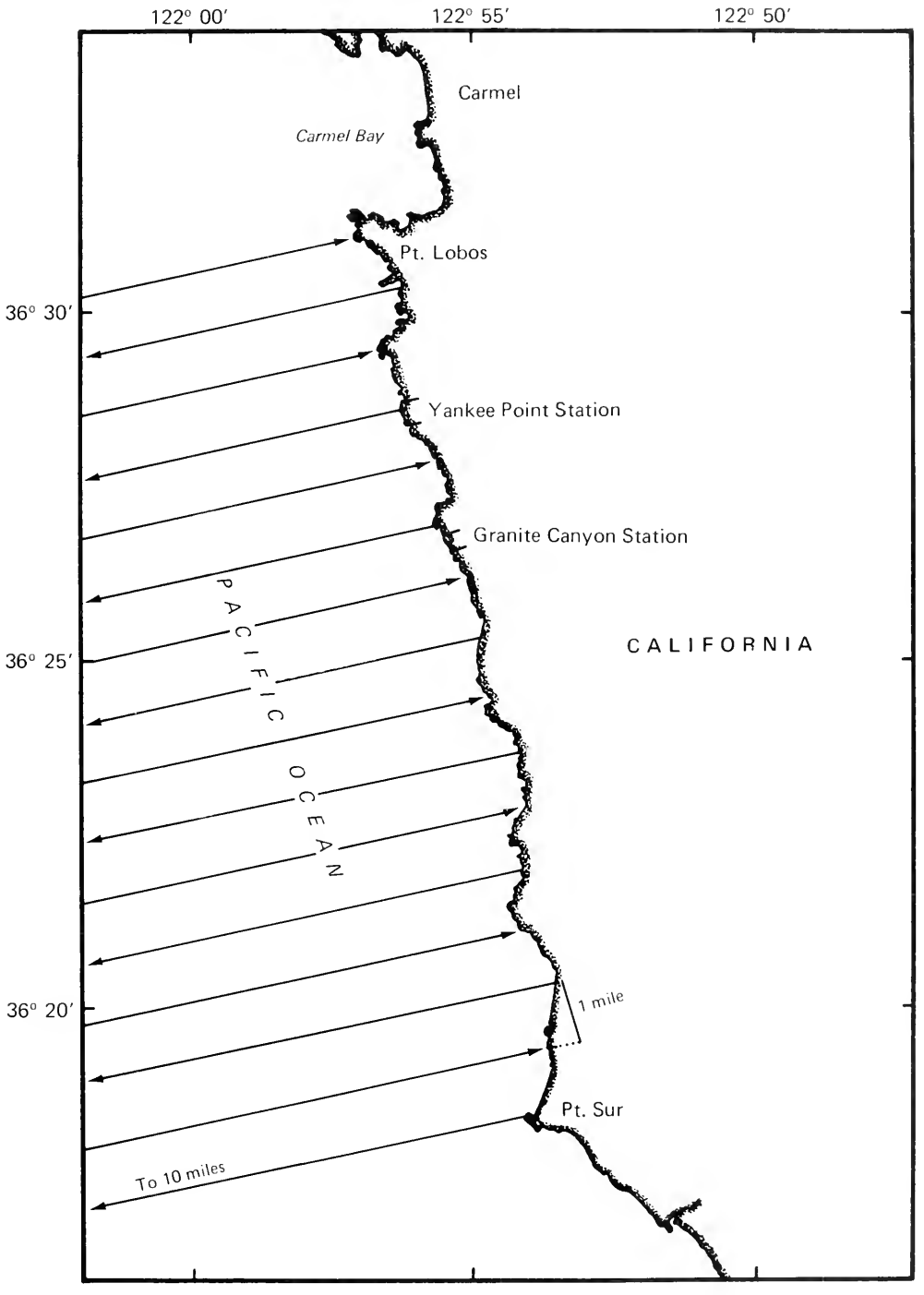

FIGURE 2.—The California coast south of Monterey, showing census stations and aerial transect lines for gray whale study.

sus results was not addressed in Reilly et al. (1980). We report here a quantitative appraisal of this effect, and account for it in our abundance estimation.

METHODS

Field Methods: Shore Census

The exact seasonal duration of the annual census changed only slightly from year to year, but it usually began on or before 10 December and ended on or after 6 February (59 d). The watch was conducted between 0700 and 1700 h, 7 d a week, by two observers who alternated 5-h shifts.

The observers watched to the north for southward swimming whales to come into view. At first sighting of a whale or group of whales the time was recorded and an initial estimate was made of the number of whales in the group. The whales were kept under observation until they were directly offshore from the station, usually about 0.5 h later. At that time a final estimate of the number present was recorded, along with the time and an estimate of the distance of the animals offshore. Distance estimates were classified in seven intervals: 0-0.25; 0.25-0.50; 0.50-0.75; 0.75-1.0;1.0-1.5; 1.5-2.0; 2.0+ mi. Beaufort Sea state, wind direction, and notes on visibility conditions were recorded continuously throughout the day. Binoculars (7 × 50) were used regularly. Beginning in 1978-79, visibility conditions were assigned one of six ordinal categories (Table 1) for each pod observed. For data prior to 1978-79, visibility conditions were classified to within these categories during the analysis, based upon information recorded systematically during the censuses.

TABLE 1.—Gray whale census—Granite Canyon visibility codes.

Code	Condition	Description
01	Excellent	Clear day, or high clouds. No glare. Horizon visible. Effective sighting distance = 3+ mi.
02	Very good	Clear or some cloud cover. Some glare, surface ripple. Effective sighting distance = 2-3 mi.
03	Good	Some fog, haze, low clouds. Some interference from chop, surf, or glare. Effective sighting distance = 1-2 mi.
04	Fair	Fog, full overcast, light rain, haze with glare. Frequent whitecaps. Effective sighting distance = 0.5-1 mi.
05	Poor	Moderate rain or fog, large surf, bad glare, etc. Effective sighting distance = 0.25-0.5 mi.
06	None	Combination of conditions make it very difficult or impossible to see even the closest (within 0.5 mi.) whales. Heavy rain, dense fog, near darkness, etc.

Analysis Methods: Shore Census

Occasionally during the censusing, only one of the standard two sighting times per group (when first seen and when directly offshore) was recorded. Frequently when an observer came on duty at 0700 h there were whales directly offshore and no "north time" was recorded. In addition, at the end of the day at 1700 h, whales which had not yet passed directly in front of the station were often sighted to the north, and no "south time" was recorded. To correct for missing time records, a mean difference between the two times was calculated for each observer individually. Missing time records were then generated from this average, and the single time record available. The time when the animals were directly offshore was then used to categorize data for time of day analyses. Only sightings with this time falling between 0700 and 1700 h were used for abundance estimation.

The results of the 1978-79 and 1979-80 half-day observation periods were investigated by analysis of variance (ANOVA) for differences between observers and between morning vs. afternoon periods on rate of recording animals, as was previously done (Reilly et al. 1980) for the 1967-68 through 1977-78 data. We also examined the two most recent censuses for possible changes in hourly rates of recorded counts, as done previously for the 1967-68 through 1977-78 data. Again, we looked for significant depressions in the counts both at the ends of the 5-h observer periods (as an indication of observer fatigue) and at the beginning and end of the day (as an indication of daylight-mediated change in migration rate).

For any migratory species which can be censused feasibly from a fixed point, the distribution of daily counts, transformed to proportions for each migration, can be viewed profitably as a time-density distribution and modeled by various probability density functions (Mundy 1979). We previously assumed a normal distribution (Reilly et al. 1980) for all years pooled. Problems with this approach were that mean days between years were not equal and that a slight but consistent skewness occurred causing lack of fit. Consequently we have replaced the normal distribution with the more flexible gamma distribution (Pearson's Type III; Bury 1975) and modeled each year separately. The time-density model for each migration was then employed in three ways:

1) To estimate the number of whales having passed the station before the first and after the last day of the census (the "tails").
2) As a standard for comparison with observed daily results, in a determination of if, and to what degree, conditions associated with the six visibility categories affect census results.

3) To estimate the proportion of the population passing the census station on days for which the visibility conditions were worse than a critical value, as determined by the results of the visibility analysis (2).

The data on pod-size estimation from all years were examined both for differences between years and for a pattern in distance from shore.

The offshore distance frequency distribution of observations was investigated for significant differences between the two locations, as a preliminary to post facto application of correction factors for whales missed offshore.

Field Methods: Verification Experiments

The aerial transects to determine the offshore distribution of the migratory corridor were repeated in 1979-80 following our previous methods (Reilly et al. 1980). We flew a Cessna 172[3] aircraft at 305 m (1,000 ft) altitude, at a speed of 145 km/h (90 mi/h), along a series of predefined tracklines (Fig. 2). These lines were situated along a 25 km stretch of the coast which included both the Yankee Point and Granite Canyon census stations. Distances of whales from shore were calculated from the timed difference between their position and the shore edge, and the plane's speed. During 1979-80 we flew a total of 13 flights for 34 h, in periods of good to excellent visibility. Flights were continued until a number greater than the minimum sample size of whales was obtained (330) for 90% precision in correctly classifying the population into the seven distance intervals used in the shore census (Reilly et al. 1980). Sample-size determination was based upon Cochran's (1977:74-76) formulae for sampling for proportions. Data from the 1974-75 shore counts were used as a presample of the proportions expected within the distance intervals from shore. The seven-interval experimental design also presented the opportunity to analyze the data in a pooled, less demanding interval scheme, with resulting higher precision in estimating the within-interval proportions.

Additive bias corrections were previously determined from the results of the observer bias experiments regarding estimation of the number of whales present in passing groups. Specifically for estimates of group size n (see Appendix 1 for explanation of notation)

$$E[n] = \hat{n} + b_n = \begin{cases} n + 0.350 & n = 1 \\ n + 0.00 & n = 2,3 \\ n + 0.333 & n \geq 4 \end{cases} \quad (1)$$

with variances as in Appendix 2.

Analysis Methods: Verification Experiments

Aerial sightings were analyzed for effects on offshore distance estimates from: differences between the two individual observers; the side of the plane from which the whales were seen; and the period of day (morning or afternoon flight) by ANOVA. The distance distributions from the 2-yr surveys were tested by χ^2 (chi-square) for the possibility of pooling.

To address the misclassification bias suggested by the results of the 1978-79 experiments, the data from those experiments were reanalyzed by using a less demanding classification scheme of three broad intervals: 0-0.75 mi (1.2 km); 0.76-1.5 mi (2.4 km); 1.6 mi + (2.6 km). From this characterization, a series of reclassification parameters (probabilities) were calculated, ρ_{ab}, being the proportion of whales estimated to be within interval a, that were determined to be actually passing within interval b. The actual census data, structured in the same three intervals, were restructured by application of these parameters as

$$\hat{m}_b = \sum_a (m_a \rho_{ab}), \quad (2)$$

where m_a includes the whales originally classified into interval a, and $\hat{m}_b$ comprises the whales redistributed into interval b, which were originally (erroneously) estimated to be in a. For example, for $a = 1$ and $b = 1$, sightings correctly classified into interval 1 are summed into the new $\hat{m}_{b=1}$. For $a = 2, b = 1$, sightings incorrectly classified during the censuses into interval 2 are reclassified, or summed, into $\hat{m}_{b=1}$. In the case of $a = 2, b = 1, \rho_{21} = 0.2367$ of the whales originally put in interval 2 would be placed into interval 1. The redistributed census data were then compared with the "true" distribution from the aerial surveys. As a simple correction factor, the ratio of the cumulative proportions seen within 2.4 km (1.5 mi) was calculated for each year (k):

$$h(k) = C_s/C_p. \quad (3)$$

A necessary assumption of this method is that at least during periods of good or better visibility, all groups of whales passing within 2.4 km (1.5 mi) were recorded.

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

Analysis Methods: Estimation of Abundance

In fitting the probability density functions to the census data, the unit used was the estimate of the proportion of the population passing during a 24-h day. The number passing on day j was estimated as

$$\hat{n}_j = (\Sigma E[n]/t_j) \cdot 24, \tag{4}$$

where $E[n]$ is the expected value of n, i.e., the estimate of the number per group, corrected for bias as in Equation (1). The relative proportion passing on day j was estimated as

$$\hat{p}_j = \hat{n}_j/\Sigma\hat{n}_j. \tag{5}$$

Model parameters were first estimated for each year using all data points regardless of recorded visibility conditions. Data were fit by the two-parameter gamma model

$$f(j;\alpha,\beta) = \frac{1}{\alpha \cdot \Gamma(\beta)} (j/\alpha)^{\beta-1} \exp\{-j/\alpha\} \tag{6}$$

for each migration separately. The parameters of the gamma distribution, their variances and covariance, were estimated by the method of maximum likelihood (Chapman 1956; Greenwood and Durand 1960). Equality of parameters between years was tested by the F statistic (Chapman[4]),

$$F = \frac{\Sigma (x - \bar{x})^2/n - 1}{\Sigma \text{ var } (x)/n} \tag{7}$$

for $x = \alpha, \beta$.

The distribution of $\hat{p}_j$ for each year was then used to determine the effect of visibility conditions on census results. An average visibility condition was calculated for each day from all of the recorded codes (Table 1). The difference (residual) between the observed and predicted relative proportions for each day was also calculated. An ANOVA was performed on the residuals with visibility categories as groups, along with multiple range tests (Duncan's, Student-Newman-Kuels, Scheffe's). These results were used, along with an examination of the mean squared errors for each category, to set a critical level of visibility conditions beyond which there was significant interference with accurate censusing. The data were then refit by the gamma distribution using only days with visibility codes less than the critical value as points. The new set of daily predictors ($\hat{p}'_j$) from the fitted gamma model were used in the further estimation procedures.

Then, as an alternate to Equation (2), the abundance for day j was

$$\hat{n}_j = \begin{cases} [(\Sigma E[n])/t_j]\ 24 & : \text{vis} \leq \text{critical value} \quad (8a) \\ \hat{p}'_j\ (\Sigma\hat{n}_j) & : \text{vis} > \text{critical value.} \quad (8b) \end{cases}$$

That is, for days with visibility conditions less than or equal to some critical level (with levels defined as in Table 1) the average hourly sighting rate, corrected for counting bias, multiplied by 24 h, was used as the estimate of the total number of whales passing. For days with visibility conditions worse than some critical value, the estimate of the number passing came from the expected proportion for the day (from the gamma distribution model of migratory timing for that year, p'_j) multiplied by the sum of the daily estimates from the first fitting of the gamma model.

For estimating the "tails" of the migration, a slight modification of the method of Mundy (1979) was used. This method was developed to predict total run size for salmon from intermediate results of counts, given that migratory timing can be modeled. The total "run" N_j was predicted by minimizing the least squares error function

$$\text{err} = \sum_j \left(\theta_j - \frac{\Sigma n_j}{N_j}\right)^2 \tag{9}$$

which was solved for $\hat{N}_j$ (N estimated by data cumulative to day j) by

$$\hat{N}_j = \sum_j (\Sigma n_j)^2/\Sigma n_j\theta_j. \tag{10}$$

Here Mundy uses θ_j as the cumulative proportion expected to have passed by day j, and we define θ_j as that quantity less the predicted proportion missed before the first day of each census.

The final form of the abundance estimate for each year k was then,

$$N_k = \{\sum_j (\Sigma n_j)^2/(\Sigma n_j) \cdot \theta_j\} h(k). \tag{11}$$

The variance for Equation (11) was estimated in two ways. The first, S^2_0, outlined in Appendix 2, was derived from the component variances of the parameters used in the model, employing the Delta Method (Seber 1973). In the second method the data were subsampled in five 2-h samples/d. The five

[4]D. G. Chapman, Director, Center for Quantitative Science, College of Ocean Fishery Sciences, University of Washington, Seattle, WA 98195, pers. commun. March 1980.

estimates for the year were then calculated using Equation (11). A simple variance of these estimates about the mean estimate (S_R^2) was then calculated. Variances were compared for equality ($H_0: S_R^2 = S_0^2$) by the test statistic

$$\chi^2 = \frac{(n-1)S_R^2}{S_0^2}, \tag{12}$$

where χ^2 is distributed approximately as chi-squared (Freund 1962:371) with rejection regions $\chi^2 > \chi^2_{\alpha/2,\, n-1}$ or $\chi^2 < \chi^2_{1-\alpha/2,\, n-1}$.

Analysis Methods: Trends in Population Size

In order to test for a trend in population size during the 13-yr study period, two models were chosen for regression analysis. This first model was simple linear regression, the second was a weighted $\log_e$ model:

$$N_t = N_0\, e^{rt}, \tag{13}$$

where N_t is population size in year t, N_0 is year zero, or 1967 for the shore census time series. Equation (13) was fit linearly as

$$\ln N_t = \ln N_0 + rt, \tag{14}$$

with weights calculated as an inverse function of the estimated variance of N_t in the log model:

$$\begin{aligned} \mathrm{Var}(\ln N_t) &\quad [f'(N_t)]^2 \mathrm{Var}(N_t) \\ &= \mathrm{Var}(N_t)/N_t^2 \\ &= w_t^{-1}. \end{aligned} \tag{15}$$

RESULTS

Shore Census Data Base

A histogram of group sizes as recorded from the 13 annual censuses is presented in Figure 3. The overall mean was 2.086 ($S^2 = 1.974, n = 23{,}749$). The mean group sizes by year are listed in Table 2. An ANOVA indicates that there are significant differences between the mean pod sizes recorded by year ($F = 8.282 > F_{12,\infty,0.05}$). Multiple range tests (Duncan's, Student-Newman-Kuel's, Scheffe's) show that 1967-68 and 1977-78 are different from each other and the rest, while all the others are homogeneous. In the 1967-68 census the unusually high mean is attributable to one of the two observers that year. His individual mean pod was 3.123 ($S^2 = 2.651$), and was significantly different from the other observer that year, whose mean was 1.886 ($S^2 = 1.959$: $t = 24.528 > t_{\infty,0.05}$). In 1977-78 however, the two observers did not differ significantly

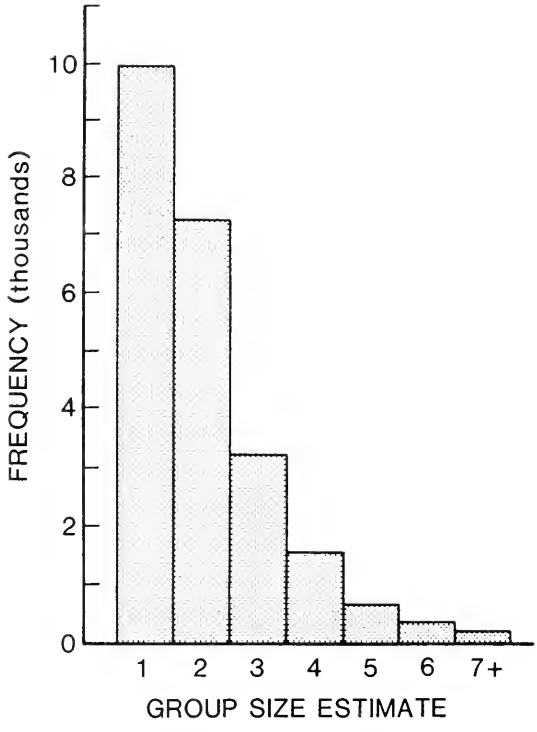

FIGURE 3.—Frequencies of group size estimates from Monterey gray whales census, 1967-68 through 1979-80, n = 23,678 observations.

TABLE 2.—Mean pod size estimates by year for the Monterey gray whale censuses, 1967-68 through 1979-80. Group membership identifies placement by multiple range tests into one of three nonsignificantly different subgroups.

Year	Mean pod estimate	SD	n	Group membership
1967-68	2.4970	3.5520	1239	3
1968-69	2.1471	2.2550	1509	2
1969-70	2.0900	2.2790	1643	2
1970-71	2.0330	1.6110	1652	2
1971-72	2.1630	1.8700	1272	2
1972-73	2.1400	1.6780	2041	2
1973-74	2.0990	1.7980	1859	2
1974-75	2.0710	1.9170	1855	2
1975-76	2.0620	1.7210	2086	2
1976-77	2.0660	1.5930	2296	2
1977-78	1.8250	1.2470	1996	1
1978-79	2.0040	2.3750	1960	2
1979-80	2.1030	1.7120	2341	2
Overall	2.0855	1.9736	23,799	

Source	df	ss	ms	F
Analysis of variance				
Between groups	12	385.7561	32.1463	8.283[1]
Within groups	23,736	92,119.1877	8.8810	
Total	23,748	92,504.9438		

[1]Significant at $\alpha = 0.05$.

from each other in mean pod size estimated (1.842, 1.829, $t = 1.1442 < t_{\infty,0.05}$) and, consequently, the difference of this year's data from others cannot be credited to one aberrant observer.

There was a significant increase in mean group size as a function of distance from shore (Fig. 4) ($F = 97.28 > F_{5,231}$). A significant linear increase in the pooled data (Fig. 4) was also noted in 10 of the 13 individual years. In the remaining 3-yr data (1968-69, 1972-73, 1978-79), the average pod size peaked at about 0.6-0.9 km (1-1.5 mi) from shore, and decreased thereafter. This may be a real between-year difference in whale behavior, but is more likely a function of the varying abilities of the observers themselves.

There are highly significant differences between years in the frequency of observations recorded within offshore distance intervals ($\chi^2 = 2{,}340$, df = 24). For this analysis, a pooled three-interval distribution was used in light of the observer bias tests discussed above. Within both the Yankee Point location subset of years and the Granite Canyon subset there also exists significant heterogeneity in the offshore distribution ($\chi^2 = 1{,}077$, df = 14; $\chi^2 = 1{,}025$, df = 8, respectively). Given this, a difference between locations pooled over years ($\chi^2 = 239$, df = 2) is not surprising and also not particularly meaningful. Consequently, given the range of interyear variation, we cannot adequately test for interlocation differences in the migratory corridor and therefore have applied distance estimation corrections equally to data from both locations.

Within each year, the distribution of distance estimates was tested for a within-season change, since our verification experiments were conducted during roughly the middle third of the migration. For this, the data were divided into early (10-29 December), mid (30 December-18 January), and late (19 January-6 February) time periods. As with the first 11-yr data (Reilly et al. 1980), the 1978-79 and 1979-80 distributions have no seasonal differences indicated by contingency table analysis ($\chi^2 = 8.54, 7.13, < \chi^2_{4,0.05}$), but do have significantly different mean distance observations ($F = 16.34, 26.91 > F_{2,\infty,0.05}$). Consequently, as with the first 11 yr, only data from the middle third of the migration were used for comparison with aerial results in Equation (3).

No significant period differences were indicated for the 1978-79 and 1979-80 censuses, in the ANOVA testing for effects on numbers of whales recorded per 5-h shift, from variation between observers and from period (morning or afternoon). Similar results were obtained in the comparison of observers within each year ($F = 1.242, 2.003, F_{1,118}$). The data were therefore considered homogeneous for pooling over these factors.

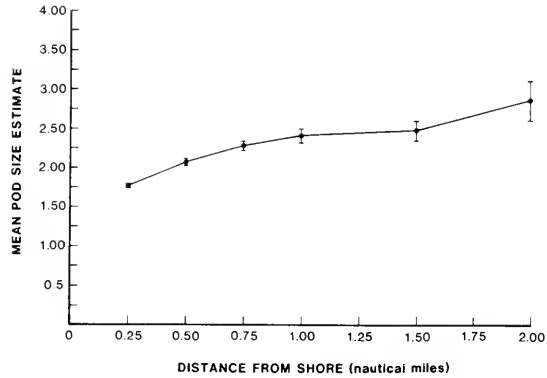

FIGURE 4.—Mean pod size estimates by distance from shore, with 95% confidence limits, from 13 annual gray whale census, 1967-68 through 1979-80, $n = 23{,}678$ observations.

The results from 1978-79 are somewhat different than the results from the first 11 yr, in the rate of whales recorded per hour of day. The mean counts show significant differences in an ANOVA ($F = 3.717 > F_{9,\infty,0.05}$) which are due to the depressed value for 0700-0800 h (Fig. 5). Multiple range tests (Duncan's, Student-Newman-Kuel's) indicate that the hourly means (other than that for 0700-0800 h) are homogeneous.

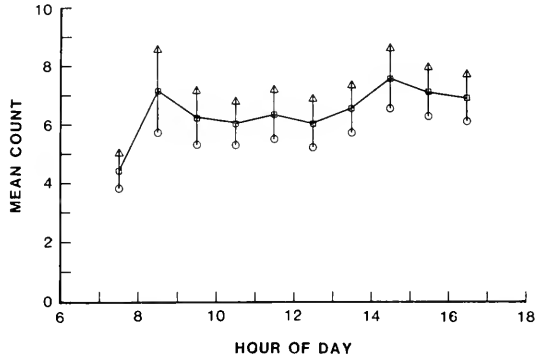

FIGURE 5.—Mean count of gray whales passing Granite Canyon Station by hour of day, with 95% confidence limits. 1978-79 and 1979-80 pooled, $n = 120$ d.

Modeling of Migratory Timing

Table 3 lists the parameters of the gamma distribution as calculated for all 13 yr, along with the mean days ($\simeq \alpha\beta$) and standard deviations ($\sqrt{\alpha \cdot \beta}$) of the annual migrations. As previously discussed, the

TABLE 3.—Parameters of the gamma models of migratory timing for each of the 13 annual gray whale censuses. $S_{\bar{x}}$ is the standard error of the scaled mean day.[1] α, β, their variances, and covariances are maximum likelihood estimates, as in Greenwood and Durand (1960).

Year	Mean day	$S_{\bar{x}}$	α	var(α)	β	var(β)	cov(α,β)	n^2
1967-68	11 January	10.05	6.0679	1.6862	3.7900	0.5758	42.4097	41
1968-69	19 January	11.13	4.8378	0.8033	6.4070	1.3028	59.0233	44
1969-70	08 January	11.68	5.0684	0.8400	6.3140	1.2042	60.8971	46
1970-71	10 January	13.09	6.6379	1.3877	4.9716	0.7036	61.9997	65
1971-72	14 January	14.58	7.9561	2.5758	3.5195	0.4367	51.3318	41
1972-73	16 January	15.16	8.8199	2.6032	3.7417	0.4094	60.7978	57
1973-74	14 January	14.47	7.5301	2.0797	4.3812	0.6278	61.4829	49
1974-75	12 January	13.12	5.6951	1.1374	5.7946	1.0430	62.5312	54
1975-76	09 January	13.09	6.0154	1.3424	4.9872	0.7662	56.3723	39
1976-77	12 January	13.17	5.6979	1.1356	5.9680	1.1456	64.5253	55
1977-78	09 January	14.10	6.7340	1.6036	4.6039	0.6833	57.9679	21
1978-79	11 January	14.38	7.1149	1.7302	4.6383	0.6598	61.7334	60
1979-80	14 January	12.82	5.1287	0.9149	7.2144	1.6887	70.8288	48

[1]The mean day is ($\alpha\beta$), scaled so that 10 December = 1.
[2]Number of days with visibility conditions of fair or better, used as points for the fit

means and variances are not equal statistically. Following adjustment on the time scale so that mean days align, however, we cannot reject the hypothesis of equality of parameters for the gamma distribution between years. For the α's, $F = 1.33 < F_{12,\infty,0.05}$. For the β's, $F = 1.54 < F_{12,\infty,0.05}$, where the F statistics were calculated as in Equation (7). Figure 6 illustrates data on daily proportions of the population passing Monterey, pooled over the 13 yr, as fit by the cumulative gamma. The use of the gamma represents a marked improvement in fit over the normal distribution, which we employed previously (Reilly et al. 1980). The error sum of squares from gamma model was 0.0179, while that from the normal fit to the same data was 0.1998, one order of magnitude greater.

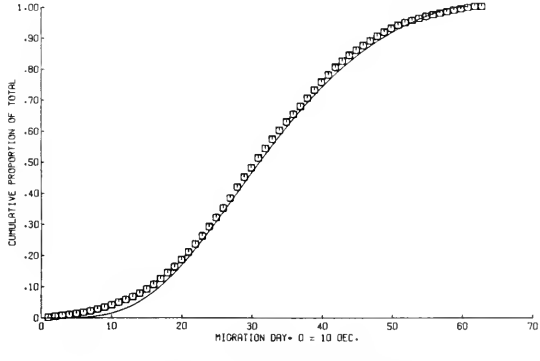

FIGURE 6.—Cumulative proportions of total count of gray whales by day (averaged) fit by the cumulative gamma function. Error sum of squares = 0.0179.

Effect of Visibility Conditions on Censusing

There are significant differences between visibility categories in the residuals (differences) of the observed from expected daily proportions of the population passing the census site (ANOVA: $F = 63.99 > F_{5,749,0.05}$). Three separate multiple range tests (Duncan's, Student-Newman-Kuel's, Scheffe's) gave the following nonsignificantly different subgroups of visibility codes, arranged in order of increasing magnitude of residuals:

1. visibility = 1, 2, 3
2. visibility = 1, 3, 4
3. visibility = 5
4. visibility = 6.

A simple interpretation of these results is that for conditions ranging from 1 (excellent) to 4 (fair), there is no significant interference from weather in shore censusing of gray whales. A plot of the mean squared residual for each category (Fig. 7) graphically illustrates this. Consequently, for days with average

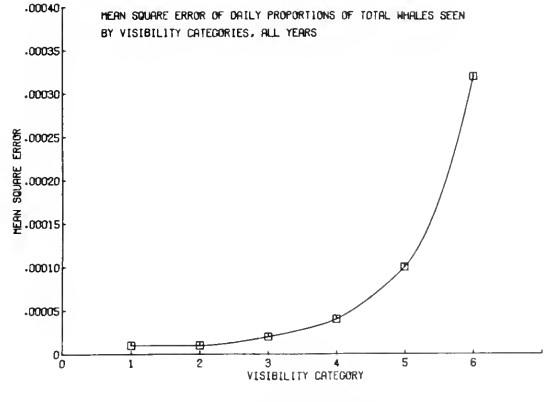

FIGURE 7.—Mean squared errors from comparison of daily proportions of total number of whales seen per season to proportions predicted by the gamma distribution, by visibility categories, all 13 yr included.

visibility of fair or better (<4) the total count for the day was estimated by Equation (8a), while for days with visibility of poor or worse (>4), it was estimated by Equation (8b). (The number of fair or better days recorded each year are listed in Table 3.)

Verification Experiments

The distance estimate data from the 1979-80 aerial survey were found to be homogeneous for pooling over sides of the plane, observers, and flight periods (Table 4). Further, the two separate years aerial data were homogeneous, and therefore pooled to form the model distribution (Table 5). This offshore frequency distribution was used as a standard for comparison with the annual observed distributions, as in Equation (3).

The values of ρ_{ab} (Equation (2)), the redistribution parameters calculated from the 1978-79 observer bias experiments, are listed in Table 6. The distance correction factors for each year $h(k)$ indicate that about 20% of passing whales are missed as a function of their distance from shore (Table 7). The cumulative proportions of the population estimated to have been observed during the census periods of around 2 mo, $\theta(k)$, indicate that between 80 and 96% of the population passed the census site during those periods (Table 7). That is, between 4 and 20% of the population passed on days before the initiation and after the termination of the annual counting efforts.

TABLE 4.—Analysis of variance for distances of sightings from shore from the 1979-80 aerial transects, with side of plane, period (morning, afternoon), and observer (Reilly, Wolman) as factors. None significant at $\alpha = 0.05$.

Source of variation	Sum of squares	df	Mean square	F
Main effects	0.385	3	0.128	0.253
side	0.062	1	0.062	0.122
observer	0.116	1	0.116	0.228
period	0.314	1	0.314	0.618
2-way interactions	1.131	3	0.377	0.743
side × obs	0.586	1	0.586	1.154
side × per	0.018	1	0.018	0.035
obs × per	0.621	1	0.621	1.224
Explained	1.516	6	0.253	0.498
Residual	124.792	246	0.507	
Total	126.308	252	0.501	

TABLE 5.—Numbers of whales observed within each of seven distance intervals from shore in aerial transects during 1978-79 and 79-80 with a χ^2 test of differences for pooling. $\chi^2 = 5.585 < \chi^2_{6,0.25}$.

Interval	Distance (mi)	1978-79 no. observed	1979-80 no. observed	Pooled (%)
1	0-0.25	14	11	2.91
2	0.26-0.5	36	33	8.02
3	0.6-0.75	41	42	9.65
4	0.76-1.0	74	88	18.34
5	1.1-1.5	148	167	36.63
6	1.6-2.0	74	61	15.69
7	2.1+	29	42	8.26
Total		416	444	

Population Estimates and Variances

The population size estimate from the 1979-80 census is 17,577, with a standard error of 2,364. Table 8 gives revised population estimates for each of the 13 yr using Equation (11), along with raw counts, variances (calculated as outlined in Appendix 2), and 95% confidence intervals (C.I.).

TABLE 6.—Values of the redistribution parameters, ρ_{ab}, and their variances.

Parameter	Value	Variance
$\rho 11$	0.6647	0.001288
$\rho 12$	0.3353	0.001280
$\rho 13$	0	0
$\rho 21$	0.2367	0.000602
$\rho 22$	0.7567	0.000614
$\rho 23$	0.0067	0.000002
$\rho 31$	0.0282	0.000386
$\rho 32$	0.8451	0.001844
$\rho 33$	0.1267	0.001558

TABLE 7.—Values of the sighting function $h(k)$, its variance, θ, the cumulative proportion predicted to have passed during the census period, and the variances of θ, for each of 13 annual gray whale censuses.

Year	$h(k)$	Var $h(k)$	θ_k	Var θ_k
1967-68	1.212	0.00958	0.8004	0.00434
1968-69	1.219	0.01143	0.9398	0.00094
1969-70	1.218	0.01076	0.9546	0.00069
1970-71	1.214	0.00889	0.9660	0.00052
1971-72	1.215	0.00619	0.8774	0.00207
1972-73	1.212	0.00857	0.9546	0.00069
1973-74	1.213	0.00848	0.9208	0.00128
1974-75	1.207	0.00642	0.9451	0.00085
1975-76	1.217	0.01112	0.9134	0.00141
1976-77	1.218	0.01170	0.9340	0.00104
1977-78	1.218	0.01607	0.9276	0.00116
1978-79	1.213	0.00659	0.9451	0.00085
1979-80	1.217	0.00929	0.9340	0.00104

TABLE 8.—Raw counts, final population estimates, their variances, standard deviations, and 95% confidence intervals for each of 13 annual grey whale censuses.

Year	Raw count	Population estimate	Variance (derived)	SD	95% confidence limits
1967-68	3,077	13,095	1,628,883	1,276	(10,593, 15,597)
1968-69	3,265	11,954	2,388,470	1,545	(8,925, 14,983)
1969-70	3,399	12,408	2,622,599	1,619	(9,234, 15,582)
1970-71	3,264	11,177	1,050,782	1,625	(9,168, 13,186)
1971-72	2,667	10,414	842,864	918	(8,615, 12,213)
1972-73	3,684	14,534	1,817,229	1,348	(11,892, 17,176)
1973-74	3,889	14,676	2,426,376	1,558	(11,623, 17,729)
1974-75	3,836	13,110	1,864,729	1,366	(10,434, 15,786)
1975-76	4,295	15,919	3,545,588	1,803	(12,228, 19,610)
1976-77	4,720	16,621	3,233,889	1,798	(13,096, 20,146)
1977-78	3,717	14,811	5,163,965	2,272	(10,357, 19,265)
1978-79	3,927	13,676	1,270,429	1,127	(11,467, 15,885)
1979-80	4,924	17,577	5,558,979	2,364	(11,943, 22,211)

Table 9 lists the mean of five subsample population estimates for each year, and the alternate variances (S_R^2) estimated from these, as well as statistics comparing variances from both methods. In 5 of the 13 yr, the variances from different methods are not equal, with the subsample estimates being generally larger. In all cases, however, the estimates are of the same general order of magnitude.

TABLE 9.—Mean estimates from five 2-h/d subsamples of each year's data, with variance (from the mean). These variances are compared with those derived for each year independently (col. 4) by χ^2 test.

Year	Mean estimate ($n = 5$)	Variance (from mean)	Variance (derived, Table 8)	χ^2
1967-68	12,301	2,326,235	1,628,883	5.7129
1968-69	11,336	474,113	2,388,470	[1]0.7940
1969-70	12,226	4,183,815	2,622,599	6.3011
1970-71	11,567	5,595,042	1,050,782	[1]21.2985
1971-72	9,745	956,377	842,864	4.5307
1972-73	15,532	9,522,245	1,817,229	[1]20.9600
1973-74	14,992	5,050,008	2,426,376	8.3252
1974-75	13,641	1,858,617	1,864,729	3.9869
1975-76	15,001	10,096,117	3,545,588	[1]11.3901
1976-77	15,833	920,392	3,233,889	1.1384
1977-78	13,588	515,923	5,163,965	[1]0.3996
1978-79	13,557	1,737,235	1,270,420	5.4698
1979-80	17,337	8,668,263	5,558,979	6.2373

[1]Significant at $\alpha = 0.05$.

Changes in Population Size, 1967-68 to 1979-80

There was a significant, positive rate of change in gray whale population size of 2.5%/yr during the 13 yr observed. The annual estimates are plotted, along with 95% C.I., in Figure 8. The unweighted simple linear model results are

$$N_t = 11{,}502.29 + 390.3 \cdot t. \qquad (16)$$

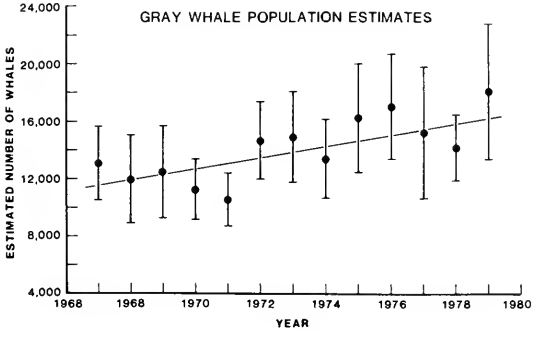

FIGURE 8.—Population estimates for the California stock of gray whales for 13 yr (1967-68 to 1979-80) with 95% confidence intervals. Fitted line is from exponential regression weighted by variances.

The coefficient of determination is 0.516, the slope is significant ($t = 3.427 > t_{11,0.05}$), and the 1980 population level estimate from this model is 16,186, with 95% C.I. (14,608, 17,763). The weighted log, model results are

$$\ln N_t = 9.3313 + 0.02513 \cdot t. \qquad (17)$$

The retransformed intercept is 11,285 for the 1967 population level. The slope is also significant ($t = 2.61 > t_{11,0.05}$), and is an estimate of the net annual rate of increase. Expressed as a percentage, $r = 2.513$ with a standard error of 0.964. The estimated 1980 population level from this model is 15,647 with 95% C.I. (13,450, 18,201).

DISCUSSION

Five areas of investigation were mentioned at the beginning of this paper as necessary to extrapolate confidently from counts of whales passing during daylight hours to estimates of total population size. We have addressed four of these quantitatively: 1) Animals missed as a function of their distance from shore, 2) animals missed due to poor visibility conditions, 3) miscounting of the number per pod, and 4) whales passing before and after the census period. The fifth area, night travel rates (and extrapolation of daylight counts to cover these), has not been adequately addressed to date by direct observation. Our last 2-yr data show a lower count for 0700-0800 h. The low value for this hour can be interpreted in two ways: The counts may be reduced due to limited visibility during the first half of this hour before the sun is up over the coastal mountains, or the animals are in fact increasing their rate of travel as the sun rises, having slowed down at night. As discussed previously (Reilly et al. 1980), the small amount of direct evidence that does exist on night travel rates, from Cummings et al. (1968) and Rugh and Braham (1979), supports the concept of a constant 24-h rate. Lacking conclusive data on this, and for consistency, we have treated the abundance estimation for these last years in the same manner as the earlier years. That is, an hourly mean rate calculated for the 10 sampled hours is used to extrapolate over the 14 h of darkness each day. If in fact the rate is slower at night, then our estimates are biased upward by an unknown proportion. For example, if the whales slow down at night to about one-half of the daytime rate of travel, our estimate from 1979-80 would be reduced from 17,577 to 12,450. Estimates from the other 12 censuses would be similarly reduced. If the rate is indeed constant, and the depressed 0700-0800 h rates for

the last two censuses are a result of limited light, then our estimates for these 2 yr are biased downward, but only by a small amount.

Because the night rate is the single largest extrapolation of the estimation procedure, more direct evidence on this would be highly desirable. Perhaps radiotelemetric studies in progress by Mate and Harvey (1979)[5] will help to clear up remaining ambiguity on this point.

The mean estimated group size increased with increasing distance from shore. This prompts two varying interpretations: This result may be an accurate depiction of whale behavior, or it may be an indication of greater sightability of larger groups farther offshore. The correction used here for whales missed offshore is based upon the assumption of equal sightability of groups, independent of group size within 1.5 mi (2.4 km), during periods of unhampered visibility. If the distribution of group sizes is in fact uniform with respect to shore, and small groups are missed near the outside of the 1.5-mi (2.4 km) zone, our population estimates would be biased downward.

Even after correction for varying amounts of poor visibility conditions and proportions of the population missed offshore, there is a considerable amount of year-to-year variation within the significant increase noted here. This may be due to further effects of visibility conditions or to unaccounted variation between counters. It also may be due, in part, to varying proportions of the population overwintering north of the Monterey area during different years. An investigation into the possible relationships of the changes in migratory timing to seasonal environmental events in the Arctic Ocean and North Pacific is in progress and may help clarify this problem.

The annual estimates presented here are slightly higher than those reported earlier (Reilly et al. 1980), especially for years with many days of poor visibility, primarily due to correction for this factor. The variances presented are also of a slightly greater magnitude than those previously reported. These are probably a more realistic representation of the variation inherent in the estimates, because they now include consideration of variation from both the effect of visibility conditions, and the inconsistency of estimating distances to passing whales. The general magnitude of the derived variances was independently corroborated by the subsampling exercise.

Regarding the current population level, we have produced three estimates: 17,577 from the latest census, 16,186 extrapolated from a simple linear model of increase, and 15,647 extrapolated from the weighted log model of increase. The 95% confidence intervals of all three overlap the point estimates. Given the range of extrapolations employed, the most conservative route is to choose the lowest, 15,647, as the "best" estimate of current population size.

A statistically significant increase in population level of about 2.5%/annum was calculated from these census results. If one also considers the annual harvest of about 164 whales by the Soviet subsistence fishery near the Chukotski Peninsula (Ivashin and Mineev 1978; International Whaling Commission 1979), the total net annual rate of production was probably near 3.75% for the past 13 yr. To our knowledge, this is the first empirical substantiation of a net increase in size by a whale population which was under exploitation.

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APPENDIX 1.—NOTATION

$\hat{n}$ = estimate of the number of whales in a passing group.

m_a = number of whales estimated to be within interval a during the regular censuses.

$\hat{m}_b$ = number of whales classified into interval b after restructuring by Equation (2).

b_n = mean bias for estimates of the number of whales in pods of n individuals.

ρ_{ab} = the proportion of the whales estimated to pass within offshore distance interval a which are actually passing within interval b.

k = the year of the census, with the 1967-68 census scaled as year 1.

$h(k)$ = offshore distance distribution correction factor for year k.

C_s = cumulative proportion of whales sighted between the shore and 1.5 mi (2.4 km) during the regular census.

C_p = cumulative proportion of the population predicted to have passed between the shore and 1.5 mi (2.4 km), by aerial transect verification.

$\hat{n}_j$ = estimate of the total number of whales passing the census site during day j, from actual counts, or from the gamma distribution, depending upon the visibility conditions.

$\Sigma\hat{n}_j$ = sum of the daily estimates.

t_j = number of hours during which a watch was conducted on day j.

$\hat{p}_j$ = the relative proportion of the population estimated to have passed the station on day j, from direct observation.

$\hat{P}_j$ = the relative proportion of the population expected to have passed the station on day j, from the gamma model.

$\hat{\theta}_j$ = the cumulative proportion of the population expected to have passed the station up to and including day j, less the proportion which passed prior to the first census day.

α = scale parameter of the gamma distribution.

β = shape parameter of the gamma distribution.

a,b = intervals of distance from shore.

N = total number of whales in the population.

$\hat{N}_j$ = estimate of the total number of whales in the population from data cumulative to day j.

$\hat{N}_k$ = estimate of population total for year k, using data cumulative to the last day of the census.

S_0^2 = variance of the estimate of the population total derived from the components of the estimation model (Equation (11)) by the Delta Method (see Appendix 2).

S_R^2 = variance of the estimate of the population total from data subsamples.

APPENDIX 2.—VARIANCE ESTIMATION

For $\hat{n}_j = (\Sigma E[n]/t_j) \cdot 24$:

$$\text{var}\{E[n]\} = \begin{cases} 0.464 ; n = 1 \\ 0.000 ; n = 2,3 \\ 0.612 ; n \geq 4 \end{cases} \text{ from Reilly et al. (1980).}$$

$\text{var}(\hat{n}_j) = (24/t_j)^2 \cdot \{\Sigma \text{var} E[n]\}$, by the Delta Method (Seber 1973).

For $n_j = (\Sigma \hat{n}_j) \cdot p_j$:

$\text{var}(\hat{n}_j) = (\hat{p}_j)^2 \text{ var}(\Sigma \hat{n}_j) + (\Sigma \hat{n}_j)^2 \text{ var}(\hat{p}_j)$,

where $\text{var}(\Sigma \hat{n}_j) = \Sigma \text{ var}(n_j)$ as above, assuming $\text{cov}(\hat{n}_j, \hat{n}_{j-1}) \simeq 0$, and

$\text{var}(\hat{p}_j) = (\delta p/\delta\alpha)^2 \text{var}(\beta) + (\delta p/\delta\beta)^2 \text{var}(\alpha) + 2(\delta p/\delta\beta)(\delta p/\delta\beta) \times \text{cov}(\alpha,\beta)$, by the Delta Method, and

$\text{var}(\alpha)$, $\text{var}(\beta)$, and $\text{cov}(\alpha,\beta)$ are estimated as in Greenwood and Durand (1960).

For $\hat{N}_k = (\sum_j \hat{n}_j)^2/\Sigma \hat{n}_j \cdot \theta_j) \cdot h(k)$:

$\text{var}(\hat{N}_k)$ is approximated by the Delta Method (as in $\text{var}(\hat{n}_j)$ and $\text{var}(\hat{p}_j)$), with component variances

$\text{var}(\theta) \simeq \theta(1 - \theta)/n$,

$\text{var}\{h(k)\} = (-C_p/C_s^2)^2 \text{ var}(C_p) + (1/C_p)^2 \text{ var}(C_s)$,

$\text{var}(C_p) = C_p(1 - C_p)/n$,

$\text{var}(C_s) = \text{var}(\hat{n}_b)$, in which

$\text{var}(\hat{n}_b) = b_a(\hat{n}_a/\Sigma \hat{n}_a)^2 \cdot \Sigma \text{var}(\rho_{ab})$, and

$\text{var}(\rho_{ab}) = \sum_a (\rho_{ab})(1 + \rho_{ab})/n_a$.

MESOPELAGIC FISHES EATEN BY FRASER'S DOLPHIN, *LAGENODELPHIS HOSEI*[1]

BRUCE H. ROBISON[2] AND JAMES E. CRADDOCK[3]

ABSTRACT

Examination of the stomach contents of three specimens of the rare pantropical dolphin, *Lagenodelphis hosei*, showed them to have been feeding on a mixed diet of mesopelagic fishes, shrimps, and squids, with fishes by far the most important component. Ecologically and morphologically the prey fishes comprised three types: A group of elongate, solitary, vertically mobile species; deep-bodied, aggregative, nonmigratory fishes; and thick-bodied, dark colored nonmigrators. Based on the known vertical distribution patterns of the prey species, the three dolphins had been feeding at depths near 250 and 500 m. The large sizes and species composition of the prey fauna indicate that the dolphins were feeding selectively, ignoring the smaller, more abundant vertically migratory species that dominate the upper mesopelagic midwater fish fauna of the eastern tropical Pacific. The estimated nutritional value of the ingested prey is similar to the values reported for related cetaceans maintained in captivity.

Until recently Fraser's dolphin, *Lagenodelphis hosei*, was known only as a skeleton, collected before 1895 from a beach in Sarawak, Borneo, and deposited in the British Museum of Natural History. From these bones, F. C. Fraser described the species in 1956, but it was not until 1971 that living specimens were observed and recognized as *L. hosei* (Perrin et al. 1973a). Subsequent reports have appeared which suggest a pantropical distribution (Tobayama et al. 1973; Caldwell et al. 1976; Miyazaki and Wada 1978). Most of the accumulating information on this rare and little-known dolphin is concerned with its distribution and anatomical distinctions, although Tobayama and his colleagues briefly described the stomach contents of a specimen found at Kamogawa, Japan.

Fitch and Brownell (1968, 1971) have demonstrated the usefulness of fish otoliths found in cetacean stomachs as reliable indicators of prey identity and, in some cases, of feeding depths. The shape of these characteristic structures is often species-specific, and they are relatively resistant to digestion. Other bones, such as dentaries, urohyals, and opercular, can also be helpful as indicators if digestion has not progressed too far (Miyazaki et al. 1973). There is a nearly direct relationship between otolith dimensions and standard length for adult fishes (Fitch and Brownell 1968); thus the sizes of the ingested fish can be quantified by comparing otolith measurements with otolith and standard length data from fish collected by trawling. These size data can in turn be used to estimate the nutritional value of the ingested fish by referring to data on their chemical composition (e.g., Childress and Nygaard 1973).

In addition to the information they provide about a predator's feeding habits (Perrin et al. 1973b), stomach content analyses are also valuable for estimating predation pressure on the prey fauna. With regard to predation by nekton on micronekton, such data may be of particular value because this major trophic link is one of the most poorly understood aspects of oceanic community dynamics.

MATERIAL AND METHODS

We examined the stomach contents of three female specimens of *Lagenodelphis hosei* that were captured by purse seine in the eastern tropical Pacific (lat. 5°N, long. 122°22'W) in May 1972 and acquired by Harvard University's Museum of Comparative Zoology. The first specimen (MCZ 52979) was about 230 cm long and carried a well-developed fetus. The sizes of the second and third individuals (MCZ 54379, MCZ 56572) were about 215 and 210 cm. The stomachs were removed intact from the specimens, which had been frozen since capture. The stomachs were thawed and opened, and their contents were gently washed through a graded series of screens to

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separate the soft tissue. After drying, the otoliths (sagittae) and other distinctive bones were picked out by hand. The bones were identified by comparison with material from fish specimens collected from both the Atlantic and Pacific Oceans by midwater trawling.

RESULTS

The first stomach contained about 1 l of material, nearly half of which was partially digested squid flesh; a roughly comparable portion was composed of fish bones. Fish muscle, squid beaks, and shrimp remains made up the small remainder. The second stomach's 2 l volume was roughly 90% fish bones, with small amounts of squid and fish flesh, shrimp carapaces, and squid beaks. No soft tissue remained in the third stomach; the volume of its contents was only about 0.125 l, and 90% of this was composed of shrimp exoskeletons. The remaining volume was due to fish bones, squid beaks, and eye lenses. Fish had clearly been the dominant component of the diets of all three Fraser's dolphins.

The three stomachs yielded 2,918 otoliths plus several hundred identifiable dentary, opercular, and cleithral bones. Table 1 presents the otolith data and the identities of the fishes they represent. An account of the most abundant fishes follows. Stomiatoid genera are classified according to Weitzman (1974).

Gonostomatidae

Otoliths of the genus *Gonostoma* are highly distinctive and easily discerned among stomach contents. The *Gonostoma* otoliths and dentary bones from the *L. hosei* stomachs are probably all from *G. elongatum.* We estimated the size of the fishes by comparing their dentary bones with those from specimens of *G. elongatum* which were collected by midwater trawling gear, albeit from Atlantic populations. The range of estimated standard lengths, 83 to 225 mm, shows that many of those ingested by the dolphins were quite large by trawl-sample standards (see Backus et al. 1965, 1969; Clarke 1974).

Sternoptychidae

Two sternoptychid genera were present in all three stomachs. Most of the *Argyropelecus* otoliths can be assigned with confidence to *A. lychnus,* while the remainder are probably from *A. affinis.* These hatchetfish occupy limited depth horizons both day and night and are common forage of large pelagic animals. Our size estimates are based on the length of cleithra from the dolphin stomachs compared with those from specimens of *A. lychnus* trawled in the eastern South Pacific and on comparisons of otoliths with trawl-caught *A. lychnus* from the eastern North Pacific. Both methods indicated that the dolphins had been feeding on a size range of about 40 to 70 mm. Here again the larger specimens ingested by *L. hosei* exceed the size of those commonly collected by trawling (Baird 1971).

Among the sternoptychid otoliths found in the dolphin stomachs, we are least certain of those tentatively designated *¿Maurolicus muelleri?* in Table 1. While this species is worldwide in distribution, and the sagittae resemble slightly digested versions of those from trawled Atlantic specimens, some uncertainty remains.

Photichthyidae

The examples of *Ichthyococcus* reported here are most likely from *I. irregularis,* which inhabits the eastern Pacific region where the three Fraser's dolphins were captured (Rechnitzer and Böhlke 1958). The peculiar configuration of *Ichthyococcus* otoliths is such that their fragile anterior projections are easily broken or dissolved, thus precluding accurate otolith length measurements. In this case we have used otolith heights for our estimates of fish size. When plotted on an otolith height vs. standard length curve for *I. irregularis* from the eastern Pacific, the otolith heights of these specimens suggest that the individuals caught by the dolphins ranged from 40 to 69 mm (Fig. 1). The largest otoliths from the dolphin stomachs are at the upper size limit of those available for comparison from trawl collections.

Chauliodontidae

Chauliodus otoliths and dentary bones were present in all three dolphin stomachs. We estimate the average standard length at about 180 mm, based on dentary length. These fishes have wide vertical ranges and exhibit irregular patterns of diel migration. Their movements appear to be related to their role as predator of vertically mobile gonostomatids, sternoptychids, and myctophids. Among the species which inhabit the eastern Pacific, it is most likely that the abundant remains attributable to this genus are from *C. barbatus.*

Paralepididae

Adult barracudina otoliths were present in all three

TABLE 1.—Otoliths and other fish bones identified from the stomach contents of three specimens of *Lagenodelphis hosei* from the eastern tropical Pacific.

Family-species	Stomach #1	Stomach #2	Stomach #3	Total	Rank	Other bones	Calculated length (mm)
Serrivomeridae							
Serrivomer sp.	4	1	3	8			
Argentinidae							
Nansenia sp.	7	6	5	18			
Bathylagidae							
Bathylagus sp.	11	9	16	36			
Opisthoproctidae							
Dolichopteryx spp.	14	9	5	28			
Gonostomatidae							
Gonostoma ¿elongatum?	66	81	37	184	5	dent.	83-225
Sternoptychidae							
Argyropelecus lychnus							
Argyropelecus affinis	68	59	50	177	6	cleith.	40-70
¿Maurolicus muelleri?	61	16	35	112	11		25-35
Photichthyidae							
Ichthyococcus ¿irregularis?	69	49	2	120	9		40-69
Vinciguerria ¿lucetia?	3	1	2	6			
Cheliodontidae							
Chauliodus ¿barbatus?	103	80	55	238	3	dent.	85-200
Unidentified stomiatoids	37	7	0	44			
Unidentified alepocephalids	2	7	5	14			
Paralepididae					13		200-300
Paralepis sp.	1	13	0	14			
Notolepis sp.	8	15	0	23			
Sudis sp.	8	7	26	41			
Unidentified paralepidids	0	4	5	9			
Evermannellidae							
Evermannella ¿ahlstromi?	49	39	31	119	10		35-90
Scopelarchidae							
Scopelarchus guentheri	51	45	31	127	8		80-160+
¿Scopelarchoides nicholsi? *¿Rosenblattichthys volucris?*	29	29	9	67	15		65-140
Scopelosauridae							
Scopelosaurus sp.	0	0	2	2			
Myctophidae							
Benthosema panamense	0	10	0	10			
Bolinichthys ¿longipes?	8	7	10	25			
Diaphus spp.	10	21	12	43			
Diogenichthys laternatus	2	6	4	12			
Hygophum spp.	8	11	5	24			
Lampadena luminosa	80	153	22	255	2		75-105
Lampadena urophaos *Lampadena* sp.	2	7	0	9			60-70
Lampanyctus ¿nobilis?	68	33	2	103	12		70-120
Lampanyctus ¿idostigma?	67	80	61	208	4		60-95
Lampanyctus ¿parvicauda?	6	12	0	18			
Myctophum spp.	12	10	3	25			
Protomyctophum spp.	12	5	38	55			
Symbolophorus ¿evermanni?	5	0	0	5			
Unidentified myctophids	0	29	29	58			
Neoscopelidae							
Scopelengys sp.	0	1	0	1			
Bregmacerotidae							
Bregmaceros sp.	8	8	6	22			
Melanonidae							
Melanonus sp.	45	12	14	71	14		120-220
Melamphaidae							
Melamphaes sp.	14	26	6	46			
Poromitra sp.	0	2	0	2			
Scopelogadus m. bispinosus	23	59	61	143	7		30-65
Diretmidae							
Diretmus argenteus	55	187	121	363	1	operc.	60-285
Anoplogasteridae							
Anoplogaster cornuta	2	5	2	9			
Chiasmodontidae							
Pseudoscopelus sp.	2	9	3	14			
Nomeidae							
Cubiceps cressa	8	2	0	10			
Totals	1,028	1,172	718	2,918			

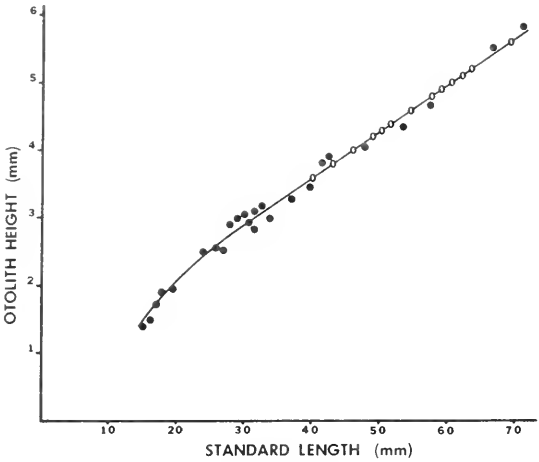

FIGURE 1.—Otolith height vs. standard length curve for *Ichthyococcus irregularis*. Solid circles represent specimens collected by midwater trawls, from which the curve was drawn. Open circles represent otoliths found in the dolphin stomachs, from which the fish sizes were estimated.

dolphin stomachs, and at least three genera are represented. Comparative material of these little-known fishes is rare, since adults are seldom captured (Rofen 1966) but the abundance of their larvae (Ahlstrom 971, 1972) and juveniles suggests that they are quite numerous. These fishes are inadequately sampled by current trawling gear and our knowledge about their ecological relationships is meager. The sizes of the otoliths that we found in the dolphin stomachs indicate that they were feeding on barracudinas of a size range uncommon in trawling collections, but because little comparative material is available, we cannot reliably estimate their lengths except to say that the majority of individuals were probably between 200 and 300 mm long.

Evermannellidae

Evermannellids are also midwater predators whose adult stages and ecology are poorly understood because of a scarcity of material. In contrast to the paralepidids, their larvae are less common in the eastern tropical Pacific (Ahlstrom 1971, 1972), yet they outnumbered barracudinas in the dolphin stomachs. Evermannellids are known to consume vertically migrating micronektonic fishes and squids, but apparently they do not migrate regularly themselves. Their sagittae are quite distinctive, and based on comparative material from the western Pacific, we estimate the sizes of the ingested fish to range from 35 to 90 mm long.

Scopelarchidae

Like the two preceding families, the "pearl-eyes" are mesopelagic predators, adept at eluding trawling gear. Based on the size range of the otoliths, *L. hosei* had been feeding upon large, adult specimens. At least three kinds of scopelarchid otoliths are present in the material; the most numerous are most likely to be from *Scopelarchus guentheri*. We estimate the size range of these individuals to be from 80 to >160 mm, based on an extrapolation from trawl-caught specimens from the western Pacific. This greatly exceeds the known size range of *S. guentheri* (Johnson 1974).

Myctophidae

Lanternfishes of the family Myctophidae are found throughout the world ocean as more than 225 species in a wide variety of niches and depth ranges. Myctophids commonly provide the bulk of the vertically migrating fish fauna which contribute to sound scattering layers. At least 10 genera are represented by the otoliths we found in the dolphin stomachs, but the majority are from *Lampadena* and *Lampanyctus*. In addition to being the most numerous, the otoliths from these two genera were obviously from much larger individuals than those of the less abundant myctophids. We believe that most of the smaller otoliths, many of which are heavily eroded, may have entered the dolphin stomachs secondarily as stomach contents of predatory fishes or squids. Among these smaller myctophids are several vertically migrating types and surface-oriented species (e.g., *Diogenichthys laternatus, Benthosema panamense, Symbolophorus evermanni).*

The *Lampadena* otoliths represent three species: *L. luminosa*, which is by far the most abundant; *L. urophaos*; and a form which has not yet been described (Fitch and Brownell 1968; Nafpaktitis and Paxton 1968). We estimate the size range of the ingested individuals of *L. luminosa* to be 75 to 105 mm and that of *L. urophaos* to be 60 to 70 mm. *Lampanyctus* otoliths are also divisible among three species: *L. nobilis, L. idostigma,* and *L. parvicauda.* Large individuals of these two genera often live as deep as 1,000 m, and either forego the vertical migration patterns typical of other myctophids or are easily able to avoid trawling gear near the surface.

Melamphaidae

Adult melamphaids are generally robust fishes found at mesopelagic depths in all oceans. They are

not generally known to be regular diel vertical migrators, although smaller individuals are usually found at shoaler depths, and there is evidence that the juveniles of at least one species do migrate vertically (Keene 1973). *Scopelogadus mizolepis bispinosus* is the only member of its genus known to inhabit the area where the Fraser's dolphins were captured. Adults are usually found below 400 to 500 m (Ebeling and Weed 1963). Based on the otolith height vs. standard length relationships of *S. beani* and *S. m. mizolepis* from the Atlantic and *S. m. bispinosus* from the eastern Pacific, more than half of the ingested *Scopelogadus* were between 40 and 65 mm long.

Diretmidae

Diretmus argenteus, the most abundant fish in the dolphin stomachs, is another poorly understood mesopelagic species. The sketchily known details of its natural history suggest that it is a deep-dwelling (ca. 400 to 800 m), nonmigrating fish which inhabits broad temperate and tropical areas of the Atlantic, Pacific, and Indian Oceans (Woods and Sonoda 1973). We have found euphausiid shrimp and lanternfish remains in the few *Diretmus* stomachs we have examined. Except for the absence of bioluminescent organs, they resemble the hatchetfishes in external appearance. While many smaller individuals were also present, the characteristic opercular bones and otoliths indicate that the majority of the ingested fishes were between 180 and 285 mm SL.

Crustaceans

In contrast to the relatively large size of many of the ingested fishes, the crustacean remains (Table 2) in the three dolphin stomachs were generally at the upper limit of the size range, which is collected by trawling gear. This suggests that midwater trawls are capable of sampling the full size range of the crustacean species involved but probably not that of the fishes. Like the fishes, however, these shrimps are relatively deep-living species, occupying depths of at least 200 m at night and 400 to 700 m by day.

TABLE 2.—Crustaceans identified from the stomach contents of three specimens of *Lagenodelphis hosei* captured in the eastern tropical Pacific.

Family-Species	Stomach #1	#2	#3	Total
Oplophoridae				
Acanthephyra smithi	10	25	7	42
Acanthephyra curtirostris	0	2	0	2
Notostomus sp. (P) ¿*longirostris*? ¿*pattentissimus*?	2	1	1	4
Systellaspis braveri	0	1	0	1
Systellaspis debilis	0	1	0	1
Pasiphaeidae				
Pasiphaea truncata	3	6	3	12
Sergestidae				
Sergestes (sergia) *inequalis*	0	0	7	7
Sergestes (sergia) sp.	0	1	0	1
Totals	15	37	18	70

Nutrition

In order to estimate the approximate nutritional value of the fish portion of the stomach contents we relied upon caloric values calculated for midwater fishes reported by Childress and Nygaard (1973). They found a range of 57.7 to 165.8 kcal/100 g wet weight for fishes which were morphologically and ecologically similar to the ones eaten by the dolphins. We multiplied these figures by length/weight relationships of from 0.067 to 0.189 g/mm (our data from the same kinds of fishes), the estimated length ranges of the species (based on otolith length vs. standard length relationships), and half the number of otoliths in each stomach. The rough estimates of nutritional value were not less than 5×10^4 cal for the first stomach, 6×10^4 cal for the second, and 4×10^4 cal for the third. We do not know if the otoliths we found are the result of a single day's feeding or that of some other time interval. However, the lack of large numbers of heavily eroded otoliths in the stomachs suggests that their residence time was relatively short.

Similar logic and calculations based on Childress and Nygaard (1974) lead to estimated values of 6×10^3 cal, 2×10^4 cal, and 8×10^2 cal for the crustacean portions of the stomach contents of the three Fraser's dolphins.

The total estimated caloric values for fish and crustaceans ingested by *L. hosei* are within the same order of magnitude as the value that can be calculated from the daily feeding rates of similar cetaceans which have been kept in captivity (Sergeant 1969). While we have not included the nutritional value of the ingested squids in these estimates, the very small proportion of the diet represented by squids suggests that their contribution was negligible.

DISCUSSION

The presence of otoliths in the stomach of a pelagic top carnivore does not necessarily mean that their original owners were ingested directly. Rather it is quite likely that some of these persistent remnants were first consumed by predatory fishes or squids and transferred via their stomachs as they, in turn,

were eaten by *L. hosei.* We take the presence of dentary, cleithral, and opercular bones, however, as evidence of direct ingestion, since these structures are more subject to dissolution by digestive action than are otoliths. The absence of remains from intermediate predators (e.g., scombroids, trichiuroids) suggests that no further trophic-level steps were involved.

The fishes which are most abundantly represented in the three dolphin stomachs can be separated into three groups based on morphological and ecological similarities. *Diretmus, Argyropelecus,* and *Ichthyococcus* are all silvery, deep-bodied, large-eyed forms which inhabit upper mesopelagic depths between 250 and 450 m in the eastern tropical Pacific (Robison 1973) and commonly occur in loose aggregations. They possess gas-filled swim bladders which undoubtedly make excellent echolocation targets. These fishes do not undertake regular, extensive, diel vertical migrations. They eat copepods, euphausiids, and small fishes which are associated with vertically mobile sound scattering layers (SSL).

Lampanyctus, Lampadena, and *Scopelogadus* are dark, thick-bodied fishes with medium-sized eyes and regressed or fat-filled swim bladders as adults. They occupy lower mesopelagic depths between 500 and 750 m (Robison 1973), and while smaller individuals may be significant components of SSL's, specimens of the size range ingested by *Lagenodelphis hosei* are not known to be regular vertical migrators. Their food consists primarily of SSL crustaceans and fishes.

Chauliodus, Gonostoma, Scopelarchus, the evermannellids, and paralepidids are solitary, slender, fast-swimming predators which prey upon micronektonic (ca. 10-60 mm) fishes and crustaceans. These fishes exhibit wide mesopelagic depth ranges between 305 and 1,250 m (Robison 1973), they do not have swim bladders, and they undertake varying degrees of vertical migration which are probably related to the movements of their prey.

Tobayama et al. (1973) found otoliths from *Ichthyococcus elongatus, Polyipnus asteroides* (Sternoptychidae), and *Diaphus elucens*? to be most numerous in the stomach of a specimen of *L. hosei* collected off Japan. These authors concluded that the fishes were eaten at a relatively shallow depth at night. However, it is likely that only *Polyipnus* could have been taken near the surface. The two other species were probably taken no shallower than 300 m, day or night.

Furthermore, the inclusion of Coryphaenoididae in their listing of prey means that deep feeding must have occurred, although the use of this name is misapplied. Coryphaenoididae is an obsolete name for the deep-living fishes of the family Macrouridae (it is unlikely that they meant Coryphaenidae, since the latter fishes do not possess otoliths). It is also possible that the otoliths in question are from *Melanonus*, since the sagittae of these fishes are easily mistaken for those of macrourids. The report of *P. asteroides* by these authors may also be in error, since Baird (1971) stated that this species is known only from the western North Atlantic.

As a collector of midwater fishes, *L. hosei* provides a distinctly different perspective on the composition of the mesopelagic fauna than that obtained by conventional sampling methods. Many of the ingested fishes were as large or larger than the maximum size of specimens that have been collected by nets. In addition, fishes such as *Diretmus,* which are rare in trawl collections, were shown to be surprisingly abundant.

The relative abundances of the fish species found as dolphin food do not reflect the relative abundances of midwater fish species in the eastern tropical Pacific as determined by trawling or larval surveys (Ahlstrom and Counts 1958; Ahlstrom 1971, 1972; Robison 1973). *Vinciguerria lucetia,* which is one of the most common fishes in trawl hauls, is represented in the stomachs by only six otoliths. Only 12 otoliths were found from *Diogenichthys laternatus*, which is the most abundant species in larval surveys.

These small, vertically migratory species have been shown to be important in the diet of the spinner porpoise, *Stenella longirostris,* in the eastern tropical Pacific (Perrin et al. 1973b). The spotted porpoise, *S. attenuata,* which cooccurs with the spinner, was shown to feed primarily on epipelagic fish and squid in the same study. While the number of *L. hosei* stomachs we examined was too small for a valid comparison of feeding with *S. longirostris* and *S. attenuata,* the low degree of similarity between prey fish types suggests that each of the three cetacean species has a different feeding strategy. Additional support for this conclusion comes from the evidence that only *L. hosei* consumes crustaceans (Perrin et al. 1973b).

Based on our understanding of the fishes whose remains we examined, we conclude that the Fraser's dolphins had been feeding selectively, by depth and by prey size. Location and ingestion took place in near or total darkness, regardless of time. Two depth horizons were hunted, each containing a different variety of mesopelagic fishes. The shallowest level was not less than 250 m, and the deepest was not less than about 500 m. The Fraser's dolphins fed with similar success at each depth.

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ABUNDANCE, MOVEMENTS, AND FEEDING HABITS OF HARBOR SEALS, *PHOCA VITULINA*, AT NETARTS AND TILLAMOOK BAYS, OREGON

ROBIN F. BROWN AND BRUCE R. MATE[1]

ABSTRACT

Patterns of seasonal abundance of harbor seals at Netarts and Tillamook Bays, Oregon, were documented by recording numbers of seals hauling out on tidally exposed sand flats in both bays. Harbor seal abundance at Tillamook Bay peaked during pupping (May-June) and molting (August) periods, while peak abundance at Netarts Bay coincided with the annual return (October-November) of chum salmon, *Oncorhynchus keta*, to a hatchery on Whiskey Creek. Observations of seals preying on adult salmon resulted in estimated losses of 6.1, 7.2, and 1.5% of the total chum returns for 1978, 1979, and 1980, respectively, due to seal predation in the Whiskey Creek area. Other prey species of harbor seals at Netarts Bay were identified by the recovery of prey hard parts from seal feces collected on haul-out areas. The Pacific sand lance, *Ammodytes hexapterus*, was the most frequently identified prey item. Ten species of flatfish (Order Pleuronectiformes) were identified as harbor seal prey with five species (*Parophrys vetulus*, *Glyptocephalus zachirus*, *Citharichthys sordidus*, *Microstomus pacificus*, and *Lyopsetta exilis*) ranking among the seven most frequently occurring food items. In general, benthic and epibenthic fish appeared to be important in the harbor seal diet. Distributions, abundances, and estimated sizes of identified prey species indicated that harbor seals had fed both in Netarts Bay and in the nearshore ocean. Movements of radio-tagged harbor seals between Netarts Bay and Tillamook Bay were common (45.4% of tagged seals made at least one move between bays). Tagged harbor seals frequented at least four different estuaries and one coastal haul-out area, ranging from 25 to 550 km from the tagging area.

The Pacific harbor seal, *Phoca vitulina richardsi* (Shaughnessy and Fay 1977), a year-round resident of Oregon, is commonly found in estuaries, along isolated shorelines, and on nearshore rocky islets. Before protection was afforded the harbor seal by the Marine Mammal Protection Act of 1972, a combination of bounties offered by the State of Oregon and traditional harassment from commercial and sport fishermen kept these animals at relatively low numbers in most bays and rivers. During the years following 1972, the numbers of harbor seals seen in many of Oregon's estuaries began to increase. At Netarts Bay, where the Department of Fisheries and Wildlife at Oregon State University operated a hatchery for chum salmon, *Oncorhynchus keta*, a similar increase in harbor seal abundance was observed (Lannan[2]).

A primary objective of the hatchery program at Netarts Bay was to rebuild the vestigial stock of chum salmon that returns annually to Whiskey Creek (Lannan 1975). Each year, during the months of October and November, predation by harbor seals on returning adult chum salmon was observed near the mouth of Whiskey Creek by hatchery staff. Our study of harbor seals in this area was initiated to learn how harbor seals use Netarts Bay and its resources. The specific objectives of this study were to 1) document the seasonal abundance of harbor seals (adults and pups) hauling out in Netarts Bay and in Tillamook Bay, the nearest estuary also used by harbor seals; 2) examine possible movements of harbor seals between Netarts and Tillamook Bays; 3) estimate the level of predation on returning chum salmon by harbor seals near the hatchery; and 4) identify other food items of harbor seals using Netarts Bay.

STUDY AREA AND METHODS

Netarts and Tillamook Bays are located on the northern Oregon coast, 110 and 95 km south of the Columbia River, respectively (Fig. 1). Harbor seal abundance in the bays was monitored by recording the number of animals hauled out on sand flats exposed during low tides. All counts were made from the shoreline using a 45× spotting scope. The numbers of harbor seals were recorded at a minimum of twice per month from May 1977 through November 1981 at Netarts Bay and from June 1978 through November 1981 at Tillamook Bay. A student's *t*-test was used to ascertain statistical differences in ob-

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[2]J. E. Lannan, Department of Fisheries and Wildlife, Oregon State University, Marine Science Center, Newport, OR 97365, pers. commun. April 1977.

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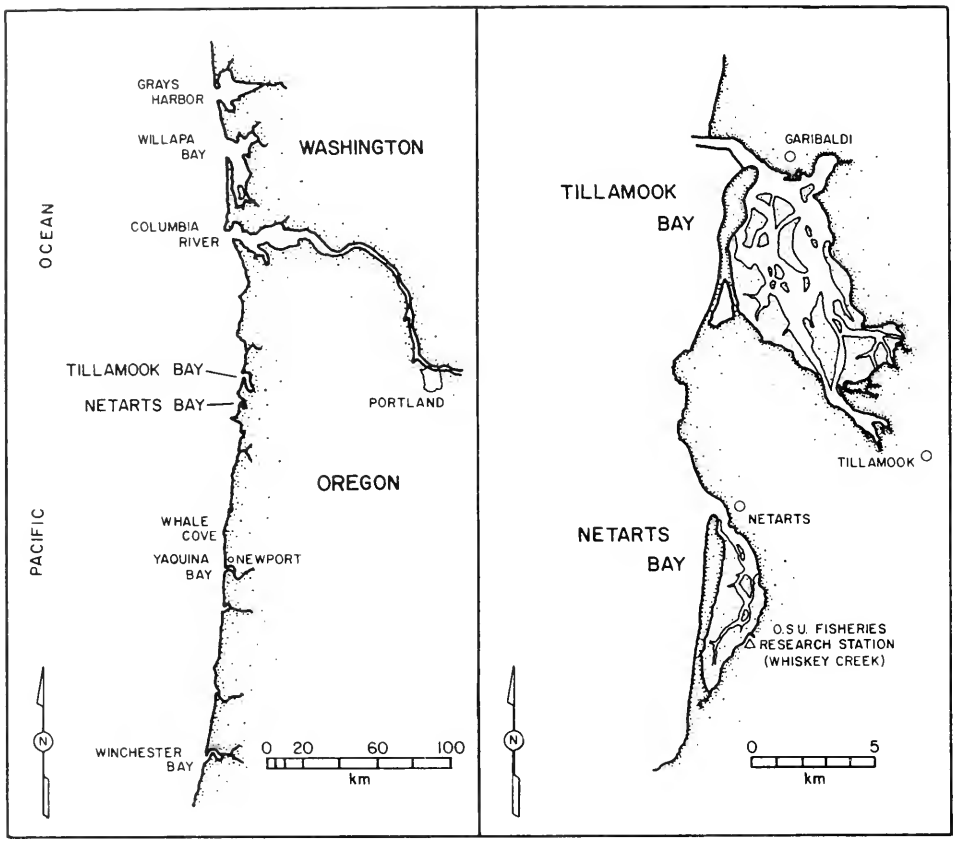


FIGURE 1.—Harbor seal study area of Netarts and Tillamook Bays on the northern Oregon coast.

served abundances between years.

To examine movements, 12 harbor seals were captured in August and October 1978, using a modified gill net (Brown 1981), and tagged with numbered plastic cattle tags and radio transmitters (Telonics Inc., Mesa, Ariz.[3]). The plastic tags were placed in the webbing of each hind flipper of all harbor seals, and radio tags were attached by an anklet to a hind appendage of 11 seals. Each transmitter package (84 g) was operated on a discrete frequency between 148 and 149 MHz, allowing identification of individual animals. Movements of tagged harbor seals were documented by identification of plastic tags and by reception of radio signals from seals carrying transmitters. Radio signals could be received only when tagged animals were out of the water. All haulout sites in Netarts and Tillamook Bays were checked visually and by radio for tagged harbor seals during a minimum of seven low tides per month, from August 1978 through June 1979. An additional 36 harbor seals were tagged and released at Netarts and Tillamook Bays in 1979, 1980, and 1981. Movements of these harbor seals were not monitored on a regular basis.

Harbor seals preying on chum salmon near the mouth of Whiskey Creek were observed during daylight hours from a 4 m high blind using binoculars and a spotting scope. The observation area included the lower 25 m of the creek and a semicircular area centered at the creek mouth and extending out onto the bay at a radius of about 200 m. Whiskey Creek enters Netarts Bay in its shallow upper reaches so that low tides prevent chum salmon from returning to the hatchery. Only when the rising tide has flooded this area can chum salmon approach and enter the creek. Harbor seals use this area only when the tide is high enough to allow them deepwater access or averaged over all observation periods, about 2.5 h before and after the peak of each high tide.

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

The numbers of chum salmon taken by harbor seals in the Whiskey Creek area were estimated by multiplying observed predation rates by the estimated number of hours that seals fed in this area. The observed predation rate was the number of chum salmon seen taken by harbor seals per hour of observation. The number of hours that harbor seals could feed near Whiskey Creek was estimated to be 5 h per high tide over the total number of high tides during each chum salmon run. The impact on the chum salmon return through predation by harbor seals near Whiskey Creek was then calculated as:

$$\text{Percent of total salmon taken by seals} = \frac{\text{estimated no. of salmon taken by seals}}{\text{total no. salmon taken at hatchery} + \text{estimated no. salmon taken by seals}} \times 100$$

Other food items of harbor seals using Netarts Bay were identified by prey hard parts recovered from feces collected on haul-out areas. Harbor seals were not purposely disturbed to gather feces. Samples were collected on an opportunistic basis when harbor seals left the haul-out areas before the flooding tide had covered them. Fecal samples were frozen after collection and later thawed and emulsified in either a 5% buffered Formalin solution or 70% isopropyl alcohol for a period of 24 h. Prey hard parts were removed and stored dry after samples were washed with water over a 0.5 mm sieve.

To estimate the size of fish taken by harbor seals, otoliths removed from fecal samples were measured under a dissecting microscope with an ocular micrometer and, when possible, compared with the lengths of otoliths from fish of known sizes. Data on otolith length versus standard length of fish were gathered from available specimens in collections at the School of Oceanography at Oregon State University. A simple linear regression was performed on these data. Standard body lengths (SL) of fish consumed by harbor seals were estimated for 12 prey species. A subsample of 621 Pacific sand lance, *Ammodytes hexapterus*, otoliths (20.9% of the total number recovered) from 11 randomly selected fecal samples (29.7% of those samples that contained Pacific sand lance otoliths) was measured to estimate the size range of this prey species.

RESULTS AND DISCUSSION

Seasonal Haul-Out Patterns

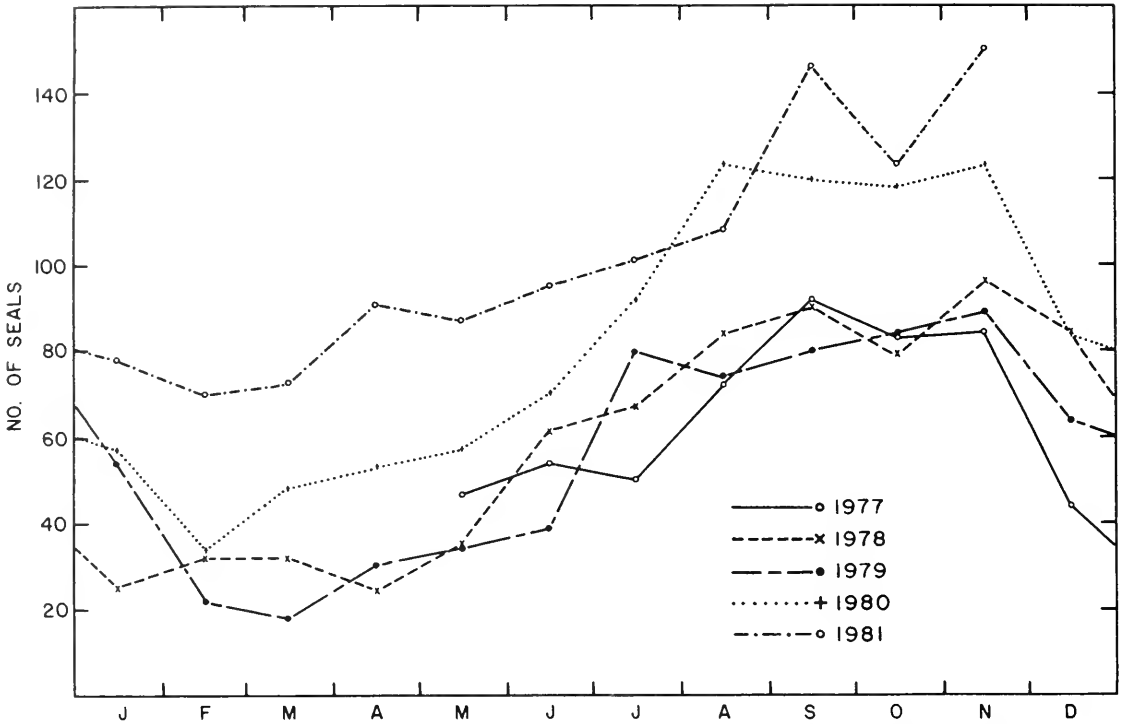
Examination of mean monthly counts of harbor seals hauled out in Netarts Bay revealed a seasonal cycle of low abundance in late winter and early spring, an increase through late spring and summer to a peak in late fall-early winter, followed by a mid-winter decline. With the exception of 1977, the highest annual counts were made during the month of November (Fig. 2). Seasonal numbers of harbor seals hauled out in Tillamook Bay showed a general trend of peak abundance during the spring and summer months with relatively lower numbers at other times of the year (Fig. 3).

An increase in the use of Netarts Bay haul-out areas was observed over the latter part of the study period (Fig. 2). Numbers of harbor seals hauled out during the period of peak annual abundance (September-November) were significantly greater in the years 1980-81 than during 1978-79 ($P<0.05$). Similarly, from February through April (annual low abundance) a significantly greater number of harbor seals hauled out during 1980-81 than during 1978-79 ($P<0.05$). There was no apparent change in numbers of harbor seals using Tillamook Bay over the study period (Fig. 3).

In Netarts and Tillamook Bays, pupping began during the first 2 wk of May and peaked in the first 2 wk of June. Molting seals were first observed in late July and the process was generally complete for all animals by early September. Percentages of pups among groups of harbor seals hauled out in the study area during the peak of the pupping periods of 1978-81 ranged from 16.3 to 21.4% at Netarts Bay and from 14.2 to 17.8% at Tillamook Bay (Table 1). Pup counts at Netarts Bay were made at close range and it is unlikely that any newborn pups were missed. However, counts made from aerial photographs have shown that ground censuses at Tillamook Bay underestimated pup abundance and that actual pup percentages in this part of the study area may have been closer to 22.4% in 1980 and 24.3% in 1981 (Jeffries[4]). Similar percentages were reported for harbor seals in British Columbia (20.0%) by Bigg (1969), in northern Puget Sound (13.2 to 19.4%) by Calambokidis et al.,[5] and in the Columbia River and adja-

[4]S. J. Jeffries, Washington State Department of Game, Marine Mammal Project, 53 Portway St., Astoria, OR 97103, pers. commun. August 1982.

[5]Calambokidis, J., K. Bowman, S. Carter, J. Cubbage, P. Dawson, T. Fleischner, J. Schuett-Hames, J. Skidmore, and B. Taylor. 1978. Chlorinated hydrocarbon concentrations and the ecology



	J	F	M	A	M	J	J	A	S	O	N	D
1977					47	54	61	73	110	107	109	55
1978	34	32	32	26	41	70	74	99	100	115	127	97
1979	66	26	23	30	45	46	86	84	100	103	107	85
1980	89	41	69	74	64	86	103	128	123	138	167	83
1981	78	94	95	106	100	108	101	121	161	154	205	

FIGURE 2.—Seasonal abundance of harbor seals at Netarts Bay, Oreg., shown by a plot of monthly mean numbers of seals hauled out in the bay. Listed at bottom of figure are monthly maximum numbers of seals observed on haul-out areas.

cent waters, including Netarts and Tillamook Bays (10.0%), by Everitt et al.[6]

Seasonal increases in numbers of harbor seals hauled out in many areas are common during the pupping and molting periods (Johnson and Jeffries 1977[7]; Everitt et al. 1979; Johnson and Johnson 1979[8]; Stewart 1981). Prior to giving birth, female harbor seals may seek out areas preferred for parturition and nursing. Roffe (1981) described the departure of harbor seals from the Rogue River by the end of April, presumably to use sites more

TABLE 1.—Maximum pup counts, number of non-pup animals present during counts, and number of pups expressed as a percentage of the total number of animals present for the 1978, 1979, 1980, and 1981 harbor seal pupping seasons at Netarts and Tillamook Bays, Oreg.

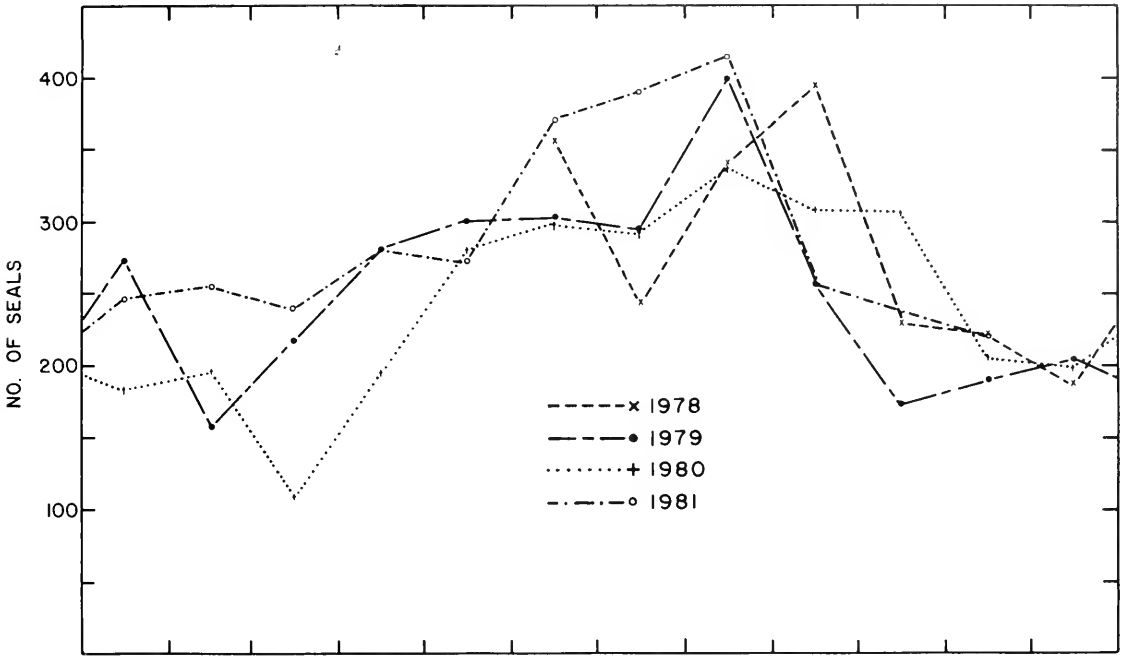
Year	Pups	Netarts	Tillamook Bay
1978	Pups	15	63
	Non-pups	55	381
	Pups/total (×100)	21.4%	14.2%
1979	Pups	9	58
	Non-pups	36	334
	Pups/total (×100)	20.0%	14.8%
1980	Pups	16	55
	Non-pups	80	254
	Pups/total (×100)	16.7%	17.8%
1981	Pups	15	70
	Non-pups	77	330
	Pups/total (×100)	16.3%	17.5%

and behavior of harbor seals in Washington State waters. The Evergreen State College, Olympia, WA 98505, 121 p.

[6]Everitt, R. D., R. J. Beach, A. C. Geiger, S. J. Jeffries, and S. D. Treacy, 1981. Marine mammal-fisheries interactions on the Columbia River and adjacent waters, 1980. [First] Annual Report March 1, 1980 to October 31, 1980. Wash. State Dep. Game to Northwest and Alaska Fish. Cent., Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115, 109 p.

[7]Johnson, M. L., and S. J. Jeffries. 1977. Population evaluation of the harbor seal (*Phoca vitulina richardi*) in the waters of the State of Washington. Contract Report to the U.S. Marine Mammal Commission, Washington, D. C., 27 p. National Technical Information Service, 5285 Port Royal road, Springfield, VA 22151

[8]Johnson, B. W., and P. A. Johnson. 1979. Population peaks during the molt in harbor seals. *In* Abstracts from presentations at the Third Biennial Conference of the Biology of Marine Mammals, October 7-11, 1979, Seattle, Wash., p. 31.



	J	F	M	A	M	J	J	A	S	O	N	D
1978						444	262	375	437	273	260	229
1979	273	200	304	285	392	353	353	485	289	191	255	207
1980	183	195	138	260	312	314	394	434	386	316	250	198
1981	246	307	325	359	330	456	390	414	310	236	220	

FIGURE 3.—Seasonal abundance of harbor seals at Tillamook Bay, Oreg., shown by a plot of monthly mean numbers of seals hauled out in the bay. Listed at bottom of figure are monthly maximum numbers of seals observed on haul-out areas.

desirable for birth and care of young. Beach et al.[9] identified females with neonates in Grays Harbor and Willapa Bay, Wash., and in Tillamook Bay, Oreg., (Jeffries footnote 4) that were tagged as pregnant females in the Columbia River. No pups were observed in the Rogue River and very few were seen in the Columbia River. Peaks in seasonal abundances of harbor seals during the winter months have been observed in the Rogue (Roffe 1981) and Columbia Rivers (Everitt and Jeffries[10]), although this pattern has been less commonly reported.

Local changes in harbor seal abundance may occur in response to variations in the availability of food (Scheffer and Slipp 1944; Fisher 1952; Graybill 1981). Beach et al. (footnote 9) suggested that the winter increase in harbor seal abundance in the Columbia River occurred in response to the presence of eulachon, *Thaleichthys pacificus*, in the river at that time. At Netarts Bay, the late fall return of chum salmon constitutes the only regular occurrence of a salmonid species in the Bay (Lannan footnote 2). The coincidence of peak harbor seal abundance and the chum salmon run suggests that this highly seasonal food source may have influenced harbor seal abundance in the bay.

At Tillamook Bay, seasonal peaks in harbor seal numbers and salmonid abundance did not coincide. The numbers of harbor seals declined to low annual levels from September through December while steelhead, *Salmo gairdneri*; chinook salmon, *Oncorhynchus tshawytscha*; coho salmon, *O. kisutch*; and chum salmon were passing through the estuary (Heckeroth[11]). High counts of harbor seals during the summer did, however, coincide with peaks in annual abundances of northern anchovy, *Engraulis mordax*;

[9]Beach, R. J., A. C. Geiger, S. J. Jeffries, and S. D. Treacy. 1982. Marine mammal-fisheries interactions on the Columbia River and adjacent waters, 1981. Second Annual Report November 1, 1980 to November 1, 1981. Wash. State Dep. Game to Northwest and Alaska Fish. Cent., Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115. NWAFC Proc. Rep. 82-04, 186 p.

[10]Everitt, R. D., and S. J. Jeffries. 1979. Marine mammal investigations in Washington State. *In* Abstracts from presentations at the Third Biennial Conference of the Biology of Marine Mammals, October 7-11, 1979, Seattle, Wash., p. 18.

[11]D. Heckeroth, Oregon Department of Fish and Wildlife, 6617 Officers Row, Tillamook, OR 97141, pers. commun. September 1978.

surf smelt, *Hypomesus pretiosus*; shiner perch, *Cymatogaster aggregata*; Pacific herring, *Clupea harengus pallasi*; and English sole, *Parophrys vetulus*, in Tillamook Bay (Forsberg et al.[12]). All five species were identified as prey of harbor seals using Netarts Bay (see results of fecal analysis) and have been commonly reported as food of harbor seals in other areas (Pitcher 1980a; Bowlby 1981; Graybill 1981; Calambokidis et al. footnote 5; Beach et al. footnote 9).

The differences in seasonal abundances of harbor seals at Netarts and Tillamook Bays may be in part related to the quality of habitat available for pupping and nursing. As in other areas (Johnson and Jeffries footnote 7), harbor seals at Netarts and Tillamook Bays use more haul-out sites within each bay during the pupping season than at other times of the year. Females with pups tend to form smaller, more isolated groups, usually in the more remote parts of the estuaries. Tillamook Bay, because of its greater size and more varied bottom topography, has a larger number of small channels in the upper portions of the bay. These channels rarely carry boat traffic and so offer access to a substantially greater number of preferred haul-out areas for female-pup pairs.

Movements of Tagged Harbor Seals

Between August 1978 and March 1979, 5 of 11 radio-tagged harbor seals (45.4%) made at least one move from Netarts Bay to Tillamook Bay (a distance by sea of about 25 km). Three of the five harbor seals made at least one trip from Netarts Bay to Tillamook Bay and back, and one visited both bays at least twice (Fig. 4). The propensity for movement seemed to vary among individuals. One harbor seal (no. 900) moved between Netarts and Tillamook Bays at least three times during the first 19 d following its release. Another animal (no. 580) was resighted more often and more regularly (27 times in 9 mo) than any other seal, yet was always found at Netarts Bay. Harbor seals carrying plastic tags have been identified at Netarts Bay up to 29 mo after tagging.

Long-range movements of harbor seals tagged in 1979, 1980, and 1981 include one harbor seal that traveled 75 km south (Whale Cove; Fig. 1) and later returned to Netarts Bay, and another animal that was found hauled out among a large group of harbor seals about 220 km south of the tagging site (Winchester Bay; Fig. 1). Single flipper tags from two harbor seals were recovered during commercial fishing operations at two locations. One tag was found entangled in a set herring gill net in Humboldt Bay, Calif., 550 km south of Netarts Bay, and another tag was recovered in a scallop drag fishing operation 75 km north of the tagging site.

Similar evidence of haul-out site fidelity and long-distance movements in harbor seals has been reported for other areas. A newborn pup, flipper-tagged on Tugidak Island, Alaska, was found 3 yr later <5 km from the tagging site (Divinyi 1971). Bonner and Witthames (1974) reported the dispersal of 55 flipper-tagged juveniles from the Wash, East Anglia, England, and their subsequent recovery up to 250 km from the tagging area. Pitcher and McAllister (1981) radio-tagged 35 harbor seals in Alaska and reported that while 8 animals had used haul-out areas, ranging from 24 to 194 km from the tagging site, 23 were found only at the hauling area where they were captured.

Predation on Chum Salmon at Whiskey Creek

Predation on chum salmon by harbor seals was not often seen in other parts of the bay. Harbor seals clearly took advantage of the concentrations of fish that occurred as chum salmon funneled from the wide open bay into the narrow mouth of Whiskey Creek. Harbor seals preying on chum salmon in this area took an estimated 6.1, 7.2, and 1.5% of the 1978, 1979, and 1980 returns, respectively (Table 2). It is important to note that while the average number of harbor seals feeding in this area per high tide was similar from year to year, the percent loss of each

TABLE 2.— Estimated impacts on 1978, 1979, and 1980 chum salmon returns at Netarts Bay, Oreg. through predation by harbor seals in the Whiskey Creek area.

	1978	1979	1980
Observation hours[1] (days)	44(11)	76.5(15)	91.6(28)
Mean estimated no. seals feeding/high tide	5.0	4.1	5.4
No. salmon seen taken by seals	22	12	24
No. salmon trapped following observation periods	432	242	3,015
Total no. salmon trapped	1,774	539	4,972
Observed predation rate (salmon/hour)	0.5	0.2	0.3
Estimated no. hours seals fed in area during run	230	210	255
Estimated no. salmon taken by seals	115	42	76.5
Percent of total return taken by seals (95% C.L.)	6.1(±4.9)	7.2(±5.5)	1.5(±0.9)

[1]Observation periods averaged 4.1 and ranged from 1.2 to 7.3 h in duration.

[12]Forsberg, B. D., J. A. Johnson, and S. M. Klug. 1977. Identification, distribution, and notes of food habits of fish and shellfish in Tillamook Bay, Oregon. Federal Aid Progress Reports, Fisheries, Contract No. 14-16-0001-5456RBS, Research Section, Oregon Department of Fish and Wildlife, 117 p.

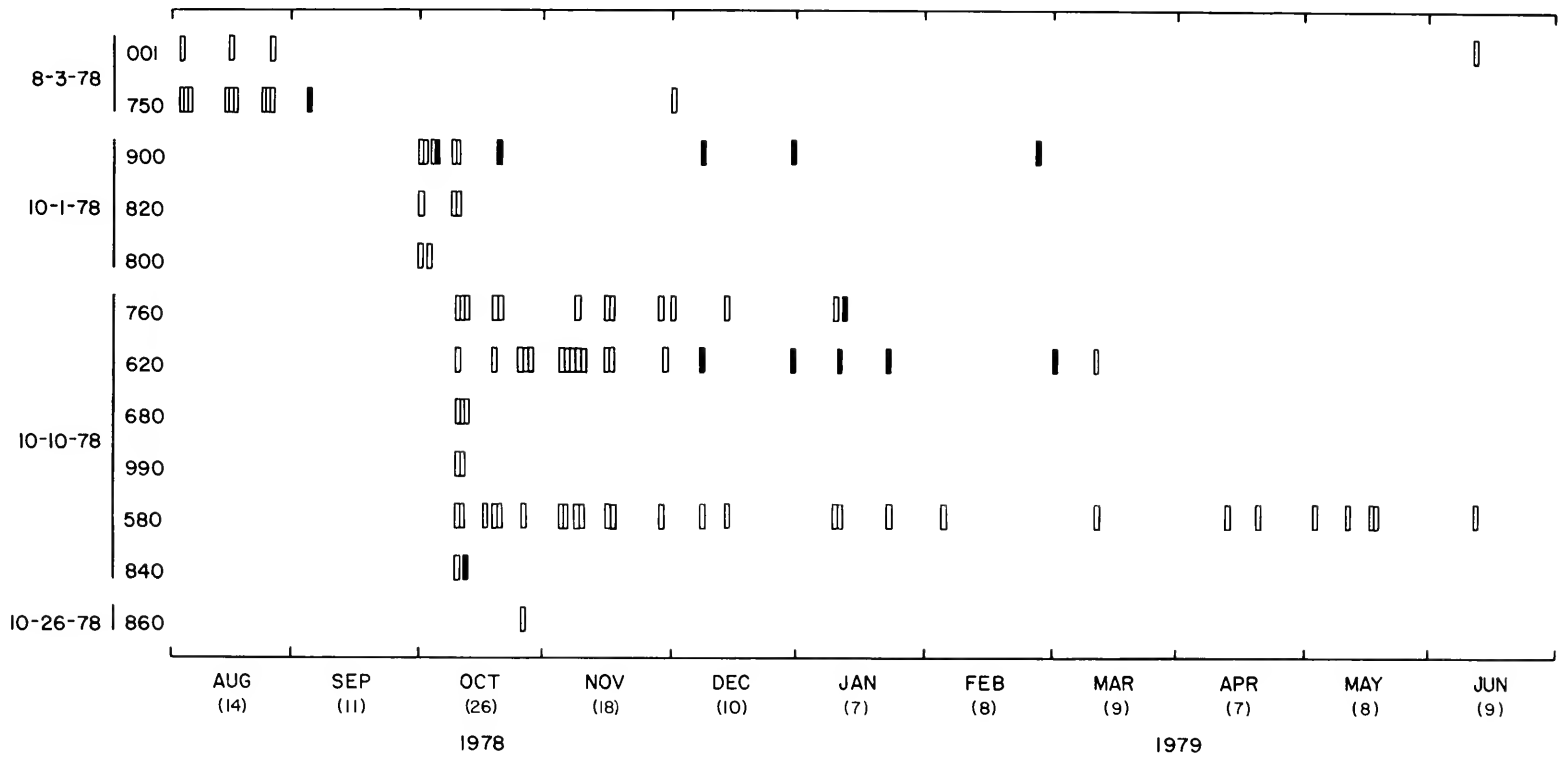


FIGURE 4.—Summary of radio signal receptions and visual sightings of 12 harbor seals captured, tagged, and released at Netarts Bay, Oreg. (tagging date appears at left margin). Open and closed boxes represent identification of tagged seals at Netarts and Tillamook Bays, respectively. Figures in parentheses under months are resighting efforts in number of haul-out periods (low tides) per month that were checked for tagged seals.

return declined as the number of returning chum salmon increased. The hydrography of this area may set an upper boundary on predation by limiting the number of harbor seals that can occupy the area and the amount of time during which feeding can occur.

These estimates assume that predation rates were equal during both day and night high tides. Night feeding by harbor seals has been reported as common behavior in many areas (Scheffer and Slipp 1944; Spalding 1964; Boulva and McLaren 1979; Roffe 1981). Generally, more chum salmon return to the Netarts Bay hatchery on high tides at night, resulting in a potential for greater losses at this time. However, as visual predators, harbor seals may be less successful at capturing free-swimming chum salmon at night. In the unlikely event that no predation occurred at night, the estimated losses would be half those presented in Table 2. Unrecorded feeding events within the observation area were believed to be few since harbor seals usually bring large fish, such as salmon, to the surface at least once during consumption. The predation estimates presented here may underestimate the overall impact on the return, since any predation on salmon occurring in other parts of the bay was not considered.

Other Harbor Seal Prey Items

Identifiable prey hard parts (fish otoliths and teeth) were found in 95 (63.3%) of 150 harbor seal fecal samples collected at Netarts Bay from May 1977 through August 1979. Teeth from hagfish (*Eptatretus* sp.) were present in six samples; teeth of the arrowtooth flounder, *Atheresthes stomias*, were found in three samples; and 3,800 fish otoliths were recovered from 91 samples, representing a total of at least 27 different prey species (Table 3). Since the majority of those samples containing identifiable prey hard parts (91.5%) were collected during the months of August, September, and October, some of the species listed in Table 3 may be only seasonally important in the diet of harbor seals in this area. The presence or absence of chum salmon otoliths in the harbor seal feces could not be documented, since attempts to collect samples during the chum salmon returns were unsuccessful. The 12 prey species for which size was estimated ranged from 40 to 280 mm SL (Table 4).

Otoliths of the Pacific sand lance, found in 37 (38.9%) of the 95 samples containing identifiable hard parts, were the most common in the collection. A minimum of 1,503 Pacific sand lance was represented, with a mean number per sample of 40.6 (range of 1-338 per sample). These fish may have been taken by harbor seals within Netarts Bay. In a limited survey of the icthyofauna of Netarts Bay, the size range of Pacific sand lance found by Howe (1980) (60-140 mm SL) was similar to that taken by harbor seals in the present study (80-130 mm SL).

The Pacific sand lance has been frequently reported as prey of harbor seals in the northeastern Pacific (Scheffer and Sperry 1931; Calambokidis et al. footnote 5; Pitcher 1980a), but has not been identified as a numerically important prey species. Pacific sand lance otoliths were found in only 2.6% of 387 harbor seal fecal samples collected in Washington (Beach et al. footnote 9) and in just 4.0% of 296 samples collected in Oregon (Graybill 1981).

Ten species of flatfishes (Order Pleuronectiformes) were identified as food of harbor seals hauling out in Netarts Bay. Of these species, five (*Parophrysvetulus*, *Glyptocephalus zachirus*, *Citharichthys sordidus*, *Microstomus pacificus*, and *Lyopsetta exilis*) were each found in 11.6% or more of the samples. English sole otoliths were found in 30 (31.6%) of the 95 fecal samples and ranked second only to the Pacific

TABLE 3.—Fish species identified as harbor seal prey by recovery and identification of prey hard parts (otoliths and teeth) from seal fecal samples collected at Netarts Bay, Oreg. Prey items are ranked by frequency of occurrence in 95 samples that contained identifiable hard parts. The minimum number of each species represented in the entire collection is presented.

Species	Frequency		Minimum no. fish
	No.	%	
Ammodytes hexapterus	37	38.9	1,503
Parophrys vetulus	30	31.6	126
Glyptocephalus zachirus	25	26.3	79
Citharichthys sordidus	17	17.9	53
Leptocottus armatus	16	16.9	54
Microstomus pacificus	16	16.9	39
Lyopsetta exilis	11	11.6	16
Clupea h. pallasi	8	8.4	22
Allosmerus elongatus	7	7.4	10
Eptatretus sp.	6	6.3	6
Sebastes sp.	5	5.3	20
Microgadus proximus	5	5.3	6
Cymatogaster aggregata	5	5.3	24
Hexagrammos decagrammus	4	4.2	6
Thaleichthys pacificus	4	4.2	11
Anoplopoma fimbria	4	4.2	14
Citharichthys stigmaeus	4	4.2	20
Isopsetta isolepis	4	4.2	6
Hypomesus pretiosus	3	3.2	8
Atheresthes stomias	3	3.2	3
Platichthys stellatus	2	2.1	1
Engraulis mordax	2	2.1	4
Psettichthys melanostictus	2	2.1	2
Embiotocid juveniles	2	2.1	7
Salmo gairdneri	1	1.0	1
Spirinchus starksi	1	1.0	1
Merluccius productus	1	1.0	1
Radulinus asprellus	1	1.0	1
Unidentified osmerid	1	1.0	2
Unidentified embiotocid	1	1.0	1
Unidentified pleuronectid	1	1.0	1
Total			2,048

TABLE 4.—Estimated sizes of 12 harbor seal prey species based on the relationship between otolith length (OL) and standard length (SL) of collected fish specimens. Also given are the coefficient of determination (r^2) and the sample sizes of otoliths from both the collected fish specimens and the fecal samples.

Species	Regression equation	r^2	No. otoliths from		Estimated prey size (SL,mm)	
			Collected specimens	Fecal samples	Range	Mean
Ammodytes hexapterus	SL = 25.0(OL) +52.2	0.98	8	621	80-130	95
Parophrys vetulus	SL = 33.3(OL)−17.7	0.98	81	140	40-240	70
Glyptocephalus zachirus	SL = 50.0(OL)−51.0	0.96	78	113	50-280	165
Citharichthys sordidus	SL = 50.0(OL)−53.5	0.86	46	74	40-215	60
Leptocottus armatus	SL = 33.3(OL)−43.7	0.96	14	85	40-210	110
Microstomus pacificus	SL = 50.0(OL)−31.0	0.94	45	62	70-210	150
Lyopsetta exilis	SL = 50.0(OL)−15.0	0.96	47	21	80-205	135
Microgadus proximus	SL = 20.0(OL)−28.4	0.98	61	8	40-230	140
Cymatogaster aggregata	SL = 20.0(OL)−10.4	0.98	34	31	65-110	85
Citharichthys stigmaeus	SL = 33.3(OL)−11.7	0.92	61	29	50-100	65
Isopsetta isolepis	SL = 33.3(OL)− 5.3	0.96	44	10	70-260	180
Psettichthys melanostictus	SL = 50.0(OL)−44.5	0.94	14	2	100-180	140

sand lance by frequency of occurrence. However, English sole otoliths represented far fewer fish (a minimum of only 126, with a mean number of 4.2 and a range of 1-38 per sample) than did those of the Pacific sand lance. This observation may reflect differing prey densities (e.g., schooling behavior in the Pacific sand lance) or variation in the passage rates of otoliths from different species.

English sole taken by harbor seals using Netarts Bay ranged from 40 to 240 mm SL, but about 90% were under 100 mm SL. Since English sole (juveniles) ranging from 39 to 120 mm SL were common in Netarts Bay (Howe 1980) and very few under 100 mm SL were found in the nearby coastal ocean (Demory 1971), it is likely that harbor seals fed on most of these fish within the bay. In contrast, Morejohn et al.[13] found harbor seals hauling out in Elkhorn slough, Calif., had taken primarily larger (120-320 mm SL) English sole from over the oceanic shelves, rather than smaller (20-140 mm SL) sole that were widely distributed throughout the slough.

Rex, Dover, and slender sole (*Glyptocephalus zachirus*, *Microstomus pacificus*, and *Lyopsetta exilis*), ranking third, sixth, and seventh, respectively, by frequency of occurrence in the harbor seal fecal samples (Table 3), were not found in Netarts Bay by Howe (1980). Demory (1971) found small (≤180 mm SL) rex, Dover, and slender sole in no less than 20, 10, and 30 fathoms of water, respectively. These fish species, and the few larger English sole, were most likely taken by harbor seals outside of Netarts Bay. Demory (1971) also found little separation by depth of large and small flatfish of the same species. Although harbor seals had taken some larger fish, they may have selected primarily for rex, Dover, and slender sole under 200 mm SL.

Flatfishes (Order Pleuronectiformes) have been a frequently reported prey of harbor seals (Imler and Sarber 1947; Morejohn et al. footnote 13; Pitcher 1980a; Bowlby 1981) and a numerically important group. Scheffer and Sperry (1931) identified flatfish in 28.4% of 79 harbor seal stomachs collected in Washington. Beach et al. (footnote 9) reported 9 Pleuronectiforme species in 27.1% of 387 seal fecal samples collected in the Columbia River and southwestern Washington. Graybill (1981) identified 12 pleuronectid species, representing 27% of all fish identified in 296 seal fecal samples collected in southern Oregon.

There are limitations to the utility of feces collection and prey hard part identification in the analysis of feeding habits. The relative importance of different prey in the diet may be biased if the ratio between consumption of the head (i.e., otoliths and teeth) and the body is not the same for all species. Some observations suggest that the heads of large fish, such as salmon, may not be consumed as often as those of smaller ones (Scheffer and Slipp 1944; Boulva and McLaren 1979; Pitcher 1980b; Roffe 1981). Harbor seals at Netarts Bay have occasionally been observed consuming heads of adult chum salmon (average weight 4.5 kg). Thus they are able to swallow fish of considerably larger size than those identified from the otolith collection. The magnitude of this potential bias is not known.

Other sources of bias in the relative importance of identified food items included variation in rates of digestion or passage through the gastrointestinal tract of hard parts from different prey species (Pitcher 1980b). Variation in the amount of time between seal feeding and hauling out may have resulted in the otoliths of some species being eliminated in the water. Prey items that lack resistant hard parts will

[13]Morejohn, G. V., J. T. Harvey, R. C. Helm, and J. L. Cross. 1979. Feeding habits of harbor seals, *Phoca vitulina*, in Elkhorn Slough, Monterey Bay, California. Unpubl. manuscr., 30 p. Oregon State University, Marine Science Center, Newport, OR 97365.

not be identified. Even in the presence of such limitations, feces collection and prey hard part identification can provide useful information on the prey species being used by seals (Pitcher 1980b).

SUMMARY AND CONCLUSIONS

The seasonal abundance of harbor seals auling out in Tillamook Bay displayed a general peak during June, July, and August, coincident with the pupping and molting periods. These high counts did not coincide with the fall peak in salmonid abundance in the bay. Two other factors may be more important in regulating seal abundance here: 1) High densities of many smaller fish species, known to be seal prey, occur during the summer months, and 2) Tillamook Bay provides the habitat preferred by seals during the pupping season.

The peak in the seasonal abundance of harbor seals at Netarts Bay coincided with the return of chum salmon to the Whiskey Creek hatchery during the months of October and November. Conditions for successful predation were ideal here: Shallow water, narrow channels, the concentrating effect that occurs as salmon funneled into the creek, and a general lack of disturbance to feeding harbor seals. Compared with the fall, the lower numbers of harbor seals hauled out during the spring months may indicate that Netarts Bay was not a highly preferred pupping area.

The estimated losses to the Netarts Bay chum salmon returns through harbor seal predation at Whiskey Creek (1.5-7.2% per year) might have been tolerated if numbers of returning chum salmon were great enough to provide ample brood stock for future releases (Lannan[14]). However, while an attempt was being made to build the stock, any loss of eggs through predation on female spawners was considered serious.

Recovery and identification of prey hard parts from feces indicated that while feeding in Netarts Bay and in coastal waters, harbor seals appeared to select fish species that were found near the bottom of the water column. The seven top-ranking food items were benthic or epibenthic species, or, as in the case of the Pacific sand lance, spent at least some time closely associated with the bottom (Howe 1980).

As evidenced by movements of tagged animals, interchange of harbor seals between coastal estuaries was common and occurred up to distances of at least 550 km. Groups of harbor seals hauling out in different estuaries apparently do not represent isolated stocks, but may instead be part of a common population of animals. The movements of harbor seals were seemingly related to the use of particular areas specifically preferred by harbor seals for feeding, for birth and care of young, or for both.

[14] J. E. Lannan, Department of Fisheries and Wildlife, Oregon State University, Marine Science Center, Newport, OR 97365, pers. commun. March 1980.

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VARIABILITY IN MEDIAN SIZE AND AGE AT SEXUAL MATURITY OF ATLANTIC COD, *GADUS MORHUA*, ON THE SCOTIAN SHELF IN THE NORTHWEST ATLANTIC OCEAN

TERRY D. BEACHAM[1]

ABSTRACT

Median length and age at sexual maturity of Atlantic cod on the Scotian Shelf declined about 50% in most stocks between 1959 and 1979. Atlantic cod in more northerly stocks matured at older ages than did those in more southerly stocks. Males generally matured at younger ages and smaller sizes than did females. Large, immature Atlantic cod disappeared from the stocks between 1959 and 1979. During 1975-79, virtually all Atlantic cod age 5 and older were mature. The decline in median length and age at sexual maturity may be due to the commercial fishery removing larger, older immature fish, a general decline in stock biomasses between 1960 and 1975 due to heavy exploitation, or both.

Vertebrate population dynamics are determined by the composite effects of reproduction, growth, dispersal, and mortality. The median age at which individuals attain sexual maturity profoundly impacts potential population growth (Cole 1954; Stearns 1976). Size and age at sexual maturity are the direct linkage between individual growth and reproductive potential of a population, and therefore they are parameters of prime concern in population dynamics.

Atlantic cod, *Gadus morhua*, is economically the most important finfish species landed in the Atlantic region of Canada. Heavy exploitation in the 1960's and early 1970's resulted in declines in stock biomass of many Atlantic cod stocks in the Maritimes (Halliday 1976; Beacham 1980). Canadian landings of Atlantic cod on the Scotian Shelf [Northwest Atlantic Fisheries Organization (NAFO) Divisions 4VWX] (Fig. 1) increased in the late 1970's while landings by other countries, chiefly Spain and the Soviet Union (Halliday 1976), declined. The southern Gulf of St. Lawrence cod stock (Division 4T) also supports an extensive fishery (Beacham 1980).

Spawning biomass of a stock is of direct concern in the management of a fishery and can be evaluated, when the abundance and proportion mature at each age are known. The presence of Atlantic cod in several areas of NAFO Subarea 4 (McKenzie 1956; McCracken 1959; Templeman 1962; Martin and Jean 1964) presented an opportunity to investigate variation in median size and age at sexual maturity of Atlantic cod among areas. The major purpose of this paper is to present historical changes in median size and age at maturity for Atlantic cod in NAFO Subdivisions 4Vn and 4Vs and Divisions 4W and 4X and to attempt to account for some of this variability among cod in these areas.

MATERIALS AND METHODS

Data analyzed in this paper were collected during 1959-79 from groundfish surveys of the Canadian research vessels MV *Harengus*, *E. E. Prince*, and *A. T. Cameron*. In 1970, annual stratified random design groundfish surveys were initiated on the Scotian Shelf with the July surveys of the *A. T. Cameron*. Previous to 1970, surveys were not always conducted annually in the areas examined for the present analysis. Annual values for median (50% mature point) length and age at sexual maturity of Atlantic cod on the Scotian Shelf before 1970 were calculated from any survey during the summer, not only July. Maturity ogives based on length and age were calculated for four periods in the study, each corresponding to about a 5-yr interval. All surveys conducted in each interval were included in the calculation of the maturity ogives. All Atlantic cod in the surveys for which maturity stage was recorded and either length or age were known were included in the determination of median size and age at maturity. Details of the surveys, including vessels and gear used and areas surveyed, were outlined by Halliday and Koeller (1981). Fork length (centimeters) and maturity stage

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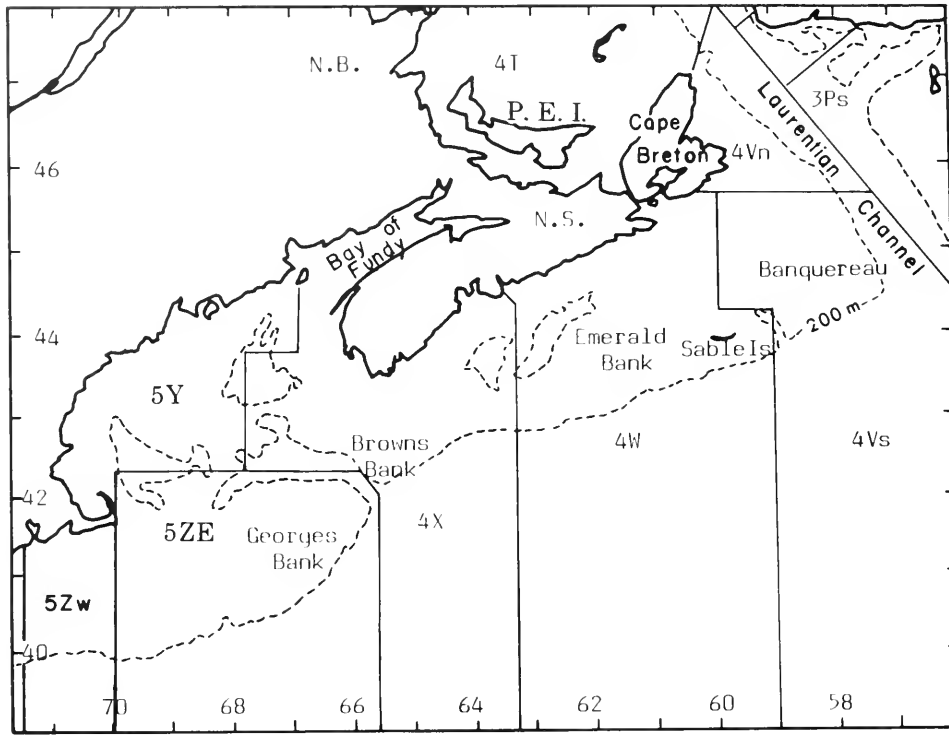

FIGURE 1.—Northwest Atlantic Fisheries Organization areas on the Scotian Shelf (Divisions 4VWX).

of Atlantic cod were recorded at sea, and otoliths were saved for later age determination according to the method of Kohler (1964). The validity of using otoliths in determining age of Atlantic cod was demonstrated by Kohler (1964) and May (1967). Powles (1958) outlined the classification of the gonads used in assessing maturity stage for this study.

The transition from immature to the mature condition in fish usually occurs over a range of length and age in the form of a sigmoid curve. From the percentages of mature Atlantic cod (gonads in ripening, ripe, spawning, spent, or recovering condition) in 2 cm length intervals in the survey or period under consideration, the median length at sexual maturity (L_{50}) was calculated by probit analysis following the technique of Leslie et al. (1945). Median age at sexual maturity (A_{50}) was calculated in a similar way by grouping the data in 1-yr intervals. Maturity ogives were plotted by eye. In some cases on the Scotian Shelf, annual values for median size and age at sexual maturity could not be calculated because Atlantic cod were not sampled in that year or because so few Atlantic cod were sampled that insufficient data were available for probit analysis.

RESULTS

Subdivision 4Vn

Atlantic cod caught in Subdivision 4Vn may be derived from three stocks. Atlantic cod from Division 4T overwinter in Subdivision 4Vn (McCracken 1959; Martin and Jean 1964), so that Atlantic cod caught between January and April may be from the Division 4T stock. Atlantic cod from Subdivision 4Vs migrate into Subdivision 4Vn during the summer, and Halliday (1974) assumed that Atlantic cod caught by commercial otter trawlers in Subdivision 4Vn during May-December were migratory cod from Subdivision 4Vs or Division 4W. There is also a local stock in Subdivision 4Vn that is exploited by the inshore fishery. Research vessel trawl surveys have been used previously to assess stock status of the inshore cod stock (Beacham et al. 1980), so it was assumed in the present analysis that the inshore stock was sampled by the surveys.

The L_{50} values of Atlantic cod sampled in Subdivision 4Vn declined from a high of 61 cm for males and 65 cm for females in 1959 to a low of 34 cm for males and 32 cm for females in 1978, but increased in 1979

(Fig. 2). Females generally matured at greater median lengths than did males, and with the difference between the sexes greater in the 1960's than in the 1970's.

The A_{50} values indicate trends similar to those of length, being about 5.7 yr for males and 6.7 yr for females in 1960, reaching a minimum in 1978 of 2.6 yr for both males and females, and increasing in 1979 (Fig. 3). During 1959-63, males tended to mature at younger ages than did females, but since 1969, median age at maturity between sexes has been similar. No values were calculated for 1975 and 1976 because of small sample sizes.

Maturity ogives based on length and age were calculated for four periods in this study, each corresponding to a 5-yr interval. L_{50} values during 1959-64 were 52 cm for males and 55 cm for females, but declined significantly ($P<0.01$) to 36 and 34 cm, respectively, during 1975-79. The trend towards the removal of larger, immature fish with time was apparent (Fig. 4). The transition from the all immature to 100% mature condition occurred over progressively shorter length ranges.

Changes in percent mature by age indicate an increase in percent mature at age through time (Table 1). There was a particularly striking increase in rates of maturity for males and females ages 3 and 4. About 90% of age-4 females were mature during 1975-79, whereas only 4% were classified as mature during 1959-64. During 1959-64, A_{50} for males was 5.4 yr and that of females 6.3 yr, whereas during 1975-79, these values were 2.8 yr for both males and females, the decline being significant ($P<0.01$). A_{50} declined faster in males than in females. These data also indicate that older, immature Atlantic cod disappeared from the area through time, probably through commercial exploitation.

TABLE 1.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Subdivision 4Vn, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male		
2	0.0 (102)	0.0 (5)	0.0 (94)	21.1 (19)
3	1.6 (126)	0.0 (15)	5.4 (92)	57.1 (67)
4	23.2 (168)	48.0 (25)	50.6 (85)	81.4 (94)
5	44.3 (131)	66.7 (18)	86.1 (129)	93.6 (60)
6	67.5 (197)	77.8 (9)	97.4 (76)	100.0 (37)
7	73.3 (206)	100.0 (16)	100.0 (57)	100.0 (10)
8	81.2 (117)	94.1 (17)	100.0 (27)	100.0 (12)
9	90.6 (96)	100.0 (14)	100.0 (13)	100.0 (11)
10	94.4 (71)	100.0 (1)	80.0 (5)	100.0 (9)
11	100.0 (38)	100.0 (6)	100.0 (3)	100.0 (2)
A_{50}	5.40(5.23-5.58)	4.39(4.01-4.79)	4.04(3.91-4.17)	2.80(2.54-3.08)
		Female		
2	0.0 (85)	0.0 (8)	0.0 (77)	9.5 (22)
3	0.0 (124)	5.3 (19)	6.1 (99)	63.1 (71)
4	4.0 (152)	50.0 (24)	34.3 (102)	90.0 (117)
5	17.3 (127)	66.7 (15)	83.6 (140)	100.0 (65)
6	49.1 (218)	91.7 (12)	97.7 (88)	100.0 (48)
7	64.2 (243)	100.0 (21)	98.4 (62)	100.0 (26)
8	76.6 (154)	100.0 (19)	100.0 (41)	100.0 (21)
9	91.6 (107)	93.3 (15)	100.0 (16)	100.0 (6)
10	91.2 (91)	100.0 (5)	100.0 (9)	100.0 (4)
11	94.7 (38)	100.0 (10)	100.0 (6)	100.0 (1)
12	89.5 (19)	100.0 (5)	100.0 (2)	100.0 (2)
13	100.0 (12)	100.0 (7)	100.0 (2)	100.0 (3)
A_{50}	6.34(6.19-6.51)	4.20(3.88-4.55)	4.20(4.07-4.33)	2.78(2.59-2.99)

Subdivision 4Vs

L_{50} for Atlantic cod in Subdivision 4Vs had the same general decreasing trend with time as in other areas, declining from 51 cm for males and 54 cm for females in 1959 to about 35 cm for males and 33 cm for females in 1977 (Fig. 5). There appeared to be a rapid drop in the median length at maturity in the early 1970's, and an increase since 1977. However, given the variability in the measurements, it is uncertain if these were actual trends or due to sampling variability.

A_{50} displayed trends similar to those of length, being about 5.6 yr for males and 5.7 yr for females in 1959, and declining to about 2.4 yr for males and 2.3 yr for females in 1977 (Fig. 6). Atlantic cod matured, on average, at older ages in the early 1960's than did those in the 1970's. Males again tended to mature at smaller sizes and younger ages than did the females.

The maturity ogives for length indicate trends similar to Atlantic cod in Subdivision 4Vn for the periods under consideration. Larger, immature fish have been eliminated from the stock over time, and the transition from the immature to the mature state occurred over a smaller length interval with time (Fig. 7). During 1959-64, the transition from 0% mature to 100% mature occurred over a 40 cm interval of length for both males and females, but from 1975 to 1979, this transition occurred over a 20 cm length interval. L_{50} values in 1959-64 were 47 cm for males and 44 cm for females, but these values declined to 38 cm for both males and females in 1975-79 ($P<0.01$).

Changes in percent mature by age indicate marked increases over time for age-3 and -4 Atlantic cod (Table 2). However, the data for the 1965-69 interval were sparse and may not be indicative of the stock in this period. These data also indicate that between 10 and 15% of age-2 Atlantic cod became mature in 1975-79, whereas virtually no age-2 Atlantic cod were mature in the 1960's. This trend was also apparent in Atlantic cod caught in Subdivision 4Vn. During 1959-64, median age at maturity for males was 5.4 yr and that of females 5.2 yr, whereas in 1975-

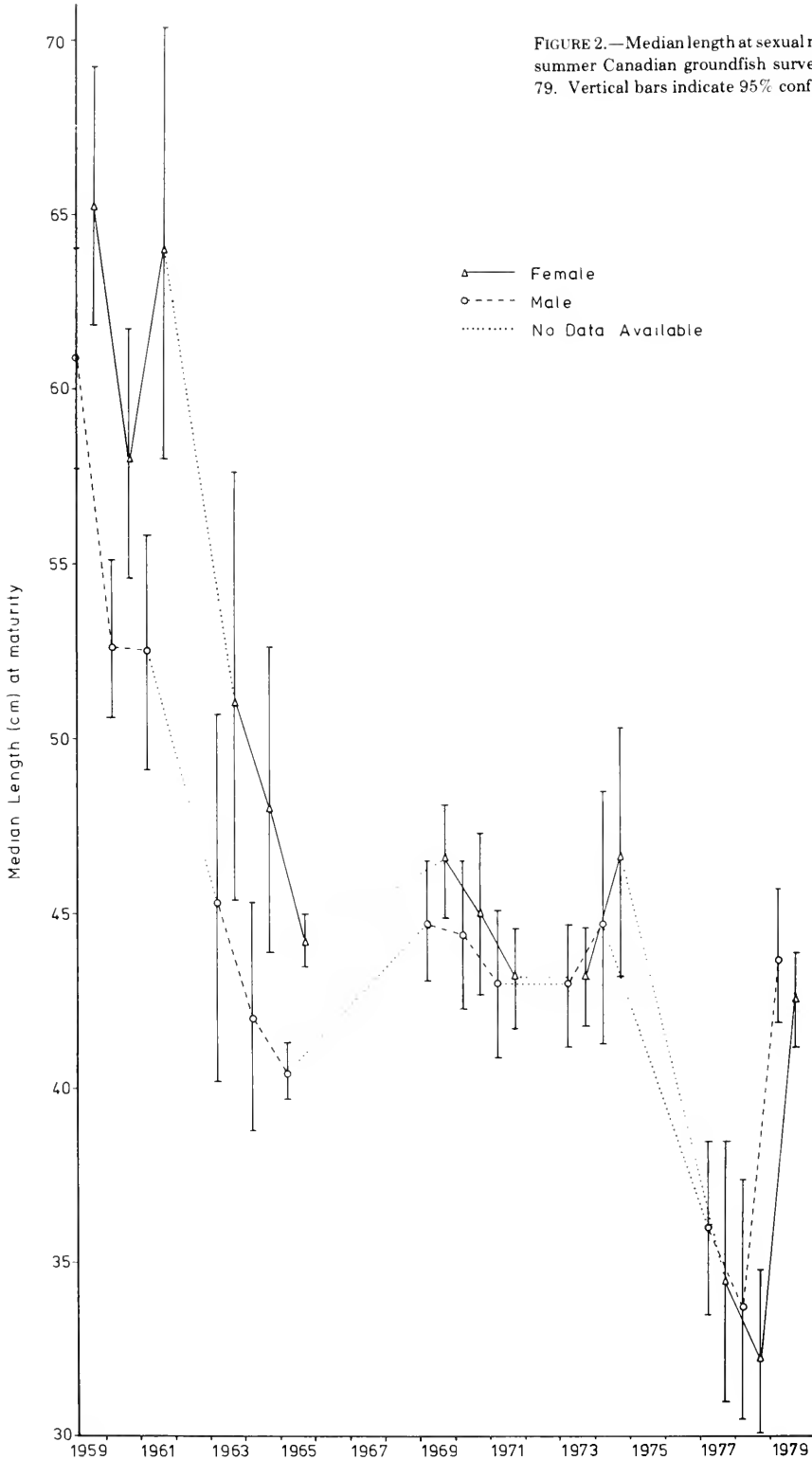

FIGURE 2.—Median length at sexual maturity for Atlantic cod during summer Canadian groundfish surveys in Subdivision 4Vn, 1959-79. Vertical bars indicate 95% confidence limits.

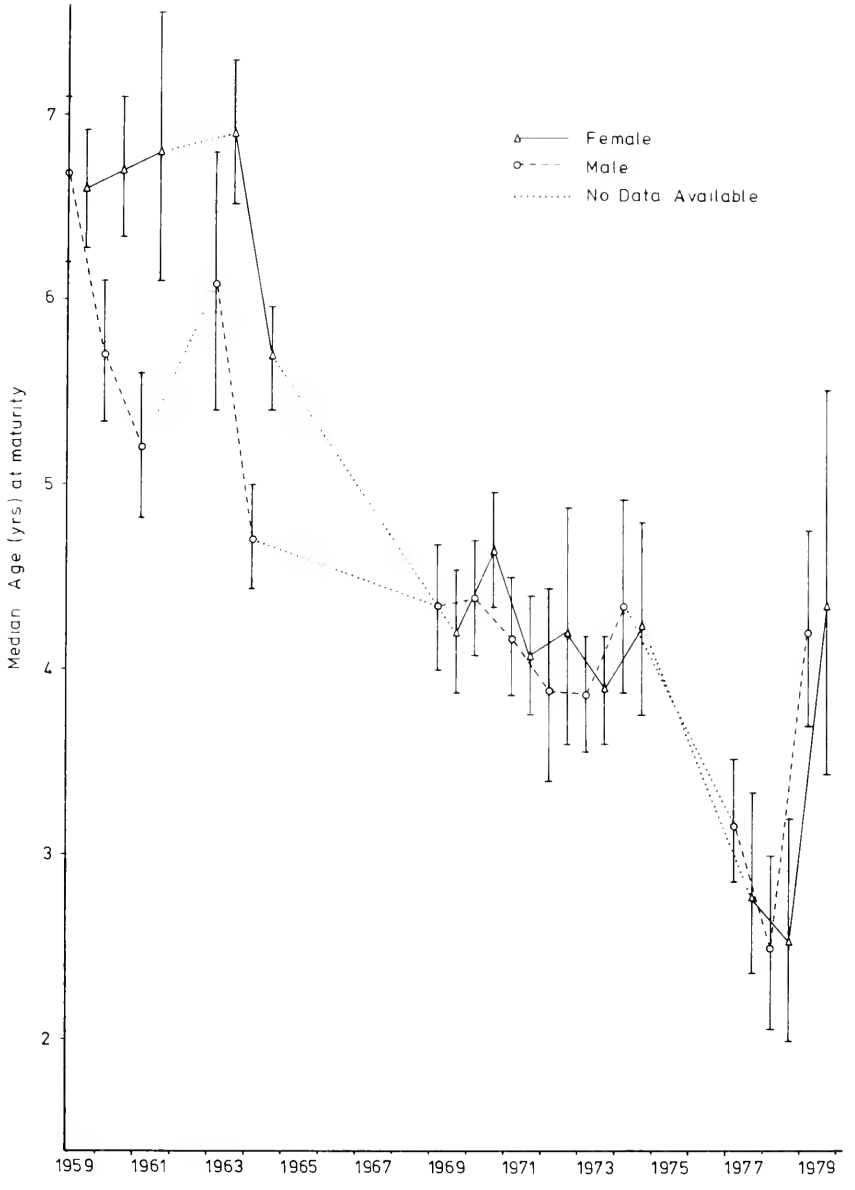

FIGURE 3.—Median age at sexual maturity for Atlantic cod during summer Canadian groundfish surveys in Subdivision 4Vn, 1959-79. Vertical bars indicate 95% confidence limits.

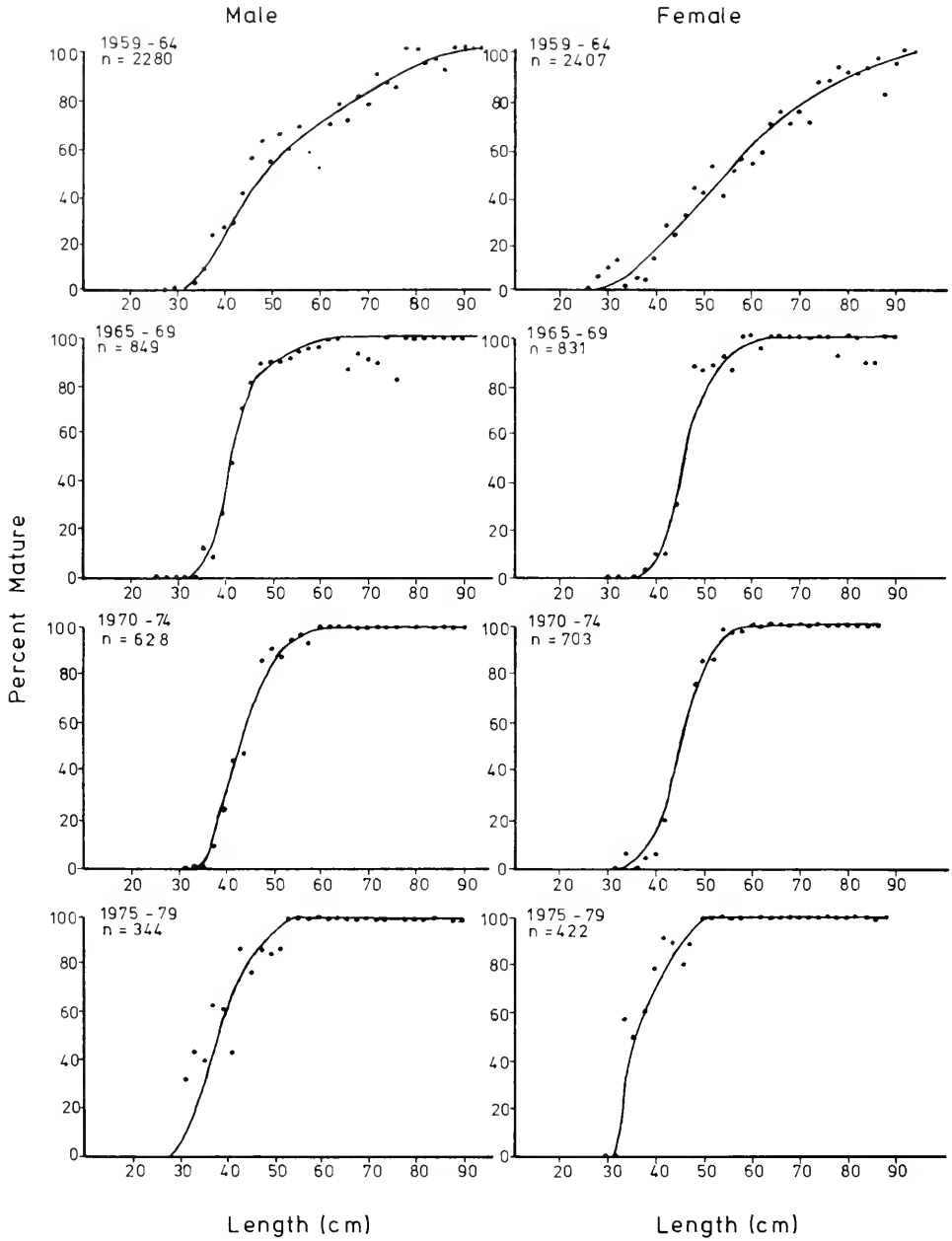

FIGURE 4.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Subdivision 4Vn, 1959-79.

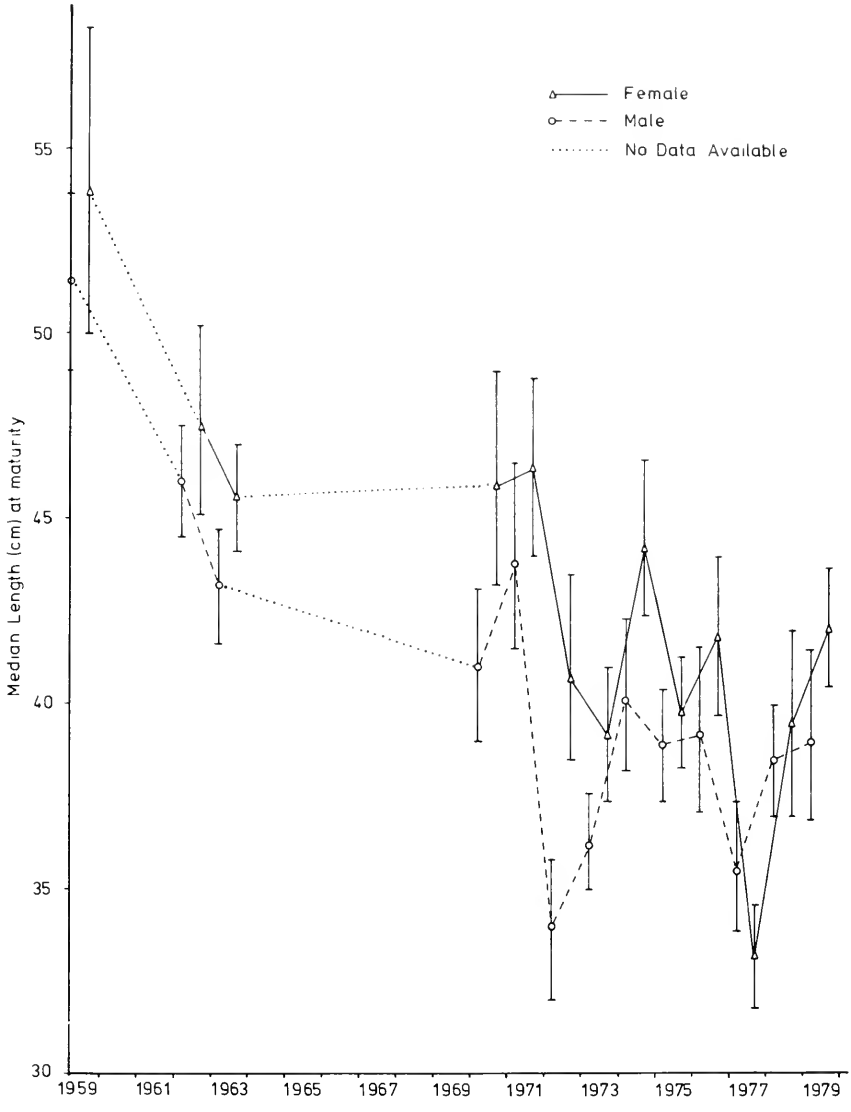

FIGURE 5.—Median length at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Subdivision 4Vs, 1959-79. Vertical bars indicate 95% confidence limits.

79, median age was 2.7 yr for males and 2.9 yr for females, a significant decline ($P<0.01$).

Division 4W

Atlantic cod populations in Subdivision 4Vs and Division 4W are considered to be a unit stock for management purposes (Gray 1979). There were similar trends in L_{50} between Atlantic cod in Subdivision 4Vs and those of Division 4W (Fig. 8). In particular, there was a rapid decline in L_{50} between 1969 and 1972, with L_{50} for males declining from 48 to 37 cm in 4 yr, and with values for females declining from 50 to 36 cm. Subsequently, L_{50} values for both sexes have generally remained below 40 cm. Atlantic cod in Division 4W were similar to those of the other areas in regards to a decrease in L_{50} with time. The difference in lengths in which males and females attained maturity was greater in the 1960's than in the 1970's, indicating that the rate of decline in L_{50} was faster in females than in males.

A_{50} values declined over time until the early 1970's (Fig. 9). A low value of 2.2 yr for males and 2.3 yr for females was reached in 1978, a decrease of about

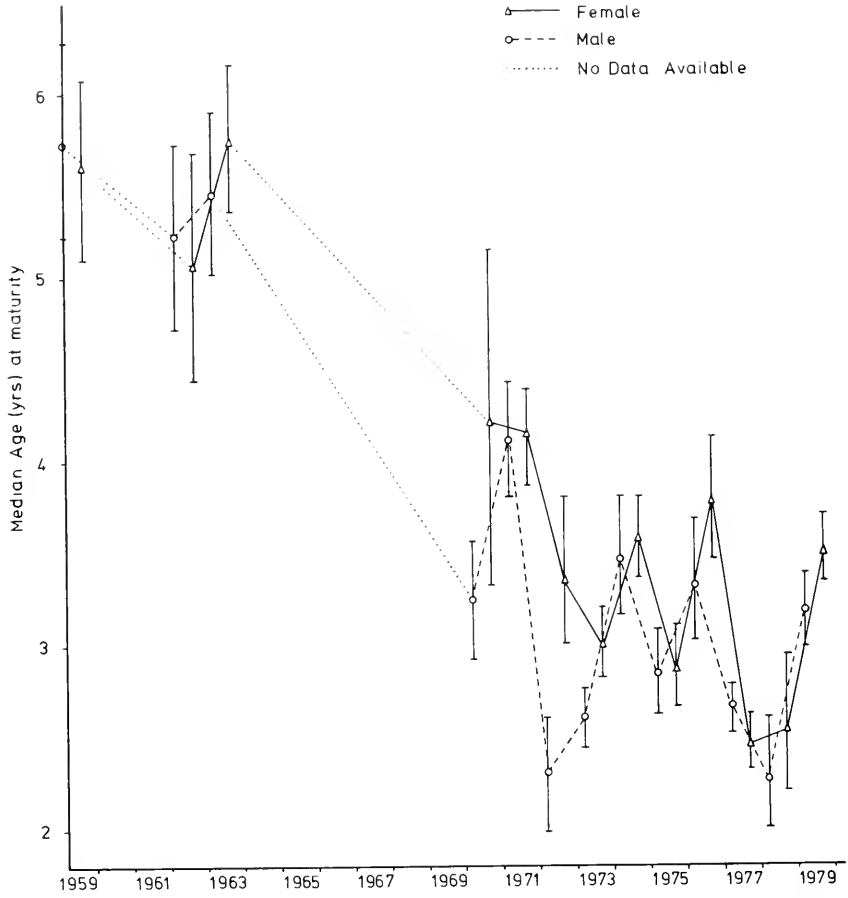

FIGURE 6.—Median age at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Subdivision 4Vs, 1959-79. Vertical bars indicate 95% confidence limits.

TABLE 2.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Subdivision 4Vs, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79	Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male					Female		
1	0.0 (19)	— (0)	0.0 (44)	0.0 (23)	1	25.0 (4)	— (0)	0.0 (46)	0.0 (9)
2	0.0 (60)	25.0 (4)	13.2 (250)	15.2 (126)	2	0.0 (79)	0.0 (1)	5.7 (299)	10.0 (142)
3	2.5 (121)	75.0 (8)	40.0 (205)	62.9 (251)	3	2.0 (102)	75.0 (12)	25.0 (228)	55.7 (266)
4	10.4 (106)	78.3 (23)	80.1 (141)	91.7 (140)	4	23.0 (100)	85.7 (14)	59.9 (157)	91.0 (163)
5	37.4 (83)	100.0 (11)	95.6 (90)	95.9 (119)	5	38.8 (80)	100.0 (9)	95.9 (98)	97.4 (107)
6	74.2 (93)	90.9 (11)	97.9 (48)	100.0 (36)	6	76.0 (121)	94.1 (17)	97.2 (72)	100.0 (50)
7	88.1 (109)	100.0 (9)	100.0 (37)	100.0 (24)	7	89.4 (113)	100.0 (8)	100.0 (23)	100.0 (28)
8	87.9 (66)	100.0 (1)	100.0 (11)	100.0 (17)	8	81.8 (77)	100.0 (2)	100.0 (15)	100.0 (6)
9	87.2 (39)	100.0 (1)	100.0 (2)	100.0 (12)	9	88.5 (52)	100.0 (3)	100.0 (6)	100.0 (5)
10	94.4 (36)	100.0 (2)	100.0 (1)	100.0 (5)	10	100.0 (49)	— (0)	100.0 (5)	100.0 (3)
11	90.9 (11)	100.0 (1)	100.0 (3)	— (0)	A_{50}	5.19(6.19-6.51)	2.45(1.61-3.77)	3.53(3.41-3.65)	2.86(2.76-2.97)
12	80.0 (10)	100.0 (1)	— (0)	— (0)					
13	100.0 (1)	100.0 (1)	— (0)	100.0 (1)					
A_{50}	5.43(5.23-5.64)	2.40(1.37-5.44)	3.07(2.96-3.18)	2.72(2.60-2.83)					

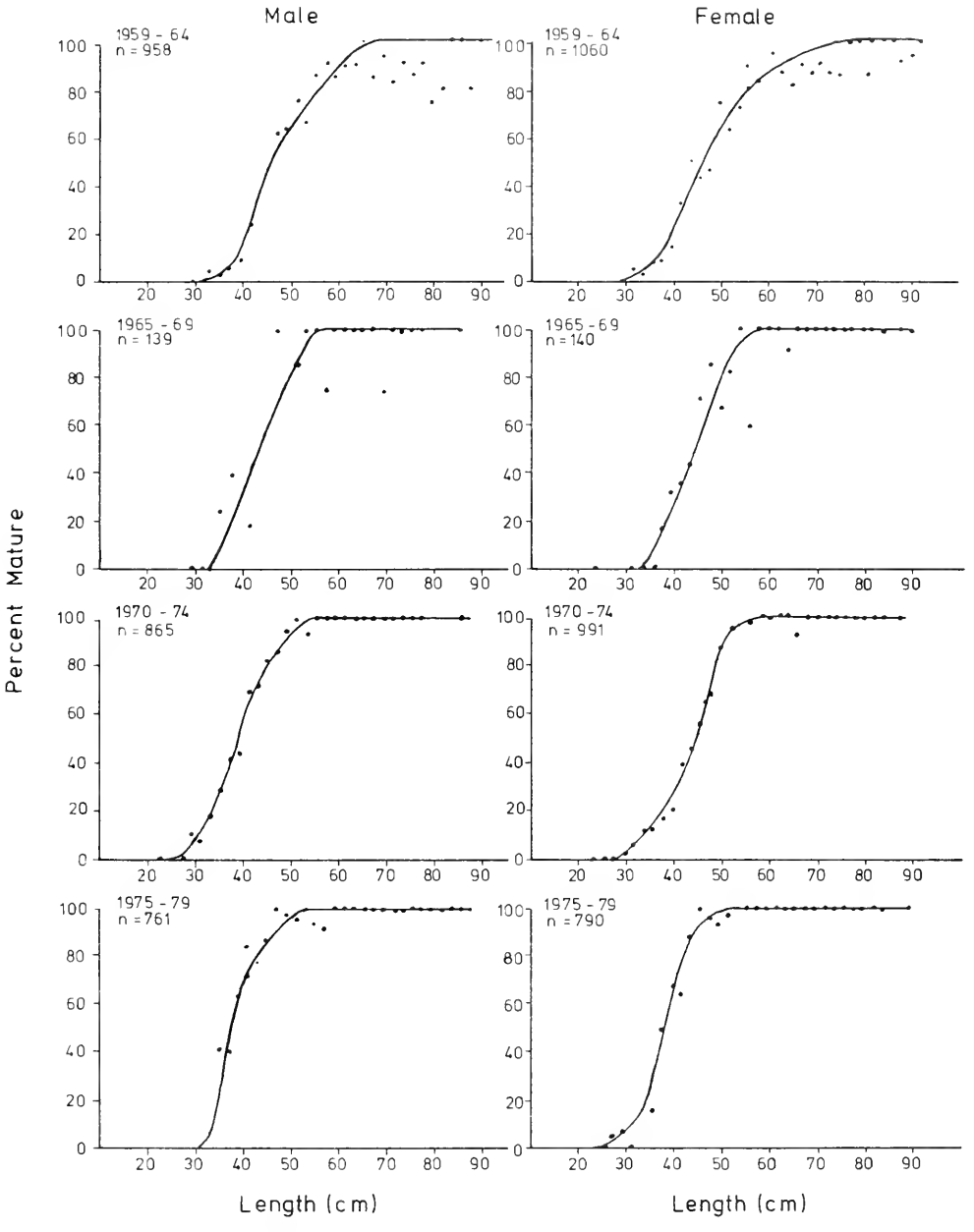

FIGURE 7.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Subdivision 4Vs, 1959-79.

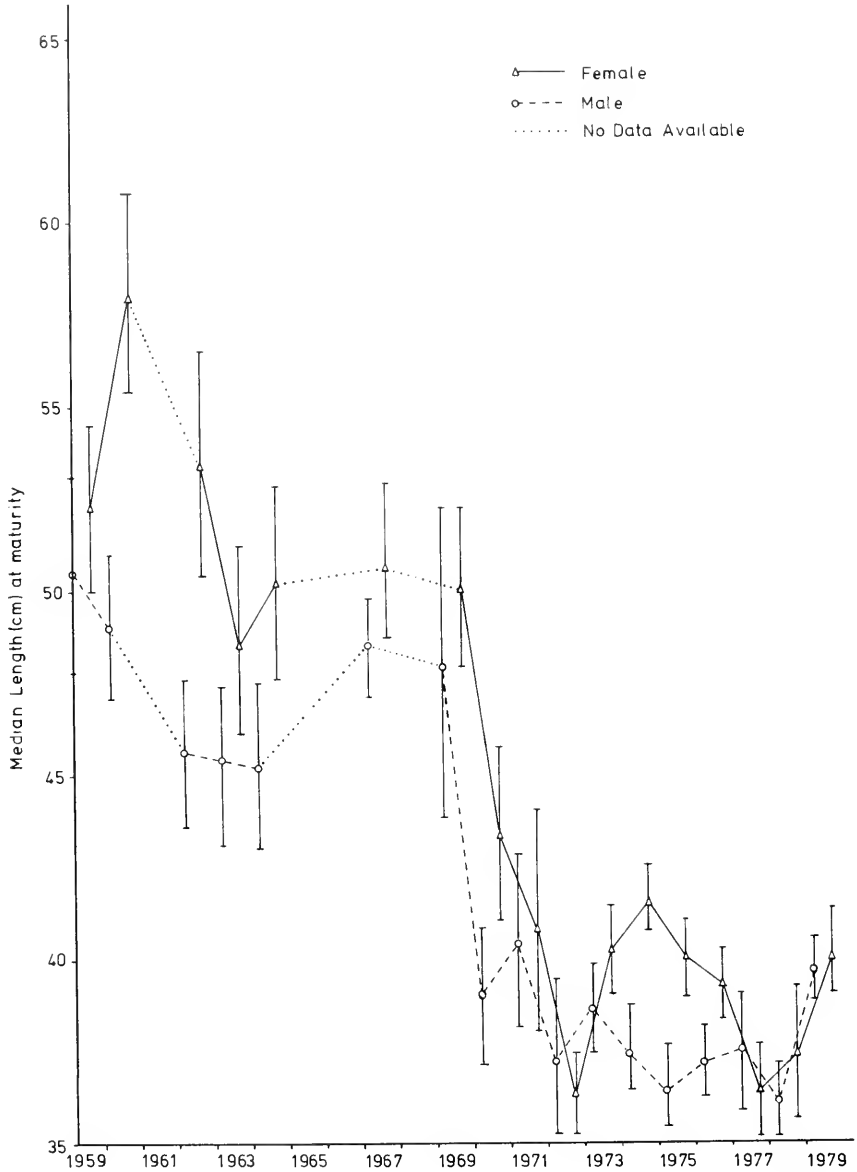

FIGURE 8.—Median length at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4W, 1959-79. Vertical bars indicate 95% confidence limits.

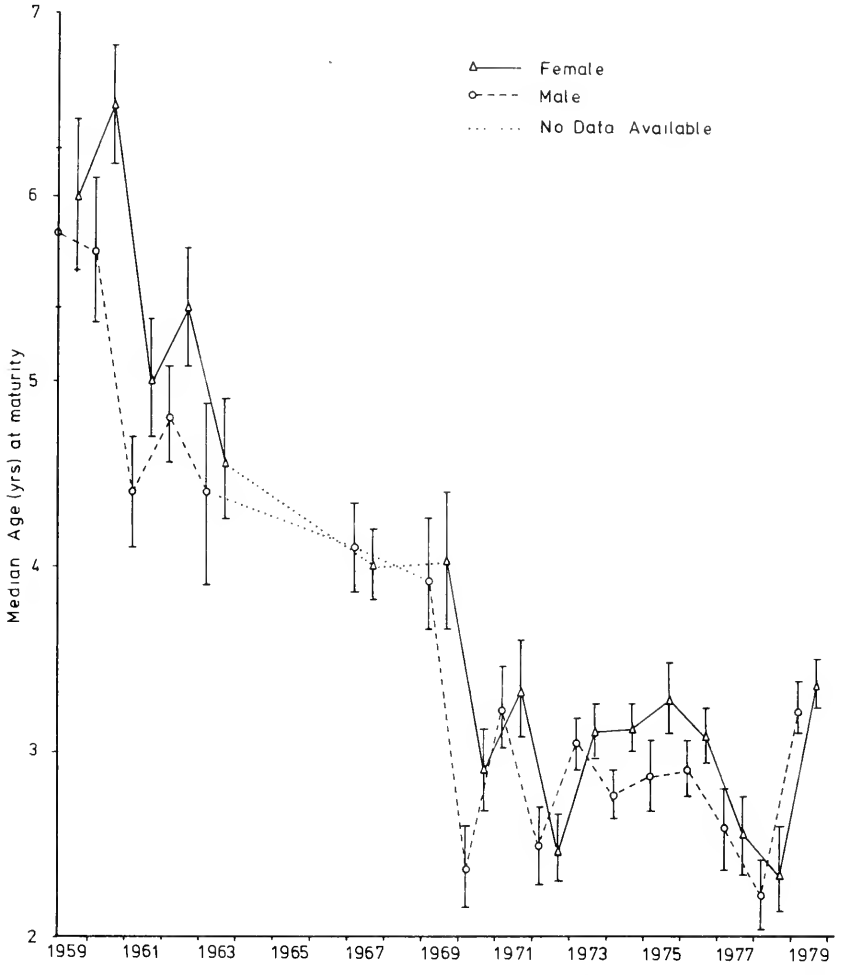

FIGURE 9.—Median age at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4W, 1959-79. Vertical bars indicate 95% confidence limits.

60% from the 1959 values. The A_{50} value increased in 1979, though further data are necessary to determine if this is a general trend.

The maturity ogives, based on length, indicated that the trend for elimination of larger, immature Atlantic cod seen in other cod in other areas was also present in this area (Fig. 10). L_{50} values for Atlantic cod in 1959-64 were 46 cm for males and 52 cm for females, but in 1975-79, these values were 37 and 39 cm, respectively. The values in 1975-79 were lower than those in any of the previous three periods ($P<0.05$). The trend for a transition from an immature to a mature state over a smaller length interval through time was also apparent. The transition occurred over a 45 cm length interval in 1959-64, but over a 25 cm interval in 1975-79.

Changes in percent mature by age indicate an increase through time (Table 3), and males and females ages 3-5 showed marked increases in percent mature over time. Age-2 Atlantic cod also showed marked increases, with about 18% of the males and 11% of the females classified as mature in 1975-79, whereas <1% were mature during 1959-64. A_{50} values in 1959-64 were 4.7 yr for males and 5.0 yr for females, and these values declined in 1975-79 to 2.7 yr for males and 2.9 yr for females ($P<0.01$). These trends are indicative of a shifting of the A_{50} to younger ages.

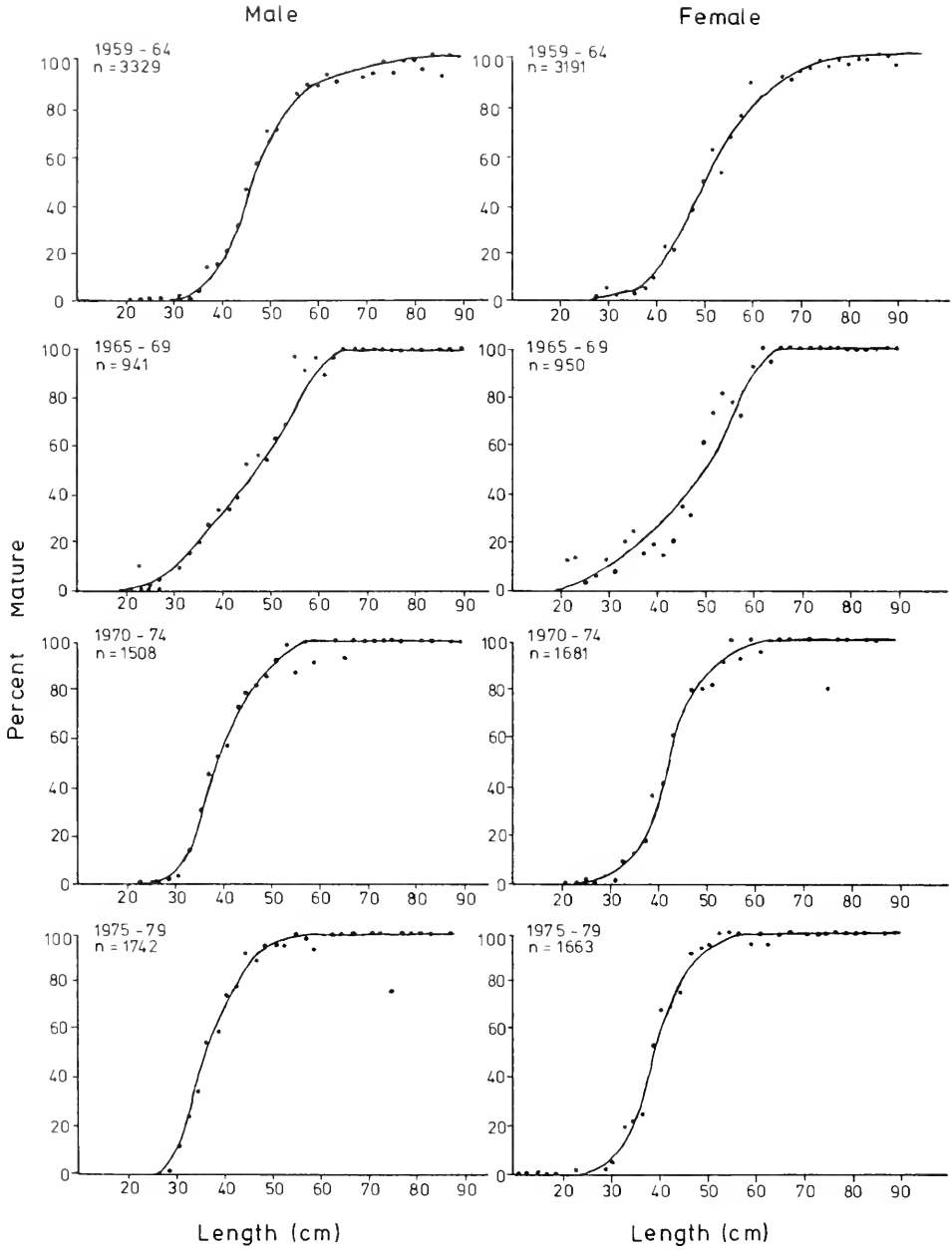

FIGURE 10.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Division 4W, 1959-79.

TABLE 3.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Division 4W, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male		
1	0.0 (59)	0.0 (7)	0.0 (146)	0.0 (120)
2	0.7 (143)	7.4 (81)	16.1 (416)	17.5 (307)
3	5.0 (282)	25.3 (178)	51.7 (395)	65.6 (466)
4	26.3 (205)	48.6 (177)	82.8 (250)	89.3 (421)
5	57.7 (208)	91.2 (91)	87.7 (114)	94.3 (261)
6	83.6 (280)	95.8 (71)	91.3 (46)	97.9 (95)
7	90.0 (250)	98.4 (63)	100.0 (36)	100.0 (26)
8	99.3 (141)	100.0 (14)	100.0 (17)	100.0 (6)
9	97.2 (71)	100.0 (12)	100.0 (4)	100.0 (2)
10	93.1 (58)	100.0 (14)	100.0 (3)	— (0)
11	100.0 (21)	100.0 (1)	100.0 (1)	100.0 (1)
A_{50}	4.69(4.58-4.80)	3.72(3.58-3.86)	2.94(2.85-3.03)	2.67(2.59-2.76)
		Female		
1	0.0 (60)	0.0 (4)	0.0 (144)	0.0 (106)
2	0.6 (177)	10.1 (79)	8.2 (486)	11.0 (287)
3	7.0 (259)	17.2 (221)	43.6 (404)	54.3 (421)
4	14.6 (212)	36.3 (171)	73.9 (284)	88.4 (445)
5	45.7 (184)	81.9 (72)	91.8 (134)	99.3 (228)
6	75.4 (236)	89.8 (49)	95.0 (40)	98.2 (110)
7	90.2 (245)	90.6 (64)	97.1 (34)	100.0 (31)
8	95.9 (170)	100.0 (14)	100.0 (15)	100.0 (4)
9	95.2 (105)	100.0 (17)	100.0 (14)	100.0 (4)
10	100.0 (77)	100.0 (14)	100.0 (12)	— (0)
A_{50}	4.95(4.83-5.07)	4.16(3.99-4.35)	3.19(3.11-3.28)	2.87(2.80-2.95)

Division 4X

Atlantic cod in Division 4X are managed as a separate unit, though inshore and offshore stocks may mix. Trends in L_{50} were not as clear as in other stocks, although there was a decrease with time until 1978 (Fig. 11). The L_{50} values were 51 cm for males and 52 cm for females in 1963, but these values had declined to 38 cm for males and 35 cm for females in 1978. Females generally attained maturity at greater lengths than did males, but there has been little difference between sexes over time. The data suggest that there was a decrease in L_{50} in 1970-71, as happened in 4VsW Atlantic cod.

A_{50} values have declined with time, but age samples in the early 1960's had small sample sizes. There was a rapid decline in A_{50} between 1969 and 1972 with values for males declining from 3.9 to 2.2 yr and for females from 5.0 to 2.4 yr (Fig. 12). In 1978, A_{50} values were calculated to be <2 yr for both males and females. Males generally matured at younger ages than did females.

The maturity ogives, based on length, indicate that there has been some elimination of larger, immature fish from Division 4X Atlantic cod with time, but that the transition from the immature to the mature state during 1975-79 still occurred over the largest length interval of the areas analyzed, being about 35 cm for males and 40 cm for females (Fig. 13). In 1959, L_{50} was 57 cm for males and 46 cm for females, but these values declined to 45 cm for both males ($P<0.05$) and females during 1975-79. The 100% mature value during 1975-79 was not attained until lengths were >65 cm.

Changes in percent maturity with age indicate an increasing trend with time, but the increase in percent maturity with time has not been as marked as in other Atlantic cod stocks (Table 4). A_{50} values in 1959-64 were 4.8 yr for males and 3.7 yr for females, but during 1975-79 these values declined to 2.8 yr for males ($P<0.01$) and 2.9 yr for females ($P<0.05$). Increases in percent mature were most apparent in males ages 2-5 and females ages 2-4. Median age at maturity has been generally <3 yr in the 1970's.

TABLE 4.—Percentage of sexually mature Atlantic cod by age and sex caught during Canadian groundfish surveys in Division 4X, 1959-79. Sample sizes are in parentheses for individual ages and 95% confidence limits for A_{50} (years).

Age (yr)	1959-64	1965-69	1970-74	1975-79
		Male		
1	0.0 (2)	— (0)	0.0 (47)	0.0 (35)
2	0.0 (12)	0.0 (30)	15.3 (183)	21.1 (204)
3	16.2 (37)	8.6 (58)	59.5 (227)	56.3 (288)
4	29.3 (75)	72.7 (55)	83.4 (169)	81.7 (355)
5	47.1 (68)	98.2 (55)	92.7 (123)	93.4 (182)
6	72.9 (59)	98.0 (50)	97.4 (78)	97.1 (136)
7	88.2 (51)	100.0 (19)	97.6 (42)	100.0 (63)
8	100.0 (60)	100.0 (11)	100.0 (22)	100.0 (35)
A_{50}	4.76(4.52-5.01)	3.69(3.54-3.84)	2.83(2.72-2.94)	2.78(2.67-2.89)
		Female		
1	0.0 (0)	— (0)	0.0 (50)	0.0 (56)
2	10.0 (20)	0.0 (31)	13.7 (182)	15.6 (238)
3	24.3 (37)	8.9 (56)	55.6 (216)	57.0 (335)
4	57.8 (90)	64.4 (45)	73.1 (197)	83.5 (351)
5	81.5 (81)	87.7 (57)	83.5 (121)	85.2 (250)
6	77.8 (54)	100.0 (57)	94.5 (91)	93.6 (125)
7	94.9 (59)	100.0 (21)	97.4 (39)	96.3 (80)
8	96.2 (26)	100.0 (10)	100.0 (25)	100.0 (34)
9	100.0 (8)	100.0 (5)	100.0 (16)	100.0 (18)
A_{50}	3.72(3.44-4.01)	3.84(3.66-4.02)	3.03(2.90-3.17)	2.88(2.77-2.99)

Comparisons Among Areas

Several trends were apparent when all areas were considered in the multiyear grouping of groundfish surveys. Median lengths at maturity tended to decline through time in all areas in which Atlantic cod were surveyed (Table 5). The differences in L_{50} values among Atlantic cod decreased with time, so that values for Atlantic cod in all areas except those in Division 4X were similar in the period 1975-79.

In an analysis of trends in A_{50}, there was a trend for younger ages at maturity over time. Differences among areas generally decreased with time, so that in the period 1975-79, A_{50} values were about 2.7 yr for

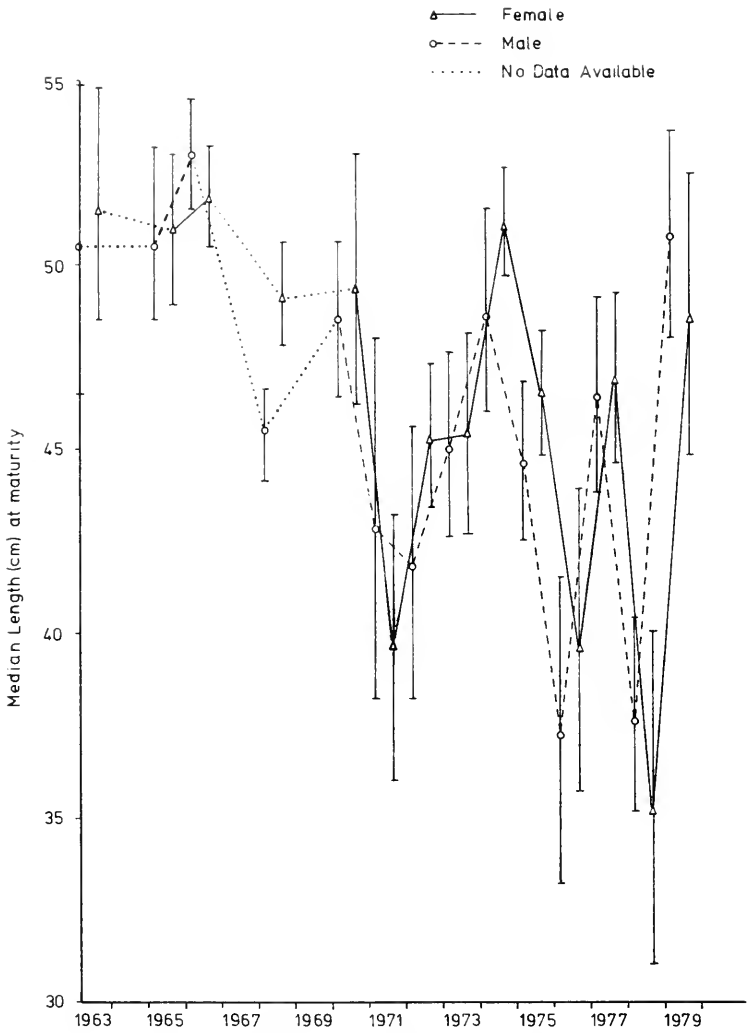

FIGURE 11.—Median length at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4X, 1959-79. Vertical bars indicate 95% confidence limits.

males and about 2.9 yr for females on the Scotian Shelf. Bottom water temperatures derived from the groundfish surveys indicated that Subdivision 4Vn had the coldest water temperatures during 1970-74 (3.6°C) and Division 4X the warmest (6.9°C), with the rest of Scotian Shelf temperatures between these extremes. There was a general trend for greater A_{50} values to be found in stocks in colder waters, and Atlantic cod growth rates on the Scotian Shelf were correlated with water temperature (Beacham 1982), so there was a trend for stocks that have a lower growth rate to have a higher median age at sexual maturity.

DISCUSSION

The Atlantic cod stocks on the Scotian Shelf were subject to high rates of exploitation in the 1960's and early 1970's and consequently declined in biomass (Gray 1979). The declines in median size and age at sexual maturity were thus concurrent with declines in stock biomass. However, with the introduction of quota management and improved recruitment, stock biomasses have generally increased since 1975.

The mean size and age of Atlantic cod in the landings of the commercial fishery in Subarea 4 have declined with time (Beacham 1982), but this cannot

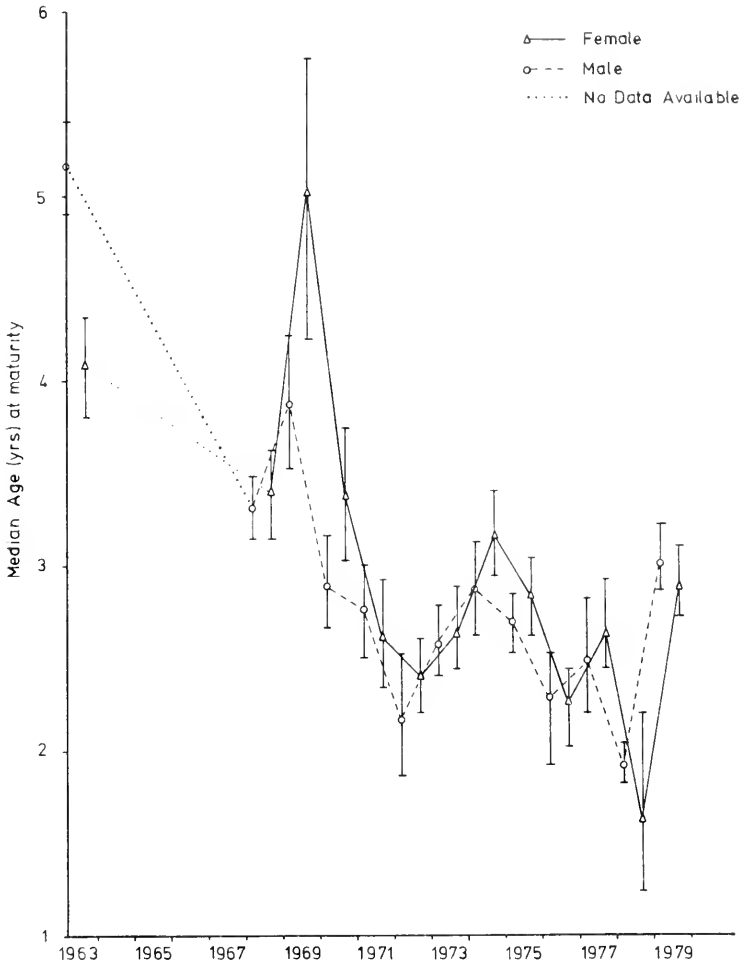

FIGURE 12.—Median age at sexual maturity for Atlantic cod caught during summer Canadian groundfish surveys in Division 4X, 1959-79. Vertical bars indicate 95% confidence limits.

account for the decline in median size and age at sexual maturity. Larger Atlantic cod are less abundant than they once were, but during 1975-79, virtually all Atlantic cod 60 cm long were mature in the stocks examined, while in the 1960's, 50% of 60 cm Atlantic cod could be immature. For the decline in median size and age at sexual maturity to be accounted for by a decline in mean size and age of the stock, sampling gears in the 1960's would have to have selected larger, immature fish while avoiding smaller, mature ones, an unlikely situation.

Median length and age at maturity of the 4VsW Atlantic cod stock declined rapidly between 1969 and 1972. Nominal catches from this stock peaked in 1968, with over 80,000 t reported by all countries, and with the Spanish catch reported at over 50,000 t (Halliday 1976). Halliday noted that there were sharp declines in the catch rates of Spanish pair trawlers subsequent to 1968. The rapid decline in median size and age at sexual maturity subsequent to 1968 may suggest that these parameters were responding rapidly to a decrease in stock biomass, although this interpretation is open to question. Stock biomasses have increased in the late 1970's (Beacham et al. 1980; Gray 1979), but there has been no corresponding increase in median size or age at maturity.

Median length and age at sexual maturity for Atlantic cod in the northwest Atlantic have been an area of some research. Variability in median length at sexual

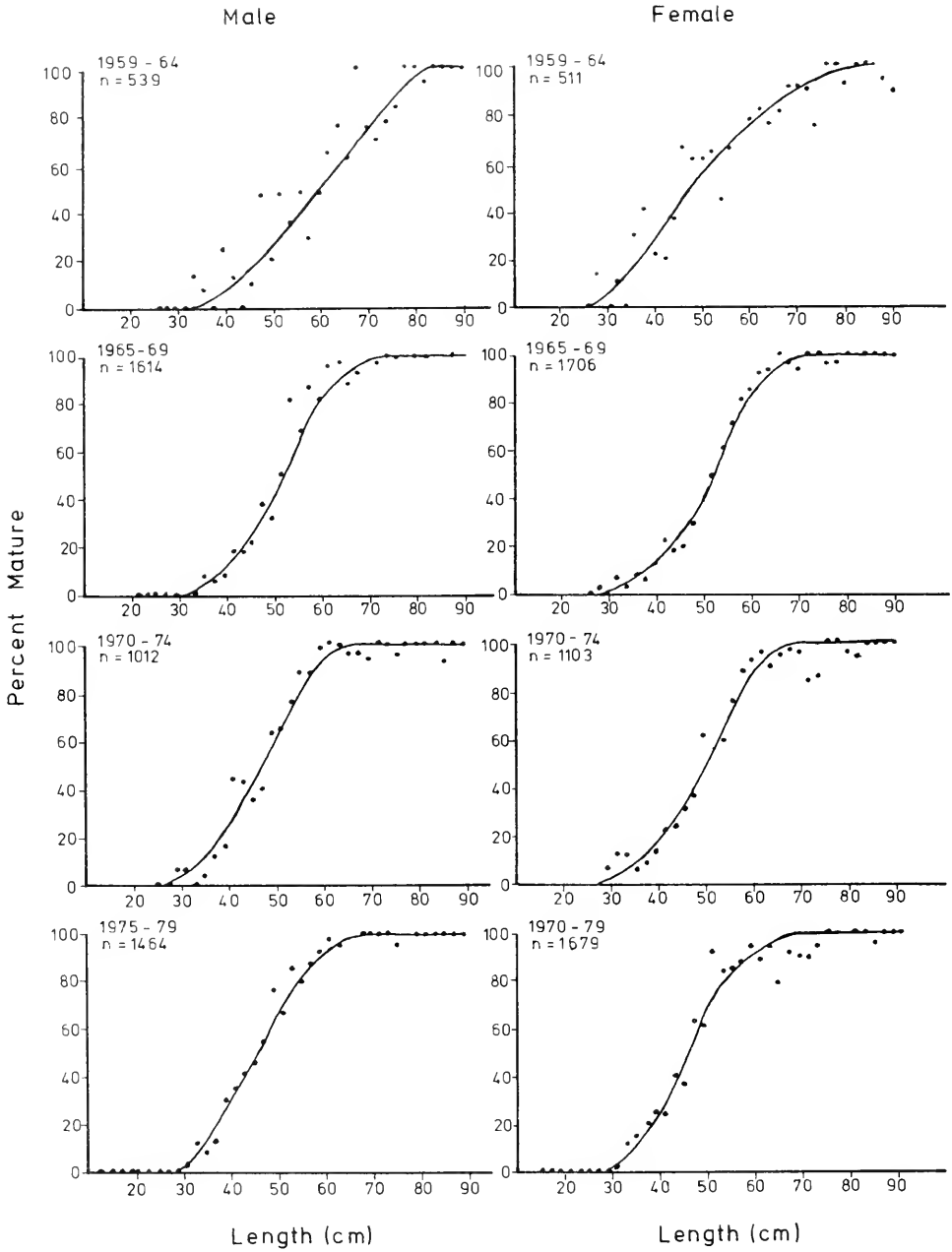

FIGURE 13.—Maturity ogives for Atlantic cod caught during Canadian groundfish surveys in Division 4X, 1959-79.

TABLE 5.—Median length (cm) at sexual maturity of Atlantic cod in areas 4Vn, 4Vs, 4W, and 4X, as calculated from Canadian groundfish surveys from 1959-64, 1965-69, 1970-74, and 1975-79. 95% confidence limits are in parentheses. Sample sizes are indicated in Figures 4, 7, 10, and 13.

Division	1959-64	1965-69	1970-74	1975-79
		Males		
4Vn	51.82	41.08	42.62	36.31
	(49.96-53.75)	(40.22-41.95)	(41.66-43.61)	(33.73-39.10)
4Vs	47.31	42.26	38.46	37.59
	(45.84-48.83)	(40.21-44.42)	(37.68-39.25)	(36.83-38.37)
4W	46.01	43.54	39.27	37.23
	(45.19-46.85)	(42.38-44.73)	(38.63-39.92)	(36.64-37.84)
4X	57.09	49.16	45.67	44.74
	(54.99-59.27)	(48.30-50.04)	(44.64-46.71)	(43.83-45.67)
		Females		
4Vn	54.55	44 85	44.09	34.11
	(53.37-55.77)	(44.21-45.50)	(43.29-44.89)	(31.73-36.67)
4Vs	43.70	43.31	42.26	37.61
	(37 12-51.88)	(40.47-46.36)	(41.44-43.10)	(36.83-38.42)
4W	52.00	45.66	41.68	38.88
	(51.55-52.45)	(44 25-47.12)	(41.03-42.34)	(38.27-39.49)
4X	46.08	48.68	47.91	44.77
	(42.86-49.55)	(47 80-49 57)	(46.75-49.10)	(43.94-45.62)

maturity for Division 4T Atlantic cod was investigated by Powles (1958), who found that during the summers of 1955 and 1956, median lengths at maturity for females were between 52 and 57 cm, and those for males between 50 and 53 cm. Wiles and May (1968) found that, by grouping data between 1947 and 1966, the median lengths at sexual maturity in the northern Gulf of St. Lawrence cod stock (Divisions 3Pn-4RS) were 46 cm for males and 50 cm for females, corresponding to median ages at maturity of 5.1 and 6.1 yr, respectively. Minet (1978), investigating the same stock in 1973, found results very similar to those of Wiles and May (1968). Pinhorn (1969) found similar results for Atlantic cod in Subdivision 3Pn in 1952, but median ages apparently increased to 6.3 yr for males and 6.7 yr for females in 1957. Fleming (1960) found that Atlantic cod in the same area matured between 6.6 and 6.8 yr from 1947 to 1950. Thus it appears for the northern Gulf of St. Lawrence cod stock, there has not been a marked decline in median age at sexual maturity with time. Hansen (1949) reported that size and age at maturity of Atlantic cod in the West Greenland stock declined from 1917 to 1936, an analogous trend to that indicated for Atlantic cod on the Scotian Shelf by the present study.

Gunter (1950) found that fish inhabiting regions of higher water temperature grew faster initially, attained sexual maturity earlier, and were of smaller final size than the same species in regions of lower water temperature. However, Fleming (1960) found that Atlantic cod in the Labrador area of Newfoundland attained sexual maturity at younger ages, but grew more slowly than did Atlantic cod in stocks further south. Fleming attributed this result to Atlantic cod in poorer environments maturing earlier than those in more favorable environments. The present study, in agreement with Gunter's (1950) conclusions, indicated that Atlantic cod stocks inhabiting regions with warmer water temperature matured earlier than did those in colder regions.

Median size and age at maturity are heavily dependent upon growth rate. Molander (1925) found that in Baltic witch flounder, *Glyptocephalus cynoglossus*, stocks with faster growth rates matured at younger ages but at larger lengths than did fish in slower growing stocks. During 1975-79 in the present study, Atlantic cod tended to mature at the same length (Table 5), but northern stocks matured at older ages than did Atlantic cod in more southerly stocks. Alm (1959) noted that faster growing fish attained sexual maturity earlier than did slower growing fish, and the results of the present study support that conclusion.

Growth rates in Atlantic cod have been shown to be inversely related with stock biomass (Lett and Doubleday 1976; Beacham 1980), with growth rates increasing as stock biomass declines. Templeman and Bishop (1979) attributed a decline in median age at maturity in haddock, *Melanogrammus aeglefinus*, to an increase in growth rate coincident with declining stock density, an idea that implicitly assumes a minimum threshold or minimum range for size at maturity. They also suggested that a decline in median length at maturity occurred, owing to a decrease in growth rates, implicitly assuming a minimum threshold for age at maturity. If Templeman and Bishop's (1979) assertions are general, then declines in median length and age at maturity should not occur concurrently.

All the Atlantic cod stocks examined in the present study showed a downward trend both in median size and median age at sexual maturity with time. Several hypotheses would explain these events. However, to the extent that size and age at maturity are genetically determined (Alm 1959), fish which mature at smaller sizes or younger ages had a selective advantage during the intensive fishery that has occurred on many of the Atlantic cod stocks since 1960 in Subarea 4. These genotypes reproduce before being fully recruited to the fishery, whereas genotypes that mature at larger lengths or older ages tend to be removed before reproduction. This process could contribute to the decreasing abundance of larger, immature fish with time and account for the shifting of the maturity ogives towards smaller sizes and younger ages. Size-selective fishing has been postulated to account for declines in size of individuals through the disproportionate removal of fast-growing individuals (Ricker et al. 1978; Favro et al. 1979). It may be, therefore, that late-maturing genotypes were removed from the Atlantic cod stocks in a period of heavy exploitation.

Environmental and genetic effects are difficult to separate. There may be a lag effect if size and age at sexual maturity have not increased at the same rate as stock biomass. Because fish attaining maturity at low stock biomass remain mature with increasing biomass, then the lag in increase in size and age at maturity results from year classes spawned under high stock biomass conditions requiring a longer period to attain maturity. There was an increase in median size and age at maturity in 1979 for Atlantic cod stocks on the Scotian Shelf, but further data are necessary to determine if this will be continuing. If median size and age at sexual maturity increase in the next 5-10 yr to levels similar to those between 1959 and 1964, this would suggest that these parameters were responding to stock biomass with a lag effect, although this interpretation is confounded by a decline in fishing intensity and thus selection. However, if median size and age at sexual maturity remain at the 1975-79 levels or decrease for the next 5-10 yr, this would suggest that there has been a genetic change within the stocks, with Atlantic cod maturing at larger sizes and older ages being selected against.

The rapid recoveries of many groundfish stocks during periods of restricted exploitation after heavy fishing, with no apparent genetic change, suggest that biomass has greater influence on variability in population parameters than do genetic changes. Heavily exploited stocks of North Sea cod and haddock recovered rapidly during World War II, when fishing mortality was reduced (Gulland 1971). Pacific halibut, *Hippoglossoides stenolepis*, stocks recovered from low population levels with no apparent genetic change (Miller 1957).

In summary, the present study has indicated that there has been a decline in median length and age at sexual maturity for Atlantic cod in several areas in NAFO Subarea 4 in the 1960's and 1970's. However, whether this decline can be ascribed to genetic or to environmental changes cannot be determined because application of the selective force (fishing intensity) concurrently changes the environment (stock biomass). Controlled selection experiments may provide some indication of potential for genetic change in Atlantic cod.

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MORPHOLOGY AND DEVELOPMENT OF HATCHERY-CULTURED AMERICAN SHAD, *ALOSA SAPIDISSIMA* (WILSON)[1]

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ABSTRACT

Morphometrics and meristics of larval *Alosa sapidissima* (Wilson) were examined and are described for hatchery-reared samples. *Alosa sapidissima* morphometrics and body proportion ratios change with ontogeny in the larval stages. Head and snout length, eye diameter, and body depth exhibit a curvilinear relationship with increasing standard length, while preanal and predorsal length show a linear relationship with increasing standard length.

Predorsal and preanal myomere counts decrease during ontogeny with corresponding anterior dorsal fin migration and shortening of the gut. Other meristics indicate that median fin development is completed between 17 and 21 mm SL, while paired fin development is completed between 23 and 28 mm SL. A developmental sequence of the various caudal fin components shows a distinction between preflexion, flexion, and postflexion larvae. The developments of hypurals and notochord flexure are important in distinguishing larval and early juvenile stages of development.

Pigmentation shows a greater number and density of melanophores on cultured than field-sampled specimens. Stellate melanophores are found to contract and migrate on cultured samples. A sequence of pigmentation changes with ontogeny is described and compared with two sympatric species.

The American shad, *Alosa sapidissima* (Wilson), is a commercially and recreationally important clupeid commonly found in western North Atlantic coastal waters from Newfoundland, Canada, to the St. Johns River, Fla. (Hildebrand 1963; Scott and Crossman 1973; Chittenden 1969; Leim 1924; Watson 1968). Life history studies of *A. sapidissima* have been limited primarily to the juvenile and adult stages of development (Carscadden and Leggett 1975; Chittenden 1969; Leim 1924).

The sequence of egg development for *A. sapidissima* has been adequately described by Hildebrand (1963), Watson (1968), and Marcy (1976). Leim (1924) described yolk-sac larvae and field-sampled larvae up to 28 mm in length. Hildebrand (1963) described yolk-sac larvae and briefly described the larval development through the juvenile stage. Mansueti and Hardy (1967), Lippson and Moran (1974), and Jones et al. (1978) all summarized the early development of *A. sapidissima*. The approach previously used to describe *A. sapidissima* appears to be the static technique, which describes a few larvae over selected or sampled size ranges.

This paper describes the development of *A. sapidissima* from yolk absorption through the juvenile stage of development, using the dynamic description approach of Moser and Ahlstrom (1970). Special attention is given in this work to morphology, meristics, and pigmentation; early caudal osteology is examined from sequential samples and a sequence of ossification is also described.

METHODS

Eggs were cultured in a flow-through system designed by Blair (1976). Apparatus used in the system included three to five 10-l culture jars. A constant flow rate was maintained into an open trough of running water. The trough contained specially designed baskets fitted with saran screen for holding the newly hatched *A. sapidissima*. Larvae were sequentially sampled daily for the first 30 d, then weekly until the end of a 100-d sampling period. Samples were preserved by the method recommended by Berry and Richards (1973), in 10% buffered Formalin[4].

Two developmental series of larvae were used. Specimens in the first series were used for morphometric data, pigment patterns, and larval il-

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lustrations. Those in the second series were cleared and counterstained by the method used by Dingerkus and Uhler (1977) for meristic and caudal osteology studies. Selected specimens in the first series were subsequently used for staining in the second series, after measurements, pigment patterns, and illustrations were completed. Field specimens of *A. sapidissima* were also examined by the counterstaining technique.

Morphometrics were taken by using an ocular micrometer, calibrated to the nearest 0.1 mm, in a dissecting microscope and a dial caliper, calibrated to the nearest 0.1 mm. Measurements follow closely those of Houde et al. (1974) and are described as follows:

Total Length (TL): Tip of snout to end of caudal finfold complex in yolk sac and preflexion larvae, and to end of the longest superior procurrent caudal ray in flexion and postflexion larvae.

Notochord-Standard Length (SL): Tip of snout to tip of notochord in yolk sac, preflexion, and early flexion larvae; tip of snout to base of hypural plate in flexion and late flexion larvae; and tip of snout to the point midway between the tenth superior procurrent caudal ray and the first inferior caudal ray in postflexion larvae and juveniles. Unless otherwise noted in the text, all references to lengths of larvae refer to standard lengths. The use of this criteria for standard length measurements is based on that set forth by Richards et al. (1974).

Preanal Length (PAL): Tip of snout to end of anus measured along the midline of the body. This measurement is also used to describe the location of the anal fin for specimens that have shown development of the anal fin complex.

Predorsal Length (PDL): Tip of snout to break in finfold for specimens in yolk sac or very early preflexion stage of development; tip of snout to origin of first dorsal ray measured along the midline of the body for fish exhibiting dorsal fin development. If dorsal rays were not evident, then measurement was made at the origin of the first dorsal radial bone.

Head Length (HL): Tip of snout to posterior margin of auditory vesicle in yolk sac and early preflexion larvae; tip of snout to posterior margin of opercular membrane and bone when development was evident.

Eye Diameter (HED): Horizontal diameter between anterior and posterior edges of the fleshy orbit.

Snout Length (SNTL): Tip of snout to anterior margin of fleshy orbit on the eye.

Body Depth (BD): Vertical height of the body measured at origin of the first dorsal ray.

All morphometrics were taken on the left side of the fish body. Damaged specimens were not used; doubtful measurements were eliminated from the study. Meristics were taken from cleared and counterstained flexion and postflexion specimens per the methods of Berry and Richards (1973).

RESULTS

Morphology of Larvae

Morphometrics for larval *A. sapidissima* are presented in Table 1. *Alosa sapidissima* body proportions change during ontogeny with the most abrupt changes occurring between 12 and 18 mm SL. HL, SNTL, HED, and BD all exhibit curvilinear growth with increasing SL. PAL and PDL exhibit linear growth with increasing SL.

SL was used to examine development of *A. sapidissima* with respect to the other morphometric data. Inspection of Figure 1 and a high coefficient of determination ($r^2 = 0.998$) indicate a strong linear relationship. SL length fluctuated between 97.5 and 92.4% of the TL for larvae measured. There were no changes in the TL and SL relationship between 8 and 13 mm, where it remained at 96%. Changes in this relationship were seen in the early postflexion stage of development, between 18 and 23 mm (Table 1), when the SL decreased from 97.2 to 95.7%. The SL/TL ratio averaged 96.5% for larvae <15 mm and 95.5% for larvae 15-31 mm. The decrease in body proportion for the SL/TL relationship is related to caudal fin development, particularly notochord flexure between 12 and 15 mm, along with development of the first and second hypural plates.

PAL exhibited a steady decrease from 95% for 8 mm larvae to 65.4% for 31 mm larvae. Examination of Figure 2, along with a high coefficient of determination ($r^2 = 0.969$), also tends to indicate a linear relationship. At 18 mm SL, where the PAL/SL ratio is invariate, transformation occurs from the flexion to postflexion stage. The major changes in this relationship were seen between 23 and 27 mm TL (Table 1). Over this TL range, the gut is shortened and transformations to the postflexion stage became evident, which tends to account for the decrease in the PAL and SL relationship.

PDL decreased with increasing SL (Table 1). There appear to be three distinct size intervals at which the PDL decreases (Fig. 3). The dorsal fin migrates forward as dorsal rays develop and SL increases. This

TABLE 1.—Morphometrics (in mm) for larval American shad, *Alosa sapidissima*. $\bar{x}$ = Mean; SD = Standard deviation; R = Range; * = Missing values; ** = One value only; TL = Total length; SL = Standard length; PAL = Preanal length; PDL = Predorsal length; PPL = Prepelvic length; HL = Head length; SNTL = Snout length; HED = Horizontal eye diameter; BD = Body depth.

Size (mm)	N	Stat.	TL	SL	PAL	PDL	PPL	HL	SNTL	HED	BD
8	9	$\bar{x}$	8.64	8.38	7.55	*5.60	—	1.23	0.20	0.36	0.61
		SD	0.174	0.212	0.230	—	—	0.086	0.026	0.033	0.055
		R	8.40-8.90	8.10-8.70	7.25-7.95	—	—	1.15-1.32	0.15-0.23	0.31-0.40	0.51-0.70
9	39	$\bar{x}$	9.64	9.31	7.65	*6.24	—	1.37	0.20	0.40	0.61
		SD	0.265	0.276	0.201	0.255	—	0.090	0.036	0.047	0.072
		R	9.00-9.99	8.60-9.67	7.13-7.96	5.72-6.60	—	1.17-1.62	0.11-0.25	0.31-0.51	0.43-0.76
10	23	$\bar{x}$	10.43	10.01	8.12	6.60	—	1.46	0.21	0.46	0.62
		SD	0.360	0.340	0.196	0.152	—	0.114	0.059	0.053	0.109
		R	10.00-10.97	9.50-10.60	7.81-8.57	6.30-6.94	—	1.25-1.71	0.11-0.32	0.33-0.55	0.52-0.83
11	16	$\bar{x}$	11.36	10.97	8.79	7.09	*5.05	1.64	0.26	0.49	0.70
		SD	0.284	0.298	0.251	0.183	0.566	0.130	0.045	0.031	0.076
		R	11.02-11.72	10.60-11.42	8.41-9.25	6.88-7.38	4.65-5.45	1.40-1.81	0.19-0.36	0.43-0.51	0.58-0.85
12	5	$\bar{x}$	12.49	12.05	9.52	7.63	**4.97	2.06	0.32	0.50	1.02
		SD	0.242	0.246	0.313	0.287	—	0.073	0.025	0.024	0.018
		R	12.17-12.71	11.78-12.28	9.55-10.28	7.25-8.00	—	1.96-2.10	0.30-0.36	0.46-0.52	1.01-1.05
13	2	$\bar{x}$	13.51	13.00	10.99	8.25	**5.57	2.34	0.37	0.61	1.26
		SD	0.325	0.707	0.594	1.089	—	0.332	0.099	0.014	0.071
		R	13.28-13.74	12.50-13.50	10.57-11.41	7.48-9.02	—	2.10-2.57	0.30-0.44	0.60-0.62	1.21-1.31
14	2	$\bar{x}$	14.24	13.65	11.40	8.76	5.58	2.40	0.44	0.71	1.31
		SD	0.042	0.283	0.212	0.509	0.198	0.071	0.035	0.141	0.014
		R	14.21-14.27	13.45-13.85	11.25-11.55	8.40-9.12	5.44-5.72	2.35-2.45	0.41-0.46	0.61-0.81	1.30-1.32
15	2	$\bar{x}$	15.75	15.34	12.22	8.98	**6.57	2.90	0.54	0.76	**1.54
		SD	0.099	0.148	0.134	0.078	—	0.014	0.085	0.071	—
		R	15.68-15.82	15.23-15.44	12.12-12.31	8.92-9.03	—	2.89-2.91	0.48-0.60	0.71-0.81	—
16	4	$\bar{x}$	16.46	16.05	12.60	9.20	*6.30	3.00	0.61	0.74	1.74
		SD	0.191	0.130	0.092	0.114	0.445	0.065	0.021	0.045	0.130
		R	16.24-16.63	15.93-16.17	12.50-12.72	9.07-9.31	6.00-6.81	2.96-3.06	0.58-0.63	0.70-0.80	1.62-1.86
17	1	$\bar{x}$	17.46	16.91	13.55	9.78	7.28	3.02	0.55	0.80	1.88
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
18	1	$\bar{x}$	18.28	17.77	13.58	9.75	7.19	3.57	0.68	1.01	1.96
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
20	2	$\bar{x}$	20.47	19.63	13.96	10.83	8.55	4.25	1.01	1.16	2.46
		SD	0.134	0.417	0.028	0.544	0.382	0.070	0.028	0.064	0.148
		R	20.37-20.56	19.33-19.92	13.94-13.98	10.44-11.21	8.28-8.82	4.20-4.30	0.99-1.03	1.11-1.20	2.35-2.56
21	2	$\bar{x}$	21.05	19.44	13.56	9.40	—	4.21	1.11	1.33	2.39
		SD	0.071	0.042	0.353	0.332	—	0.056	0.035	0.148	0.028
		R	21.00-21.10	19.41-19.47	13.31-13.81	9.16-9.63	—	4.17-4.25	1.08-1.13	1.22-1.43	2.37-2.41
23	2	$\bar{x}$	23.26	22.28	15.41	10.43	—	4.91	1.26	1.73	3.80
		SD	0.127	0.537	0.290	0.184	—	0.276	0.226	0.184	0.163
		R	23.17-23.35	21.91-22.66	15.20-15.61	10.30-10.56	—	4.71-5.10	1.11-1.42	1.60-1.86	3.68-3.91
24	1	$\bar{x}$	24.28	23.13	15.00	11.41	—	5.62	1.33	1.75	4.04
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
25	3	$\bar{x}$	25.24	23.98	15.01	10.20	**10.08	5.83	1.43	2.15	5.02
		SD	0.110	0.583	0.775	0.061	—	0.105	0.165	0.165	0.322
		R	25.15-25.36	23.46-24.61	14.15-15.65	10.13-10.25	—	5.73-5.94	1.32-1.62	1.96-2.26	4.68-5.32
27	1	$\bar{x}$	27.05	25.76	16.94	11.88	**11.63	6.76	1.83	2.07	5.39
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
28	3	$\bar{x}$	28.34	26.61	17.39	12.60	12.46	6.76	1.78	1.99	5.37
		SD	0.104	0.079	0.371	0.051	0.157	0.157	0.090	0.055	0.570
		R	28.27-28.46	26.52-26.67	16.99-17.72	12.54-12.64	12.28-12.57	6.64-6.94	1.73-1.88	1.94-2.05	4.83-5.97
29	2	$\bar{x}$	29.54	28.17	18.57	12.22	12.17	6.61	1.55	1.86	5.46
		SD	0.445	0.487	0.375	0.430	0.410	0.156	0.071	0.198	0.156
		R	29.22-29.85	27.82-28.51	18.30-18.83	11.93-12.50	11.88-12.46	6.60-6.72	1.50-1.60	1.72-2.00	5.35-5.57
30	1	$\bar{x}$	30.93	29.50	19.50	**12.91	12.60	6.65	1.99	2.11	5.90
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
31	1	$\bar{x}$	31.25	29.66	19.55	**12.93	12.68	8.15	2.12	2.64	6.38
		SD	—	—	—	—	—	—	—	—	—
		R	—	—	—	—	—	—	—	—	—
Total	122										

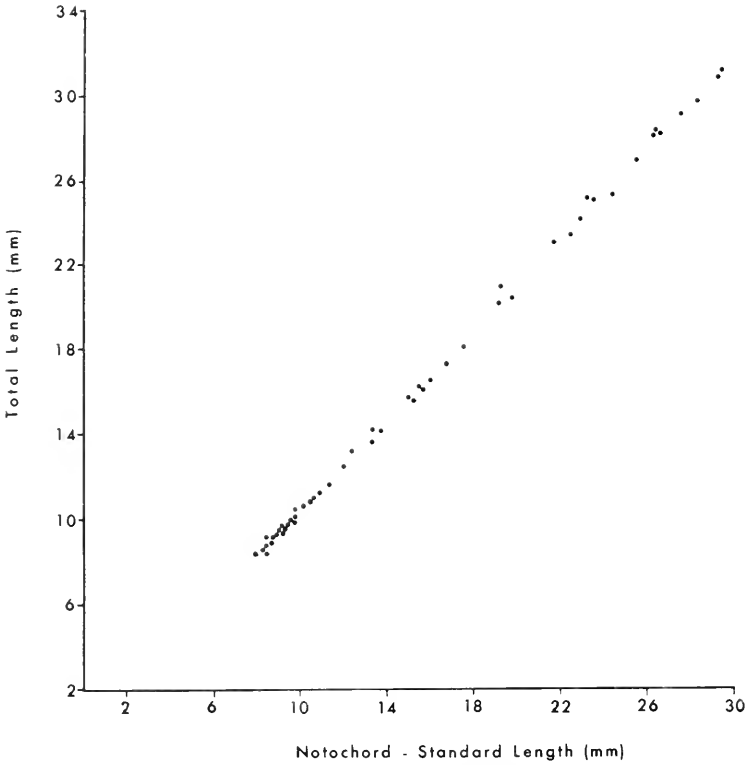

FIGURE 1.—Scatterplot of TL/SL for larval *Alosa sapidissima*. Regression equation: TL = −0.30 + 1.06 SL; $r^2 = 0.998$.

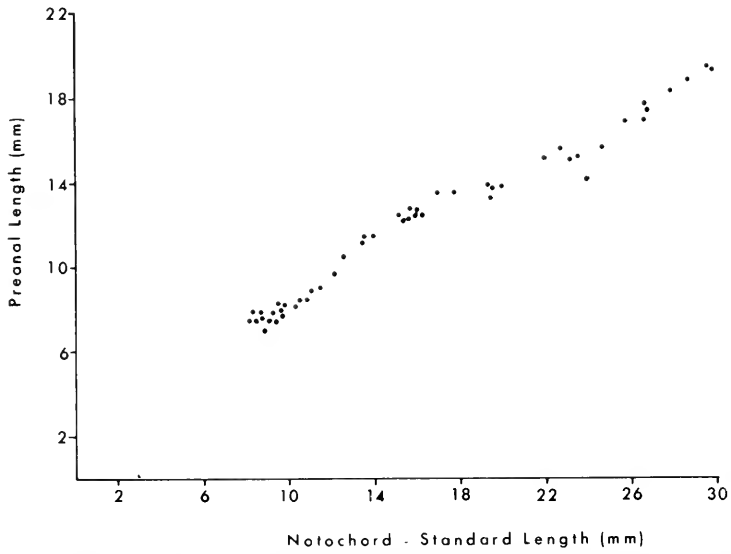

FIGURE 2.—Scatterplot of PAL/SL for larval *Alosa sapidissma*. Regression equation: PAL = 2.18 + 0.60 SL; $r^2 = 0.969$.

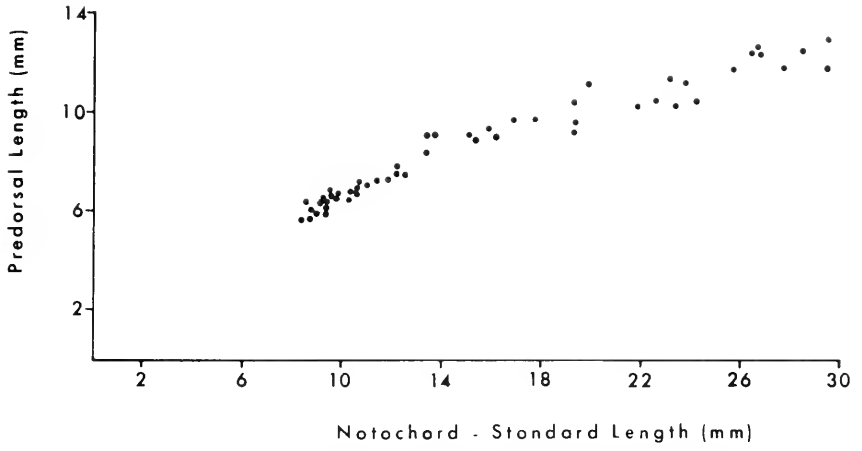

FIGURE 3.—Scatterplot of PDL/SL for larval *Alosa sapidissima*. Regression equation: PAL = 2.62 + 0.39SL:$r^2 = 0.964$.

accounts for the decrease in predorsal body proportions from 66.7 to 43.6% of the SL. This decrease is reported to be common for clupeoid larvae (Ahlstrom 1968; Houde et al. 1974; Jones et al. 1978).

Larvae of *A. sapidissima* are relatively big-headed in comparison to their thin nonrobust body in the preflexion and flexion stages. Head development is prominent in larvae between 8 and 11 mm. Five branchial arches, jaws, and two pairs of recurved teeth in the lower jaw were also evident in larvae this size. HL averages 14.7% of SL between 8 and 11 mm (Table 1). At 12 mm, HL increases to 17.0% of SL. An increase of 1.2% is evident in the HL/SL relationship for larvae 12-17 mm. HL increases from 20.1 to 27.5% of SL in larvae 18-31 mm.

The HL/SL relationship is not as obvious in late flexion and postflexion larvae because the body has become more robust. Examination of Figure 4 at first tends to indicate a linear relationship between HL and SL. However, there appears to be a point in Figure 4 at the transformation between the flexion and postflexion stages (18 mm SL) where the HL/SL relationship may exhibit allometric growth. Fitting the data to the model for an allometric growth curve (Sokal and Rohlf 1969) produced a higher coefficient of determination ($r^2 = 0.992$). Thus the HL/SL ratio

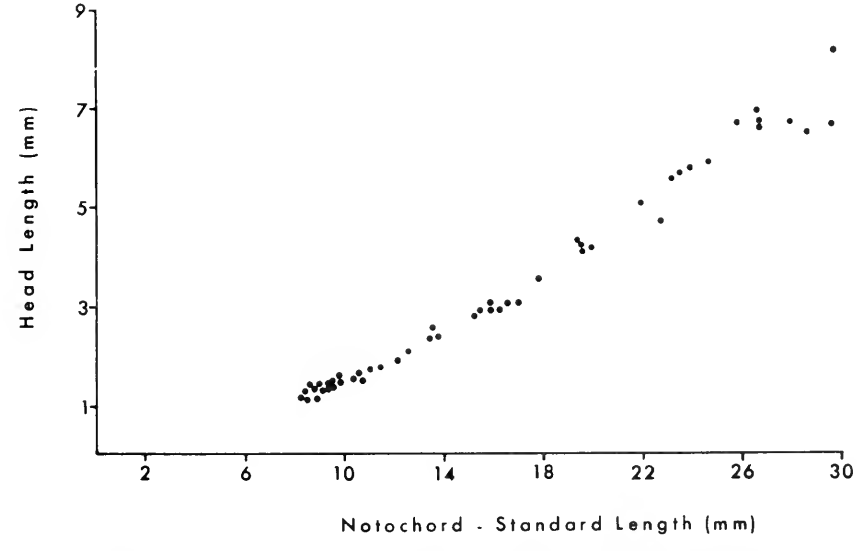

FIGURE 4.—Scatterplot of HL/SL for larval *Alosa sapidissima*. Regression equation: ln (HL) = ln 0.05 + 1.50 ln (SL):$r^2 = 0.992$.

probably exhibits a positively allometric relationship.

HED shows an allometric growth relationship with SL. Both HED and SL were log-transformed to fit the linear regression of these two morphometric variables (Fig. 5). HED are variable for a given size interval; at 23 mm SL they vary between 1.60 and 1.86 mm, and at 29 mm SL between 1.72 and 2.00 mm (Fig. 5). Most of the variability occurs between 19 and 31 mm SL, after the transformation from flexion to postflexion larvae. Very little variation occurs in the preflexion and flexion stages (6-18 mm SL).

SNTL appears to exhibit allometric growth with respect to SL (Fig. 6). Both SNTL and SL were log-transformed to fit a linear relationship between these two variables. Snout lengths are variable for a given size range in the postflexion stage, while very little variation occurs within individual size ranges between 6 and 18 mm SL (Fig. 6).

BD exhibits allometric growth with respect to SL (Fig. 7). Increases in BD indicate corresponding increases in body weight and body volume. As the SL and BD increase, the body shape becomes more streamlined, changing from a thin rodlike shape to a deep-bodied, streamlined shape in *A. sapidissima*.

Myomeres

Myomere counts have been shown to be useful for identifying clupeoid genera (Ahlstrom 1968; Houde et al. 1974). The total number of myomeres ranged from 54 to 58; most of the larvae had 55 or 56 myomeres. The number and distribution of myomeres relative to body morphology are shown in Table 2.

The distribution of myomeres was examined in relation to predorsal and preanal body measurements. Predorsal myomeres decreased in number with increasing SL. Predorsal myomere counts decreased

TABLE 2.—Distribution of myomeres relative to other body morphology for *Alosa sapidissima* larvae. N = Number of specimens counted; $\bar{x}$ = Mean myomere counts; R = Range of myomere counts.

Size interval (mm SL)	Preanal myomeres			Postanal myomeres			Predorsal myomeres		
	N	$\bar{x}$	R	N	$\bar{x}$	R	N	$\bar{x}$	R
8.0- 9.0	11	48.4	45-52	9	12.3	10-14	11	33.9	31-36
9.1-12.0	18	46.1	43-51	17	11.6	10-14	18	30.7	28-35
12.1-15.0	9	44.4	42-48	7	14.6	11-16	9	28.5	26-33
15.1-18.0	7	41.3	39-43	7	15.6	13-17	7	23.3	21-26
18.1-21.0	3	39.0	36-42	—	—	—	3	22.6	21-24
21.1-24.0	4	38.5	35-43	—	—	—	4	21.0	20-23

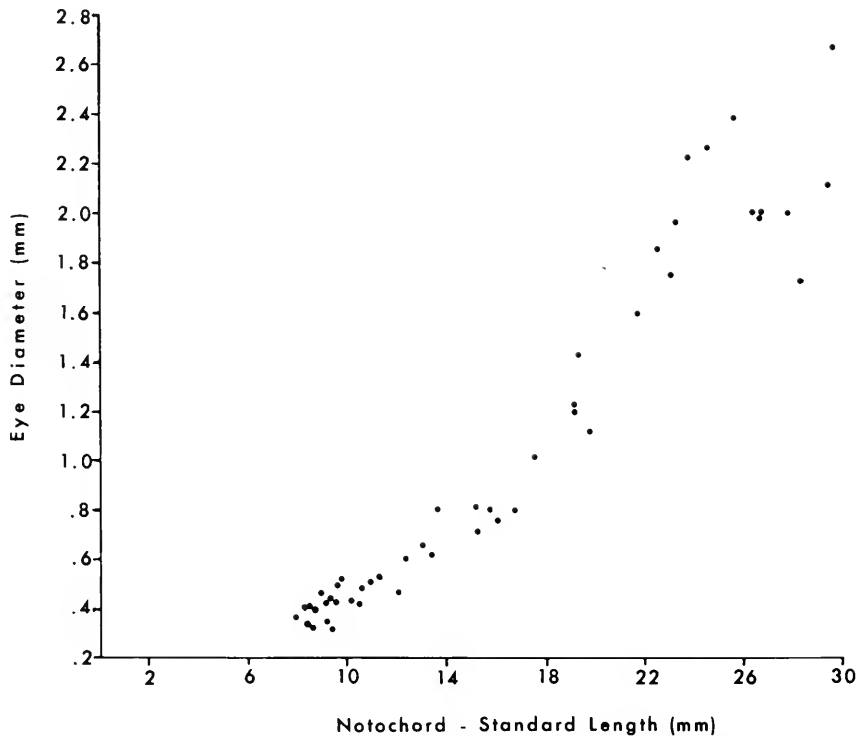

FIGURE 5.—Scatterplot of HED/SL for larval *Alosa sapidissima*. Regression equation: $\ln(\text{HED}) = \ln 0.01 + 1.59 \ln(\text{SL})$: $r^2 = 0.973$.

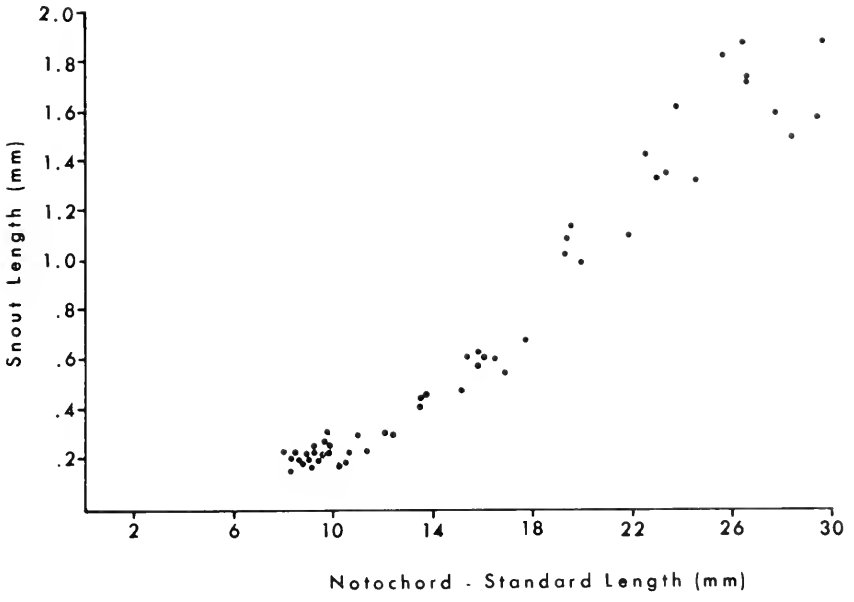

FIGURE 6.—Scatterplot of TL/SL for larval *Alosa sapidissima*. Regression equation: $\ln (SNTL) = \ln 2.31 + 2.01 \ln(SL)$:$r^2 = 0.964$.

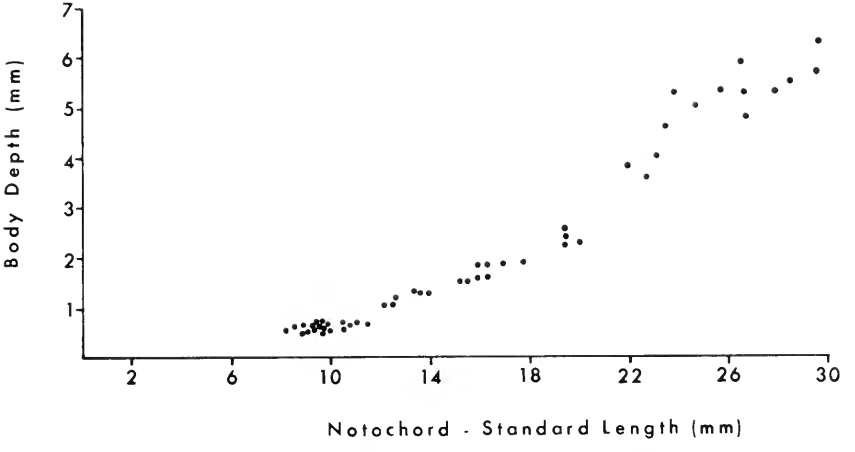

FIGURE 7.—Scatterplot of BD/SL for larval *Alosa sapidissima*. Regression equation: $\ln (BD) = \ln 4.91 \ln + 2.14 \ln (SL)$:$r^2 = 0.977$.

from a mean of 33.9-21.0 for the larvae examined ($N = 52$). Significant changes in predorsal myomere counts were seen in the 12.1-18.0 mm SL size interval (Table 2). There is, however, considerable variation in predorsal myomere counts for all size intervals, as shown in Table 2.

Counts for preanal myomeres decreased with increasing SL and decreasing PAL. There was a decrease in the mean number of preanal myomeres from 48.4 to 38.5 for the larvae examined. This decrease parallels the shortening of the gut as the SL increases.

The mean number of postanal myomeres increased with the shortening of the gut and increasing SL. An increase from a mean of 12.3 to 15.6 postanal myomeres was evident for the larvae examined ($N = 40$; Table 2). No information is available in this study for postanal myomere counts in larval *A. sapidissima* >18.0 mm SL.

Fin Development

Median and paired fin development is indicated in Tables 3 and 4 for both hatchery-cultured and field-sampled specimens. A summary of the fin development of cultured specimens is presented in Table 5. Development of the median fins (dorsal, anal, and caudal), including ossification of rays, is first evident between 9.0 and 12.5 mm SL. Median fin development is completed between 17 and 21 mm SL. Paired fin development is not truly evident until larvae are in the late flexion or early postflexion stages. Development of the paired fins was complete when larvae were between 23 and 27 mm SL (Table 5).

The dorsal fin exhibits the earliest development of all fins. Dorsal fin radials first appear in larvae 8.0-9.0 mm SL (Table 5). Radials appear as buds and are not fully developed at this stage.

The developmental sequence for the various components of the caudal complex is described from the first appearance of cartilaginous structures to a gradual ossification and fusion of bones in the caudal complex. The criteria used to place larvae into one of the three larval stages of development are similar to that described by Tucker (1978). Description of the sequence of caudal complex development is based on 19 selected counterstained specimens (Figs. 8, 9).

Larvae between hatch and 9.5 mm SL had a straight notochord (no flexure) and showed no evidence of any support structure development (hypurals, uroneurals, neural, or haemal spines) (Fig. 8A). Early caudal fin development is evident in the late preflexion stage in larvae 9.8-11.3 mm SL. The notochord is straight, and one incipient parhypural and one to three incipient hypurals have begun to develop (Fig. 8B). The hypurals and parhypural first appear stained with Alcian Blue. There is some incipient caudal fin ray development (Table 3).

Notochord flexure starts between 11.5 and 12.6 mm

TABLE 3.—Some fin meristics for larval *Alosa sapidissima* cultured at USFWS Harrison Lake National Fish Hatchery, Va.

Notochord standard length (mm)	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Caudal rays			
					Superior procurrent	Superior principal	Inferior principal	Inferior procurrent
Preflexion larvae								
9.25	8	—	—	—	—	—	—	—
9.59	7	—	—	—	—	—	—	—
9.91	8	—	—	—	—	—	—	—
10.00	8	—	—	—	—	—	—	—
10.40	9	—	—	—	—	—	—	—
10.72	9	—	—	—	—	—	—	—
10.85	10	—	—	—	—	—	—	—
11.00	9	—	—	—	—	—	—	—
11.17	9	—	—	—	—	—	—	—
11.42	10	—	—	—	—	2	—	—
11.81	12	3	—	—	—	2	—	—
Flexion larvae								
12.12	12	—	—	—	1	2	2	2
12.28	13	—	—	—	2	4	2	2
12.50	13	8	—	—	4	7	4	—
13.45	15	9	—	—	4	9	5	2
13.50	14	—	—	—	3	9	3	3
13.85	16	12	3	—	—	9	—	—
15.44	17	15	—	—	—	10	4	4
15.93	17	19	—	—	3	10	4	5
15.94	16	8	—	—	—	10	—	—
16.15	18	9	5	—	—	10	4	4
16.17	17	—	2	—	—	10	4	4
16.91	17	17	3	—	5	10	7	—
17.77	18	15	—	—	7	10	5	5
Postflexion larvae								
19.33	18	20	—	4	7	10	7	6
19.41	18	19	8	—	5	10	5	6
19.47	18	18	10	—	8	10	9	7
19.92	17	20	13	6	8	10	9	6
21.66	18	21	—	—	7	10	9	7
21.91	18	19	—	—	8	10	9	7
23.13	19	19	11	—	8	10	9	7
23.46	19	20	—	—	8	10	9	7
24.61	19	22	15	—	8	10	9	7
25.76	19	23	15	8	8	10	9	7
26.52	19	22	16	7	8	10	9	6
26.64	19	22	14	7	8	10	9	7
26.67	19	21	16	8	8	10	9	7
27.82	19	20	16	9	8	10	9	6
28.51	19	19	16	9	8	10	9	7
29.50	19	23	15	10	8	10	9	7

TABLE 4.—Fin development meristics for postflexion (juvenile) *Alosa sapidissima*.

Standard length (mm)	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Caudal rays: Superior procurrent	Caudal rays: Superior principal	Caudal rays: Inferior principal	Caudal rays: Inferior procurrent
26.5	19	22	15	9	8	10	9	6
26.8	18	23	14	9	8	10	9	7
27.4	18	23	15	9	8	10	9	7
28.2	19	22	16	9	8	10	9	7
28.4	19	22	18	9	8	10	9	6
28.5	19	22	17	9	7	10	9	6
28.6	17	23	17	10	7	10	9	7
28.8	18	23	17	8	7	10	9	6
29.0	17	—	17	9	8	10	9	7
29.1	18	22	14	8	7	10	9	7
29.2	17	21	18	9	7	10	9	7
29.3	18	20	14	8	8	10	9	7
29.5	19	23	15	9	8	10	9	6
29.6	19	23	17	10	8	10	9	7
30.2	21	19	16	8	7	10	9	7
30.4	17	24	16	8	8	10	9	7
31.7	18	21	14	8	8	10	9	7
31.8	18	22	15	9	8	10	9	7
31.8	18	22	15	9	7	10	9	7
32.2	18	21	18	9	7	10	9	6
32.4	19	20	15	11	8	10	9	7
32.9	17	23	15	8	8	10	9	7
33.0	17	21	16	10	7	10	9	6
33.4	17	20	17	8	7	10	9	6
36.2	18	21	18	8	8	10	9	7
37.2	18	23	16	9	8	10	9	7
37.8	18	22	17	10	7	10	9	6
38.4	17	22	14	10	7	10	9	7

TABLE 5.—Summary of fin development sequence in larvae of *Alosa sapidissima* (Wilson).

Fin	Standard length[1,2]: Buds first appear[3]	Standard length[1,2]: Rays first appear	Standard length[1,2]: Full complement of rays	No. rays in fully developed fins
Dorsal	8.0- 9.0	9.0- 9.3	17.0-20.0	17-20
Anal	11.0-11.7	11.8-12.5	19.0-21.0	19-23
Pectoral	*	13.8-19.4	23.8-25.7	14-18
Pelvic	17.0-19.0	19.0-20.0	25.0-27.0	8-10
Caudal				
Superior procurrent	—	12.0-12.5	19.0-20.0	7-8
Superior principal	—	11.0-12.0	15.0-15.5	10
Inferior principal	—	12.0-12.5	19.0-19.5	9
Inferior procurrent	—	12.0-12.5	19.0-20.0	6-7

[1]Rays were present but not necessarily ossified.
[2]Rays were stained blue or red for counting. (Blue = cartilaginous; Red = ossified bone.)
[3]Includes the radial and basipterygium bones.
*Incipient rays are evident in yolk-sac larvae, but do not stain with Alcian Blue or Alizarin Red S.

SL, and is completed by 18 mm SL. A specimen 12.1 mm SL exhibited the following characteristics of early notochord flexure: The posterior end of the notochord was beginning to tip up dorsally; one parhypural and the first four hypurals were formed; the anterior portion of the first, second, and third hypurals and parhypural absorbed Alizarin Red S stain, indicating that the structures were ossifying; the fourth hypural and the posterior portion of the first three hypurals and parhypural absorbed Alcian Blue stain; a cartilaginous haemal spine was also evident in this specimen. Another specimen, 13.2 mm SL, exhibited the following characteristics for a larvae in midflexion (Fig. 8C): The posterior end of the notochord was curved dorsally and then flattened into an S shape; five hypurals were distinct, with hypurals 1, 2, and 3 absorbing Alizarin Red S in the anterior portion of the structure; both haemal and neural spines were present, absorbing both Alcian Blue and Alizarin Red S stains; the first evidence of the first uroneural appeared in this specimen.

Late flexion larval *A. sapidissima* are characterized by complete flexure of the notochord and evidence of segregation into the uroneurals and ural vertebra (Fig. 8D). A cartilaginous sixth hypural plate is also evident. Two slightly fused epural bones are evident, along with the first formation of the neural arch. Both the neural arch and epurals appear as cartilage.

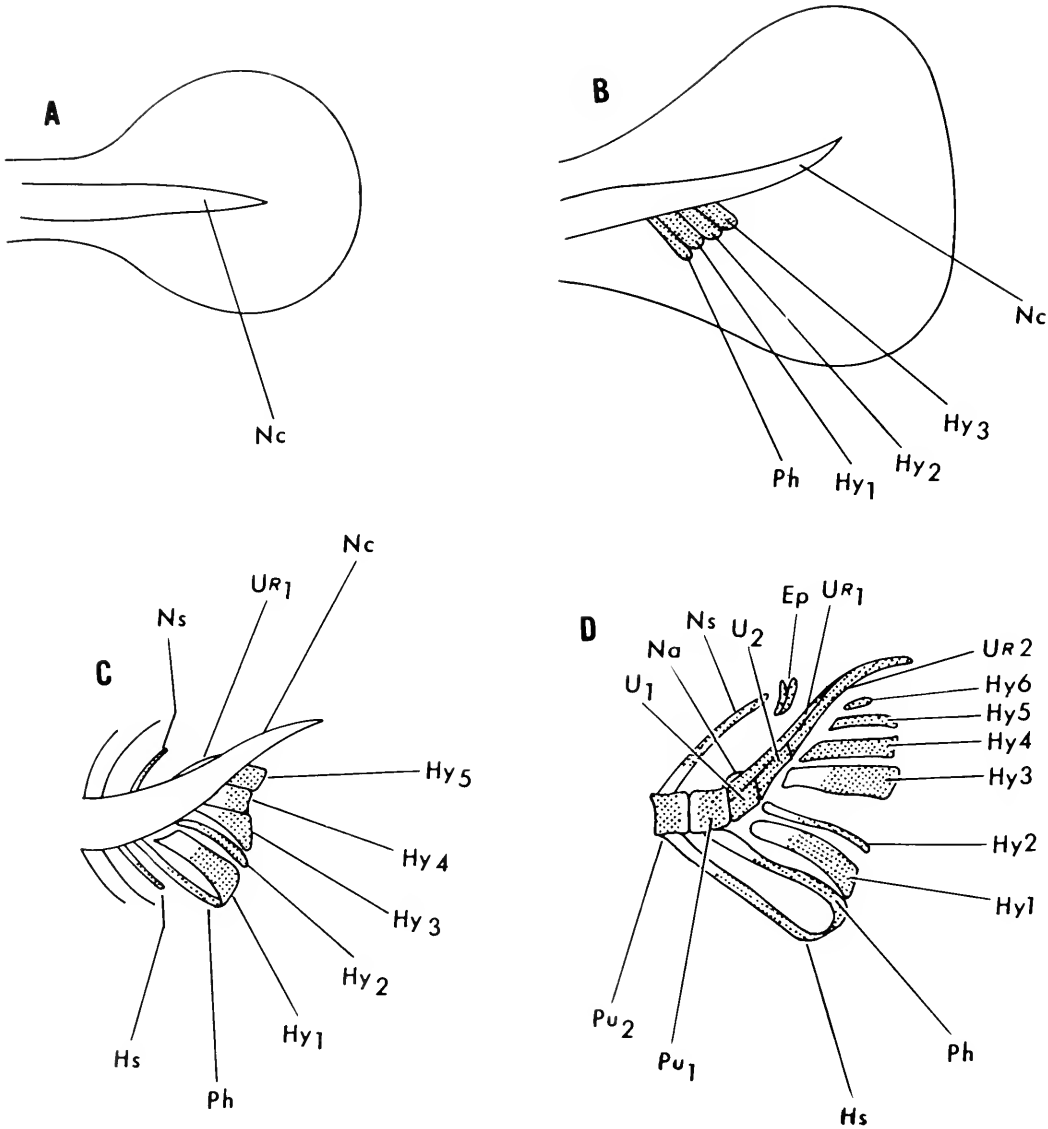

FIGURE 8.—Development of the caudal fin osteology in larval *Alosa sapidissima*. Fin rays are omitted to clearly show support osteology: (A) Farly preflexion, 9.2 mm; (B) late preflexion, 10.8 mm; (C) flexion, 13.2 mm; (D) late flexion, 16.9 mm. Hy (1-6) = hypural plates; Ep = epurals; U(1-2) = ural vertebra; Pu(1-2) = preural vertebra; Hs = haemal spine; Nc = notochord; Ur(1-2) = uroneurals; Ns = neural spine; Ph = parhypural; Na = neural arch. Clear areas indicate uptake of Alizarin Red S (except for Nc in A, B, and C), while stippled areas indicate uptake of Alcian Blue.

There appears to be a distinct cartilaginous fusion between the haemal spine and the parhypural bones (Fig. 8D).

Postflexion larval and juvenile *A. sapidissima* show complete separation between the ural and preural vertebrae (Fig. 9). The hypurals, neural and haemal spines, neural arch, and the epurals all absorbed Alizarin Red S and Alcian Blue stains. The epurals no longer were fused. The third uroneural was stained with Alcian Blue. These structures do not appear to completely ossify until well into the juvenile stage of development. A field-sampled specimen 48.0 mm SL showed complete Alizarin Red S absorption in the hypurals, ural and preural vertebrae, and the neural arch. The neural and haemal spines and parhypural exhibited proximal end absorption of Alcian Blue to preural vertebrae 1-4. The two epural bones had absorbed Alcian Blue at both the anterior and posterior

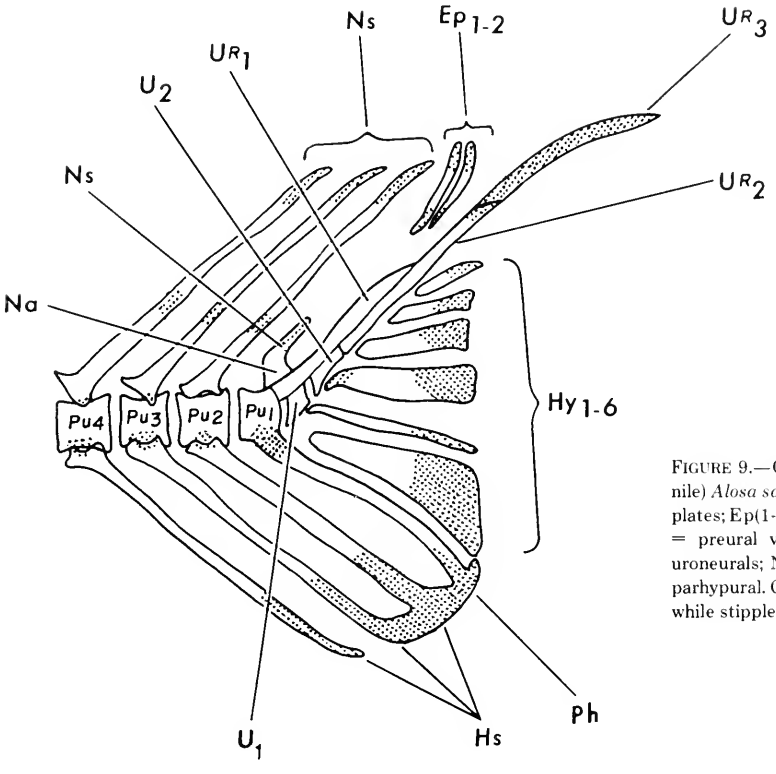

FIGURE 9.—Caudal fin osteology of a postflexion (juvenile) *Alosa sapidissima*, 29.6 mm SL. Hy(1-6) = hypural plates; Ep(1-2) = epurals; U(1-2) = ural vertebra; Pu(1-4) = preural vertebra; Hs = haemal spine; Ur(1-2) = uroneurals; Ns = neural spine; Na = neural arch; Ph = parhypural. Clear areas indicate uptake of Alizarin Red S, while stippled areas indicate uptake of Alcian Blue.

tips of the structures, with Alizarin Red S absorption in the middle.

Pectoral fin development is evident at hatch in the form of a pectoral fin fold and cartilaginous support structures. Incipient pectoral fin rays are also evident in yolk-sac larvae; however, these rays were outlined under light microscopy (25×). Development of the pectoral fin appears to be slow when compared with the other fin development characteristics (Table 5). There is a 5.6 mm range of SL over which cartilaginous pectoral fin rays first absorb Alcian Blue stain.

The pelvic fin is the last of the five median and paired fins to start and complete development (Table 5). Pelvic fin development is first evident at the transformation from flexion to postflexion larvae. The pelvic fin basipterygium first appeared during this size interval.

Pigmentation

The distribution of melanophores on *A. sapidissima* appears to be similar to that of other clupeid larvae found in Chesapeake Bay tributaries and the western North Atlantic. There is some variability in the pigmentation patterns among individuals in any given size interval; however, this variation is due in part to individual chromatophores and melanophores existing in a contracted or expanded state. The specimens illustrated in Figures 10-13 indicate the general pattern of pigmentation typical of the *A. sapidissima* specimens cultured for this study.

Newly hatched *A. sapidissima* have very few melanophores on the snout and over the brain. A newly hatched specimen, 8.2 mm SL, had one stellate melanophore on the tip of the snout and two others in a straight line, spaced at equal intervals, toward the anterior end of the eye. The eyes in this specimen and all the specimens sampled were fully pigmented by 9.5 mm SL (Fig. 10A). Three to five melanophores were present over the brain of a specimen 10.4 mm SL (2 d after hatch). A small but distinct line of melanophores is present above the yolk sac, over the pectoral symphysis and heart, in specimens 9.3-10.5 mm SL (Fig. 10A).

The number of melanophores on the snout and brain increases with increasing SL. A 10.9 mm SL specimen (Fig. 10B) showed an increased number and density of melanophores on the snout. A line pattern of stellate melanophores is developed dorsally from the snout up the midline of the skull and over the top of the brain in larvae 10.9-28.5 mm SL (Figs. 10B-13).

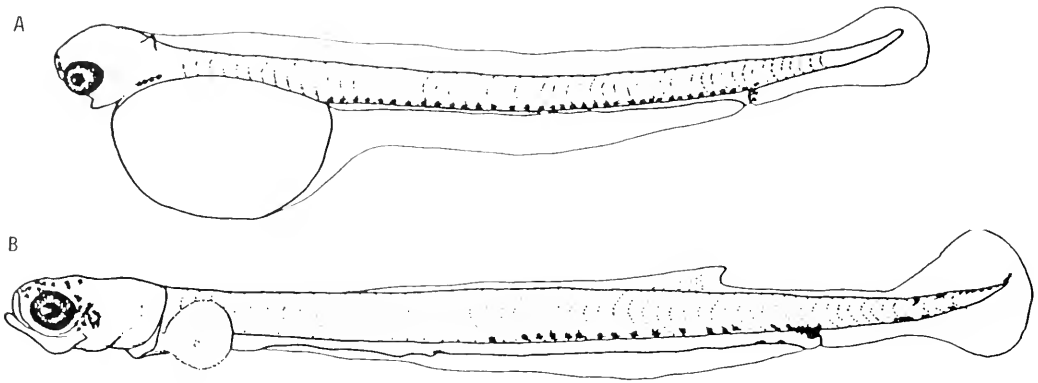

FIGURE 10.—Preflexion *Alosa sapidissima*. A, 9.3 mm SL early preflexion larva; B, 10.9 mm SL late preflexion larva.

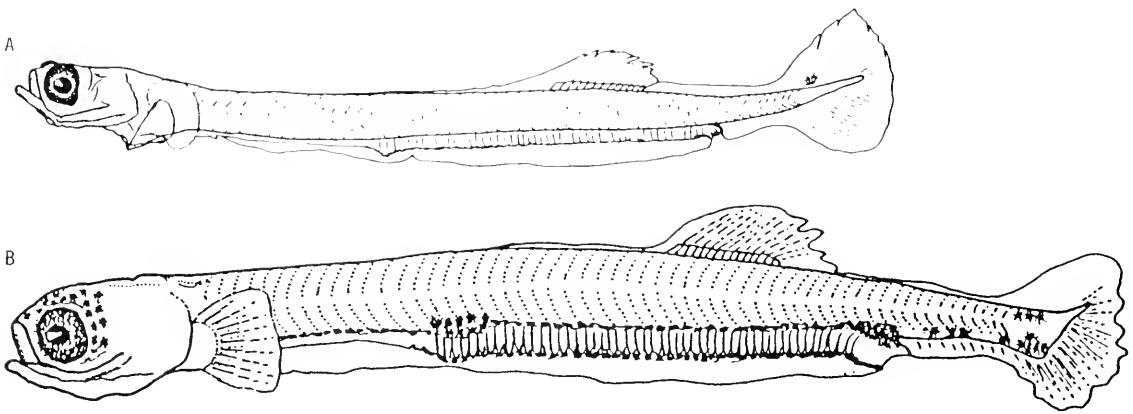

FIGURE 11.—Preflexion *Alosa sapidissima*. A, 12.7 mm SL early flexion larva; B, 15.8 mm SL midflexion larva.

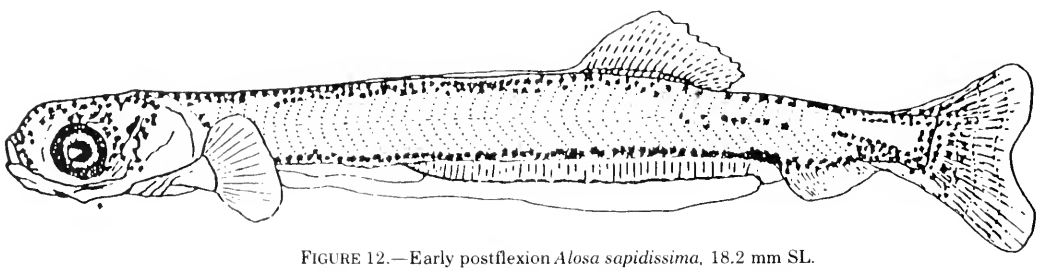

FIGURE 12.—Early postflexion *Alosa sapidissima*, 18.2 mm SL.

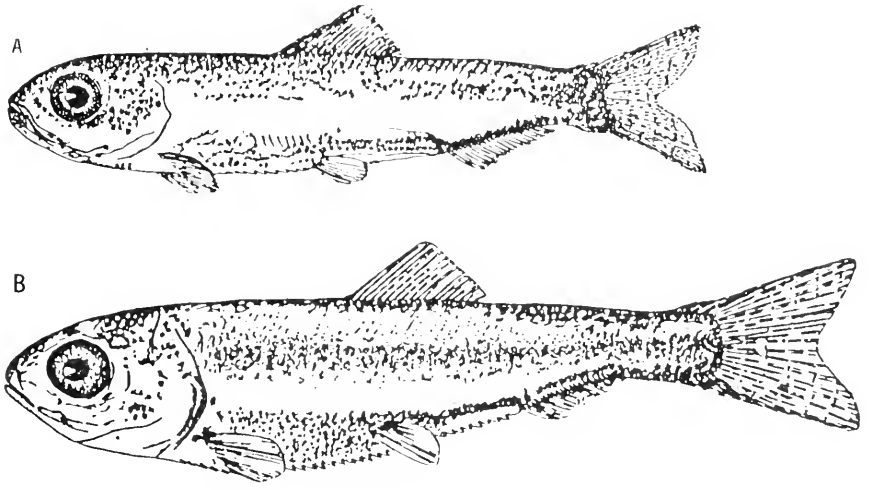

FIGURE 13.—Postflexion *Alosa sapidissima*. A, 23.4 mm SL larva; B, 28.5 mm SL larva.

The pigment pattern associated with the area posterior to the fleshy orbit of the eye, and anterior to the opercular, is variable. The density and number of melanophores around the eye increased to ~22 mm SL. Larvae in the 15-18 mm SL range exhibited most of this pigment just posterior to the fleshy orbit of the eyes, with no melanophores over the opercular bone (Fig. 11). Larvae >20 mm (Fig. 13) exhibited distinct melanophores extending from the fleshy orbit onto the opercular bone. A substantial number of the specimens examined >20 mm SL showed no increase in the actual number of melanophores. Instead, this pigment appeared to migrate, and in some cases contract, from the fleshy orbit of the eye onto the opercular bone. Field-sampled specimens >28 mm showed a reduced number and density of pigment just posterior to the fleshy orbit of the eye and a more concentrated number just anterior to the tip of the opercular bone.

Preflexion *A. sapidissima* have a series of very small, distinct melanophores along the dorsal surface of the gut. These melanophores remained distinct on the larvae to about 18 mm SL (Figs. 10-12). About 2 d after hatch, pigmentation was evident on the ventral surface of the gut. This pigment was in a dense pattern of short dash-shaped melanophores that gave the appearance of a solid line by 15 mm SL (Fig. 11). After 15 mm SL, ventral gut pigmentation contracted from a solid line pattern to a series of spaced melanophores (Figs. 11, 12).

As larvae developed into the postflexion stage, gut pigmentation became increasingly difficult to detect because of the added body tissue and weight. Shortening of the gut, with increasing SL, is seen in conjunction with the formation of larger, distinct, stellate melanophores along the dorsal gut surface (Fig. 12). There is also a dense concentration of stellate melanophores at the anus in postflexion and juvenile *A. sapidissima*.

Pigment developed along the anal fin base at 15 mm SL where one to three stellate melanophores were found in a series of specimens 15-18 mm SL (Fig. 11). The number of anal fin base melanophores increased to between 14 and 20 for 18-20 mm SL larvae (Fig. 12). Postflexion *A. sapidissima* (Fig. 13) had ~22-26 stellate melanophores in a straight-line pattern over the radials of the anal fin. This line of pigmentation was continuous from the anus, where a dense concentration of melanophores was found, to the caudal peduncle, where pigmentation associated with the caudal fin was evident.

Pigment is found at the base of the dorsal fin over the developing radials in 12 mm SL larvae. From zero to five small dorsal fin melanophores were counted on a series of 11.8-13 mm SL specimens. The number and density of melanophores associated with the dorsal fin increased as the fish grew and the dorsal fin migrated forward. Larvae in the 15-18 mm SL range have 10-19 stellate melanophores over the radials of the dorsal fin (Figs. 11, 12). Larvae >20 mm SL have a stellate melanophore directly over each radial of the dorsal fin (Fig. 13); there are 20 radials with at least one melanophore (more than one in most specimens examined) at the base of the fin.

There is a continuous pair of pigmentation stripes from the eye to the caudal peduncle along the dorsal midline. The paired melanophores anterior to the dorsal fin are distinct, appearing as two lines, while

posterior to the dorsal fin the melanophores are still paired, but coalesce into a single line.

Large stellate melanophores first appear on the posterior end of the lateral line at 18 mm SL (Fig. 12). Between 11 and 15 melanophores are evident during this transition phase between flexion and postflexion larvae. In some of the specimens examined, in the 18-20 mm SL range, pigment was in pairs, one directly above and one directly below the lateral line (Fig. 12). Between 35 and 62 large stellate melanophores were counted on specimens >20 mm SL along the lateral line posterior to the dorsal fin.

Pigment first appeared as very small light chromatophores along the lateral line anterior to the dorsal fin and posterior to the opercular bone in specimens 13-16 mm SL. These cells expanded into distinct stellate melanophores in larger specimens (Fig. 13A). The number of melanophores that could be counted along the lateral line ranged from 7 to 23 in specimens 17.7-21.9 mm SL; more than 50 melanophores were counted for larvae >23 mm SL (Fig. 13). Stellate melanophores in the large postflexion larvae (>25 mm SL) contracted into small indistinguishable melanophores along the lateral line (Fig. 13B).

Newly hatched *A. sapidissima* had no pigment associated with the notochord posterior to the anus (Fig. 10A). Pigment first appeared on the dorsal tip of the notochord at 9.8 mm SL with one to four small melanophores. At 10.9 mm SL (Fig. 10B) pigment was present as eight small melanophores on the dorsal tip and four small melanophores on the ventral tip of the notochord.

Melanophores associated with the caudal region appeared to have migrated toward the anus in larvae 11-13 mm SL. The number and density of melanophores concentrated at the end of the anus increased during this length interval (Fig. 10A). Pigment still appeared in the caudal region as larger, distinct stellate melanophores; however, the number of melanophores remained fairly constant between three and seven for larvae 11-13 mm SL.

Pigment density increased rapidly in the caudal region in larvae >15 mm SL (Figs. 11-13). Melanophores migrated onto the developing caudal rays from the caudal peduncle region, and large stellate melanophores outlined the edge of the caudal peduncle (Fig. 12).

Pigmentation reached its greatest density in larvae 23-25 mm SL (Fig. 13). The number of melanophores increased and became more concentrated in postflexion and juvenile *A. sapidissima*. Larvae >25 mm SL exhibited contraction in size of caudal stellate melanophores, which became difficult to distinguish individually.

DISCUSSION AND CONCLUSIONS

Information pertaining to the morphology of larval *A. sapidissima* presented herein reinforces the summary information presented in Mansueti and Hardy (1967), Lippson and Moran (1974), and Jones et al. (1978). In addition, this study details the ontogenic changes in body development that were previously unavailable in the literature. The earliest studies on *A. sapidissima* larval morphology by Leim (1924) and Hildebrand and Schroeder (1928) reported morphometric body proportions for selected sizes of larvae. Recent studies on the early development of *A. sapidissima* by Watson (1968), Chittenden (1969), and Marcy (1976) presented results that adequately describe the development and ontogenic changes associated with egg and yolk-sac larvae development.

The culture techniques employed in this study (Blair 1976) provided adequate samples to describe the morphological development of *A. sapidissima* over the standard length range that was previously void in the literature (yolk-sac absorption to the postflexion stage). A complete description of morphological development and body proportion ratios is now available from hatch through the adult stage. A combination of this study, Hildebrand (1963), Chittenden (1969), and Marcy (1976), provides a synopsis of the morphology and development of the egg, larva, and adult stages of *A. sapidissima*.

The range of preanal myomeres reported for cultured larval *A. sapidissima* in the present study varies slightly from that previously reported for *A. sapidissima* (Mansueti and Hardy 1967; Lippson and Moran 1974; Jones et al. 1978). Mansueti and Hardy (1967) reported 43-47 preanal myomeres up to 13 mm SL; Lippson and Moran (1974) reported 41-47 between 6 and 14 mm SL; Jones et al. (1978) reported a range of 44-50 ($\bar{x}$ = 47) preanal myomeres between 9.0 and 12.9 mm SL. These myomere ranges are lower than those determined in the present study over comparable length ranges (Table 2).

Anterior myomeres can be difficult to discern in *A. sapidissima*, because they are very crowded in the early stages of development (i.e., 8-10 mm SL range). Care was taken in this study to intensify the myomeres by immersing each larvae in glycerin. Berry and Richards (1973) stated that myomere counts can be distorted by crowding in the anterior region; the use of glycerin appears to improve the reliability of myomere counts.

Both this study and that of Mansueti and Hardy (1967) report a decrease in preanal myomere count with ontogeny and shortening of the gut, while main-

taining the same range in total myomere number (Table 2). Jones et al. (1978) did not report a decrease in preanal myomeres with shortening of the gut; rather they indicated an increase in the mean number of preanal myomeres. The information presented by Jones et al. (1978) is based on the work of Chambers et al. (1976), which compares the means and ranges of the preanal myomeres for larval clupeids. Findings of this study and information reported in Mansueti and Hardy (1967) are different from that reported by Chambers et al. (1976). Difference in sample size may explain the difference in results among the studies. Larval *A. sapidissima*, cultured for this study, exhibited a steady decrease in the PAL/SL ratio and in the mean number of preanal myomeres. These changes correspond with shortening of the gut throughout the flexion stage of development.

Ahlstrom (1968) proposed the use of dorsal fin position (PDL), and the relative number of and difference between predorsal myomeres and preanal myomeres, as an accurate method of identifying clupeid larvae. Predorsal myomere counts and ranges reported herein trace the anterior migration of the dorsal fin during ontogeny. The morphometric data in Tables 1 and 2 fulfill the previous information gap in accurate identification of larval *A. sapidissima*.

The sequence of larval fin development and developmental osteology of *A. sapidissima* has not been extensively studied. Bigelow and Welsh (1925) postulated that fin formation may be completed in *A. sapidissima* by 20 mm SL. Nichols (1966) compared the fin ray meristics of several populations of juvenile *A. sapidissima*, and his results compare favorably with this study in the number of fin rays in cultured *A. sapidissima* larvae and juveniles. The mean counts in this study of dorsal (19), anal (21), and pectoral (16) fin rays on cultured larvae and juveniles agree with the means and frequencies of meristic counts made by Nichols (1966) on juvenile *A. sapidissima* from the York River, Va.

Leim (1924), Hildebrand (1963), and Jones et al. (1978) discussed the ventral pigmentation pattern seen from yolk absorption to about 13 mm SL. Indeed, this is one of the most important characteristics in identification of larval *A. sapidissima*. Ahlstrom (1968), however, pointed out that clupeids can be difficult to identify unless precaution is taken to note the sequence of changes in the larva. This is especially true with respect to pigmentation in larval *A. sapidissima*. Leim (1924) and Jones et al. (1978) noted that specimens from freshwater are more heavily pigmented than those in brackish water. This was confirmed in the present study by comparison of field and cultured specimens of larval *A. sapidissima*. Pigmentation is heavier on the head and dorsal trunk regions of freshwater cultured larvae than on native brackish-water larvae.

The sequence of pigmentation described herein for *A. sapidissima* larvae can be used to identify *A. sapidissima* of freshwater origin, because the culture method utilized freshwater. The pattern of ventral pigment described by Leim (1924) should be used when identifying larvae in the 10-13 mm SL range from samples collected in brackish water. There is a large amount of variability in the distribution of melanophores in freshwater-cultured larvae; therefore, special care should be taken when attempting to identify and confirm larval *A. sapidissima* collected in freshwater. Additionally, meristic characters should be used in conjunction with pigmentation patterns to fully confirm identification of *A. sapidissima* from freshwater samples.

Pigmentation patterns may be useful for separating larval *A. sapidissima* from larval *A. aestivalis* and *A. pseudoharengus*. Leim (1924) used the ventral pigmentation pattern to separate *A. sapidissima* from *A. pseudoharengus*. Chambers et al. (1976) noted that the ventral pattern of pigmentation was similar for *A. aestivalis* and *A. pseudoharengus*. Ventral pigmentation patterns and size differences can be used to distinguish these species when they are in the early preflexion and postflexion stages of development. When *A. sapidissima* is in the early- to midflexion stage and *A. aestivalis* and *A. pseudoharengus* are in the mid- to late-flexion stage, misidentification can occur between these species. Morphometrics presented herein (Tables 1-5) and the work of Chambers et al. (1976) could be used to distinguish these species. Table 6 exhibits the pigmentation characteristics that distinguish larval *A. sapidissima, A. aestivalis*, and *A. pseudoharengus*. Careful examination should be made of both the pigmentation patterns (presented in Table 6) and morphometric and meristic characteristics of each of the three species to fully confirm the identification.

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TABLE 6.—Pigmentation summary for larval and juvenile *Alosa sapidissima*, and a comparison of distinguishing pigment characters with *A. aestivalis* and *A. pseudoharengus*.

Development stage and pigment area	American shad, *Alosa sapidissima*	Blueback herring, *Alosa aestivalis*	Alewife, *Alosa pseudoharengus*
Preflexion larvae			
Head region	Eye completely pigmented (9.5 mm SL). 1-9 stellate melanophores on snout (10.72 mm SL); 3-12 stellate melanophores on brain (11.42 mm SL).	Eye completely pigmented (3.1-4.0 mm TL)[1].	Slightly pigmented at hatch (>4.82 mm TL) fully pigmented (5.1 mm TL)[2]
Yolk-sac region	4-7 melanophores above yolk sac and over the pectoral symphysis and heart (9.3 mm SL).	Chromatophores scattered on ventral surface of yolk sac[1]	Scattered and irregular chromatophores (3-5 mm TL).
Notochord	1-4 melanophores (9.8 mm SL).		
Gut, trunk, and fin region	33-38 small melanophores on dorsal surface of gut (10.9 mm SL).	Irregular chromatophores below pectoral fin, melanophores, some stellate (5.1 mm TL)[1]; 4 ventral melanophores below pectoral fin (6.0 mm TL)[1].	Transparent at hatch[2]. 2 chromatophores below pectoral; 3-6 posterior to pectoral (3.2-4.8 mm TL), generally sparce and irregular; 2 series of melanophores on each side of ventral line.
Flexion larvae			
Head region	Increased melanophore density over eye, snout, and opercular bone (16-34 stellate melanophores around the eye, 13-15 mm SL).	Increased melanophore density on snout, scattered melanophores on head and operculum (8.8-8.9 mm SL)[4]	Dense scattered melanophores (9.0 mm TL)[3] over snout and between the eyes.
Paired and median fins	1-3 anal fin stellate melanophores (15-18 mm SL). Dorsal fin, 0-5 melanophores (11.8-13 mm SL), 10-19 melanophores (15-18 mm SL)	Double-line pigmentation at pectoral fin (10.4 mm TL)[1]	3 melanophores below pectoral fin (6-10 mm TL)[1,2]; melanophores more stellate on caudal fin (9.0 mm TL).
Gut and trunk region	Pigments contract to a solid line after 15 mm SL. Light chromatophores on lateral line (13-16 mm SL)	Small indistinguishable chromatophores on anterior gut; large stellate melanophores on posterior gut (8.8-8.9 mm SL)[4]	12 melanophores on dorsal surface, anterior gut (6 mm TL)[1]; 22 melanophores on ventral surface, posterior gut (6 mm TL).[1] Posterior anus pigmentation generally disappears[2] (5-9 mm TL).
Postflexion larvae and juveniles			
Head region	Paired pigment stripes from posterior orbit of eye to caudal peduncle, very heavy pigment around eye (>18.2 mm SL).	Large scattered chromatophores around eye and over snout (20.5 mm TL).	Dense pigment on snout and top of head (29-47.5 mm TL)[1].
Paired and median fins	Anal fin 14-20 stellate melanophores (18-20 mm SL); 22-26 stellate melanophores (23-29 mm SL). >20 dorsal fin melanophores (>20 mm SL)	Large indistinguishable blotches of chromatophores on caudal fin (45 mm TL).	1 large expanded melanophore between pectoral fin bases (15 mm TL)[1,2].
Gut and trunk region	Dense concentration of stellate melanophores at anus; hard to distinguish lateral line; 7-23 melanophores (17.7-21.9 mm SL); >50 melanophores (>23 mm SL)	Defined dorsal rows of melanophores (25.0 mm TL)[1]	Chromatophores increasing on dorsal lateral surface between head and caudal fin (19.1-32.2 mm TL)[1].

[1]Jones et al. (1978).
[2]Cianci (1969).
[3]Chambers et al. (1976).
[4]Norden (1980).

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SEASONAL CHANGES IN THE OVARIES OF ADULT YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*

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ABSTRACT

Seasonal changes in both macroscopic and microscopic appearance of yellowtail flounder ovaries are described, as well as seasonal changes in the gonosomatic index. Oocytes pass through seven cytologically different developmental stages. By examining seasonal changes in the relative abundance and sizes of these stages, it was found that oogenesis occurs in two broad phases, each lasting about 1 year. The previtellogenic phase begins as a new stock of oogonia arises each year, principally in the summer months following spawning. These rapidly develop into early perinucleolus oocytes, which in turn develop into resting stage oocytes by the fall. Most oocytes remain in this stage until the following spring, when they then develop into late perinucleolus oocytes. The vitellogenic phase begins as these late perinucleolus oocytes, now about 1 year old, become transformed into early maturing oocytes through the accumulation of yolk. This occurs during the late spring and summer months. Through the following fall and winter the cytoplasm completely fills with yolk as oocytes reach the late maturing stage. Shortly before spawning the following spring, the final hyaline stage of development is reached.

These results indicate that there are two synchronous groups or populations of oocytes present in the ovary at any given time. Members of the vitellogenic group are in their second year of development, and will be released in the upcoming spawning season. These are recruited from a previtellogenic group which developed during the previous year.

Seasonal changes in the microscopic appearance of the ovaries were well correlated with seasonal changes in both gonosomatic index and macroscopic appearance.

Yellowtail flounder, *Limanda ferruginea*, range along the Atlantic coast of North America from the Gulf of St. Lawrence to the Chesapeake Bay (Bigelow and Schroeder 1953). Over much of this range the species supports important commercial fisheries. Despite their economic importance, comparatively little is known of their reproductive biology. Spawning season is latitudinally dependent, with most spawning occurring from April through June in the southern portion of the range, and from May through July in the northern portion (Bigelow and Schroeder 1953; Royce et al. 1959; Pitt 1970; Smith et al. 1975; Able 1978; Colton et al. 1979). Females generally mature between 30 and 40 cm TL (total length), which is reached in 2-4 yr in the southern portion of their range (Royce et al. 1959) and in 5-8 yr further north (Scott 1954; Lux and Nichy 1969; Pitt 1970). The fecundity of Grand Bank, Newfoundland, yellowtail flounder has been related to total length and age by Pitt (1971), and Howell and Kesler (1977) related fecundity of southern New England yellowtail flounder to total length, age, and ovary weight.

The purpose of this research was to examine seasonal changes in both the macroscopic and microscopic appearance of the ovary, to examine seasonal changes in gonosomatic index (GSI), and to describe histologically the process of oogenesis. Specific questions addressed were: 1) What developmental stages does an oocyte pass through from oogonium to fully ripe egg? 2) How long does this process take, and when do the changes from one stage to the next occur? 3) How do seasonal histological changes relate to seasonal changes in both GSI and the macroscopic appearance of the ovary? These data provide baseline information against which either experimental results or field data can be compared, and which are useful in identifying environmental variables that may effect eventual fecundity.

MATERIALS AND METHODS

Data were collected from commercially landed fish at the Pt. Judith, R.I., Fisherman's Cooperative at approximately monthly intervals from June 1977 through November 1978 (Table 1). On each sampling date adult females were randomly selected from the combined catches of several vessels that had been fishing southeast of Block Island, R.I. In addition to the data collected in Rhode Island, 15 immature females were examined. They were collected by the National Marine Fisheries Service on Georges Bank in April 1979.

All specimens were measured to the nearest 0.1 cm

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TABLE 1.—Collection dates and number of yellowtail flounder examined.

Sampling date	No. of specimens examined		
	For length, weight, and maturity stage	For ovary weight	Histologically
26 Jan. 1978	90	50	25
27 Feb. 1978	90	50	25
3 Apr. 1978	100	50	25
1 May 1978	100	50	25
31 May 1978	100	50	25
27 June 1977	139	50	25
28 July 1977	106	50	25
21 Aug. 1978	100	50	25
6 Sept. 1977	50	50	25
4 Oct. 1977	100	50	25
15 Nov. 1977	7	7	7
20 Nov. 1978	50	50	25
19 Dec. 1977	46	46	25
Total	1,078	603	307

TL, then eviscerated and weighed to the nearest gram wet weight. Both ovaries from a subsample of the examined specimens were weighed to the nearest 0.1 g. A GSI was calculated for these individuals as ovary wet weight (g) divided by eviscerated wet weight (g) and expressed as a percentage.

Based on the macroscopic appearance of the ovaries, fish were classified into one of five maturity stages following a modification of the International Scale of Sexual Maturity first proposed by Hjort (1910) (Table 2).

A portion of ovarian tissue was removed from the anterior third of the eyed-side ovary from 25 fish on each sampling date (except November 1977) and fixed in Davidson's solution. The histological technique employed was developed for fish gonads by the Florida Department of Natural Resources (reported in Yevich and Barszcz 1977). Tissues were embedded in Paraplast,[2] sectioned at 6 μm, and stained using Harris' hematoxylin and Eosin Y.

Slides of tissue were prepared and scanned at 400× magnification. The first 200 oocytes encountered were classified based upon the degree of chromatin condensation, size and staining characteristics, number and placement of nucleoli, and morphological appearance of the cytoplasm and follicle cells. In 10 fish randomly chosen from the 25 individuals of each sampling date, diameters of the first 50 oocytes encountered were measured to the nearest micrometer using an ocular micrometer. Measurements were taken only on oocytes sectioned through the nucleus. Such measurements have been shown to be representative of true oocyte diameters (Foucher and Beamish 1980). The mean diameter of each oocyte type was calculated from the 10 fish in every sample. A one-way analysis of variance (ANOVA) was used to test the null hypothesis that no significant differences in mean diameter were present between samples. When significant differences were found, Student-Newman-Keuls test was employed to examine the differences between samples.

Percent frequency distributions of the different oocyte types were calculated for each sample by dividing the total number of that type by the total number of oocytes examined in the sample. These fractions were then expressed as percentages. Since the probability of an individual oocyte being cut in a

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

TABLE 2.—Macroscopic and microscopic characteristics of the different maturity stages in yellowtail flounder. Stages modified from Hjort (1910). Oocyte developmental stages are described in text.

Maturity stage	External appearance	Histological appearance
I. Immature virgin	Ovaries small (2-6 cm), slender, conical, pinkish, and generally translucent. Enveloped in a layer of silvery epithelium. No oocytes visible to the naked eye.	Mainly Stage II and IV oocytes, few >50 μm. A few Stage I and III oocytes also present. All oocytes with lightly basophilic cytoplasm. Ovarian wall from 25 to 75 μm thick.
II. Developing virgin, recovering spent	Ovaries relatively small (6-12 cm), rounded, reddish, and translucent. Ovarian wall thick. Vascularization slight.	Stage II, IV, and V oocytes predominate. Stage IV oocytes are abundant early in this maturity stage, but tend to decline as Stage V oocytes increase later in the period. Most oocytes <150 μm diameter. Ovarian wall from 250 to 400 μm thick.
III. Developing, maturing	Ovaries larger in size (>12 cm) and occupying most of ovarian cavity. Visible oocytes large, yellowish in color, and opaque. Ovarian wall thin, translucent, and granular in texture due to underlying developing oocytes.	Mainly Stage III and VI oocytes, but small numbers of Stages I, II, IV, and V also present. Stage VI oocytes increase in diameter to reach about 370 μm just prior to the ripe/running stage. Ovarian wall from 100 to 200 μm thick.
IV. Ripe	Ovaries very large and distending the body wall. Some oocytes yellowish and opaque, others transparent (hyaline) producing a speckled appearance. Vascularization heavy. Ovarian wall thin. Ova run from vent upon slight pressure.	Stage III, VI, and VII oocytes predominate. Stage VII oocytes are irregular in shape, about 400 μm in diameter, and often present in the lumen of the ovary. Ovarian wall from 50 to 100 μm thick.
V. Spent	Ovaries flaccid, bloodshot. All visible remaining oocytes clear.	Many empty and collapsed follicles with relatively few oocytes. Stage III and IV oocytes predominate, with many in transition between these two stages. Small numbers of Stage I, II, and resorbing oocytes also present. Ovarian wall from 250 to 400 μm thick.

section is proportional to its size as well as its abundance, large oocytes tend to be overestimated and small oocytes underestimated when percent frequencies are calculated. The calculated percentages, therefore, may not be exact, but they do provide indications of seasonal changes.

Size-frequency distributions of oocyte diameter were constructed for each sample by dividing the diameters into 10 μm categories. The number per category was then divided by the total number of measurements and expressed as a percentage.

To test the hypothesis that no differences existed in either frequencies of oocyte types or diameters between different regions within an ovary, or between ovaries of the same fish, chi-square contingency tests were employed to compare both size- and percent-frequency distributions from portions of tissue taken from the anterior, middle, and posterior regions of both ovaries from eight fish collected in October. Since no significant differences were found ($P>0.05$), the anterior portion of the eyed-side ovary was assumed to be representative, and this region was used exclusively in the study.

Two samples were collected in November; one in 1977 and one in 1978 (Table 1). In order to facilitate data analysis it was desirable to combine them. Mean length, weight, and GSI for both samples were compared using a Student's t-test (Snedecor and Cochran 1973). Since no significant differences were found ($P>0.25$), the samples were combined for all further analyses.

RESULTS

Macroscopic Structure and Maturity Stages

The paired ovaries lie, one on either side, in an ovarian cavity between the haemal spines and the body wall musculature. Each is shaped like an elongated cone, with the apex oriented toward the tail and the enlarged anterior end protruding slightly into the abdominal cavity. They are anchored by both connective tissue fascia and a suspensory ligament that runs from the cleithrum to the anterior end of each ovary. Very short oviducts arise from the anterior end of each ovary and terminate at the cloaca.

Percentages of fish in each of the different maturity stages are given in Table 3. Stage I (Immature virgin) females were observed only in the collection made in April by the National Marine Fisheries Service. None were found among those fish landed commercially, since fishermen generally discard small immature fish. Stage II (Developing virgin, recovering spent) females were seen from May through early October. Their percentage was relatively low in May, but increased to 66% by June. In July and August all fish were in this category. A rapid decline in the percentage of Stage II females occurred from September (81%) to October (7%). Stage III (Developing, maturing) females were present from September through May. In early September, 19% of the fish were in this stage. The percentage increased to 93% by October, and all fish were in this stage from November through at least February. Percentages then declined from 91% in April to only 7% in late May. Stage IV (Ripe) females were observed only in April (9%), early and late May (17 and 31%, respectively), and June (24%). Stage V (Spent) females were seen only in May and June.

Gonosomatic Index

When the relationship between GSI and fish length was examined using functional linear regression (Ricker 1973), a significant positive relationship was

TABLE 3.—Seasonal changes in gonosomatic index (GSI) and percentages of yellowtail flounder in the different maturity stages. Stages are modified from Hjort (1910).

Sampling date	GSI (mean ±2 SE)	Stage II (developing virgin, recovering spent)	Stage III (developing, maturing)	Stage IV (Ripe)	Stage V (Spent)
1/26/78	11.79±1.10	—	100	—	—
2/27/78	11.26±1.58	—	100	—	—
4/3/78	18.54±1.70	—	91	9	—
5/1/78	13.49±2.29	4	68	17	11
5/31/78	11.53±2.78	12	7	31	50
6/27/77	3.32±0.51	66	—	24	10
7/28/77	2.46±0.17	100	—	—	—
8/21/78	3.81±0.22	100	—	—	—
9/6/77	3.20±0.22	81	19	—	—
10/4/77	3.87±0.34	7	93	—	—
11/15/77 and 11/20/78	4.95±0.37	—	100	—	—
12/19/77	6.96±0.62	—	100	—	—

found ($P<0.001$). Since this variable was dependent on fish length, and since mean fish length was significantly different between samples (ANOVA, $P<0.05$), the sample means of GSI were adjusted for length using analysis of covariance (Snedecor and Cochran 1973).

Adjusted mean monthly GSI values showed a seasonal pattern (Table 3). Values were highest in early April, then fell sharply to their lowest value by late July. From July through September GSI values remained low, then began to rise gradually to reach about 11% by the following January and February. A sharp increase was observed from late February through early April.

Histology of the Ovaries

The ovarian wall is comprised of three tissue layers (Fig. 1A). The outermost layer (tunica albuginea) is fibrous connective tissue. Internal to this are two layers of smooth muscle tissue. Fibers of the external layer are oriented perpendicularly to the long axis of the ovary, while fibers of the inner smooth muscle layer run parallel to the long axis. Ovigerous folds (lamellae) arise from inner layers of the ovarian wall and extend into the lumen. Margins of these folds are covered by epithelial cells. The entire ovary is enclosed in a thin peritoneum.

Oogenesis was divided into seven developmental stages based upon the cytological characteristics of the cells. Although the developmental stages through which teleost oocytes pass are quite similar from species to species (Wallace and Selman 1981), the nomenclature used, and the number of stages defined, differs considerably between investigators. The terminology used here generally follows that of Yamamoto (1956a). The developmental stages are defined as follows:

Stage I—Oogonia (Fig. 1B): Small (5-29 μm), spherical to slightly oval in shape. Nucleus spherical and large, occupying most of cell. Chromatin material appearing as thin threads. One prominent, deeply basophilic nucleolus located at periphery of nucleus. Nucleoplasm clear. Cytoplasm very thin and faintly basophilic. Usually associated with a single potential follicle cell. Most often found in small groups, or "nests" of 4 or 5.

Stage II—Early perinucleolus (Fig. 1B): Small (10-78 μm), and angular to round in shape. Nucleus spherical and large. Chromatin material forming chromosomes characteristic of meiotic prophase. Two to five deeply basophilic large nucleoli located near periphery of nucleus. Nucleoplasm slightly basophilic. Cytoplasmic volume greater than in oogonia and deeply basophilic. Surrounded by a single layer of flattened follicle cells (theca).

Stage III—Resting (Fig. 1C): Small to intermediate in size (23-140 μm), and spherical in shape. Nucleus spherical and large. Chromatin dispersed, granular, and lightly basophilic. Three to ten deeply basophilic nucleoli arranged peripherally just inside nuclear envelope. Cytoplasm divided into two concentric zones; the inner deeply basophilic and dense, and the outer only slightly basophilic and less dense. Boundary between zones usually poorly defined. Single layer of flattened follicle cells surround oocyte (theca).

Stage IV—Late perinucleolus (Fig. 1D): Small to intermediate in size (39-174 μm) and spherical in shape. Nucleus spherical and large. Chromatin material dispersed, causing nucleoplasm to appear granular. Five to twenty deeply basophilic nucleoli arranged peripherally around inner surface of nuclear envelope. Cytoplasm lightly basophilic. Oocyte surrounded by a single layer of flattened follicle cells (theca).

Stage V—Early maturing (Fig. 2A, B): Intermediate to large in size (52-260 μm), and spherical in shape. Nucleus large and spherical. Chromatin material dispersed. Ten to twenty basophilic nucleoli arranged peripherally, just inside nuclear envelope. Cytoplasm containing either yolk vesicles (Fig. 2A) or yolk globules (Fig. 2B) in its outer region. Follicle is composed of a thin inner acidophilic zona radiata and two outer layers of follicle cells; an inner granulosa and an outer theca.

Stage VI—Late maturing (Fig. 2C, D): Large (104-474 μm), and spherical in shape. In early stages (Fig. 2C), nuclear envelope is distinct, nucleoplasm is lightly acidophilic, and numerous nucleoli are located peripherally in nucleus. Cytoplasm is completely full of yolk globules. In later stages (Fig. 2D), nuclear envelope is indistinct, and nucleus is irregularly shaped. Nucleoli dispersed throughout the slightly acidophilic nucleoplasm. Lampbrush chromosomes often apparent. Nucleus may be located either centrally or toward the periphery of the cell. Zona radiata thick, and radial striations are apparent. Two layers of follicle cells are located external to the zona radiata; an inner granulosa and an outer theca.

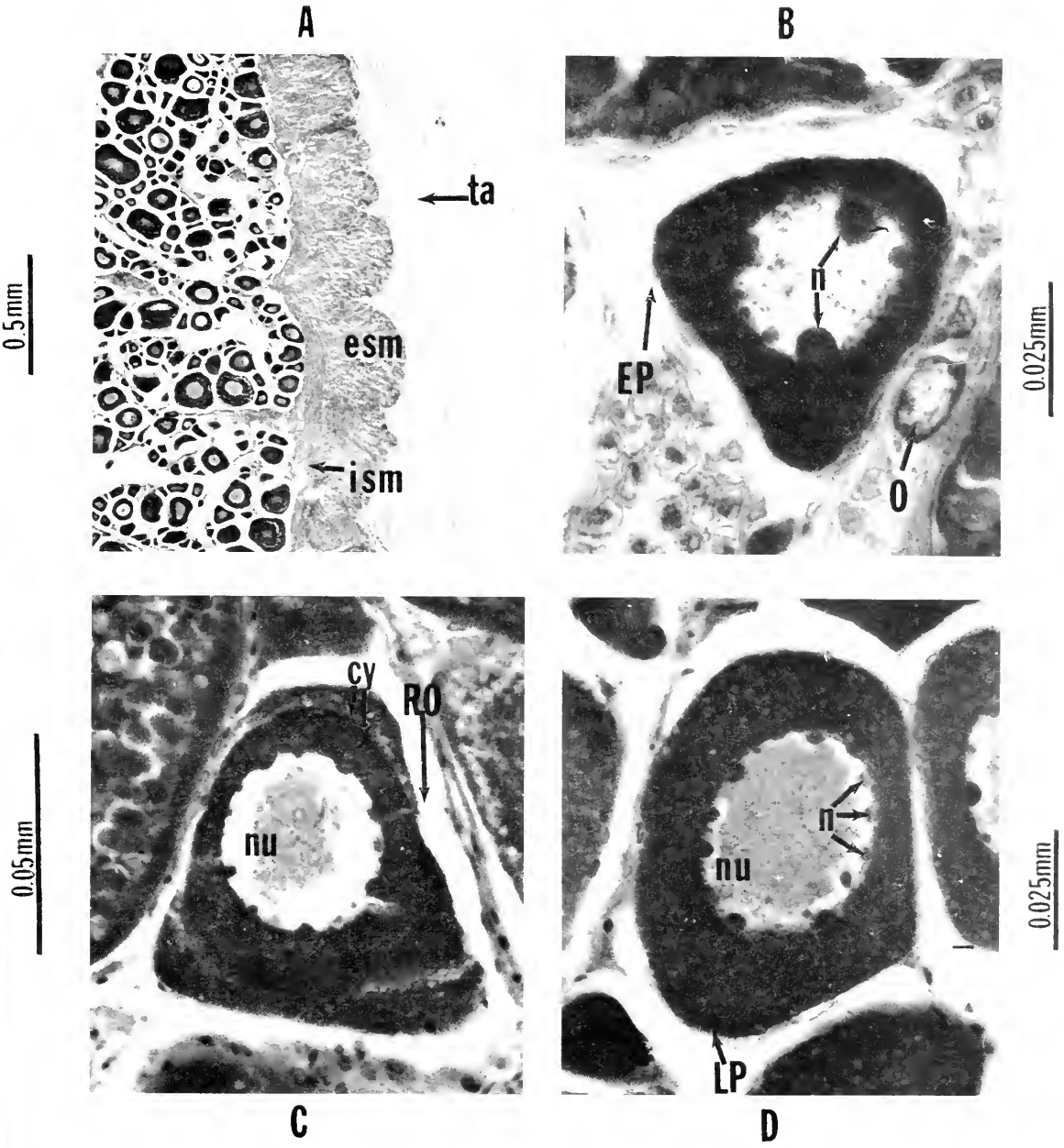

FIGURE 1.—A. Cross section of the ovary wall in a postspawning yellowtail flounder. B. Oogonia and early perinucleolus stage. C. Resting oocyte stage. D. Late perinucleolus stage. cy = cytoplasm, EP = early perinucleolus oocyte, esm = external smooth muscle, ism = internal smooth muscle, LP = late perinucleolus oocyte, n = nucleolus, nu = nucleus, O = oogonia, RO = resting oocyte, ta = tunica albuginea.

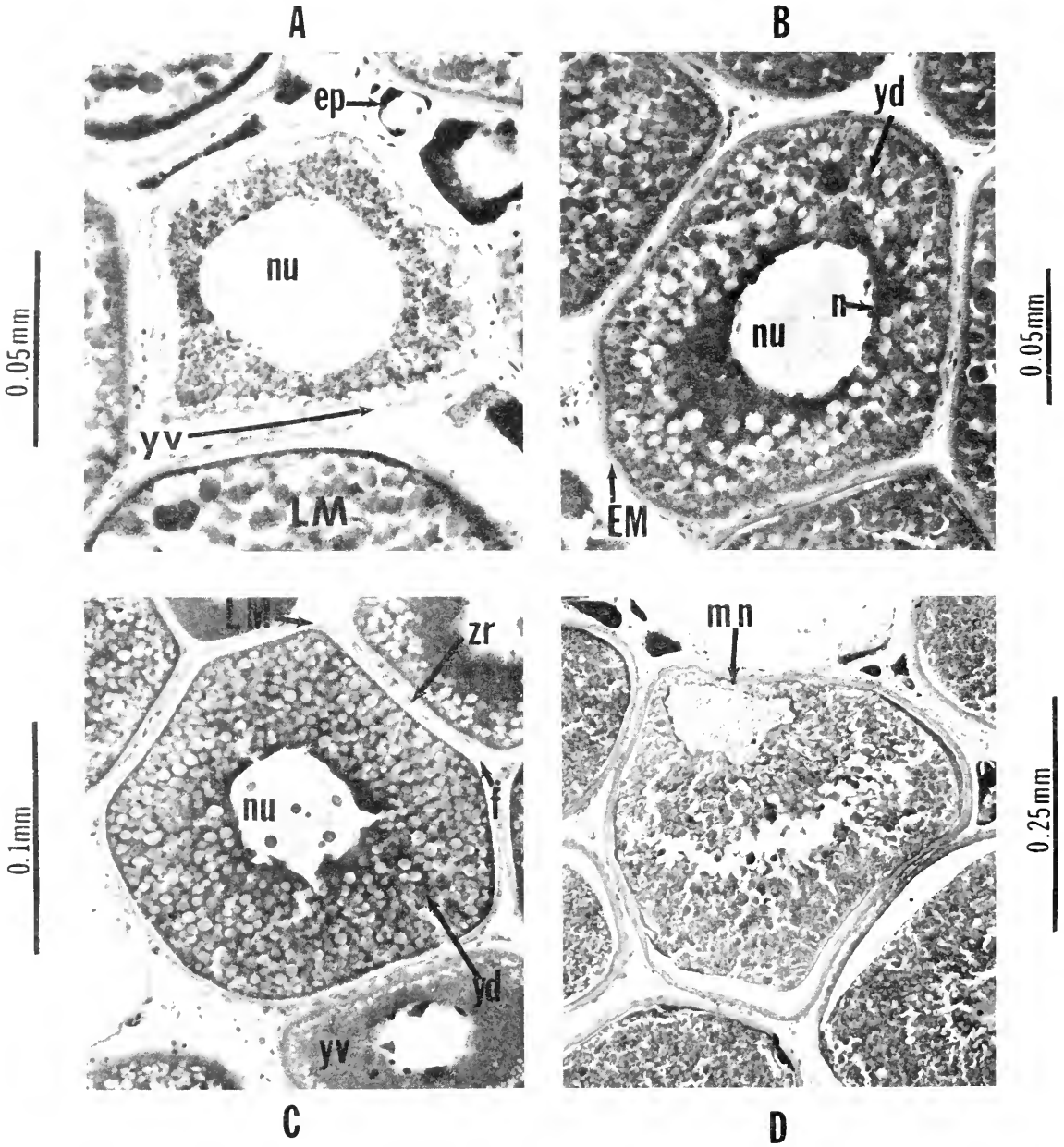

FIGURE 2.—A. Early maturing stage of the yellowtail flounder with yolk vesicles. B. Early maturing stage acquiring yolk. C. Late maturing oocyte. D. Migrating nucleus of late maturing oocyte. EM = early maturing oocyte, ep = early perinucleolus oocyte, f = follicle cell layer, LM = late maturing oocyte, mn = migrating nucleus, n = nucleolus, nu = nucleus, yd = yolk droplet, yv = yolk vesicle, zr = zona radiata.

Stage VII—Hyaline (Fig. 3A): Large (about 400 μm) and irregularly shaped, presumably due to histological processing. Nucleus, seen only at the beginning of this stage, is irregularly shaped and located near margin of cell. Early in this stage the yolk globules begin to break up, allowing the yolk to coalesce. At conclusion of this stage, interior of cell is completely homogeneous, with no yolk globules or nucleus apparent. Zona radiata is thin, and no radial striations are seen. Follicle layer external to the zona radiata is absent.

In addition to the above seven developmental stages, there were two types of regressing oocytes:

Type I—Corpora atretica (Fig. 3B): Large and irregularly shaped. Size variable, but generally from 150 to 300 μm. Characteristics similar to either early maturing or late maturing oocytes except that the zona radiata is broken and collapsed inward. Follicle cells are hypertrophied, lightly basophilic, and invade the cytoplasm. Comparatively few yolk globules remain, and those present are indistinct. Found only in prespawning fish.

Type II—Resorbing (Fig. 3C): Cytoplasmic characters similar to those of either late maturing or hyaline oocytes. Entire cell is collapsed inward, and zona radiata is broken in numerous places. Found only in postspawning fish. Size variable, but generally from 350 to 400 μm.

Seasonal Changes in Microscopic Appearance

When the relative abundances of the different developmental stages of oocytes were calculated for each sampling date, seasonal differences were apparent (Table 4; Figs. 4, 5). The mean diameter of some oocyte types also showed seasonal changes

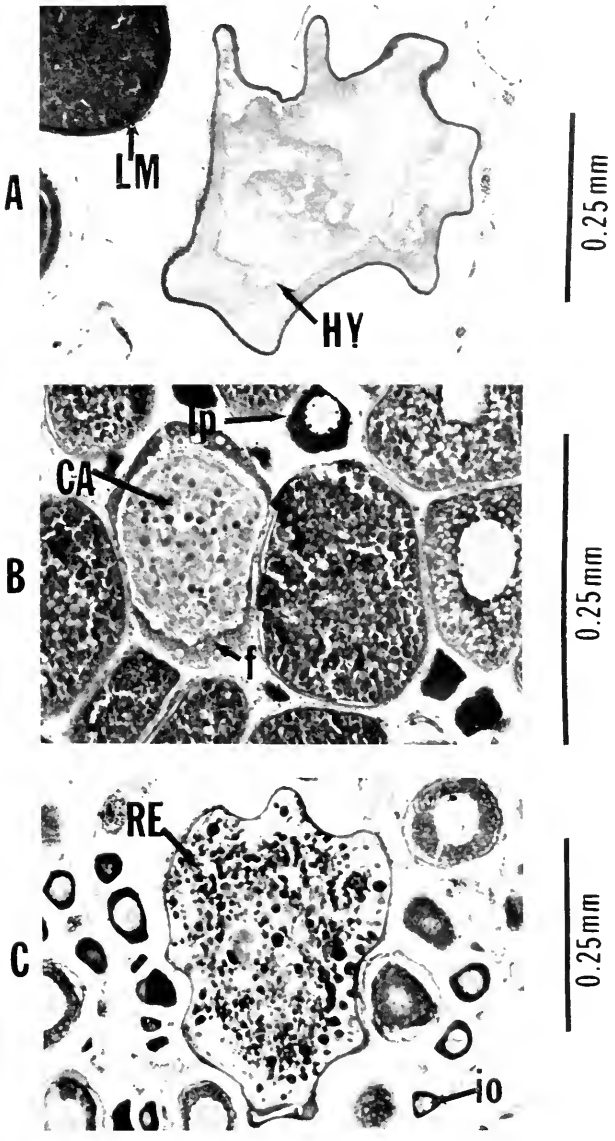

FIGURE 3.—A. Hyaline oocyte of the yellowtail flounder. B. Corpora atretica in a ripening fish. C. Resorbing oocyte in a spent fish. CA = corpora atretica, f = hypertrophied follicle layer, HY = hyaline oocyte, io = immature oocyte, LM = late maturing oocyte, lp = late perinucleolus oocyte, RE = resorbing oocyte.

TABLE 4.—Seasonal changes in frequency (%) of different oocyte developmental stages in yellowtail flounder. n = number of cells examined. Developmental stages and regressing type are described in text.

Sampling date	n	Developmental stages							Regressing type
		I	II	III	IV	V	VI	VII	I
1/26/78	5,000	1.42	4.86	17.90	4.94	—	69.54	—	1.28
2/27/78	5,000	0.52	3.88	23.84	—	0.68	69.28	—	1.80
4/3/78	5,000	2.70	5.04	24.00	1.24	1.08	63.64	2.02	0.28
5/1/78	5,000	2.28	8.28	13.86	8.04	8.44	57.44	1.60	0.06
5/31/78	5,010	5.17	7.12	32.29	1.34	18.14	26.91	8.98	0.04
6/27/77	5,000	2.34	26.64	1.92	38.42	22.20	8.06	0.30	—
7/28/77	5,000	2.96	39.94	—	27.38	29.72	—	—	—
8/21/77	5,000	8.08	41.22	—	22.28	28.42	—	—	—
9/6/77	5,000	4.66	44.46	—	16.98	33.90	—	—	—
10/4/77	4,978	11.05	12.17	25.15	7.31	9.68	34.63	—	—
11/15/77 and 11/20/78	6,400	5.59	11.89	14.81	8.75	6.66	52.19	—	0.11
12/19/77	4,900	2.38	5.35	20.75	7.06	3.71	60.55	—	0.14

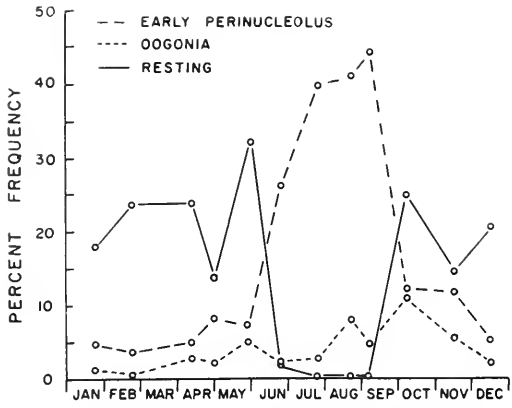

FIGURE 4.—Seasonal changes in the percent frequencies of oogonia, early perinucleolus, and resting stage oocytes in yellowtail flounder.

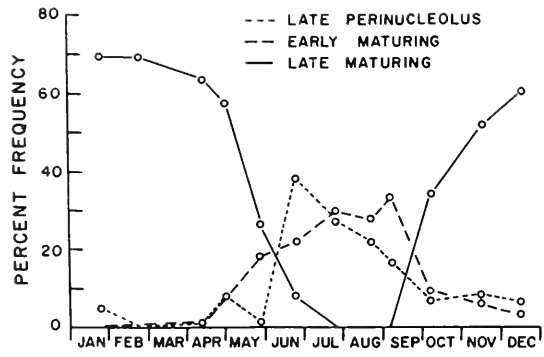

FIGURE 5.—Seasonal changes in the percent frequencies of late perinucleolus, early maturing, and late maturing stage oocytes in yellowtail flounder.

(Table 5; Figs. 6, 7), as did their size-frequency distribution (Fig. 8).

Oogonia were present year-round in variable percentages (Table 4), but showed a tendency to be more abundant during the summer and early fall (Fig. 4). No significant differences in mean diameter were apparent between months ($P>0.05$).

Early perinucleolus oocytes were also present on all sampling dates, but marked seasonal changes in abundance were apparent (Table 4). Relatively few were seen from October through May, but their percentage increased sharply from June through September (Fig. 4). Although their size stayed fairly constant over the year, a significant decrease in mean diameter was noted between September and October, and April and May ($P<0.05$), while a significant increase ($P<0.05$) was seen between February and April (Fig. 6). Most early perinucleolus oocytes were from 21 to 30 μm in diameter in all months except June, July, and September when their modal size increased to 31-40 μm (Fig. 8).

Resting oocytes were present only from October through June (Table 4). From September to October their percentage increased sharply, then fluctuated from about 14 to 32% through the following May when they began a sharp decline in abundance (Fig. 4). The percentages of early perinucleolus and resting oocytes were inversely related. As the percentage of early perinucleolus oocytes declined from September to October, the percentage of resting oocytes increased. An opposite situation was noted from May to June (Fig. 4). From October through December the mean diameter of resting oocytes increased (Table 5). It remained fairly constant through April, and then began a gradual decline through June (Fig. 6). The size-frequency distributions of resting oocytes widely overlapped those of early perinucleolus, late perinucleolus, and early maturing oocytes. Modal diameter was relatively small in October, increased

from November through April, and then decreased in May (Fig. 8).

Although resting oocytes remained histologically similar from October through February, changes began to occur in April and May. The boundary between the cytoplasmic zones became very indistinct and eventually disappeared as the inner zone became less basophilic. Accompanying this transition, the number of nucleoli increased, and in some oocytes a peripheral ring of yolk vesicles appeared in the cytoplasm.

Late perinucleolus oocytes were observed in all months except February (Table 4). Their abundance increased sharply during June and then began a gradual decline through October (Fig. 5). Coincidentally, there was a decrease in the percentage of resting oocytes (Fig. 4). The mean diameter of late perinucleolus oocytes showed little seasonal change with the exception of a significant ($P<0.05$) increase in size from July to August followed by a significant decline from August to September (Fig. 7). The size-frequency distributions of this oocyte stage overlapped those of all other oocyte types except for late maturing. Beginning in April some late perinucleolus oocytes had a narrow, clear area in the cytoplasm just inside the follicle layer.

The percentage of early maturing oocytes increased fairly steadily from April through September, and then declined through December (Fig. 5). As their abundance increased from May to June, the percentage of resting oocytes decreased (Fig. 4). Although the percentages of both early maturing and late perinucleolus oocytes increased from May to June, the percentage of late perinucleolus oocytes peaked in June and then declined, while the peak percentage of early maturing oocytes was not seen until September, about 3 mo later (Fig. 5). The mean diameter of early maturing oocytes increased steadily from April through August, declined from August to October, and then remained fairly constant through February (Fig. 7). The size-frequency distributions of early maturing oocytes overlapped those of both resting and late perinucleolus oocytes in the months when they were present together. A continuous size-

TABLE 5.—Seasonal changes in mean diameter (μm) (±1 SD) of different oocyte developmental stages and regressing types in yellowtail flounder. Developmental stages and regressing types are described in the text.

Sampling date	Developmental stage							Regressing type	
	I	II	III	IV	V	VI	VII	I	II
6/27/77	13.47±1.97	36.20±4.62	71.62± 8.74	78.17± 5.39	129.74± 8.05	372.03±45.44	413.43±36.65	—	397.43±35.88
7/28/77	10.23±1.71	31.90±4.22	—	76.59± 6.84	142.00± 9.93	—	—	—	—
8/21/78	11.47±3.53	36.31±6.11	—	95.50±10.57	151.79±13.43	—	—	—	—
9/6/77	12.99±1.69	36.87±4.86	—	77.70±10.21	133.15±22.10	—	—	—	—
10/4/77	12.64±1.58	28.55±5.39	59.57±13.37	67.50±12.22	102.73± 9.45	170.98±32.35	—	—	—
11/15/77 and 11/20/78	11.58±2.60	32.40±4.21	65.79± 4.19	79.81±12.09	105.68±15.30	204.46±26.44	—	171.63±48.48	—
12/19/77	9.56±1.19	29.57±6.58	77.68± 2.55	77.10± 5.80	121.60±19.69	249.58±19.81	—	229.20±38.56	—
1/26/78	12.75±3.31	35.16±5.73	76.85± 8.79	70.89±22.24	—	294.43±19.94	—	203.67±30.39	—
2/27/78	10.00±1.43	28.41±6.31	78.35± 6.86	60.10±13.46	116.27±21.08	293.71±23.15	—	234.00±36.77	—
4/3/78	13.15±3.09	37.86±8.30	76.85± 8.79	—	92.90± 6.65	324.43±37.84	404.18±37.43	246.11±33.75	—
5/1/78	12.65±0.61	21.14±3.32	74.89± 8.48	76.35±14.35	96.53± 9.26	313.55±18.90	403.00±33.00	231.33±45.52	—
5/31/78	11.45±3.52	26.41±2.52	73.02± 9.82	78.75±17.32	108.87±20.10	349.12±12.90	399.00±32.71	228.80±41.75	366.36±51.29

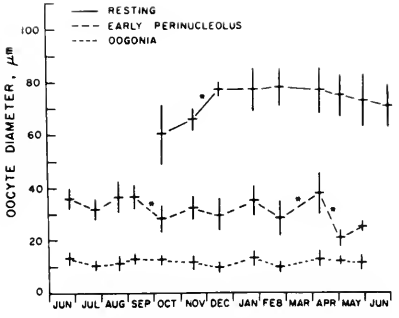

FIGURE 6.—Seasonal changes in diameter (mm) of ogonia, early perinucleolus, and resting stage oocytes in yellowtail flounder. Horizontal bar = mean, vertical bar = mean ± 1 SD, *indicates a significant difference (ANOVA, Student-Newman-Keuls, $P<0.05$) between adjacent means.

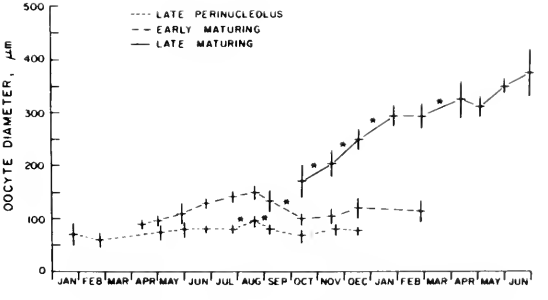

FIGURE 7.—Seasonal changes in diameter (mm) of late perinucleolus, early maturing, and late maturing stage oocytes in yellowtail flounder. Horizontal bar = mean, vertical bar = mean ± 1 SD, *indicates a significant difference (ANOVA, Student-Newman-Keuls, $P<0.05$) between adjacent means.

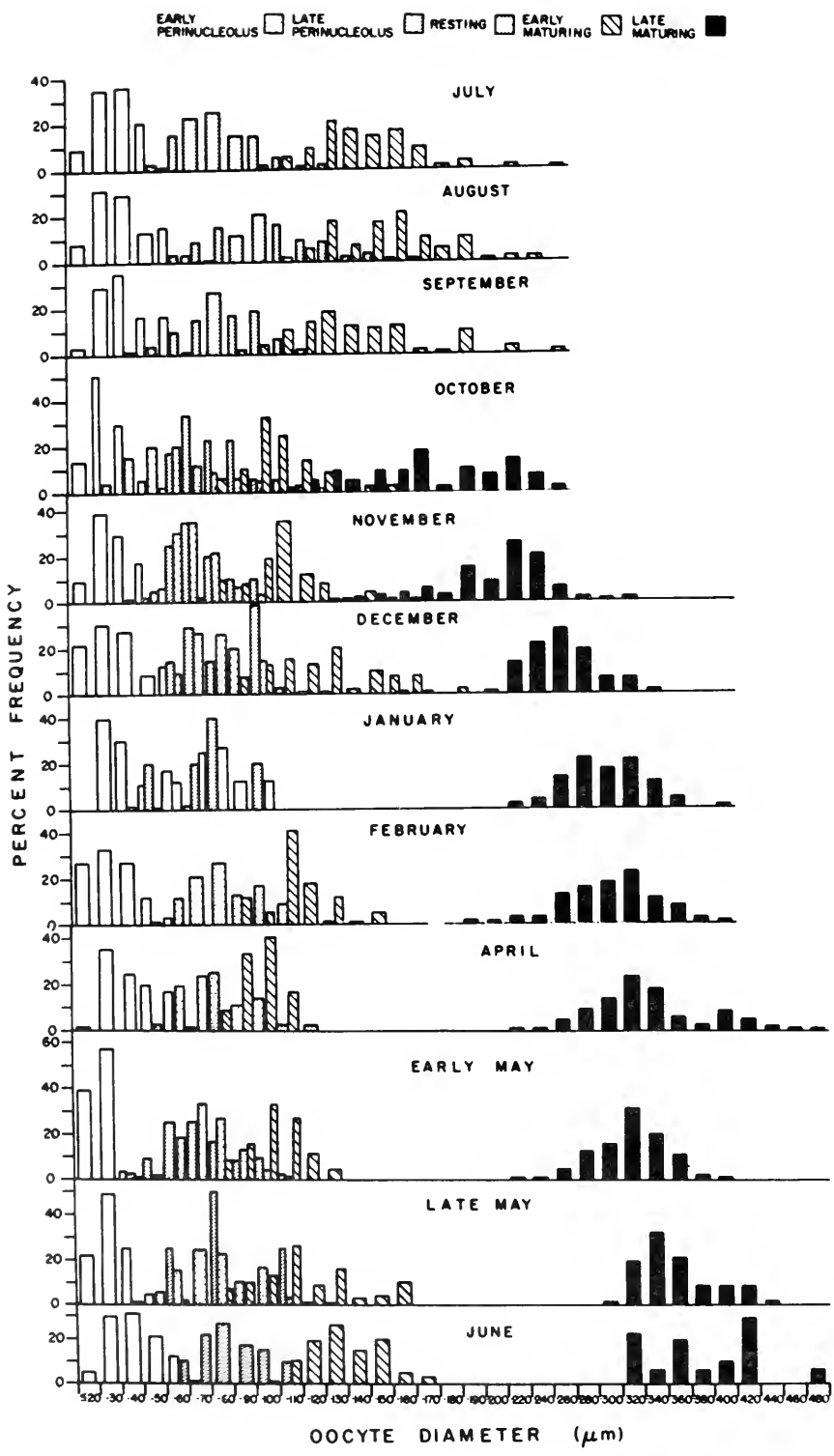

FIGURE 8.—Size-frequency distributions of yellowtail flounder oocytes from July through June.

frequency distribution was seen between early and late maturing oocytes from October through December. The continued growth of late maturing oocytes caused the distributions to become discontinuous by February (Fig. 8).

Late maturing oocytes were present from October through June (Table 4). Their abundance increased steadily from September through January, remained fairly constant through April, and then declined sharply in May and June (Fig. 5). Their mean diameter increased from October through June (Fig. 7). This increase was reflected in their progressively larger size-frequency distributions (Fig. 8).

Hyaline oocytes were present in relatively small percentages from April through June (Table 4). Their mean diameter was about 400 μm (Table 5). Corpora atretica (Regressing Type I) were seen from November through May in very small percentages (Table 4). There was a slight tendency for them to be more abundant in January and February.

DISCUSSION

The developmental events observed in yellowtail flounder oocytes are very similar to those described for most other teleosts (see review by Wallace and Selman 1981). Development can be divided into two broad phases. In the first, or previtellogenic phase, growth is slow and comparatively few cytoplasmic changes occur. The second, or vitellogenic, phase is characterized by rapid growth and the deposition of large amounts of yolk in the cytoplasm. The previtellogenic phase includes the oogonia, early perinucleolus, resting, and late perinucleolus developmental stages. While oogonia were found throughout the year, their abundance tended to be somewhat higher from August through October. Similar patterns of year-round presence, with peak abundances in postovulatory fish, have been reported by many others (Barr 1963; Crossland 1977; Htun-Han 1978; Khoo 1979). Since oogonia represent the initial stage in the process of oogonesis, and thus the reserve from which all oocytes will eventually develop, the timing and location of their production are of considerable interest (see review by Tokarz 1978). Braekevelt and McMillan (1967), studying the brook stickleback, *Eucalia inconstans*, suggested that they arose mitotically from residual oogonia that remained in the ovary from year to year. Bowers and Holliday (1961) concluded that in the herring (*Clupea harengus*), oogonia were derived annually from primary germ cells, while others including Wheeler (1924), Yamamoto (1956a), and Foucher and Beamish (1980) working with *Pleuronectes* (= *Limanda*) *limanda*, *Liopsetta obscura*, and *Merluccius productus*, respectively, concluded that at least some oogonia arose from follicle cells following ovulation. In addition to the site of production, the life history stage during which production occurs may differ from species to species. Many investigators (Barr 1963; Shirokova 1977; Htun-Han 1978; Monaco et al. 1978) have observed mitotic activity in oogonia of mature fish, suggesting that a new stock of oogonia arises during each reproductive cycle. Hickling (1935) and Yamamoto (1956b) saw no evidence of mitotic activity and concluded that the total reserve stock of oogonia had been produced prior to sexual maturity. While no mitotic divisions were apparent in this study, the fact that oogonia were usually present in small groups is an indication that such divisions were occurring but were overlooked due to the very small size of the oogonia. Furthermore, if the total reserve fund of oogonia, representing all future oocytes, were present in the ovary of a fish as fecund as yellowtail flounder (Howell and Kesler 1977), it seems likely that their abundance would have been considerably higher than observed. Because of these observations, and the seasonal changes in the abundance of oogonia, it seems reasonable to conclude that a new stock of oogonia is produced each year in yellowtail flounder, primarily in the months following spawning.

The sharp increase in abundance of early perinucleolus oocytes following spawning indicates that oogonia were rapidly being transformed into early perinucleolus oocytes at this time. Since few intermediate types were observed, it must be assumed that the transition was rapid.

The coincidental decline in the percentage of early perinucleolus oocytes and the increase in resting oocytes seen in September indicate that some early perinucleolus oocytes are converted into resting oocytes at this time. This is further indicated by their overlapping size-frequency distributions and their cytological similarity. This transformation was accompanied by a division of the cytoplasm into two concentric zones. Similar cytoplasmic zonation has been noted in a variety of species including *Clupea harengus* (Bowers and Holliday 1961), *Gadus morhua callarias* (Shirokova 1977), *Gadus merlangus* and *G. esmarkii* (Gokhale 1957), *Liopsetta obscura* (Yamamoto 1956a), and *Pleuronectes* (= *Limanda*) *limanda* (Wheeler 1924). Recent studies (see review by Guraya 1979) suggest that this apparent zonation may be due to aggregates of ribonucleoprotein particles having been extruded through the nuclear membrane. When these aggregates become surrounded by cytoplasmic organelles (not seen in this study) they are variously known as "yoke nuclei" or

"Balbiani bodies." While the function of these remains unknown, Guraya (1979) has suggested that they act as centers for the formation, multiplication, and accumulation of organelles and materials needed for yolk deposition.

The mean diameter of resting oocytes increased from October to December, remained fairly constant from December to April, and then declined from April through June. The increase was presumably caused by progressively older, and therefore larger, early perinucleolus oocytes entering the resting stage. The decline in mean size seen during the spring was probably due to the larger ones having been transformed into late perinucleolus oocytes.

Resting oocytes rapidly declined in abundance from May to June and were absent by July. Coincident with this decline was an increase in late perinucleolus oocytes. This observation, combined with their similarities in mean size and overlapping size-frequency distributions, indicates that resting oocytes were transformed into late perinucleolus oocytes. During this transformation the zonation in the cytoplasm was lost, the number of nucleoli increased, and the cytoplasm became less basophilic.

The vitellogenic phase of oogenesis contains the early and late maturing types as well as hyaline oocytes. It begins as the late perinucleolus oocytes develop into early maturing oocytes. As indicated by their relative changes in seasonal abundance and size-frequency distributions, this changeover occurs primarily during the late spring and summer months. In large late perinucleolus oocytes a ring of vacuole-like structures is seen near the periphery of the cytoplasm. Oocytes of this type have alternatively been described as yolk vesicle (Yamamoto 1956a; Khoo 1979), early or primary vitellogenic (Monaco et al. 1978; Htun-Han 1978) or vacuolated (James 1946) oocytes. This stage marks the beginning of vitellogenesis during which the oocyte rapidly grows in size and accumulates yolk. Yolk vesicles apparently originate from the Golgi complexes (Yamamoto and Onozata 1965; Yamamoto and Oota 1967) and contain mucopolysaccharides which represent the first form of yolk inclusions (Yamamoto 1956a; Malone and Hisaoka 1963; Khoo 1979). Yamamoto (1956c) and Khoo (1979) have reported that in the later stages of vitellogenesis the yolk vesicles are displaced to the periphery of the oocyte and gave rise to the cortical alveoli which, after fertilization, contribute to water hardening of the egg. Simultaneous with the appearance of these vesicles the beginning of the zona radiata was seen between the follicle cells and the cytoplasm. As early maturing oocytes continued to develop, yolk globules became interspersed with the yolk vesicles near the periphery of the cytoplasm. These globules represented the second form of yolk inclusions which have been shown in other species to contain proteins, phospholipids, and fats (Yamamoto 1957; Khoo 1979).

As yolk continued to accumulate toward the nucleus the mean diameter of early maturing oocytes continued to increase. The significant decrease in mean diameter of this stage noted from September to October was due to the larger early maturing oocytes being classified as late maturing. This is demonstrated in their size-frequency distributions where it can be seen that size classes formerly dominated by early maturing oocytes had become predominantly late maturing oocytes. As expected, the percentages of early maturing oocytes declined as the percentages of late maturing oocytes increased. Following this transformation, mean oocyte diameter increased rapidly.

Beginning in April late maturing oocytes began to be transformed into hyaline oocytes preparatory to their release from the follicle. At this time the yolk globules began to break open allowing the yolk to coalesce. Accompanying this was an increase in size, presumably due to the absorption of fluid, which caused the zona radiata to become thin.

The low percentage of hyaline oocytes observed is an indication that spawning is intermittent during the breeding season, with only a portion of the late maturing oocytes taking in fluid and being discharged at one time. Following the expulsion of the ripe ovum, the remaining follicle collapses into an irregular mass, decreases in size, and disappears shortly after spawning.

The year-round presence of some oogonia and early perinucleolus oocytes indicates that a small amount of oogonia production and subsequent development into early perinucleolus oocytes occur throughout the year. Although not established, it is assumed that those early perinucleolus oocytes produced during the late fall and winter enter the resting stage until the following spring. Small percentages of late perinucleolus and early maturing oocytes were also present year-round. The small percentage of late perinucleolus oocytes from October through January indicates that not all of them had developed into early maturing oocytes over the late spring and summer months. Presumably these would have begun to accumulate yolk during the late fall and early winter months. This would account for the small percentages of early maturing oocytes seen at this time.

The percentages of the two types of regressing oocytes were very small. Corpora atretica (Regressing Type I) were seen only in prespawning fish, and

were formed as either early or late maturing oocytes ceased to develop and began to be resorbed. Even in the samples where most abundant (January and February), they accounted for <2% of the oocytes examined. The persistence of corpora atretica and corpora lutea in certain species has led some investigators to conclude that they are the source of ovarian hormones (see review by Ball 1960). The very small percentages of corpora atretica seen in this study suggest that in yellowtail flounder these structures either disappear rapidly or are formed very infrequently. Similar low percentages have been reported in numerous other teleosts (Wheeler 1924; Yamamoto 1956a; Barr 1963; Davis 1977). Resorbing oocytes (Regressing Type II) were observed even more infrequently, and only in postspawning fish. Because of their scarcity in the samples, no percentages were calculated. The infrequency of the two types of regressing oocytes indicates that the vast majority of oocytes which reach the vitellogenic phase continue to develop and are released during spawning. Those few which cease to develop or remain in the ovaries after spawning are quickly resorbed.

These data indicate that the development of a fully mature yellowtail flounder egg requires 2 yr. During the first year, which begins after spawning, oocytes pass through the previtellogenic phase which includes oogonia, early perinucleolus, resting, and late perinucleolus developmental stages. In the second year of development, oocytes pass through the vitellogenic phase and are then released. This phase begins as late perinucleolus oocytes, now about 1 yr old, develop into early maturing oocytes during the spring and summer. By the fall of their second year the oocytes have accumulated large amounts of yolk in the cytoplasm and have reached the late maturing stage. Over the following winter and early spring months they continue to accumulate yolk and increase in size. During the spawning season, batches of late maturing oocytes enter the hyaline stage and are then released. This apparently occurs intermittently throughout the breeding season until virtually all late maturing eggs become hyalinated and are released.

At any given time then, there are two populations or year classes of oocytes present within adult yellowtail flounder ovaries. These include a population of small, previtellogenic oocytes which develops over 1 yr, and a second population of larger vitellogenic oocytes which are recruited from the previtellogenic population. Members of the vitellogenic population are in their second year of development and will mature and be released in the upcoming breeding season. Ovaries such as this have been described as "group synchronous" (Wallace and Selman 1981).

The events described in the process of oocyte maturation fit closely with seasonal changes in both GSI and the macroscopic appearance of the ovaries. Maturity Stage II (Developing virgin, recovering spent) ovaries were seen from May through October. These ovaries contained only oogonia, early and late perinucleolus, and early maturing oocytes. The relatively small size of these oocyte developmental stages (<150 μm diameter), and the absence of late maturing and hyaline oocytes, resulted in these ovaries being relatively small and translucent. As expected, in postspawning months when fish with ovaries of this type accounted for >50% of the sample (June-September), mean GSI values were very low. Stage III (Developing, maturing) fish were observed from September through May. Due to the presence of large early and late maturing oocytes, their ovaries were enlarged, yellowish in color, and granular. As the percentages of fish in this maturity stage increased from September to October, mean GSI values increased. From November through at least February, all fish had ovaries in this maturity stage. Mean GSI values rose during this time due to the increasing size of the late maturing oocytes present. Ripe fish (Stage IV) were present from April through June. Mean GSI was highest in April since all fish examined were either still maturing or ripe. The first spent fish (Stage V) were found in early May, and by the end of May 50% of the fish had spawned. Loss of eggs through spawning caused these ovaries to be flaccid and bloodshot, and mean GSI values decreased as the spawning season progressed.

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SIZE AT MATURITY AND FECUNDITY OF ROCK CRABS, *CANCER IRRORATUS*, FROM THE BAY OF FUNDY AND SOUTHWESTERN NOVA SCOTIA

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ABSTRACT

Rock crabs, *Cancer irroratus*, were collected from lobster traps, trawls, and by divers in the Bay of Fundy and southwestern Nova Scotia, 1980-81. Estimates of maturity were similar using gonad examination, measurements of chela height, and abdominal width/carapace width ratios. The carapace width (CW) at which 50% of male and female rock crabs were mature was estimated to be 62 and 49 mm, whereas the onset of maturity was estimated to be 40 and 27 mm CW, respectively. Ovigerous females (range 41-100 mm CW) were heavier than nonovigerous females and males of the same carapace width, and carried from 47,130 to 567,690 eggs per female. Rock crabs in the Bay of Fundy and southwestern Nova Scotia appear to mature at a larger size than rock crabs from more southern waters.

The rock crab, *Cancer irroratus* Say, 1817, (Decapoda: Brachyura), is common along the Atlantic coast of North America from Labrador to South Carolina (Rathbun 1930; Squires 1966; Nations 1975). In Canadian waters, *C. irroratus* is generally found near the coast (depth <20 m) and is abundant in the southern Gulf of St. Lawrence (Caddy and Chandler 1976; Stasko 1976; Campbell 1979). At present, *C. irroratus* is underutilized due to high processing costs and limited market demand. Consequently, rock crabs are fished primarily as an incidental bycatch in the lobster fishery and, except in certain areas, are generally discarded or occasionally used as bait in lobster traps. Bigford (1979) summarized the numerous studies on the biology and ecology of *C. irroratus*. Little information exists on the reproductive biology of *C. irroratus* in its northern range, especially the Bay of Fundy and southwestern Nova Scotia (Krouse 1972, 1976, 1980; Scarratt and Lowe 1972; Elner and Stasko 1978; Elner and Elner 1980).

Size at maturity and fecundity are important parameters in determining reproductive potential and for managing a crab fishery. Crabs can be considered mature when males can mate successfully (Hartnoll 1969) and females are capable of extruding eggs. Although egg-bearing by female crabs is an obvious indication of functional maturity, depending on the season and other factors, a proportion of mature females may be found without external eggs at any given period. Estimation of maturity in these nonovigerous females and males can be determined by internal examination of the gonads (physiological maturity) and/or measurement of external morphological secondary sexual characteristics (functional maturity). This paper reports on the physiological and functional maturity, fecundity, and weight relations of different size-groups of *C. irroratus* males and females collected from the Bay of Fundy and southwestern Nova Scotia waters (Fig. 1).

METHODS

Male and nonovigerous female *C. irroratus* were collected near Alma, Beaver Harbor, and Grand Manan, New Brunswick, and at Scots Bay, Delap Cove, and Port Maitland, Nova Scotia, by lobster fishermen who used conventional lobster traps during March-July 1980 (Fig. 1). Additional samples were collected by divers on the southwestern shore of McNutt Island near Shelburne, Nova Scotia, during July 1981. Ovigerous *C. irroratus* were caught in lobster traps near Alma and on the eastern side of Passamaquoddy Bay, using bottom trawls during January-June 1980 and December 1980-February 1981.

The rock crabs were frozen individually in plastic bags within 6 h of capture and stored at ca −20°C. Prior to examination, the rock crabs were thawed at room temperature. We recorded the carapace width (CW, widest distance between the tips of the anterolateral spines of the carapace), the height of the

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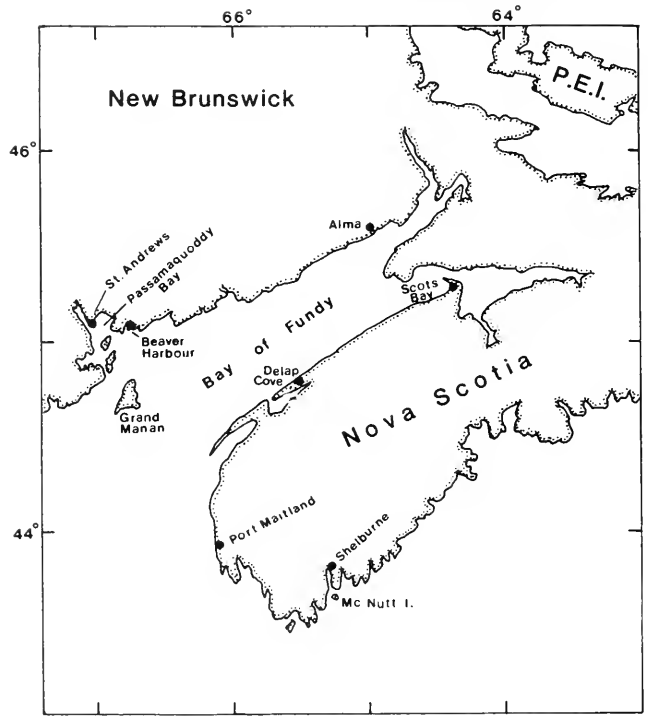

FIGURE 1.—Location of areas sampled for rock crabs in the Bay of Fundy and southwestern Nova Scotia.

left chela (Fig. 2), width of the sixth abdominal segment (see figure 4 in Bigford 1979) to the nearest 0.1 mm, whole body wet weight to the nearest 0.01 g, sex, and gonad stage (Table 1) for each crab. Eggs only were removed from ovigerous females and preserved in 5% Formalin[3] for 24 h then dried to a constant weight at 70°C for 48 h. The total number of eggs was calculated from the weight of the total egg mass divided by the average weight of an egg estimated from the known number (counted under dissecting microscope) and weight of three subsamples of about 500-1,000 eggs.

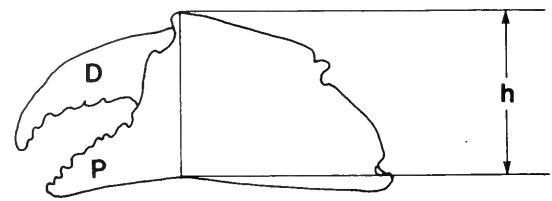

FIGURE 2.—Diagram of a male rock crab left chela indicating the chela height (h) measurement taken; D = dactyl; P = propus.

Gonad stages (Table 1) were based on a modified version of Haefner (1976) who indicated six stages of

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

TABLE 1.—Stages in gonad development of rock crab, *Cancer irroratus* (modified from Haefner 1976).

Stage of development	Male	Female
1. Undeveloped	Gonads not detectable without microscope.	
2. Slight	Vasa deferentia evident. Testes small or not apparent. Colorless. 0-8 small, developing spermatophores per 0.1 mm².	Ovaries threadlike. Colorless to white. No oocytes.
3 Moderate	Testes and vasa deferentia of approximately equal weight or vasa deferentia slightly heavier. Gonads quarter to half volume of hepatopancreas. White. 8-35 well-developed spermatophores per 0.1 mm².	Ovary half volume of hepatopancreas. White to light orange. Oocyte diameter 0.1-0.5 mm.
4 Developed	Gonads half volume of hepatopancreas. Vasa deferentia more than 3 times heavier than testes. White. >30 well-developed spermatophores per 0.1 mm².	Ovary volume approximately equal to that of hepatopancreas. Light orange to orange. Oocyte diameter 0.2-0.5 mm.
5. Well developed	Gonads dominant organ. White. >100 well-developed spermatophores per 0.1 mm².	Ovary larger than hepatopancreas. Orange to red. Oocyte diameter 0.2-0.5 mm.

gonadal development. Modifications to Haefner's classification include combining Haefner's first and second stages into a single immature stage and microscope measurements of oocytes, and examination for spermatophores. The diameters of three oocytes per ovary to the nearest 0.01 mm under a compound microscope were measured. Female *C. irroratus* were considered to be physiologically mature when ovaries were developed to greater than or equal to stage 3 since all ovigerous females had stage-3 ovaries. Male *C. irroratus* were estimated to be physiologically mature as judged by the size of the gonads and the presence of spermatophores (number per 0.1 mm^2 determined with a micrometer and microscope) in the vas deferentia (Table 1). About 10% of the vas deferentia of each gonad stage was subsampled and examined for the presence of spermatophores under 400× magnification. All males with gonad stage ≥3 had well-developed spermatophores. Stage-2 gonads were considered immature because of the low numbers of small developing spermatophores.

The proportion of physiologically mature crabs in each sex was calculated by dividing the number of mature gonad stages by the total number of gonads examined for each 5 mm CW class. The relationship between CW (X) in millimeters and proportion mature (Y) for both female and male *C. irroratus* was approximated by the logistic function:

$$Y = \frac{a}{1 + e^{b+cX}}$$

where a, the asymptote of the curve, and b and c, empirical constants, were estimated by nonlinear least squares approximation from the CW and proportion mature data using Marquardt's algorithm (Conway et al. 1970; Marquardt 1963).

Indices of functional maturity using morphometric criteria for male and female rock crabs were obtained by the following two methods: The first was to find 50% sexual maturity from the intersection of a pair of linear regressions that had the best fit (Somerton 1980a, b) to CW-chela height data; the second by dividing the abdominal width by CW for each individual crab and averaging the ratios for each 5 mm CW group.

The power curve of the linear form $\log_{10} Y = a + b \log_{10} X$ was used to approximate the relationship between CW(X) and total weight in grams (Y), and the number of eggs per female (Y), using the least squares method. Analysis of covariance was used to compare the slopes and elevations of all the regression equations (Snedecor and Cochran 1967).

RESULTS AND DISCUSSION

There were no significant differences using analysis of covariance ($P>0.05$) in size at maturity, CW-weight, or CW-fecundity relationships between rock crabs of the same sex from each sample area; therefore, the data were combined to present each relationship for one general Bay of Fundy-southwestern Nova Scotia area. Table 2 indicates that the CW-weight (g) relationship had a high correlation coefficient (r) for male, nonovigerous, and ovigerous *C. irroratus*. Although there were no significant differences between the slopes ($P>0.05$), there were differences in elevations ($P<0.001$) of the CW-weight regressions over similar CW ranges, between ovigerous females and males and between ovigerous and nonovigerous females (Table 2). Differences in elevation between male and nonovigerous females were probably not biologically significant at $P<0.05$ (Table 2). Krouse (1972) and Scarratt and Lowe (1972) also did not find a difference between males and nonovigerous females in the CW-weight relationship. We, as did Scarratt and Lowe (1972), found that ovigerous females were heavier than nonovigerous females carrying 2.2-45.2 g (wet weight) of eggs for a 41.1-100.2 mm CW range.

The CW-proportion mature relationship estimated from gonad development was described well by the logistic curve (Fig. 3). The CW at which 50% of males and females were mature was estimated at 61.7 and 48.6 mm, respectively. The smallest male found with mature gonads (stage 3) was 34.2 mm CW and the largest male with immature gonads (stage 2) was 95.1

TABLE 2.—Regression constants for the carapace width (Y) and weight (X in grams) relationship ($\log_{10} Y = a + b \log_{10} X$) for male, nonovigerous, and ovigerous rock crabs, *Cancer irroratus*. r = correlation coefficient.

Sex	Regression constants			Number	Carapace width (mm)	
	a	*b*	*r*		Min	Max
Male	−3.9422*o	3.0519	0.9948	476	15.6	137.8
Nonovigerous female	−3.9435*+	3.0667	0.9938	235	19.0	107.1
Ovigerous female	−3.7085o+	2.9921	0.9835	73	41.1	100.2

[1]Elevations followed by same symbol were significantly different: * at $P<0.05$; o and + at $P<0.001$, but there were no significant differences ($P>0.05$) between all three slopes (b) using analysis of covariance.

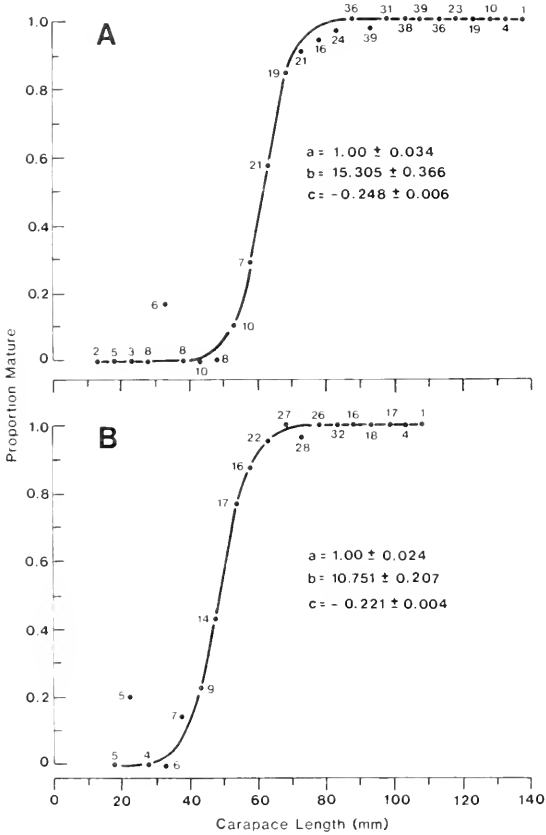

FIGURE 3.—Relationship between proportion mature based on gonad development and carapace width (CW) for (A) male and (B) female rock crabs from the Bay of Fundy and southwestern Nova Scotia. Values next to dots are numbers of crabs examined at every 5 mm CW class. a = asymptote, b and c = empirical constants followed by the 95% nonlinear confidence intervals for the logistic curve (see text for formula).

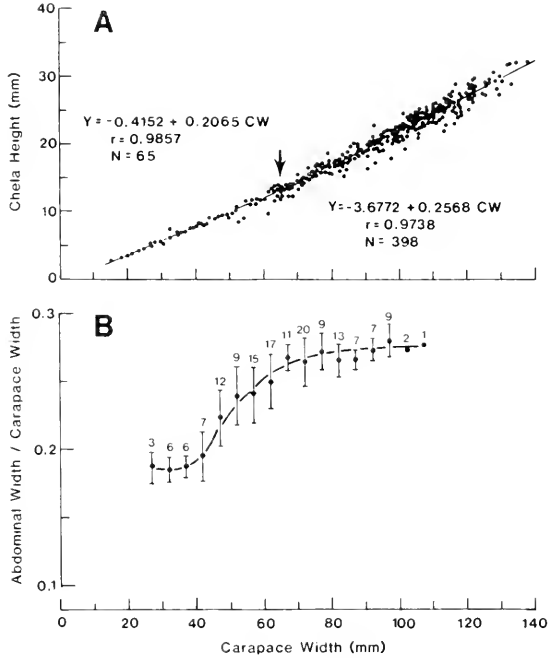

FIGURE 4.—Maturity estimation using rock crab morphometric data in relation to carapace width (CW) for (A) male chela height (Y) (arrow indicates inflection point of two regression lines or 50% maturity; r = correlation coefficient; N = number of individuals), and (B) female abdomen width/carapace width ratio (dots are means, vertical lines are ±1 standard deviations, numbers above each dot are the number of individuals measured for each 5 mm CW group).

mm CW. Most males in the 34.2-134.0 mm CW range had stage-3 gonads and in the 61.9-137.8 mm CW range had fully developed stage-5 gonads. The smallest female with mature ovaries (stage 3) was 20.2 mm CW and the largest female with immature ovaries (stage 2) was 72.2 mm CW. Many females had stage-3 ovaries in the 39.4-99.6 mm CW range, and many females had fully developed stage-5 gonads in the 44.7-105 mm CW range.

Size at 50% maturity for male rock crabs, estimated as the inflection point in the CW-chela height data, was 64.9 mm CW (Fig. 4A), which was similar (61.7 mm CW) to the estimate obtained by the gonadal inspection technique (Fig. 3A). Since only one regression line, using the best fit method (Somerton 1980a), could be obtained for the female CW-chela height data (not shown in this paper), this relationship could not be used to estimate sexual maturity in female rock crabs. The abdomen width/CW ratio was linear for males (not shown in this paper), but curvilinear for females (Fig. 4B), indicating that broadening of the abdomen is a female secondary sexual characteristic. The inflection and asymptote showing onset and 100% sexual maturity, respectively, occurred at about 37 and 77 mm CW (Fig. 4B) which is similar to that derived by gonadal inspection (Fig. 3B). Abdominal width and chela length (not height) have been used to estimate onset of sexual maturity of rock crabs by Shotton (1973) and Terretta (1973). The abdominal width/CW ratio has not been previously used for rock crabs, although commonly used for lobsters in estimating sexual maturity (Templeman 1935; Aiken and Waddy 1980). The results suggest that external morphological secondary sexual characteristics generally coincide with physiological maturity in *C. irroratus* females and males.

The presence of external eggs on females is an obvious indicator of functional maturity. The smallest ovigerous female was 41.1 mm CW, whereas most ovigerous females caught were ≥65 mm CW (Fig. 5), which generally agrees with the maturity curves based on gonad development (Fig. 3B) and ab-

dominal width/CW ratio (Fig. 4B). There were no ovigerous females in our samples between 48 and 65 mm CW; perhaps this scarcity could be attributed to sample bias owing to gear selectivity and/or spatial and temporal effects on the sizes of ovigerous females collected.

Haefner (1976) showed an increase in development of gonads in relation to CW increase for *C. irroratus* males and females captured in the mid-Atlantic Bight. In general, the present data suggest that *C. irroratus* matures at a smaller size in southern than in northern waters of eastern North America. Along the Virginia coastline, the presence of eggs on females, morphological measurements, and observations on gonads of male and female *C. irroratus* indicated individuals are mature by about 30 mm CW (Shotton 1973; Terretta 1973). Reilly (1975) found ovigerous females as small as 14 mm CW, with many ovigerous crabs collected in the 14-25 mm CW range from Rhode Island waters. In northern populations along the Maine coast, Krouse (1972) suggested that females mature at 55-62 mm CW, based on the presence of ovigerous females, although most females were ovigerous in the 70-99 mm CW range. Scarratt and Lowe (1972) examined the gonads of *C. irroratus* from Northumberland Strait and found the smallest female with mature gonads to be 60 mm CW, but the smallest female with external eggs was 65 mm CW, whereas some males had developing gonads at a 50-100 mm CW range and there were a few with ripe gonads ≥69 mm CW. The results of this study on *C. irroratus* in the Bay of Fundy and southwestern Nova Scotia generally agree with those of Krouse (1972) and Scarratt and Lowe (1972) in that most ovigerous females were ≥65 mm CW (Fig. 5).

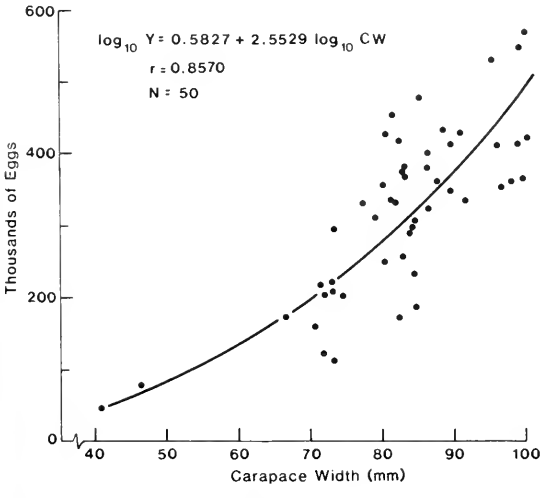

FIGURE 5.—Relationship between total number of eggs (Y) carried externally and carapace width (CW) of ovigerous female rock crabs from the Bay of Fundy and southwestern Nova Scotia; r = correlation coefficient, N = number of individuals.

The CW-fecundity relationship was described well ($r = 0.857$) by a power curve (Fig. 5). There were no significant differences ($P>0.05$) in CW-fecundity relation between newly extruded eggs (orange-red color) and well-developed eggs (pale gray-brown) and between specimens collected in 1980 and 1981, using analysis of covariance; thus the data were combined. The smallest ovigerous female (41.1 mm CW) collected had the lowest number (47,130) of eggs. A 99.8 mm CW female had the largest number (567,690) of eggs. The only other published estimates of fecundity for *C. irroratus* are from Rhode Island (Reilly and Saila 1978). There were no significant differences ($P>0.05$) between the fecundity of *C. irroratus* females in the same size range (37-88 mm CW) from Rhode Island and this study. However, larger ovigerous rock crabs (90-100 mm CW) producing a greater number of eggs (320,000-567,690) per female (Fig. 5) were observed from Bay of Fundy and southwestern Nova Scotia relative to those reported from the Rhode Island area (Reilly 1975; Reilly and Saila 1978).

Interarea variations between *C. irroratus* of size at first maturity and fecundity may be caused by a number of factors such as differences in photo-period, temperature, and food availability. Temperatures are generally cooler in northern waters, such as in the Bay of Fundy, compared with southern waters, such as off Rhode Island (Colton and Stoddard 1972). Warmer temperatures probably lead to maturity at a smaller size in *C. irroratus* compared with colder waters (Kurata 1962). Although *C. irroratus* from the Bay of Fundy may produce more eggs at larger sizes (90-100 mm CW) than female crabs off Rhode Island, we hypothesized that the reproductive potential of this species is greater in warmer southern waters where more individuals mature at smaller sizes, thereby reducing the population generation time, than those rock crabs in colder northern waters. The integration of growth, size at maturity, and fecundity information to compare the reproductive potential of *C. irroratus* from these two areas requires further study.

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LONG-TERM VARIATIONS IN THE SOUTHERN OSCILLATION, EL NIÑO, AND CHILEAN SUBTROPICAL RAINFALL

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ABSTRACT

A 120-year record of Southern Oscillation-related activity along the west coast of South America was studied in order to better understand the causes and variations in this activity with time. Significant decreases in the frequency of occurrence of moderate/strong El Niños and the related abnormally heavy amounts of Chilean subtropical rainfall were noted over the past half century. Work done by Berlage on the Southern Oscillation and findings here concerning the above decreases in activity indicate a significant change took place between 1927 and 1931. A significant decrease in average annual rainfall was noted over subtropical Chile after 1944.

Below normal pressures in the southeast Pacific subtropical high over the past 6 years coincide timewise with generally above normal sea surface temperatures over this region. An associated weakening of the southeast trade system is hypothesized to be responsible for environmental changes that contribute to the large alteration in composition of the pelagic biomass in both the Peruvian and northern Chilean fishery regions over recent years.

Recent findings on large-scale climatic fluctuations over a large part of the tropical and subtropical Pacific (Quinn et al. 1978, 1981), the availability of additional sources of corroborative evidence of these changes (Chilean subtropical rainfall data), and the establishment of an unusual trend in the Southern Oscillation indices over the past 6 yr led to our further investigation of the long-term climatic changes and their causes.

In Quinn et al. (1978) we compiled evidence on El Niño developments, their intensities, and their frequency of occurrence. However, at that time we did not consider the possibility of long-term variations in El Niño intensity with time. In Quinn et al. (1981) we found the Chilean subtropical rainfall amounts to be closely associated with the El Niño (low Southern Oscillation index anomaly)/anti-El Niño (high Southern Oscillation index anomaly) type conditions for 1875-1930. Here we have extended the rainfall records from Taulis (1934) up through 1980 (Table 1) for a study of the changes in activity with time.

In the past we noted a relationship between the Southern Oscillation indices and the productivity of the Peruvian anchoveta fishery (Quinn 1976; Quinn et al. 1978). Ordinarily when a moderate/strong El Niño occurred, the fishery suffered a significant setback, but following such events there was usually a prolonged anti-El Niño period during which the fishery recuperated. However, since the 1976 El Niño the index has remained unusually low (Fig. 1), and coincidentally there has been a startling change in the makeup of the pelagic biomass in the fishery. This change was reported in a Cerescope item (Ceres 1981) from the FAO/Norway Regional Acoustic Centre (the Centre) for Latin America in Lima, Peru. (The Centre became operational in May 1975 under

TABLE 1.—Annual rainfall amounts (in mm) at Santiago (lat. 33°26'S, long. 70°50'W) and Valparaiso (lat. 33°01'S, long. 71°39'W), Chile, for 1931-80.

Year	Santiago	Valparaiso	Year	Santiago	Valparaiso
1931	321.2	470.3	1960	193.0	208.6
1932	351.0	498.3	1961	270.0	442.0
1933	316.1	293.4	1962	210.0	228.3
1934	519.2	486.5	1963	440.0	452.9
1935	252.5	325.0	1964	160.0	261.0
1936	377.3	439.0	1965	400.0	811.0
1937	346.2	391.9	1966	434.0	450.0
1938	202.0	289.4	1967	172.0	248.0
1939	322.6	382.0	1968	70.0	89.0
1940	339.7	529.0	1969	175.0	194.0
1941	674.0	796.0	1970	325.0	229.0
1942	402.0	397.0	1971	253.0	237.9
1943	204.0	327.2	1972	574.0	443.6
1944	494.0	604.0	1973	171.0	217.8
1945	247.0	194.6	1974	417.0	391.7
1946	127.0	222.6	1975	149.0	362.8
1947	253.0	317.0	1976	189.0	299.3
1948	367.9	336.6	1977	333.0	405.2
1949	306.5	255.2	1978	403.0	472.1
1950	292.8	358.4	1979	166.0	295.6
1951	323.0	429.8	1980	292.0	440.1
1952	335.0	350.1			
1953	584.0	488.9			
1954	317.0	392.8			
1955	196.0	255.6			
1956	264.0	281.4			
1957	309.0	461.1			
1958	335.0	394.8			
1959	321.0	234.1			

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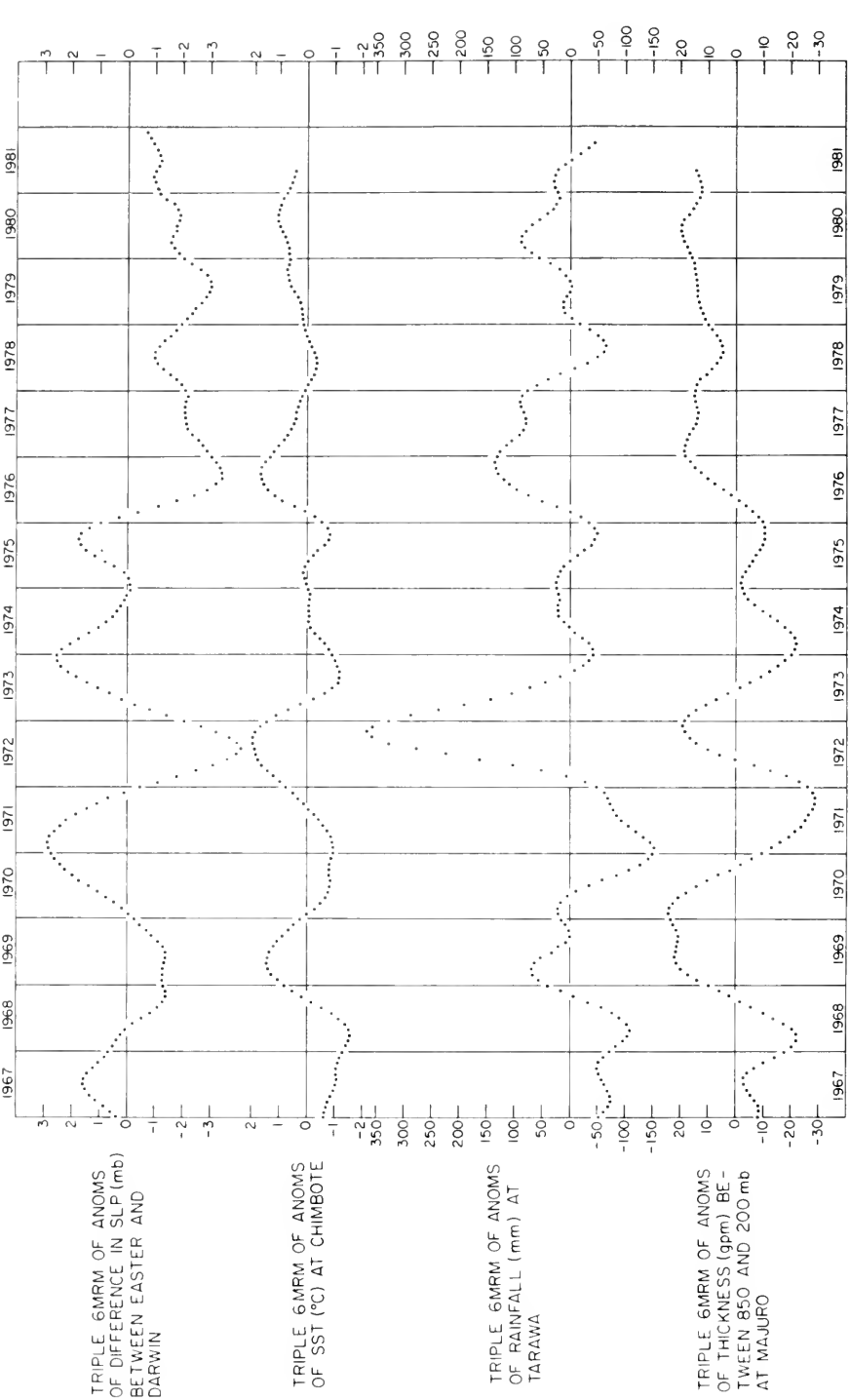

FIGURE 1.—Triple 6-mo running mean (6 MRM) plots of anomalies of the difference in sea level atmospheric pressure (millibars) between Easter Island (lat. 27°10'S, long. 109°26'W) and Darwin (lat. 12°26'S, long. 130°52'E), Australia; anomalies of sea surface temperature (°C) for Chimbote (lat. 09°10'S, long. 78°31'W), Peru; anomalies of rainfall (millimeters) for Tarawa (lat. 01°21'N, long. 172°55'E), Gilbert Islands; and anomalies of 200-850 millibar atmospheric thickness (geopotential meters) for Majuro Island (lat. 07°05'N, long. 171°23'E) for 1966-81.

a 5-yr research and training project that developed and passed on the technique for hydroacoustic surveying of fishery stocks.) Karl Johannesson, FAO team leader at the Centre during the project, mentioned that one would only have to go back to 1973 to find that about 95% of the total pelagic biomass off Peru was anchoveta, but by the end of the project it was about 30% or less. He noted that the whole ecological system had been changed after a brief recovery of the stock in early 1976. It was also noted in the Peruvian fishery that at the same time the decline in the anchoveta stock was being observed, other species, such as sardine and mackerel, began to grow (Ceres 1981). The Centre calibrated its equipment for these species, and after several surveys estimated stocks at between 5 and 8 million tons. Vondruska (1981) noted the sharp fall in Peru's production and exportation of fishmeal in 1977 and attributes it to the adverse effects of both heavy fishing and El Niño in 1976. Over the past 5-6 yr Ceres (1981) reported that the Peruvian anchoveta fishery has operated under a set of regulations covering length of season, size of individual fish taken, and maximum allowable catch.

The fisheries along the north Chilean coast, like those off Peru, are sensitive to environmental disturbances (Brandhorst et al. 1968; Cañon 1978; Quinn 1980b; Caviedes 1981). The Southern Oscillation-related El Niño type conditions affect both fisheries. Table 3 of Vondruska (1981), which extends through 1979, shows the combined Peru plus Chile fishmeal production to be particularly low in 1973, 1975, and 1977. In both fishery areas, species other than anchoveta (e.g., mackerel, sardines) have become more important over recent years. Off northern Chile there has been a decline in the anchoveta catches since 1970, but there was an extremely steep decline after 1976 (figure 4 of Caviedes 1981). Since recent environmental changes, as represented by the Southern Oscillation index trend (Fig. 1), may have played a significant part in the recent unusual west coast South American fishery changes, we wish to consider them in the light of past history and to determine the cause for the persistently low indices since 1976.

Background and definition of terms frequently used in this article follow. Southern Oscillation indices (differences in sea level atmospheric pressure between sites located in the South Pacific subtropical high pressure region and the Indonesian equatorial low region) are used to represent the Southern Oscillation (Quinn 1974; Quinn et al. 1978). In this respect it was proposed that they be used to monitor and predict Southern Oscillation-related, short-term climatic changes over the equatorial Pacific, the oceanic region off the northwest coast of South America, and the Indonesian region. Although we have used many different indices in our studies, we find the Easter-Darwin, Totegegie-Darwin, and Rapa-Darwin indices to be most effective for following and assessing developments. Details concerning processing of the index data are included in the following section.

Hushke (1959) defined El Niño as a warm ocean current setting south along the coast of Ecuador, so called because it generally develops after Christmas. In exceptional years, concurrent with a southerly shift in the tropical rain belt, he stated that the current may extend southward along the coast of Peru to lat. 12°S. When this occurs, he reported that plankton and fish are killed in the coastal waters and a phenomenon somewhat like the red tide of Florida results. Through common usage, most publishers and scientists now refer to El Niño as the exceptional year event of Hushke. Also, on learning more about El Niño and the fishery it affects, the definition has been altered accordingly, since it not only involves the thin southward flowing equatorial surface water layer but an influx of waters from the west and northwest beneath this surface layer. The invading thin surface layer has a significantly lower salinity than the subtropical surface water further to the west of the Peru coast, and it is nutrient depleted unlike the cool, highly productive Peru current and its coastal upwelled waters that usually prevail along the Peruvian coast. These infrequent invasions ordinarily set in during the Southern Hemisphere summer season, when sea temperatures are at a seasonal high, but they may set in well into the fall; and the effects may persist for a year or more. Additional symptoms of the stronger El Niño, some or all of which may be noted, are torrential downpours, flood, and erosion in the normally arid coastal lowlands of northern Peru; red tide; invasion by tropical nekton; and mass mortality of various marine organisms, including guano birds, sometimes with subsequent decomposition and release of hydrogen sulphide (Wooster 1960). It occurs at irregular intervals—may appear 2 yr in succession and then not reappear for another 3-12 yr [refers to the moderate and strong categories of Quinn et al. (1978) which seriously affect the fishery]. El Niño is the regional manifestation of a large-scale ocean-atmosphere fluctuation (Southern Oscillation), and it is brought about by relaxation from a prolonged period of strong southeast trades (represented by rising and high Southern Oscillation indices) (Quinn 1974; Wyrtki 1975). The magnitude of the southeast trade relaxation (as indicated by fall-

ing and low Southern Oscillation indices) and its timing in relation to the regular regional seasonal relaxation determine the strength of the resulting El Niño (Quinn 1979). During the period of prolonged strong southeast trades and equatorial easterlies, the south equatorial current is intensified, coinciding with an east-to-west buildup in sea level and an accumulation of warm water in the western Pacific; and, as soon as the wind stress relaxes, the accumulated water flows eastward, probably in the form of an internal equatorial Kelvin wave (Wyrtki 1975). This wave leads to the accumulation of warm equatorial undercurrent water off Ecuador and Peru and to a depression of the usually shallow thermocline there. In addition to the generation of internal Kelvin waves and Rossby waves, as discussed by Hurlburt et al. (1976) and McCreary (1976), it is assumed that the eastward-flowing currents (i.e., the North Equatorial Countercurrent, South Equatorial Countercurrent, and Equatorial Undercurrent) are intensified, and the westward-flowing South Equatorial Current is weakened when the relaxation occurs (Wyrtki et al. 1976). Hydrographic data off the coasts of Ecuador and Peru confirm the thermal structure depression and poleward spreading during El Niño (Enfield 1981); although upwelling may continue, it is from the accumulated warm water above the base of the thermocline, and this too causes coastal surface waters to be much warmer and less productive than water from the usual source, the Peru Current.

At times we use the broader connotation "El Niño type" when describing events, in order to avoid arguments as to what is and what is not an El Niño; in this way, we can account for events that evolve in a similar manner (associated with falling and low Southern Oscillation indices), but which vary in timing, intensity, and extent (Quinn et al. 1978). We will also at times refer to the contrasting anti-El Niño phase where a strengthening and strong southeast trade and equatorial easterly system prevails (associated with rising and high Southern Oscillation indices) (Quinn et al. 1978). It appears that most of the large short-term climatic changes, and their characteristic current and weather patterns over the lower latitudes of the Pacific, are associated with either El Niño or anti-El Niño phases of the Southern Oscillation.

METHODS

Data Processing

Rainfall data for Santiago and Valparaiso prior to 1931 were obtained from Taulis (1934). Rainfall data for Valparaiso 1931-80 were obtained from the Servicio Meteorologico, Armada de Chile. Rainfall data for Santiago 1931-80, La Serena 1869-1980, and Tarawa 1966-81 were obtained for applicable years from the World Weather Records (Clayton 1927, 1934; Clayton and Clayton 1947; U.S. Department of Commerce 1959, 1968) and the Monthly Climatic Data for the World (U.S. Department of Commerce 1961-81). The sea level atmospheric pressure data and upper level pressure versus geopotential height data (used to obtain atmospheric thickness data between the 850 and 200 mbar levels in Figure 1) were obtained for applicable years from previously listed U.S. Government sources. Sea surface temperature (SST) data for Chimbote were obtained from the Instituto del Mar del Peru. SST analyses for the southeast Pacific were obtained from Fishing Information (National Marine Fisheries Service 1976-80) and a continuation of those analyses for 1981-82 by Forrest Miller of the Inter-American Tropical Tuna Commission at the Southwest Fishery Center, National Marine Fisheries Service, NOAA, in La Jolla, Calif.

The use of the triple 6-mo running mean filter on monthly anomalies of various atmospheric and oceanic variables (i.e., Fig. 1) has been discussed in Quinn et al. (1978). An 11-yr running mean filter was used on the longest annual rainfall records available for Santiago and Valparaiso (Fig. 2). Our selection of the 11-yr running mean for smoothing the data was based in part on the desire for a decadal filter and in part on the sunspot cycle having an average length of 11.1 yr. Although 11-yr cycles have been suggested for various tropospheric phenomena, none of these has been substantiated (Hushke 1959).

Classifications of Activity

The classification of El Niño events by intensity was accepted from Quinn et al. (1978). Since we had a Southern Oscillation index and more reliable information concerning El Niño intensities available after 1860, our study concerning El Niño intensities, event frequencies, and the corroborative subtropical Chilean rainfall data was limited to the period from 1861 on (see Tables 2-6).

In Tables 3, 4, and 5 the rainfall classifications of <200 mm for Santiago and <300 mm for Valparaiso were selected to represent unusually dry years; and the classifications of ≥ 500 mm for Santiago and ≥ 600 mm for Valparaiso were selected to represent unusually wet years.

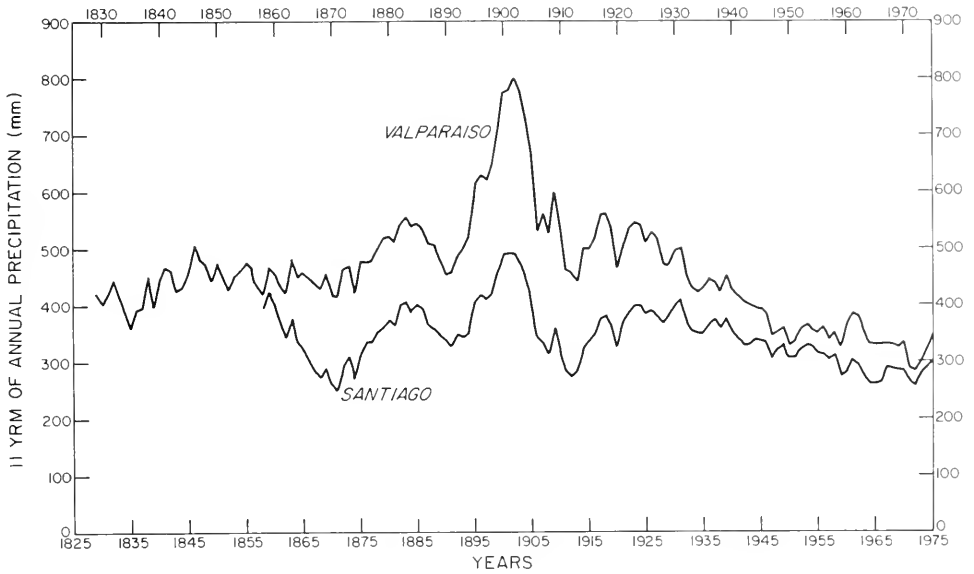

FIGURE 2.—Eleven-year running mean (11-YRM) plots of annual precipitation amounts (millimeters) for Santiago (lat. 33°26'S, long. 70°50'W) and Valparaiso (lat. 33°01'S, long. 71°39'W), Chile, for 1853-1980 and 1824-1980, respectively.

LONG-TERM VARIATIONS

Southern Oscillation-Related Activity

Large demands on the Peruvian anchoveta fishery over the past couple of decades to support fishmeal production have caused increasing concern over El Niño occurrences, since they adversely affect this fishery. As a result, many articles on El Niño, both scientific and popular, have appeared in periodicals and other news media over recent years. So much emphasis has been placed on recent El Niño-type events, regardless of intensity, that those without the historical background on this subject might think this type of activity has increased in frequency and intensity over recent years. Our findings indicate this is definitely not the case.

It was Berlage's (1957) opinion that the Southern Oscillation (the large-scale atmospheric circulation fluctuation with which El Niño is associated) was less regular and less intensively developed after 1925 than it was before. Accepting Berlage's breakpoint after the 1925 El Niño and using tables 3 and 5 in Quinn et al. (1978) to obtain times between onsets of moderate/strong events and between onsets of all events (very weak, weak, moderate, and strong), respectively, we derived the data in Table 2. The average time between event onsets, regardless of intensity, was the same for 1925-76 as it was for 1864-1925. However, the average time between onsets of the significant (moderate/strong) El Niños was much less for 1864-1925 (4.1 yr) than it was for 1925-76 (6.4 yr). Therefore, it appears that the average frequency of occurrence of the irregular atmospheric circulation fluctuations, known as the Southern Oscillation, has not changed significantly over the past 120 yr; but the number of those fluctuations resulting in moderate/strong El Niños has decreased considerably over the past half century.

In our investigation of this intensity shift, we followed up on findings in Quinn et al. (1981) which showed the Chilean subtropical rainfall fluctuations (for Santiago and Valparaiso) to be closely related to the El Niño/anti-El Niño conditions for 1875-1930.

TABLE 2.—Statistical information pertaining to the frequency of occurrence of the highly significant moderate/strong El Niño (Case I) and all events regardless of intensity (Case II) (from Quinn et al. 1978).

Period considered	No. of events[1]	No. of periods between events	Average time (yr) between events
Case I	strong/moderate		
1864-1925	16	15	4.1
1925-1976	9	8	6.4
Case II	all intensities		
1864-1925	20	19	3.2
1925-1976	17	16	3.2

[1]Here we refer to separate events, the onset times for separate events, and the interval between onset times (e.g., the 1925-26 El Niño was a single event with onset in 1925, the 1957-58 El Niño was also a single event with onset time in 1957).

The large rainfall amounts occurred in those years when moderate/strong El Niños were setting in or occurring. The frequency of occurrence of years with abnormally heavy rainfall at Santiago and Valparaiso appeared to decrease significantly after 1930 (based on contents of table IIIB of Taulis 1934 and Table 1 here). At Santiago about 23% of the years 1861-1930 had rainfall amounts ≥500 mm, whereas only 8% of the years 1931-80 had rainfall amounts in this category; and at Valparaiso 30% of the years 1861-1930 had rainfall amounts ≥600 mm, but only 6% of the years 1931-80 had rainfall amounts in this category (Table 3). Tables 4 and 5 show the rainfall category breakdown by decade for Santiago and Valparaiso, and substantiate the decrease in wet years over the past 5 decades when significant (moderate/strong) El Niños were less frequent.

The smoothed rainfall plots for Santiago and Valparaiso (Fig. 2) show prominent rainfall peaks near and shortly after the turn of the century. Over the 7-yr period 1899-1905 the average annual rainfall was extremely high at La Serena, Santiago, and Valparaiso (Table 6). During this period there were three moderate/strong El Niños (Quinn et al. 1978) which resulted in very large rainfall amounts in 5 of the 7 yr (table 5 of Quinn et al. 1981).

The prominent El Niño/anti-El Niño-related rainfall departures are primarily confined to the Chilean subtropics. Data from stations near lat. 40°S, at

TABLE 3.—Percentage of years with annual rainfall (in millimeters) in designated categories over indicated periods for Santiago (lat. 33°26'S, long. 70°50'W) and Valparaiso (lat. 33°01'S, long. 71°39'W), Chile.

Stations	Percentage of years in indicated categories							
	1861-1930		1931-1980		1861-1944		1945-1980	
Santiago	<200 mm	−500 mm	<200 mm	−500 mm	<200 mm	−500 mm	<200 mm	−500 mm
	17.1%	22.9%	22.0%	8.0%	14.3%	21.4%	30.6%	5.6%
Valparaiso	<300 mm	−600 mm	<300 mm	−600 mm	<300 mm	−600 mm	<300 mm	−600 mm
	12.9%	30.0%	38.0%	6.0%	13.1%	27.4%	47.2%	2.8%

TABLE 4.—Number of years per decade that annual rainfall was within indicated categories, the average rainfall by decade, and similar data for the 7-yr peak rainfall period (1899-1905) at Santiago (lat. 33°26'S, long. 70°50'W), Chile.

Decade	Rainfall categories in mm			Decadal annual average
	<200	200-499	≥500	
1861-1870	3	5	2	304.4
1871-1880	3	5	2	352.2
1881-1890	1	7	2	371.3
1891-1900	1	6	3	422.1
1901-1910	2	5	3	360.6
1911-1920	1	7	2	341.2
1921-1930	1	7	2	393.6
1931-1940	0	9	1	334.8
1941-1950	1	8	1	336.8
1951-1960	2	7	1	317.7
1961-1970	4	6	0	265.6
1971-1980	4	5	1	294.7
Peak period				Peak period annual average
1899-1905	1	1	5	568.5

TABLE 5.—Number of years per decade that annual rainfall was within indicated categories, the average rainfall by decade, and similar data for the 7-yr peak rainfall period (1899-1905) at Valparaiso (lat. 33°01'S, long. 71°39'W), Chile.

Decade	Rainfall categories in mm			Decadal annual average
	<300	300-599	≥600	
1861-1870	2	6	2	451.7
1871-1880	0	5	2	484.2
1881-1890	1	6	3	504.6
1891-1900	1	5	4	639.1
1901-1910	1	5	4	597.7
1911-1920	3	5	2	498.7
1921-1930	1	5	4	534.2
1931-1940	2	8	0	410.5
1941-1950	3	5	2	380.9
1951-1960	4	6	0	349.7
1961-1970	6	3	1	340.5
1971-1980	4	6	0	356.6
Peak period				Peak period annual average
1899-1905	0	2	5	906.9

TABLE 6.—Average annual rainfall and departure from overall average (DA) (in millimeters) for indicated periods at three subtropical Chilean stations: La Serena (lat. 29°54'S, long. 71°15'W), Santiago (lat. 33°26'S, long 70°50'W), and Valparaiso (lat. 33°01'S, long 71°39'W).

Period	La Serena[1]		Santiago		Valparaiso		Notes
	Avg.	DA	Avg.	DA	Avg.	DA	
1861-1930	137.0	+20.2	359.8	+20.8	530.0	+67.6	
1931-1980	91.8	−25.0	309.9	−29.1	367.6	−94.8	
1861-1944	133.9	+17.1	360.8	+21.8	515.8	+53.4	
1945-1980	80.8	−36.0	288.2	−50.8	337.6	−124.8	
1899-1905	224.9	+108.1	568.5	+229.5	906.9	+444.5	Peak period average
1861-1980	116.8		339.0		462.4		Overall average

[1]For La Serena the precipitation record is limited to 1869-1980.

times, register these Southern Oscillation-related changes, but to a lesser degree.

Additional Considerations

Although a decrease in frequency of occurrence of moderate/strong El Niños might be expected to have some affect on average annual rainfall, the rainfall records for recent decades show a sizeable decrease in amounts for El Niño, anti-El Niño, and intermediate years as well for subtropical Chile. Rainfall data (table 5 in Quinn et al. 1981 and Table 1 here) show that a significant decrease in average annual rainfall at Santiago and Valparaiso occurs after 1944. Table 6 shows large negative departures from the long-term averages at La Serena, Santiago, and Valparaiso for 1945-80. This climatic change, which is also primarily noted over subtropical Chile, indicates another source for change. It appears that the desert conditions that have prevailed over northern Chile have been spreading further southward into subtropical Chile for several decades. Discussions with Chilean scientists confirm that this is occurring.

This decrease in rainfall over the arid region between the west coast and the westernmost ranges of the high Andes also appears to be affecting western Peru. Santiago E. Antuñez[2] stated that his 70-yr regression analysis of river runoff in western Peru showed that a very serious decrease in runoff was occurring. The extremely arid zone between the west coast of South America and the westernmost ranges of the high Andes and extending from about lat. 30°S almost to the Equator (as described in Lettau and Lettau 1978) appears to be becoming increasingly arid and slowly extending southward.

Obviously the heavy rainfall that occasionally occurs over the usually arid coastal lowlands of Peru during significant El Niños cannot be directly related to the heavy rainfall occurrences over subtropical Chile, although a superficial overview of statistics from year-to-year rainfall records might so indicate. Rainfall sources for these two areas, and times of year the rainfall occurs in each, differ. The association between these occurrences is indirect; the weakening of the southeast Pacific subtropical high (as represented by low Southern Oscillation indices) with a resulting slackening in the southeast trades facilitates both developments.

Abnormal southward advances of the intertropical convergence zone over the invading warm El Niño surface waters along the coasts of southern Ecuador and northern Peru cause the heavy rainfall over the usually dry coastal lowlands. This El Niño-related rainfall occurs during the Southern Hemisphere summer and/or fall, a time when the regular annual weakening of the trades augments this irregular interannual slackening (Caviedes 1975).

Years of abnormally heavy rainfall in subtropical Chile result when storms of the westerly belt penetrate further to the north than usual into subtropical Chile during the Southern Hemisphere winter (sometimes including late fall and/or early spring) months, as a result of degeneration of the southeast Pacific high and/or displacement of the weakened high center. This is similar to what happens north of the Equator when the northeast Pacific subtropical high breaks down, and we get unusually heavy rainfall down into the southwestern United States and northwestern Mexico during the Northern Hemisphere winter.

RECENT CHANGES IN THE PERUVIAN AND NORTHERN CHILEAN ANCHOVETA FISHERIES

Up through a little beyond the first half of this century, the principal drain on the Peruvian anchoveta fishery at shallow depths was the heavy consumption by guano birds, on which Peru's guano industry depends. Demands of the fishermen over these earlier years were quite modest, and their catches extended to depths to which the birds could not reach. During significant El Niños the anchoveta were no longer abundant at shallow depths, and large numbers of guano birds died of starvation along the Peruvian coast while others left the affected area. Yet, limited demands of fishermen at that time and the great reduction and slow recovery in bird populations following El Niños permitted a suitable recovery of the fishery during the subsequent anti-El Niño periods. However, by the late 1950's the growing fishmeal industry was placing increasingly large demands on the anchoveta fishery to meet fishmeal production quotas. The anchovy fishery made Peru the leading fish-producing nation from the late 1960's through 1971 (Idyll 1973). The record catches of 1970-71 followed by the strong 1972-73 El Niño led to a precipitous drop in fishmeal production through 1973 (Fig. 3), from which there has never been a significant recovery. In 1972 and 1976, fishing continued through the principal fishing season (March-May) without taking into account the El Niños already underway. In retrospect, for these

[2]Santiago E. Antuñez, Universidad Mayor de San Marcos at Lima, Peru, pers. commun. 14 August 1978.

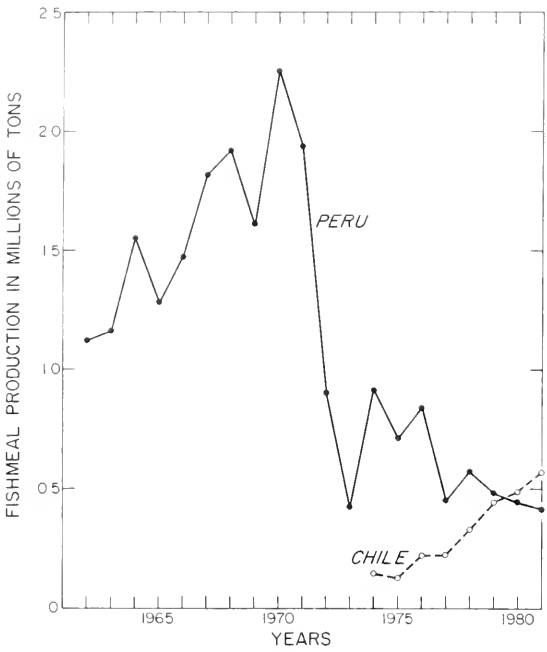

FIGURE 3.—The Peruvian fishmeal production for 1962-81 and Chilean fishmeal production for 1974-81 in millions of metric tons as obtained from National Marine Fisheries Service (1977, 1979, 1981, 1982).

cases it might have been advantageous to conserve reproductive stocks (ban fishing) in order to minimize subsequent recruitment failures. It appears that the operating regulations since the 1976 El Niño, as reported in the introductory section, were initiated much too late to benefit the anchoveta.

Available information on the fishery off northern Chile, along with the El Niño-related effects on it, is quite limited; nevertheless, contents of the introductory section and the previous section indicate it should be included in this discussion. Over the past 2 decades the fisheries off the coast of northern Chile, although not as productive formerly as those off Peru, have been likewise exploited most of this time without regard for conservation of the fish population. However, we must realize that whereas anchoveta, as a percentage of the catch, was still at the 95% level in 1973 in the Peruvian fishery (Ceres 1981), it declined from a level of 70-80% of the catch off northern Chile before 1970 to a little over 30% by 1973; and after the 1976 El Niño the percentage dropped precipitously to <10% of the northern Chilean catch for 1977, with sardines, jurel, and other fish making up the rest of the catch (figure 4 of Caviedes 1981). This would indicate that the decline in anchoveta, as a percentage of catch, showed up several years earlier off the coast of northern Chile than it did off the coast of Peru. Also, the substantial increase in other fish (e.g., jurel, sardines) was noted earlier off northern Chile than was the increase in sardines and mackerel off Peru (Ceres 1981; Caviedes 1981). It is interesting that Caviedes (1981) reported the largest jurel catches off northern Chile during the El Niño-related years of 1973, 1975, and 1977, the same years that Vondruska (1981) in his table 3 showed the combined Peru plus Chile production of fishmeal to be at its lowest levels.

Since 1976 the SST's over the tropical and subtropical southeast Pacific, as evidenced in the Fishing Information (National Marine Fisheries Service 1976-80) and Forrest Miller's continuation analyses, have remained near or above normal; and sea level pressures in the South Pacific subtropical ridge, as represented by pressures at Easter, Totegegie, and Rapa Islands, have averaged below normal over this same period. An indication that this was taking place was shown earlier in figure 7 of Quinn (1980b). Instead of having a compensating prolonged rise in the Easter-Darwin index to high positive anomalies following the deep index anomaly trough of the 1976-77 event, as one would ordinarily expect after an El Niño, the index has remained unusually low. It has averaged about 2 mbar below normal over the past 75 mo (April 1976-June 1982), and 78% of this abnormally low value was caused by the contribution of the Easter Island pressure component. In the past, it was usually during the high index anti-El Niño periods that the Peruvian anchoveta fishery recuperated. During this extended low index period the Peruvian fishmeal production has continued its pattern of decline (Fig. 3) to the extent that Peru has fallen from its position of leading fishmeal producer in the Fishmeal Exporters Organization to a number two position behind Chile for 1980 and 1981. Although Peruvian fishermen modified their efforts so as to also catch the types of fish which have recently become more numerous (e.g., mackerel and sardines), this modification was necessitated by the change in composition of the pelagic biomass (which showed a drastic reduction in the anchoveta). As mentioned before, a similar change in biomass with a drastic reduction in anchoveta also occurred in the fisheries off northern Chile, although this change off northern Chile started setting in earlier. How much of the change in fishery composition has been the result of fishing practices (e.g., overfishing) and how much can be attributed to environmental change or other ecological factors is questionable; however, it is our opinion that the recent unusual climatic trend, as represented by the abnormally low Southern Oscilla-

tion index and the greatly reduced amplitude in index fluctuations (Fig. 1), has played a significant part in bringing about this change.

DISCUSSION

Thermal and Pressure Changes and Their Effects

We were interested in determining the cause for the persistent abnormally low sea level pressures in the southeast Pacific subtropical anticyclone over the past 6 yr. Petterssen (1940) explained that in the central parts of anticyclones, or belts of high pressure, the air is stagnant or slowly moving, and it therefore has sufficient time to adjust its temperature and moisture content to the underlying surface. The circulation around anticyclones is divergent, and properties absorbed in the central parts are, therefore, spread over large areas, while turbulence and convective currents gradually distribute the absorbed properties to higher levels (Petterssen 1940). Our limited studies at other marine locations illustrate this adjustment of properties in the overlying atmosphere to changes in the underlying ocean surface (Quinn 1977, 1980a, b; Quinn et al. 1981). Rises in SST relate to rises in surface air temperature, falls in sea level pressure, and increased thicknesses between pressure levels aloft. Falls in SST relate to falls in surface air temperature, rises in sea level pressure, and decreased thicknesses between pressure levels aloft. Talara data in figure 13 and table 4 of Quinn (1980a) show close correlations between SST, surface air temperature, and sea level pressure; however, on the average there is about a 1 mo lead on the part of SST changes over the associated changes in air temperature and sea level pressure. (Changes in sea level on the average lead changes in SST by 1 mo at Talara.) Figures 6 and 7 of Quinn et al. (1981) show close associations between SST and thickness changes between pressure levels aloft, and Table 2 of this article indicates thickness changes between pressure levels near the surface precede related changes in thickness between pressure levels at higher altitudes.

In our opinion, it is primarily the relatively persistent in-sync relationship over the past 6 yr, between the generally above normal SST's and the generally below normal sea level pressures over the subtropical southeast Pacific, which has caused the below normal Southern Oscillation index and the reduced amplitude of fluctuations in this index. As a representation of the Southern Oscillation, the index trend would indicate a significant reduction in amplitude of the Southern Oscillation over this period. How much longer this low index condition will prevail and what will cause a return to the large fluctuations of the past are not apparent at this time. However, a slow occasionally interrupted rise in the index has been noted over the past several years.

The below normal pressures in the subtropical high signify a generalized weakening of the associated southeast trades and equatorial easterlies, and the reduced amplitude of the index fluctuations signifies a reduction in the El Niño/anti-El Niño extremes in Southern Oscillation-related activity.

It appears to us that the generally weaker southeast trades and their reduced fluctuations in strength, which have prevailed over the past 6 yr, would not be capable of building up to the type of relaxation response called for by Quinn (1974), Wyrtki (1975), and Wyrtki et al. (1976), where Wyrtki's so-called "back sloshing" of the built-up water accumulation in the western Pacific produces a significant El Niño. Under existing conditions we would expect weaker responses to the smaller buildups, such as the 1979-80 event reported by Donguy et al. (1982). This event would be considered a relaxation response to the small 1978 anti-El Niño buildup. (Note the 1978 index peak in Figure 1.)

Changes in strength of the southeast trades and equatorial easterlies bring about changes in the Peru (offshore and coastal) current and equatorial current systems, and the Peru-Chile undercurrent, as discussed in the introductory section; and they, in turn, cause environmental changes in the Peruvian and north Chilean coastal fisheries. In addition to the generally above normal subtropical surface water temperatures, we also note that the Chimbote SST anomalies remain generally high during this period of low index anomalies (Fig. 1). One cannot fail to note the sharp drop in the anchoveta contribution to the overall catch after the 1976 El Niño in both the Peruvian and north Chilean fisheries; also, in both of these fishery areas the catch of other types of fish increased over this same period (Ceres 1981; Caviedes 1981).

Monitoring and Predicting the Changes

Considering the monitoring and prediction of El Niño, it must be realized that when the use of the Easter-Darwin index was initially proposed (Quinn 1974), it was intended for use on large interannual fluctuations leading to the onset of relatively strong events (e.g., 1957, 1972). This was particularly true for purposes of prediction, since the time involved in

relaxation from a pre-event index peak to a projected index trough determines to a large extent how far in advance of event occurrence the outlook can be given (Quinn 1978). Nevertheless, we did find the indices useful in predicting the very minor 1975 event and moderate 1976 event. And, when we look at Figure 1, we can see that even the very small changes in index anomaly trends are reflected in the trends of other variables over various parts of the tropical Pacific. Additional Southern Oscillation-related changes in other variables over the tropical and subtropical region are shown in more detail in Quinn (1980a, b) and Quinn et al. (1978, 1981). Since Berlage (1957, 1966) and Troup (1965) indicated that the Southern Oscillation was not only involved with the South Pacific subtropical high, but also to some extent with the North Pacific subtropical high region, we monitor a Ship N-Darwin index (Quinn 1979). (With the demise of Ship N, we started using data obtained for its former coordinates: lat. 30°N, long. 140°W.) The northeast trades can contribute significantly to the equatorial easterly flow.

When one considers the nature of the short-term climatic changes and the time leads/lags in the involved variable changes, as shown in the articles referenced in the previous paragraph, one realizes that the significant changes in the atmospheric centers of action (the semipermanent highs and lows that appear on mean charts of sea level pressure; e.g., the South Pacific subtropical high, the Indonesian equatorial low, the North Pacific subtropical high) take place more nearly on the time scale of the oceanic circulation and thermal pattern changes. Therefore, the centers of action are more likely to respond measurably to significant oceanic changes and vice versa; it is through monitoring and projecting these involved large-scale, long-term changes that we are most likely to have a suitable basis for our short-term climatic outlooks. Results will be reflected in the influence these slower changing, large-scale features exert on the developments and trajectories of the rapidly moving transient storms that affect our day-to-day weather and sea conditions.

Significant changes in fishery populations also take place on the time scales of the large changes in atmospheric centers of action, oceanic circulation, and oceanic thermal anomaly patterns. In our opinion, through the monitoring and projection of appropriate pressure and circulation indices and other related variables such as sea level, SST, etc., a suitable basis for outlooks on fishery environmental changes and fishery catches could be provided. For the north Chilean fishery, in addition to the Southern Oscillation indices, we would also recommend use of the Easter-Quintero and Easter-Antofagasta 850 mbar height difference indices of Quinn (1980b). They can be used to represent interannual changes in strength of the low level flow (south to north components) over that part of the southeast Pacific with which we would be concerned. In the case of fisheries we will not only be concerned with interannual changes, but also the longer term changes such as those noted in the previous section.

CONCLUDING REMARKS

After seeing what has been happening to the Peruvian and north Chilean fisheries over the past decade or more, and how they are similarly affected by large-scale ocean/atmosphere changes, the need for a well-coordinated study of this west coast South American fishery region as a whole becomes apparent. In the past, investigations have been limited by the areas covered and the objectives of scientists involved. Most of the studies have been concentrated on the Peruvian coastal region. Investigations should cover an area extending in length from near the Equator to lat. 30°-35°S, and in width from the coast out to about 600 km seaward. Participants should include fisheries biologists, marine ecologists, physical oceanographers, meteorologists, and chemical oceanographers.

We will be interested in monitoring the current climatic situation to see what brings about an emergence from the extended period of abnormally low Southern Oscillation indices and the greatly reduced amplitudes in fluctuations of these indices.

We will also be interested in further investigation of the very long-term climatic changes that have been occurring over western South America between the coast and the westernmost ranges of the Andes. This will include further study of the following noted changes in rainfall characteristics over subtropical Chile: 1) The decrease in frequency of abnormally heavy El Niño-related rainfall after 1930, and 2) the sizeable decrease in average annual rainfall after 1944.

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PERCENT SIMILARITY: THE PREDICTION OF BIAS

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ABSTRACT

An equation is developed which predicts the percent similarity index between replicate samples from an association with specified structure and heterogeneity. A second equation gives a first approximation of the variance between replicate indices. The magnitude of the expected index depends not only upon the heterogeneity of the species but also upon the number of species, their abundance, and their diversity. Because of these dependencies, care must be used in interpreting the percent similarity index.

Many community ecologists use the percent similarity index (PSI; here symbolized by I) to compare the species composition of different communities or community subsets (Whittaker and Fairbanks 1958; Miller 1970; Murdoch et al. 1972; Hicks and Tahvanainen 1974; Donaldson 1975; Haedrich et al. 1975; Silver 1975; Haedrich and Krefft 1978; Reid et al. 1978; Silver et al. 1978; Abramsky et al. 1979). This index, derived from the Bray-Curtis similarity coefficient (Boesch 1977) was proposed by Whittaker (1952) and may be expressed as

$$E(I) = \sum_{i=1}^{n} \min [E(p_{i,1})\, E(p_{i,2})]$$
$$= 1 - 0.5 \sum_{i=1}^{n} |E(p_{i,1}) - E(p_{i,2})|,$$

where I is the similarity index between two communities (1 and 2), n is the total number of species in the combined species list, and $p_{i,1}$ and $p_{i,2}$ are the proportions of species i in the two associations such that, within each association,

$$\sum_{i=1}^{n} p_{i,1} \text{ and } \sum_{i=1}^{n} p_{i,2} = 1.00.$$

A variant of this index is based upon the percent composition instead of proportions and equals $I \times 100\%$. From this variant comes the common designation "percent similarity index." The present study is developed in terms of proportions but the familiar name is retained. All conclusions in this paper are applicable to both forms of the index, although the formulae must be scaled accordingly.

The theoretical range of the percent similarity index is from 0.0 for two associations with no species in common to 1.0 for two identical associations. In actuality, a value of 1.0 is unlikely to be observed even between replicate samples of the same association[2] because species abundance fluctuations in the field, often augmented by sampling errors in the laboratory, reduce the index below 1.0. At present, the only means of estimating the magnitude of this bias is to count replicate samples within each of the two (or more) associations being compared, or to obtain the index between replicate samples by means of computer simulation. Both are time consuming. Recognition of this bias has led to the development of several different similarity indices in which certain types of bias are reduced (Morisita 1959; Lance and Williams 1966; Horn 1966; Grassle and Smith 1976; Wolda 1981). Nevertheless, the percent similarity index remains popular because of its simplicity.

The following paper develops the mathematical formulae relating the percent similarity index expected between replicate samples and its variance to the abundances of the component species and the variances and covariances of the abundance estimates. Equations are developed for the specific case of bias introduced by subsampling error in the laboratory where the magnitudes of the variances and covariances may be controlled. However, when estimates of these parameters are available for field populations, the general equations may be applicable to the estimation of I between replicate field samples. The equations not only offer a method of evaluating I, but provide insight into the influence of changes in community structure (i.e., the number of component species, and their abundances, variances, and diversity) on the bias of the similarity index.

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[2]The precise definition of "association" may vary considerably from study to study. It will generally have spatial dimensions and may have a temporal dimension as well.

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METHODS

The diversity index used in this paper is the standardized Shannon-Wiener index (Fager 1972):

$$H' = (H - H_{min})/(H_{max} - H_{min})$$

where $H = -\sum_{i=1}^{n} p_i \ln p_i$

$$H_{max} = \ln n$$

$$H_{min} = \ln T - \left[\frac{(T - n + 1)}{T}\right] [\ln(T - n + 1)]$$

p_i = proportion of species i
T = total number of individuals in the sample
n = total number of species in the sample.

Use of 1 − Simpson's diversity index (Fager 1972) gave similar results.

Development of the theoretical equations for I and its variance ($s^2(I)$) was accompanied by computerized simulation modeling to examine the accuracy of the equations; values predicted by the equations were compared with those observed in the simulation studies. Two measures of accuracy were used:

$$\text{relative error} = [|\text{predicted} - \text{observed}|/\text{predicted}] \times 100\%$$

$$\text{relative bias} = [(\text{predicted} - \text{observed})/\text{predicted}] \times 100\%.$$

Species distributions sampled in the simulation studies were independent and normal. The consequences of these two assumptions are evaluated in detail in a later section. In each simulation the relationship between the mean and variance ($\sigma_i^2/\mu_i = q$) was held constant for all species in an association. This was a convenience, not a necessary condition.

To determine empirically the values of I and $s^2(I)$ for an association, 100 pairs of replicate samples were drawn; the value of I was calculated for each pair and the mean and variance were determined over the 100 pairs. These values, I and $s^2(I)$, were compared with the values $\hat{I}$ and $\hat{s}^2(I)$ estimated from the statistics observed in each sample of an independent set of 100 single samples drawn from the same association. The comparison allowed determination and correction of the bias of the predictive formulae for mean and variance and the determination of the variance of the estimate. The number of species in the association, their abundances, variances, and diversity were varied independently to examine their influence on the value of I and $s^2(I)$ and on the accuracy of the values estimated by the formulae.

To examine any errors introduced by use of the normal distribution in the simulations, a second series of simulations was run to sample species distributed independently according to a negative binomial distribution (Bliss and Fisher 1953). The negative binomial distribution is generally characterized by the parameters μ and $k = \mu^2/(\sigma^2 - \mu)$. However, an alternative parameter $q = (\mu/k) + 1 = (\sigma^2/\mu)$ is identical to the parameter q used throughout this study to express population heterogeneity. Thus, I have chosen to define negative binomial distributions by q rather than k. In these simulations, the parameters used in the formulae for the expected similarity index and its variance were not estimated from single samples but were the given parameters of the distribution.

RESULTS

Percent Similarity Index

An equation for predicting the similarity index between replicate samples from one association is

$$\hat{I} = 1 - \frac{0.5642}{\tau^2} \sum_{i=1}^{n} \{[\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i,T) + \mu_i^2\sigma^2(T)]\}^{1/2},$$

where n is the total number of species, μ_i and $\sigma^2(x_i)$ are the mean and variance of the estimate of abundance of the ith species, τ and σ^2 (T) are the mean and variance of the estimate of abundance of the total number of individuals, and $\sigma^2(x_i,T)$ is the covariance between x_i and T (Appendix Equation (5)).[3] The goal of this study is to estimate, from a single sample of an association, the value of $\hat{I}$ expected between replicate samples. Thus, the parameters necessary for Appendix Equation (5) must be obtained from one sample or must be independently known. The observed abundances, x_i, and T are unbiased estimators of the true mean abundances. To simplify the estimation of the variance and covariance components in the present study, two assumptions have been made: 1) The component species are independently distributed, which may be strictly true only under controlled laboratory conditions, as when a subsample is drawn

[3] These statistics must be applicable to the association represented by $\hat{I}$. Thus, if the association has a temporal dimension, this must be represented by the means and variances.

from a sample; and 2) the variance of a single species may be obtained from a predetermined relationship between the mean and the variance: $\sigma^2(x_i) \approx q\mu_i \approx qx_i$. A relationship between mean and variance has been demonstrated for phytoplankton subsampled in the laboratory (Venrick et al. 1977; Venrick 1978), although the validity of this approximation in field populations remains to be investigated.

Using these simplifying relationships and correcting for biases, Appendix Equation (5) becomes

$$\hat{I} = 1 - 0.5765(q/T^3)^{1/2} \sum_{i=1}^{n} (Tx_i - x_i^2)^{1/2},$$

(Appendix Equation (7)).

It is evident from Appendix Equations (5) and (7) that the expected similarity index between replicate samples is a function of many of the parameters of the association: total number of species, their abundance and heterogeneity, and diversity. These relationships are interactive. The relationship between $\hat{I}$ and the number of species when T is held constant (Fig. 1) is nonlinear, with $\hat{I}$ approaching 1.0 as n approaches 1. Increasing the heterogeneity (q) or decreasing the total number of individuals (T) decreases the expected similarity and increases the dependence of $\hat{I}$ on n. When abundances of component species, rather than T, are held constant, the value of $\hat{I}$ is essentially independent of n, except at very low species numbers (Fig. 2). The relationship between $\hat{I}$ and diversity is approximately linear for values of $H' > 0.2$, the value of $\hat{I}$ decreasing as diversity increases (Fig. 3), but the slope of the relationship depends upon the other parameters. Although $\hat{I}$ is related to total abundance (T), scaling the abundance data by some factor (as when counts per sample are standardized to some different sample area or volume) does not alter the expected similarity index, since the values of T and q are automatically scaled by the same factor while $\sigma^2(x_i)$, $\sigma^2(T)$, and $\sigma^2(x_i,T)$ are scaled by the square of that factor and the factor cancels out in both Appendix Equations (5) and (7).

Variance of I

Appendix Equations (5) and (7) predict the value of $\hat{I}$ likely to be observed between replicate samples from a specified association. This is a mean value which has a variance associated with it. Unfortunately, it was not possible to calculate an exact expression for $\hat{\sigma}^2(I)$. However, in some situations the approximate equation may be useful:

$$\hat{\sigma}^2(I) = \frac{\beta q}{T^3} \sum_{i=1}^{n} (Tx_i - x_i^2)$$

where β is obtained from Figure 4 (Appendix Equation (9)).

Comparison of Appendix Equations (7) and (9) indicates that $\hat{\sigma}^2(I)$ is related to $(1 - \hat{I})$; lower similarity indices have larger associated variances. In general, the relationship between the variance of I

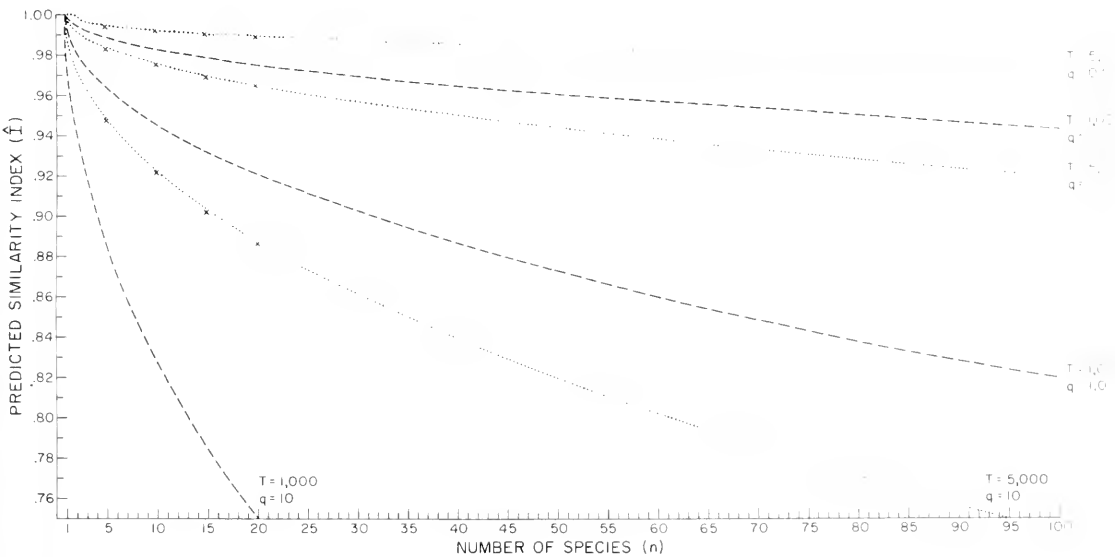

FIGURE 1.—Relationship between $\hat{I}$ and the number of species (n) for associations of different heterogeneity (q) and total number of individuals (T). In all cases, diversity (H') = 1.0. For each curve, abundance (x_i) is a constant. Curves are derived from Appendix Equation (7). X's indicate values of I observed in computer simulation and are included to indicate the accuracy of the equation.

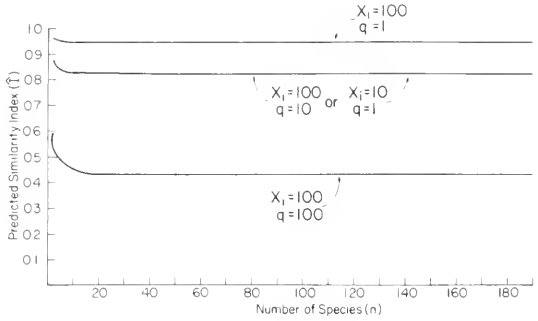

FIGURE 2.—Relationship between $\hat{I}$ and the number of species (n) for associations with different abundances (x_i) and heterogeneity (q). In all cases, diversity (H') = 1.0. For each curve, total number of individuals (T) is a constant. Curves are derived from Appendix Equation (7).

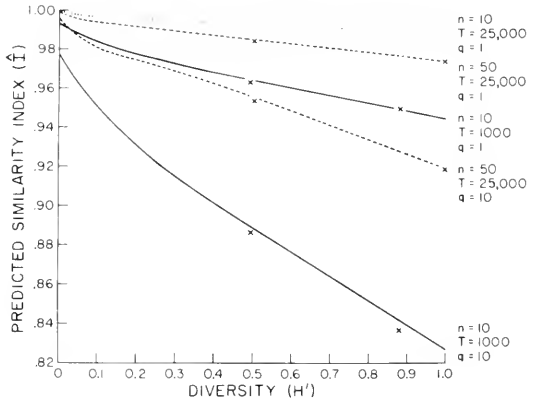

FIGURE 3.—Relationship between $\hat{I}$ and diversity (H') for associations with different numbers of species (n), total abundance (T), and heterogeneity (q). Curves are derived from Appendix Equation (7). X's indicate values of I observed in computer simulation and are included to indicate the accuracy of the equation.

and the underlying community structure is opposite in direction from that of $\hat{I}$. However, the behavior of $\hat{\sigma}^2(I)$ is mediated somewhat by the simultaneous dependence of the factor β on community structure (Figs. 4,5). Thus, although $\hat{I}$ shows a negative relationship with numbers of species, the relationship between $\hat{\sigma}^2(I)$ and n is also inverse, but much weaker (Kendall correlation, $0.05 < P < 0.10$). While $\hat{I}$ decreases continuously with increasing diversity, $\hat{\sigma}^2(I)$ increases with diversity, but stabilizes or decreases at high diversities. The dominant influence on the variance of I is the population heterogeneity, q. As evident from Appendix Equation (9), an order-of-magnitude increase in q produces an order-of-magnitude increase in $\hat{\sigma}^2(I)$.

CONSIDERATION OF ASSUMPTIONS

Two assumptions underlying this study are admittedly unrealistic and require further consideration:

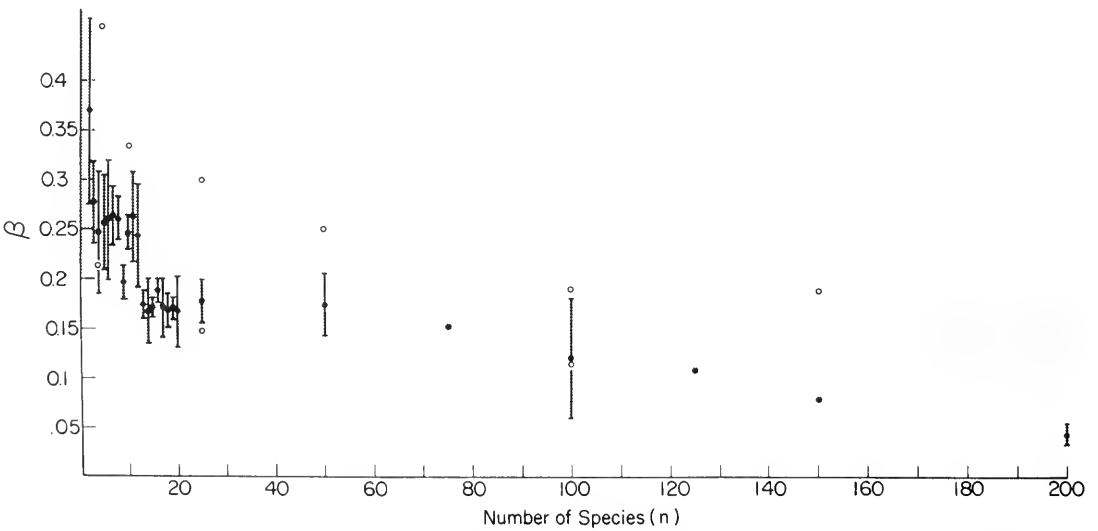

FIGURE 4.—Relationship between the value of β in Appendix Equation (9) and the number of species (n). Vertical bars are 95% confidence intervals from five estimates with diversity (H') = 1.0 and heterogeneity (q) = 0.1, 0.5, 1.0, 5.0, and 10. Dots are single estimates. Open circles are maximum values of β observed when H' varied from 0.0 to 1.0. Shaded area approximately delimits the range of observed values of β.

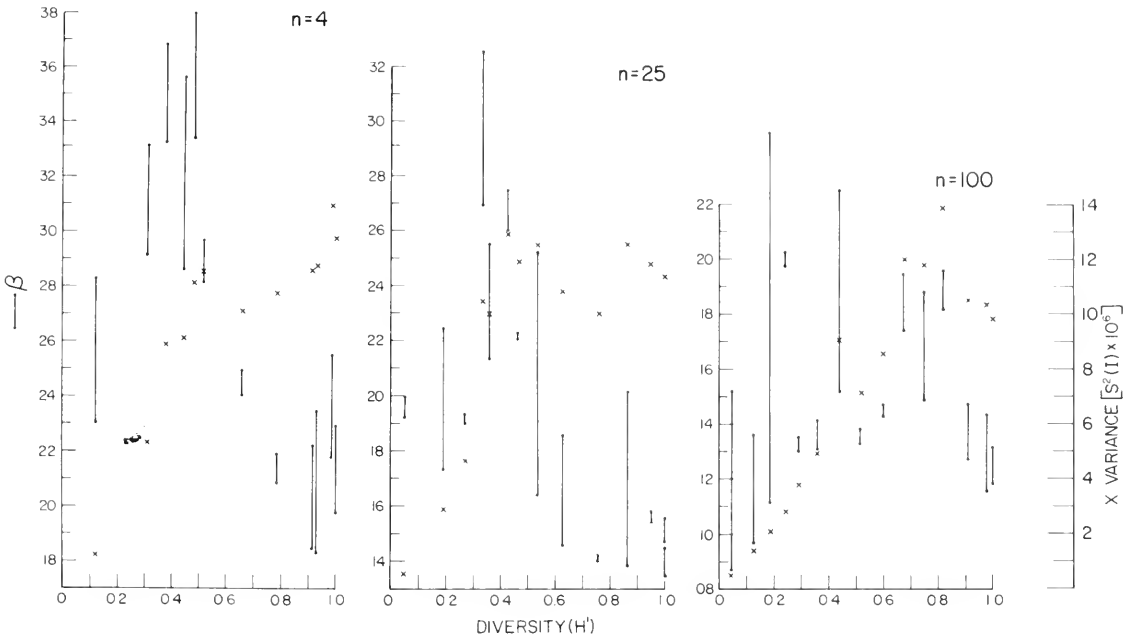

FIGURE 5.—Relationship between the value of β in Appendix Equation (9), the observed variance of I, and the diversity of the association (H'). X's represent the mean values of $s^2(I)$ observed in two or more sets of 100 replicate pairs of samples. Vertical bars represent the range of β values, each based upon single estimates of $\hat{\sigma}^2(I)$ from 100 samples, total abundance (T) = 12,500, heterogeneity (q) = 1.0.

1) The assumption of independence of species abundances may be justified in some situations, as when a sample is thoroughly mixed before subsamples are drawn, but it is probably unrealistic when applied to species in the field. However, this assumption is a convenience, not a necessity. If an independent measure of species covariance is available, the covariance between species i and the population total may be calculated and entered into Appendix Equation (5). Any positive covariance between component species increases the expected similarity index over that predicted by Appendix Equation (7) (decreasing bias). Perfect covariance between all species results in an index of 1.00. Thus, the effect of any positive covariance on the value of $\hat{I}$ is the greatest in those associations for which the expected bias is large, i.e., small samples from associations with many species, high diversity, and/or great heterogeneity.

The effect of negative covariance is less easily anticipated. For any two species, the value of $\sigma^2(x_i, T)$ is decreased, lowering the value of $\hat{I}$. However, for associations of more than two species, perfect negative covariance does not exist. Large negative correlations between some species are likely to be accompanied by positive correlations between others, so that the overall effect on $\hat{I}$ may be minimal.

2) The assumption of normality of species distributions is necessitated by the use of the theoretical expected relationship between a range and a variance; however, this relationship has not been determined for other distributions. To examine the consequences of the use of the normal distribution, a final series of simulations was run to sample species distributed independently according to the negative binomial distribution which has given satisfactory fit to numerous field distributions (Bliss and Fisher 1953 and references therein; Holmes and Widrig 1956). The 39 simulations investigated values of q between 1.1 and 10. (The negative binomial is not defined at $q = 1$.) Corresponding values of k ranged between 0.44 and 900 depending upon the means and variances of the species.

In 38 of the 39 simulations, the value of I observed between replicate samples from negative binomial distributions was higher than the value predicted by Appendix Equation (7). Major deviations occur in those associations in which all species are heterogeneous and rare. In these cases, the normal distribution predicts large numbers of negative abundances, which are impossible in reality. For instance, in an association of 100 species, all with a mean abundance $\mu_i = 4$ and $q = 10$ ($k = 0.444$), the relative error of Appendix Equation (7) is 240%; in an association of 50

species, all with $\mu_i = 8$ and $q = 10.0$ ($k = 0.889$), the error drops to 25%. For the same two associations, when the heterogeneity is reduced so that $q = 1.1$ ($k = 40$ and 80, respectively), the error is reduced to 1.0 and 0.6%, respectively. This effect of rare, patchy species is less important in associations of lower diversity, dominated by a few abundant species. When such extreme associations were eliminated from consideration, the average relative error and bias were 1.6 and −1.6%, respectively, for 32 simulations. Thus, with the exception of the extreme case of small samples from a diverse, patchy association, the accuracy of Appendix Equation (7) appears to be independent of the underlying species frequency distributions. More important, the similarity index derived from negative binomial distributions shows the same relationships with the underlying community structure as does the index derived from normal distributions, decreasing either with increasing diversity, increasing numbers of species, or increasing heterogeneity (Fig. 6).

The variance between values of I from replicate samples of negative binomial distributions is satisfactorily predicted by Appendix Equation (9). In 38 of the 39 simulations, the observed variance fell within the predicted range (Fig. 7). Thus, it appears that use of the normal distribution in the present study does not restrict the applicability of the results and that the general conclusions of the paper are independent of the frequency distribution being sampled.

APPLICATIONS

An earlier study of small-scale variability of oceanic diatoms (Venrick 1972) was based upon abundances in a series of 10 samples at each of three depths in each of two environments. The 10 samples from the 10 m depth in the subarctic Pacific were selected arbitrarily to examine the performance of Appendix Equations (7) and (9). The diatom flora consisted of nine species and was strongly dominated by one ($H' = 0.23$). Although the concordance between the four dominant species was marginally significant (Kendall concordance, $P \sim 0.10$), the species were assumed to be independently distributed. The necessary parameters for the formulae ($\bar{x}_i$, $\overline{T}$, and q) were calculated from the means of the 10 samples. Observed values of q were strongly correlated with mean abundance; a single, representative value was calculated from individual q values weighted by each species' mean proportion. (Individual q values could easily have been used.) Appendix Equation (7) predicts a similarity index between field samples of 0.9101. The actual observed values, calculated between five random independent pairs of samples,

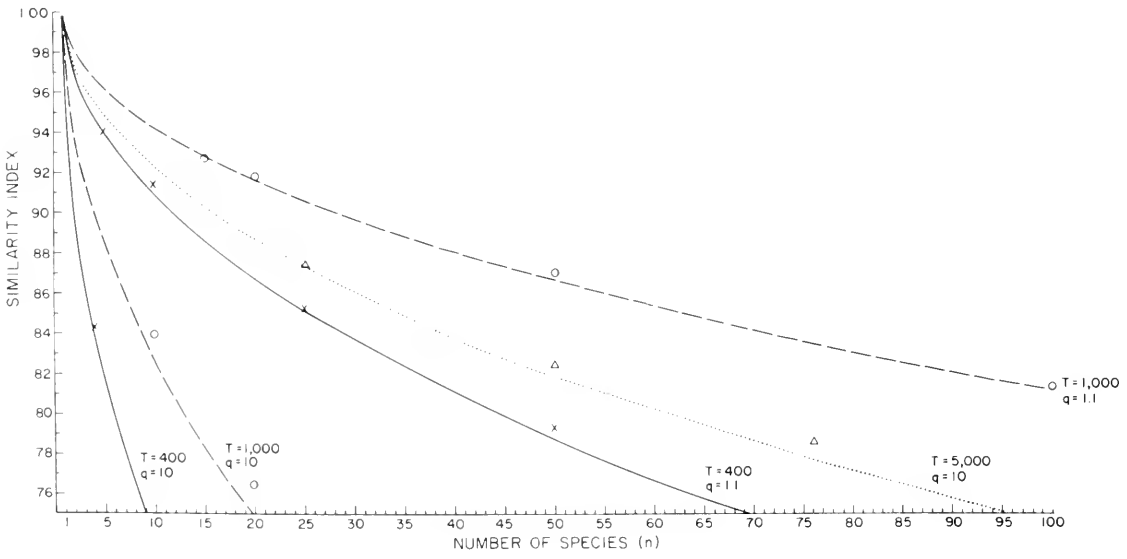

FIGURE 6.—Estimation of I from a negative binomial distribution. Curves are the value of $\hat{I}$ from appendix Equation (7) plotted against species number for five associations of different total abundance (T) and heterogeneity (q). For all associations diversity (H') = 1.0. Symbols indicate the value of I observed between replicate samples from corresponding associations of species distributed according to a negative binomial distribution. Each point is the mean of 100 replicate pairs.

range from 0.878 to 0.969 with a mean value of 0.9232. Appendix Equation (9) and Figure 4 predict a variance between replicate I values of between 1.00×10^{-3} and 2.54×10^{-3}. The observed variance is 1.48×10^{-3}.

This example is admittedly artificial; given replicate samples from the association of interest, the appropriate measure of the maximum expected similarity index is that observed between independent pairs of the replicate samples. Use of Appendix Equations (7) and (9) is unnecessary. Nevertheless, the example illustrates the accuracy of the equations when applied to field conditions, even when covariance between species is assumed to be negligible and the variances of species abundances are expressed as a simple function of the means.

McGowen and Walker (1979:211) present the percent similarity indices between samples of oceanic zooplankton. In order to estimate the bias of the index, they counted replicate aliquots of six samples and calculated the values of I between the replicates. They generously made their raw data available (five of the six samples), and the Appendix Equations (7) and (9) and Figure 4 were used to estimate the value of $\hat{I}$ expected from each single sample. A rough approximation of q between replicates was derived from a different set of 17 replicate counts of samples taken on the same cruise from the same location. Scanning the data suggested a relationship between q and the mean abundance, and the data were therefore arbitrarily divided into three categories according to abundance and separate values of q calculated for each category.

The results are presented in Table 1. The five values of I observed between the five replicate pairs of samples are compared with the 10 values and the probable ranges calculated from the equations, using the statistics observed in each sample. Only once does the observed value fall outside the estimated interval. This is good agreement (exact probability = 0.40). This is a situation in which, given some independent estimate of q, Appendix Equations (7) and (9) might have been used to estimate the magnitude of the bias in I introduced by laboratory procedures, thereby eliminating the necessity of counting replicate aliquots of single samples.

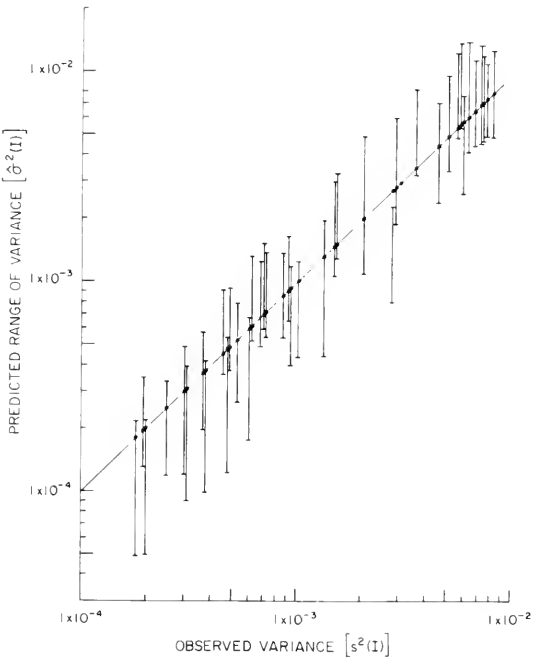

FIGURE 7.—Estimation of $\hat{\sigma}^2(I)$ from a negative binomial distribution. Vertical bars indicate the probable range of $\hat{\sigma}^2(I)$ derived from Appendix Equation (9) and Figure 4. Abscissa indicates the observed $s^2(I)$ between 100 values of I from replicate samples from associations of species distributed according to a negative binomial distribution. Values are from the simulations used for Figure 5. Diagonal line indicates values were $\hat{\sigma}^2(I) = s^2(I)$.

TABLE 1.—Similarity index (I) between counts from replicate aliquots of a single sample: observed (McGowan and Walker 1979) and expected ($\hat{I}$, Appendix Equation (7)). The probable range is based on the equation for the 95% confidence interval using a variance estimated from Appendix Equation (9) and Figure 4. Samples were collected in September 1968 near lat. 28 N, long. 155 W.

A. The Data Set

Sample no	Depth interval (m)	Sample characteristics			
		T	H	n	Maximum β
1a	100-225	671	0 757	58	0 24
1b		886	0 753	69	0 23
2a	225-350	847	0 686	54	0 25
2b		842	0 649	58	0 25
3a	0-25	576	0 779	35	0 28
3b		670	0 794	33	0 29
4a	25-50	844	0 643	52	0 25
4b		960	0 624	55	0 25
5a	50-75	835	0.740	59	0 24
5b		626	0 757	54	0 25

Values of q: $q = 5.6$ for $x_i \geq 100$
$q = 1.8$ for $100 > x_i \geq 10$
$q = 1.0$ for $10 > x_i$

B. Results

Sample no.	Observed I	Predicted $\hat{I}$	Predicted $\hat{\sigma}^2(I)$ ($\times 10^{-3}$)	Probable range of I
1a	0.8472	0.8427	0.5438	0 7970-0 8884
1b		0.8367	0.6363	0 7873-0.8861
2a	0.8680	0.8628	0 6588	0.8125-0 9131
2b		0.8643	0 6742	0 8134-0.9152
3a	0.9168	0 8490	1 0592	0.7852-0.9128
3b		0 8589	0 9609	0 7981-0.9197
4a	0.8676	0 8648	0.8059	0 8092-0 9204
4b		0 8698	0.7478	0.8162-0.9234
5a	0 8701	0.8412	0 8464	0 7842-0.8982
5b		0.8304	0 9556	0.7679-0.8929

Venrick (1982) discussed data on the vertical distribution of phytoplankton samples from four stations at one location in the central Pacific. For the present study, counts from samples of 15 and 120 m depths (representing shallow and deep phytoplankton associations, respectively) were used to generate values of I between the field samples. Appendix Equations (7) and (9) were used to estimate the magnitude of $\hat{I}$ arising from laboratory subsampling error. A predetermined relationship between laboratory sampling error and mean abundance (Venrick 1982) is available from which to estimate the value of q. The parameters of each sample were used to calculate the value of $\hat{I}$ expected between replicate counts of that sample and the maximum probable range (Table 2). For the 15 m samples, one-half of the indices observed between field samples fall within the range expected from the equations. At least for these samples, it appears that differences between samples in the field may be largely attributed to handling and counting errors. For the 120 m samples, none of the observed indices fall within the expected range. At this depth there appear to be "real" differences between field samples.

The indices observed at 120 m are lower than those at 15 m. The extent to which this is due to heterogeneity of species abundances, as opposed to shifts in number of species, diversity, or total abundance, may be assessed by calculating the standardized I value:

$$\hat{I}' = I/\hat{I}$$

where I is the observed value and $\hat{I}$ is the maximum expected value calculated from Appendix Equation (7). For each observed value of I, two values of $\hat{I}$ are available, one from each sample. When two samples are similar in species content, a representative value of $\hat{I}$ may be obtained by calculating a new value of $\hat{I}$ from pooled data. This is time consuming and, when samples are dissimilar, the resultant value of $\hat{I}$ may not represent either of the original samples. In general, it seems preferable to use the mean of the individual $\hat{I}$ values.

The comparison of standardized I' values for the phytoplankton data is presented in Table 3. In five of the six cases, the I' values at 120 m are lower than the corresponding value at 15 m. This shift in I' values with depth cannot be attributed only to changes in number of species or diversity. Assuming no depth-related change in the laboratory error, this indicates an increase in the spatial or temporal variability of abundances at greater depths. In the complete analysis (Venrick 1982), the source of this heterogeneity is postulated to be vertical displacement of vertically stratified populations.

TABLE 2.—Similarity index (I) observed between replicate field samples compared with maximum expected index calculated from Appendix Equation (7). The probable range is based on the equation for 95% confidence interval using a variance estimated from Appendix Equation (9) and the largest likely β from Figure 4. All samples were collected near lat. 28° N, long. 155° W.

A. Predicted Laboratory Bias

Sample depth and no.	Date	T	H'	n	Maximum β	$\hat{I}$	$\sigma^2(I)_2$ ($\times 10^{-2}$)	Probable range
15 m:								
1	6/05/77	1,574	0.438	37	0.28	0.8975	0.1976	0.8104-0.9846
2	6/13/77	1,051	0.669	40	0.27	0.8005	0.4321	0.6716-0.9293
3	6/20/77	664	0.538	36	0.28	0.7777	0.6956	0.6142-0.9411
4	8/19/78	1,897	0.328	43	0.27	0.9055	0.1347	0.8336-0.9774
120 m:								
1	6/05/77	1,475	0.672	57	0.24	0.8586	0.1540	0.7817-0.9355
2	6/13/77	1,051	0.669	51	0.25	0.8773	0.1009	0.8150-0.9396
3	6/20/77	1,196	0.639	59	0.24	0.7840	0.4372	0.6544-0.9136
4	8/19/78	597	0.768	55	0.25	0.7625	0.3170	0.6522-0.8729

q values: $q = 0.271$ species counted in entire 265 ml sample
$q = 2.13$ species counted in 44% of the sample
$q = 41.01$ species counted in 0.9% of the sample
(from Venrick 1982)

B. Observed I between field samples. Underlined values are those within the expected range if I values from replicate counts from same sample.

Sample depth and no.	1	2	3	Sample depth and no.	1	2	3
15 m:				120 m:			
2	0.579			2	0.573		
3	0.681	0.659		3	0.487	0.339	
4	0.732	0.502	0.649	4	0.403	0.299	0.462

TABLE 3.—Comparison of two phytoplankton associations using the standardized I: $I' = I/\hat{I}$. Original values of I are given in Table 2.

Sample depth and no.	Mean $\hat{I}$			I'		
	1	2	3	1	2	3
15 m:						
2	0.849			0.682		
3	0.838	0.789		0.813	0.835	
4	0.901	0.853	0.842	0.812	0.589	0.771
120 m:						
2	0.868			0.660		
3	0.821	0.831		0.593	0.408	
4	0.811	0.820	0.773	0.497	0.365	0.598

DISCUSSION AND CONCLUSIONS

In spite of the numerous approximations and assumptions which underlie the formulae for the percent similarity index and its variance, the formulae appear to be good predictors. This is true even when the equations are applied to actual species abundances which are unlikely to fulfill all the conditions met by computer simulation (i.e., normality and independence of species distributions and accurate knowledge of heterogeneity).

An important result of this study is the elucidation of the relationship between the bias of I and such community parameters as the number of species, their abundances, heterogeneity, and diversity. Decision about the importance of these dependencies is hampered by the vagueness of the concept "similar", i.e., that which is being measured by I. In my own mind, the concept is strongly linked to differences of relative abundances, and ultimately to q. In some situations the dependency of I on factors other than heterogeneity may be desirable, or at least irrelevant, as, for instance, when I values within one set of items are compared with I values between that set and a different set. Silver (1975) calculated values of I between the diatom associations in the stomachs of several salps and compared these with the indices between salps and nearby water samples. Finding no difference, she concluded that salps are nonselective feeders. In this comparison, any differences in any of the community parameters between the first set of indices (salp-salp) and the second (salp-water) are directly related to the concept of selective feeding and are validly confounded into a similarity index. A similar situation is presented by time series of I values (e.g., Miller 1970; McGowan and Walker 1979) where all comparisons are within the same general system and temporal changes in species number or diversity are important aspects of the evolution of the system, as measured by changes in I.

On the other hand, I values from within quite different systems are occasionally compared, leading to decisions about the relative similarity of items within the systems. In a study of plants ad homoptera in fields (Murdoch et al. 1972), several fields were surveyed for plant and insect abundances. Values of I between fields were lower for plants than for insects, leading to the conclusion that "the insect assemblages on different fields are more alike than are the plants." To the extent that the observed difference could reflect only different biases of the index in the two systems (caused, for instance, by different numbers of species of plants and insects), this conclusion seems unjustified. Such a comparison between plants and insects would be validated by the use of standardized I' values to remove the contribution of species number, abundances, and diversity so that the index accurately reflects the heterogeneity of the two systems.[4]

Numerous similarity indices have been proposed with different theoretical frameworks and different attributes. Intercomparisons have given different results depending upon the conditions of the comparison and the evaluation criteria (Morisita 1959; Grassle and Smith 1976; Pielou 1979; Bloom 1981; Wolda 1981). There is little evidence to suggest that other similarity indices are independent of the underlying community structure, nor is there reason to expect the relationships to be similar to those observed for the percent similarity index. The ultimate selection of a similarity index is less important than a thorough understanding of the behavior of that index under various conditions. Without such background information, interpretation of any similarity index is subject to serious error.

ACKNOWLEDGMENTS

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[4]Elsewhere in the paper these authors use a value of I which has been corrected for internal heterogeneity of the associations.

LITERATURE CITED

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APPENDIX

Derivation of Formulae for $\hat{I}$ and $\hat{\sigma}^2$ (I), the Percent Similarity Index and Its Variance

The Percent Similarity Index

General Case

In the equation defining the percentage similarity index,

$$I = 1 - 0.5 \sum_{i=1}^{n} |E(p_{i,1}) - E(p_{i,2})|, \qquad (1)$$

where n is the total number of species in samples 1 and 2, $p_{i,1}$ and $p_{i,2}$ are the proportions of species i in samples 1 and 2, and the expression $|p_{i,1} - p_{i,2}|$ is the range (w) of a sample of size two and its expected value can be related to the standard deviation of the underlying normal population by the equation $\sigma_i = 0.8862\, w_i$ (Dixon and Massey 1969, table A-8b (2)). Thus

$$E\,[|p_{i,1} - p_{i,2}|] = \sigma(p_i)/0.8862.$$

Substitution of this expression in Equation (1) gives

$$\hat{I} = 1 - 0.5642 \sum_{i=1}^{n} \sigma(p_i). \qquad (2)$$

The proportional abundance of species i, p_i, is the ratio of the abundance of that species, x_i (or μ_i) to the total number of individuals in the sample, T (or τ). The variability of p_i is a function of the variance of x_i and the variance of T. When variances are small relative to mean values, the variance of p_i may be approximated by

$$\hat{\sigma}^2(p_i) = [\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i, T) + \mu_i^2\sigma^2(T)]/\tau^4 \qquad (3)$$

and

$$\hat{\sigma}(p_i) = \{[\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i,T) + \mu_i^2\sigma^2(T)]/\tau^4\}^{1/2} \qquad (4)$$

(Yates 1953; the equation may also be derived using the differential theory of variances, or delta method, Seber 1973).

The substitution of Equation (4) into Equation (2) gives an equation for $\hat{I}$:

$$\hat{I} = 1 - \frac{0.5642}{\tau^2} \sum_{i=1}^{n} \{[\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i, T) + \mu_i^2\sigma^2(T)]\}^{1/2} \qquad (5)$$

Single Sample Case

In order to estimate $\hat{I}$ from a single sample, some independent method of estimating $\sigma^2(x_i)$, $\sigma^2(T)$, and $\sigma^2(x_i, T)$ must be available. In the following derivation, two assumptions are made: 1) The variance can be expressed as a function of the mean, e.g., $\sigma^2(x_i) \sim (q)(\mu_i)$; and 2) species are independently distributed so that $\sigma^2(x_i, T) = \sigma^2(x_i)$. Values of x_i and T from a single sample are unbiased estimates of μ_i and τ.

When the above approximations are introduced into Equation (4), the expression for $\hat{\sigma}(p_i)$ becomes

$$\hat{\sigma}(p_i) = [(q/T^3)(Tx_i - x_i^2)]^{1/2}$$

and

$$\sum_{i=1}^{n} \hat{\sigma}(p_i) = \sum_{i=1}^{n} [(q/T^3)(Tx_i - x_i^2)]^{1/2} \qquad (6)$$

The accuracy of Equation (6) was examined over a spectrum of values of q and T using computer simulation. Associations of 10 species with prescribed means and variances were sampled 10 times. The abundances of the species in each sample were converted to proportions and, for each species, the standard deviation of these proportions within the 10 samples was calculated. These observed standard deviations were then summed over all species to give one simulated value of $\sum_{i=1}^{n} \sigma(p_i)$. For comparison, the observed values of x_i and T from each sample and the prescribed value of q were entered into Equation (6) to give 10 predicted estimates of $\sum_{i=1}^{n} \hat{\sigma}(p_i)$. Each set of 10 samples was repeated 10 times in a run. Over 44 runs, sampling associations with a broad range of diversities and values of q from 0.1 to 50, the mean relative error and bias of the estimate of $\sum_{i=1}^{n} \hat{\sigma}(p_i)$ were 2.9 and -2.5%, respectively.

Substitution of Equation (6) into Equation (2) gives an expression for $\hat{I}$ in which all parameters may be estimated from one sample:

$$\hat{I} = 1 - 0.5642\,(q/T^3)^{1/2} \sum_{i=1}^{n} (Tx_i - x_i^2)^{1/2}.$$

The factor 0.5642 is expected to be increased somewhat by the demonstrated bias in the estimation of

$\sum_{i=1}^{n} \hat{\sigma}(p_i)$ and may also be affected by any biases resulting from approximating $|p_{i,1} - p_{i,2}|$ by $\alpha(p_i)$. Thus, the equation for $\hat{I}$ was expressed as

$$\hat{I} = 1 - \alpha(q/T^3)^{1/2} \sum_{i=1}^{n} (Tx_i - x_i^2)^{1/2},$$

and the magnitude and properties of α were investigated by computer simulation (described in Methods). In a total of 260 runs, the mean value of α was 0.5765 (95% confidence interval: 0.5751 - 0.5780). The magnitude of α appears to be independent of the number of species in the association (n varied from 5 to 200; Kendall correlation, $P > 0.20$) and their diversity (H' varied from 1.0 to 0.03; run test, $P > 0.20$). There is a relationship between the magnitude of α and the value of q (Friedman two-way ANOVA over 20 values of n and 5 values of q; $P < 0.01$). However, over the range of q values investigated, the change in the value of α is small (Appendix Table 1). For practical purposes, this correlation may be ignored and the overall mean value of α employed. Thus, the equation for estimating the percent similarity index between replicate samples becomes

$$\hat{I} = 1 - 0.5765(q/T^3)^{1/2} \sum_{i=1}^{n} (Tx_i - x_i^2)^{1/2}. \qquad (7)$$

The relative error of this estimate, determined from computer simulation, is small and independent of the number of species, their abundances, and their diversity. There is a direct relationship with the square root of q, reflecting the dependence of α on q. For values of q of 0.1, 1.0, and 10, the mean relative error was 0.005, 0.022, and 0.53%, respectively.

APPENDIX TABLE 1.—The relationship between α and q (population heterogeneity). Each value α is the mean of 40 runs, with n varying between 3 and 200 and diversity varying between 0.50 and 1.00. Friedman 2-way ANOVA is significant and may indicate a linear trend. (Friedman 2-way ANOVA: $\omega = 0.0915$, m = 40, $n = 5$, $P \sim 0.01$.)

q =	0.1	0.5	1.0	5.0	10.0
α =	0.5749	0.5763	0.5789	0.5761	0.5797

Variance of the Percent Similarity Index

A first approximation to the variance of the similarity index, like Equations (2), (5), and (7), is based upon the analogy between the absolute value of a difference and the range of a sample of size two. The expected relationship between the variance of a standard deviation estimated from a range and the variance of the population being sampled is known (Dixon and Massey 1969, table A-8b(1)):

$$\hat{\sigma}^2(0.886|p_{i,1} - p_{i,2}|) = 0.571\ \sigma^2(p_i)$$
$$\hat{\sigma}^2(|p_{i,1} - p_{i,2}|) = 0.7274\ \sigma^2(p_i).$$

An expression for the variance of the similarity index then becomes

$$\hat{\sigma}^2(I) = \sigma^2(1 - 0.5 \sum_{i=1}^{n} |p_{i,1} - p_{i,2}|)$$
$$= 0.25 \sum_{i=1}^{n} \sigma^2(|p_{i,1} - p_{i,2}|)$$
$$= 0.1818 \sum_{i=1}^{n} \sigma^2(p_i).$$

Using the delta approximation (Equation (3)) this becomes

$$\hat{\sigma}^2(I) = \frac{0.1818}{\tau^4} \sum_{i=1}^{n} [\tau^2\sigma^2(x_i) - 2\mu_i\tau\sigma^2(x_i, T) + \mu_i^2\sigma^2(T)].$$

Squaring Equation (6) and substituting gives an expression which may be used with single samples:

$$\hat{\sigma}^2(I) = 0.1818\ (q/T^3) \sum_{i=1}^{n} (Tx_i - x_i^2). \qquad (8)$$

However, this equation, based on the addition of variances, assumes independence of the components which is not valid in the present case where the components are fractional parts of a sample and must sum to 1.0. The consequences of these interdependencies were investigated empirically by expressing Equation (8) as

$$\hat{\sigma}^2(I) = \frac{\beta q}{T^3} \sum_{i=1}^{n} (Tx_i - x_i^2) \qquad (9)$$

and examining the effect on β of varying the underlying population parameters.

β is dependent upon the number of species (Kendall correlation, $P < 0.01$), decreasing as n increases (Fig. 4). The value is independent of T (Kendall correlation, $P > 0.20$) and, unlike α, appears independent of q (Friedman 2-way ANOVA, $P > 0.25$). The relationship of β to diversity is nonlinear and appears linked to the relationship between the variance of I and diversity (Fig. 5). At low diversities both $\hat{s}^2(I)$ and β increase as H' increases. At higher diversities, $\hat{s}^2(I)$ reaches a plateau or decreases while β decreases

more sharply. Thus, minimum values of β are associated with values of $H' < 0.25$ and $H' \sim 1.0$, while maximum values occur at some intermediate value of H', possibly influenced by the number of species.

The shaded area in text Figure 4 approximately encompasses the maximum and minimum values of β observed empirically over a broad range of H'. Much of the variability in the estimated β apparent in Figures 4 and 5 is due to errors in the empirical determination of the true variance of I; with 100 samples in each estimate, 95% confidence intervals are $0.47\,s^2 - 1.35\,s^2$. Although the value of β cannot be determined with sufficient accuracy to allow Equation (9) to be used to establish confidence intervals about predicted values of $\hat{I}$, nevertheless the figure can be used to provide conservative estimates of β so that Equation (9) may aid in decisionmaking.

NOTES

SURVEY OF POLYCHLORINATED BIPHENYLS IN SELECTED FINFISH SPECIES FROM UNITED STATES COASTAL WATERS

Polychlorinated biphenyls (PCB's) were manufactured commercially under the trade name Aroclor[1] by Monsanto Chemical Company, the sole U.S. producer. They were first marketed in 1929 and thereafter found extensive industrial applications until domestic production ceased in 1977. The PCB's, as a class of organic chemicals containing typically 20-70% chlorine, have certain chemical and physical properties that make them particularly useful (Broadhurst 1972; American National Standards Institute, Inc. 1974). They are extremely stable and chemically inert compounds, resistant to decomposition by heat, have a high dielectric constant, and are nonflammable. They have been used as insulating fluids in electrical transformers and capacitors, heat exchange fluids, hydraulic fluids, paints, plasticizers, printing inks, retardants, and carbonless copy paper. Because they are carcinogenic to animals, the use of PCB's has been restricted except in closed-system applications thereby minimizing but not eliminating their loss into the environment. As a result of their widespread industrial production and inherent resistance to degradation, PCB's have become ubiquitous and persistent environmental contaminants and have been found in the fatty tissues of a wide range of aquatic and land animals (Anas and Wilson 1970; Bagley et al. 1970; Addison et al. 1972; Claeys et al. 1975; Spagnoli and Skinner 1977; Smith et al. 1977).

The deleterious biological effects of PCB's have been extensively documented during the last decade with particular emphasis on embryo toxicity and a variety of sublethal effects in the consuming animal (Kinter et al. 1972; Aulerich et al. 1973; Hansen et al. 1974; Healton 1974[2]; Barsotti and Allen 1975[3]). Concern over accumulation of PCB's in foods (fish, dairy products, eggs, poultry, and animal feed ingredients) and the possible exposure of the U.S. population to their toxic effects led to the proposed Food and Drug Administration's (FDA) regulatory action of 1973, establishing limits for the amounts of PCB's that may be present in food as a result of contamination (Gardner 1973).

The tolerance set for fish at that time was 5.0 parts per million (ppm) on a wet weight basis. Recent toxicological data on PCB's, however, have caused the FDA to consider the need to lower these limits. In particular, a reduction in the tolerance level from 5.0 to 2.0 ppm is under active consideration by the FDA (Schmidt 1974).

Unlike freshwater fish (for which considerably higher PCB levels have been reported), marine fish have been considered to be largely uncontaminated, at least relative to the 5.0 ppm guideline. Limited "market basket" surveys by FDA have indicated PCB levels in common commercial saltwater species to average <0.2 ppm (Jelinek and Corneliussen 1975). Surveys of this type tend to be misleading, however, because of the emphasis on popular commercial seafoods that are low in fat content.

Fish samples screened for PCB contamination under the National Pesticide Monitoring Program indicate that estuarine pollution levels are declining (Butler and Schutzmann 1978). However, the experimental design and intent of this program emphasizes juvenile rather than adult, market-size fish. Although the results of an EPA-NOAA estuarine monitoring program conducted during 1976-77 indicate few high PCB levels according to the 5.0 ppm guideline for the fishes examined (Butler[4]), several species and/or geographic locations clearly stand out as candidates for more detailed investigation. The estuarine and near coastal waters of the United States are receiving the heaviest load of PCB's (Harvey et al. 1974), many of which find their way into the sediments through absorption by particulates, thus providing a potentially enormous sink of contamination for eventual though gradual release into the marine ecosystem. The food chain magnification of PCB's (and many other organic contaminants) is complex, reflecting the diversity of interspecies relationships and physiological characteristics of in-

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

[2]Healton, D. C. 1974. Review of PCB's in the Great Lakes area, U.S. Food and Drug Administration. Presented at the Governor's Great Lakes Regional Interdisciplinary Pesticide Council, Chicago, Ill., 30 p. Available Northeast Fisheries Center Gloucester Laboratory, National Marine Fisheries Service, NOAA, Emerson Avenue, Gloucester, MA 01930.

[3]Barsotti, D. A., and J. R. Allen. 1975. Effects of polychlorinated biphenyls on reproduction in the primate. Presented at the Meeting of the Federation of American Societies for Experimental Biology, Atlantic City, N.J.

[4]Butler, P.A. 1977. EPA-NOAA Cooperative Estuarine Monitoring Program. Final Report, October, 8 p.

dividual organisms. It is clear, however, that PCB's do accumulate principally in the fats of fishes and that the longer fishes are exposed to contaminated waters and food the greater will be their accumulation of PCB's.

The fish to be monitored were selected on the basis of several criteria: Importance to man (commercial and recreational), ecological importance, and their biochemical, physiological, and behavioral diversity. The sampling sites were chosen to be representative of major coastal and estuarine habitats which differ from one another in ecosystem and function (Fig. 1).

When sampled, the organisms recommended gave a cross section of trophic levels at which the different degrees of accumulation may occur. Examples of these are:

1) Plankton-feeding fishes of wide range, high in lipid content, and commercially important.
2) Benthic-feeding fishes of wide range and of commercial importance.
3) Migratory-feeding fishes, anadromous, top carnivores that migrate into and out of areas that are highly polluted and are of recreational importance.
4) Commercially important species of the mackerel family, pelagic.
5) Upper dwellers, weakly migratory, and commercially important species.
6) Species indigenous to the area being sampled which are of commercial recreational importance.

The sites from which the fish samples were collected represented known or suspected highly contaminated areas, pristine locations, and recreational and commercial areas. The Atlantic, Gulf, and Pacific coasts and one inland site were sampled.

The objective of this work was to develop extensive quantitative data on the concentration of PCB's in the edible tissues of targeted finfishes taken from the chosen areas of U.S. waters.

Materials and Methods

Collections were made between the fall of 1979 and winter of 1981. The collection sites and common names of fishes monitored are shown in Figure 1. Target species from pristine and contaminated sampling areas, supporting substantial recreational and commercial areas, were collected seasonally.

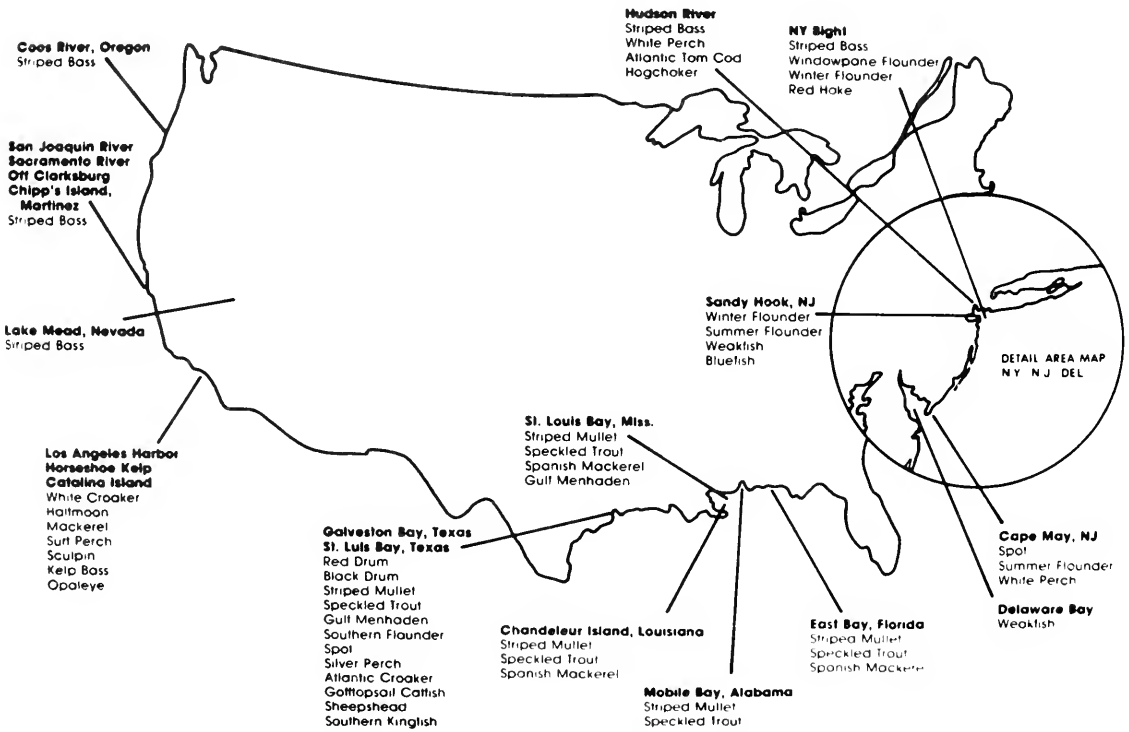

FIGURE 1.—National PCB survey sampling sites and targeted species.

Collections were made by crews operating out of Montclair State College and the New Jersey Marine Sciences Consortium Seaville Field Station; Gulf Coast Research Laboratory, Ocean Springs, Miss.; Texas A&M University of Galveston Marine Laboratory at Galveston, Tex.; University of Southern California Institute for Marine and Coastal Studies, Los Angeles, Calif.; and the Southwest Fisheries Center Tiburon Laboratory of the National Marine Fisheries Service (NMFS), Tiburon, Calif. Sampling of target species was accomplished by using appropriate gear, including beach seines, gill nets, otter trawls, and hook and line. Following capture, specimens were cooled and stored in ice. Subsequently, all specimens were measured, weighed, sexed, and aged. Fish were then filleted, the right side serving for analysis samples and the left for NMFS archives. Gonad and liver tissues also were archived for future reference. All samples were frozen in prerinsed aluminum foil prior to shipment to Gloucester. All samples were composited at the Gloucester Laboratory and consisted of equal weights of 10 deboned, skinless fillets from the right side of 10 individual fish. Target species included are shown on Table 1 and are arranged in phyletic sequence, according to families to which they belong.

Analytical procedure was in accordance with the AOAC multiresidue procedure for pesticides (Horwitz 1980). Briefly, homogenates were extracted with petroleum ether. The extract was concentrated, the solvent completely removed, and the weight of fat determined. Three grams or less of fat were taken for acetonitrile partitioning between petroleum ether. The extract was concentrated to ca. 10 ml and transferred to a florisil column. PCB's were eluted with 6% diethyl ether in petroleum ether, concentrated to 5 ml, and analyzed by gas-liquid chromatography. The florisil extract was further concentrated or diluted for eventual cleanup by silicic acid chromatography (Armour and Burke 1970). A suitable aliquot was charged onto the column. PCB's were eluted with petroleum ether, concentrated, and made up to a definite volume. An aliquot of the silicic acid extract was injected on a Perkin-Elmer Sigma 1 gas chromatograph, equipped with a Ni^{63} electron capture detector. A 6-ft by 2 mm i.d. glass coiled column consisting of 1.5% SP-2250 + 1.95 SP-2401 on 100/120 mesh Supelcoport was used as the analytical column. The carrier gas was argon/methane 95/5 at a flow rate of 20 ml/min. A makeup flow of 40 ml/min was added for a total detector flow of 60 ml/min. Injector temperature was set at 225°C, detector 300°C, and oven 200°C. The electrometer range was set at 1.0 nA. Efficiency of the column for p, p'-DDT was determined to be 931 theoretical plates per foot.

PCB's were measured by comparing total area of residue peaks with total area of peaks from appropriate Aroclor reference material. Only those peaks from samples that could be attributed to chlorobiphenyls and which were present in the chromatogram of reference material were used. PCB residues, with chromatographic patterns which were altered extensively from Aroclor references, were measured by individual peak area comparisons, using Aroclor reference material weight factors. Each PCB peak was calculated against an appropriate individual reference peak with exactly the same absolute retention time. Total PCB's were obtained by summing individual peak values.

TABLE 1.—Common and scientific names of fish species listed in phylogenetic order.

Gulf menhaden	*Brevoortia patronus*
Gafftopsail catfish	*Bagre marinus*
Red hake	*Urophycis chuss*
Atlantic tomcod	*Microgadus tomcod*
Whiting (silver hake)	*Merluccius bilinearis*
Striped bass	*Morone saxatilis*
White perch	*Morone americana*
Kelp bass	*Paralabrax clathratus*
Bluefish	*Pomatomus saltatrix*
Sheepshead	*Archosargus probatocephalus*
Weakfish	*Cynoscion regalis*
Speckled trout	*Cynoscion nebulosus*
Spot	*Leiostomus xanthurus*
Black drum	*Pogonias cromis*
Red drum	*Sciaenops ocellatus*
Silver perch	*Bairdiella chrysoura*
Atlantic croaker	*Micropogonias undulatus*
Southern kingfish	*Menticirrhus americanus*
White croaker	*Genyonemus lineatus*
Opaleye	*Girella nigricans*
Halfmoon	*Medialuna californiensis*
White seaperch	*Phanerodon furcatus*
Striped mullet	*Mugil cephalus*
Chub mackerel	*Scomber japonicus*
Spanish mackerel	*Scomberomorus maculatus*
California scorpionfish	*Scorpaena guttata*
Winter flounder	*Pseudopleuronectes americanus*
Summer flounder	*Paralichthys dentatus*
Windowpane flounder	*Scophthalmus aquosus*
Hogchoker	*Trinectes maculatus*
Pacific sanddab	*Citharichthys sordidus*
Southern flounder	*Paralichthys lethostigma*

Quality Assurance Program

Before processing any samples, a method blank (minus flesh) was run to insure that all glassware, reagents, and solvents were interference free. Each time there was a new set of samples, or occasionally to check reagents, a method blank would be processed as a safeguard against chronic contamination. Standard quality assurance practices were used with this method. For checking the accuracy of PCB determinations, check standards were prepared.

Analyses were replicated to validate the precision of the analysis. Agreement among triplicate samples extracted on the same day was ±5% of the mean. A sample was fortified with 1.0 ppm Aroclor 1254 each week to check percent recovery. The spiking solution was pipetted directly onto the homogenized flesh contained in the blender jar and worked up by AOAC multiresidue procedure. Check of final recovery precision was ±11% of the mean. Degradations of specified Aroclors 1242, 1254, and 1260 were monitored by running standard mixtures of the compounds through the entire procedure in the absence of any sample material. This was done whenever new materials or reagents were used.

Validation studies were accomplished at the 1.0, 0.5, and 0.1 ppm levels. Recovery efficiency for seven samples spiked at the 1.0 ppm level was 83.88%. At the 0.5 ppm level recovery was 85.66%, and at 0.1 ppm, 79%. Coefficient of variation ranged from 6.9 to 11.5 for the three levels. In addition, a blind sample of homogenized carp was introduced into the sampling system periodically. This sample was provided and thoroughly analyzed by J. D. Petty of the Fish and Wildlife Service, Columbia National Fisheries Research Laboratory, Columbia, Mo.

Finally, the Gloucester Laboratory participated in the ICES[5] fourth organochlorine intercalibration exercise for unspiked and spiked fish oils. The accuracy and precision of the Gloucester Laboratory exceeded the performance level accepted by ICES.

Confirmation of PCB's by GC-MS

A 12 m by 0.21 mm i.d. fused silica column (OVID-101) was coupled to a Hewlett-Packard 5992 B GC-MS (gas chromatography-mass spectrometry) and operated in the selected ion monitoring mode. Four extracts of striped bass and four extracts of white perch were analyzed by GC-MS to confirm the presence of chlorosubstituted biphenyls. Ion masses of 235, 246, 263, 292, 326, and 360 were selected. In this manner, tetrachloro, pentachloro, hexachloro, heptachlorobiphenyls, aldrin, analogues of DDT, and p,p'-DDE could be detected. The presence of chlorosubstituted biphenyls (4, 5, 6, and 7) was indicated. Also, mass spectra of some of the individual peaks were obtained and stored during production of a total ion chromatogram. Subsequently, the individual peaks were identified by comparing their spectra with those in the system's library using a library search program.

Results

Table 2 gives the mean PCB concentrations (ppm, wet weight), lipid content, length, weight, age, number of samples, and location for each of the species. A total of 270 samples were analyzed by the AOAC procedure with additional cleanup by silicic acid chromatography. PCB's were detected for all of the samples analyzed. Total PCB values of marine finfish averaged 0.33 ppm, well below the FDA limit of 5 ppm and 3/20 of the proposed 2 ppm standard.

The highest concentration measured in any species was 22.0 ppm in a white perch sampled from the Hudson River. White perch sampled from Cape May Peninsula had an average total PCB content of 0.06 ppm. The Hudson River is known to be heavily laden with PCB's. White perch fished in the Hudson River appear to be strong candidates for regulatory action. Total PCB content for white perch young-of-a-year (YOY) sampled from the Hudson River was 1.9 ppm.

Striped bass sampled from estuaries of the Hudson River averaged 1.5 ppm. Range of PCB results from five samples indicate that this species is another candidate in need of more intensive monitoring. A sample of the YOY had a total PCB content of 1.1 ppm. One sample from the New York Bight Apex had a PCB value of 3.6 ppm. The lowest PCB values for striped bass were found in Lake Mead, Nev. Striped bass fished from Coos River, Oreg., averaged 0.27 ppm. Coos River was considered one of the pristine areas for sampling striped bass. Striped bass fished from the San Francisco Delta region averaged 0.39 ppm. There is intensive agriculture in the Central Valley of this region with drainage by the Sacramento and San Joaquin Rivers into the Delta and San Francisco Bay. Sites considered to be contaminated from agricultural runoff were sampled. One sample from the Sacramento River had a PCB content of 4.00 ppm. Seventy-nine striped bass samples were analyzed from the western coastal U.S. waters. The total PCB content averaged 0.32 ppm.

Table 3 summarizes PCB values according to family grouping. The average PCB values in ppm for the following families were:

bluefish	1.2	porgies	0.07
cods	0.08	sea basses	0.04
drums	0.19	sea chubs	0.02
herrings	0.34	scorpionfishes	0.07
mackerels	0.14	surfperches	0.13
mullets	0.13	temperate basses	2.84

[5]ICES (International Council for the Exploration of the Sea). An intercalibration exercise on PCB's in biological materials carried out by 24 participants using unspiked and spiked samples of cod liver oil to determine agreement among analysts.

TABLE 2.—Total PCB content of the edible portions of targeted samples in respect to length, weight, age, and lipid content. Mean ranges are in parentheses.

Species and location	No. of samples	Length (cm)	Weight (kg)	Age (yr)	Lipid content (%)	Total PCB's (ppm)
Gulf menhaden						
Bay St. Louis, Miss.	2	18(15-33)	0.14(0.09-0.30)	3(2-3)	8.4(5.5-11.4)	0.19(0.10-0.29)
Galveston Bay, Tex	4	25(19-28)	0.21(0.14-0.34)	1(1-2)	12.6(9.8-14.5)	0.49(0.43-0.54)
San Luis Pass, Tex.	3	24(16-29)	0.20(0.08-0.31)	1(1-3)	8.6(5.3-11.1)	0.34(0.31-0.41)
Gafftopsail catfish						
Galveston Bay, Tex	2	51(44-55)	1.23(0.78-1.5)	2(1-3)	2.3(2.1-2.5)	0.10(0.04-0.17)
San Luis Pass, Tex.	2	44(27-40	1.04(0.17-2.10)	2(0+-3)	2.4(1.5-3.2)	0.10(0.04-0.17)
Red hake						
New York Bight	8				1.7(1.6-1.8)	0.10(0.03-0.34)
Atlantic tomcod						
Hudson River	1	18(17-19)	0.06(0.05-0.10)	2(2-3)	1.6(1.6-1.6)	0.10(0.10-0.10)
Silver hake						
San Luis Pass, Tex	1	26(16-30)	0.16(0.06-0.38)	1(1-2)	1.2(1.2-1.2)	0.03(0.03-0.03)
Striped bass						
Hudson River	5	20(4-32)	0.14(0.00-0.39)	4(YOY[1]-7)	2.6(2.0-3.9)	1.5(1.1-2.1)
New York Bight Apex	4	26(18-70)	0.59(0.05-4.25)	Large fishes-13 others undetermined	3.3(1.2-8.2)	1.1(0.2-3.60)
San Joaquin River, Calif. (off Antioch)	7	64(57-72)	3.54(1.86-6.52)	5(4-7)	2.1(1.3-3.0)	0.35(0.29-0.5)
Sacramento River, Calif. (off Clarksberg)	11	66(51-91)	3.83(1.53-8.88)	6(4-9)	2.5(1.4-3.7)	0.75(0.2-4.00)
Chipp's Island, Calif.	17	40(25-74)	1.04(0.18-4.53)	3(2-4)	2.4(0.8-6.0)	0.22(0.11-0.78)
Martinez Shore, Calif.	9	66(32-121)	4.22(0.34-16.20)	5(2-14)	1.7(1.0-2.8)	0.24(0.07-0.57)
Coos River, Oreg.	28	77(49-101)	7.08(1.80-15.44)	7(4-19)	2.5(1.3-5.3)	0.27(0.04-1.86)
Lake Mead, Nev	7	47(37-59)	0.95(0.55-1.37)	3(2-3)	1.3(0.6-2.4)	0.10(0.03-0.34)
White perch						
Hudson River	5	15(5-23)	0.07(0.00-0.19)	4(YOY-6)	6.1(2.6-10.7)	10.2(1.9-22.0)
Cape May Peninsula	3	22(19-28)	0.16(0.05-0.30)	—	1.5(1.1-1.8)	0.06(0.04-0.08)
Kelp bass						
Backside Catalina	2	22(19-36)	0.28(0.10-1.02)	4(2-7)	1.6(1.4-1.7)	0.03(0.02-0.04)
Frontside Catalina	2	26(16-36)	0.40(0.18-1.74)	5(3-9)	1.3(1.2-1.4)	0.05(0.04-0.06)
Bluefish						
Sandy Hook Bay	1	46(45-47)	1.13(0.99-1.27)	9(8-9)	9.0(9.0-9.0)	1.2(1.2-1.2)
Sheepshead						
Galveston Bay, Tex	1	37(31-42)	0.87(0.73-1.26)	2(2-2)	2.1(2.1-2.1)	0.06(0.06-0.06)
San Luis Pass, Tex	2	36(26-44)	0.94(0.42-1.56)	2(1-3)	1.6(1.0-2.2)	0.08(0.02-0.14)
Weakfish						
Sandy Hook Bay	6	36(9-77)	0.84(0.01-3.72)	4(YOY-10)	1.7(1.2-2.5)	0.23(0.12-0.02)
Cape May Peninsula	1	38(32-48)	0.58(0.43-1.07)	5(3-6)	3.8(3.8-3.8)	0.35(0.35-0.35)
Speckled trout						
East Bay, Fla.	5	31(25-41)	0.41(0.21-0.99)	3(3-5)	2.2(1.0-3.2)	0.18(0.03-0.61)
Mobile, Ala.	4	32(25-0.38)	0.45(0.22-0.76)	4(3-4)	5.9(2.3-10.7)	0.24(0.07-0.43)
Bay St. Louis, Miss.	4	36(24-46)	0.73(0.21-1.31)	4(3-6)	4.3(2.8-6.4)	0.10(0.05-0.25)
Chandeleur Sound, La.	1	25(18-41)	0.27(0.10-0.92)	3(2-5)	0.9(0.9-0.9)	0.02(0.02-0.02)
Galveston Bay, Tex	1	31(21-49)	0.41(0.11-1.14)	2(1-2)	4.0(4.0-4.0)	0.14(0.14-0.14)
San Luis Pass, Tex.	2	46(26-67)	1.27(0.20-3.17)	3(1-5)	3.1(0.17-4.6)	0.12(0.11-0.14)
Spot						
Sandy Hook Bay	1	30(30-31)	0.40(0.37-0.43)	—	1.8(1.8-1.8)	0.24(0.24-0.29)
Cape May Peninsula	1	15(13-16)	0.04(0.03-0.07)	4(2-4)	1.5(1.5-1.5)	0.03(0.03-0.03)
Galveston Bay, Tex.	1	16(15-19)	0.06(0.1 -0.08)	1(1-1)	2.5(2.5-2.5)	0.20(0.20-0.20)
San Luis Pass, Tex.	1	21(18-22)	0.14(0.08-0.18)	1(1-1)	1.0(1.0-1.0)	0.13(0.13-0.13)
Black drum						
Galveston Bay, Tex.	4	33(21-44)	0.60(0.14-1.34)	1(1-2)	1.5(0.6-2.3)	0.05(0.02-0.10)
San Luis Pass, Tex.	2	27(21-37)	0.41(0.15-0.70)	1(1-2)	1.5(1.3-1.6)	0.06(0.02-0.10)
Red drum						
Galveston Bay, Tex.	4	44(30-62)	1.03(0.34-2.67)	1+(0+-1+)	1.3(1.1-1.5)	0.03(0.02-0.04)
San Luis Pass, Tex.	1	51(47-54)	1.47(1.22-1.73)	1(1-2)	1.6(1.6-1.6)	0.02(0.02-0.02)
Silver perch						
Galveston Bay, Tex.	1	20(19-20)	0.12(0.11-0.12)	2(2-2)	5.2(5.2-5.12)	0.23(0.23-0.23)
San Luis Pass, Tex.	3	18(17-21)	0.08(0.04-0.15)	1(1-2)	2.6(1.6-4.3)	0.11(0.08-0.14)
Atlantic croaker						
Galveston Bay, Tex.	2	21(15-32)	0.14(0.03-0.44)	1(0+-1)	9.2(6.2-12.1)	0.22(0.13-0.31)
San Luis Pass, Tex.	1	31(28-32)	0.41(0.28-0.57)	1(1-1)	3.9(3.9-3.9)	0.09(0.09-0.09)
Southern kingfish						
San Luis Pass, Tex.	1	24(29-38)	0.47(0.31-0.68)	2(2-2)	2.2(2.2-2.2)	0.04(0.04-0.04)
White croaker						
Inside LA Harbor	2	23(20-25)	0.21(0.11-0.27)	6(5-7)	2.1(1.1-3.2)	0.75(0.74-0.76)
Outside LA Harbor	2	21(16-26)	0.16(0.08-0.28)	5(3-7)	2.1(1.0-3.2)	0.72(0.50-0.95)
Opaleye						
Frontside Catalina	1	23(18-29)	0.36(0.22-0.71)	3(2-4)	1.2(1.2-1.2)	0.01(0.01-0.01)
Backside Catalina	1	20(15-25)	0.30(0.14-0.47)	2(2-3)	0.7(0.7-0.7)	0.01(0.01-0.01)
Halfmoon						
Inside LA Harbor	2	22(17-26)	0.35(0.14-0.71)	3(2-5)	2.3(1.0-3.6)	0.04(0.01-0.07)
Outside LA Harbor	1	23(20-26)	0.23(0.13-0.35)	3(3-5)	1.1(1.1-1.1)	0.04(0.04-0.04)
Frontside Catalina	2	21(17-24)	0.27(0.14-0.35)	3(2-3)	1.1(0.7-1.6)	0.02(0.01-0.03)
Backside Catalina	2	21(17-25)	0.25(0.06-0.35)	3(2-3)	1.5(1.2-1.8)	0.03(0.01-0.06)
White seaperch						
Inside LA Harbor	1	17(15-18)	0.11(0.10-0.13)	3(2-3)	1.1(1.1-1.1)	0.13(0.13-0.13)

TABLE 2.—*Continued.*

Species and location	No. of samples	Length (cm)	Weight (kg)	Age (yr)	Lipid content (%)	Total PCB's (ppm)
Striped mullet						
Mobile Bay, Ala.	5	29(25-32)	0.42(0.28-0.67)	2(2-3)	4.4(1.7-9.5)	0.34(0.04-0.85)
East Bay, Fla.	5	29(23-33)	0.47(0.21-0.69)	2(2-3)	4.6(1.4-12.1)	0.17(0.04-0.34)
Bay St. Louis, Miss.	4	29(25-28)	0.47(0.26-0.99)	2(2-3)	3.3(1.2-5.9)	0.11(0.01-0.21)
Chandeleur Sound, La.	4	27(21-38)	0.39(0.15-0.96)	2(2-3)	3.4(2.4-4.6)	0.05(0.02-0.10)
Galveston Bay, Tex.	4	30(21-37)	0.31(0.10-0.57)	1(1-2)	2.0(1.2-3.0)	0.09(0.04-0.12)
San Luis Pass, Tex.	4	32(23-50)	0.45(0.14-1.65)	1(1-2)	3.1(1.5-7.6)	0.03(0.02-0.04)
Chub mackerel						
Inside LA Harbor	2	30(26-40)	0.39(0.23-0.79)	3(2-5)	5.2(5.0-5.5)	0.19(0.11-0.27)
Outside LA Harbor	2	231(26-39)	0.46(0.25-0.94)	3(2-4)	5.5(5.0-6.5)	0.18(0.06-0.31)
Frontside Catalina	1	31(26-37)	0.41(0.26-0.82)	3(2-4)	6.3(6.3-6.3)	0.[illegible](0.06-0.06)
Spanish mackerel						
East Bay, Fla.	2	30(26-35)	0.28(0.18-0.38)	1(1-1)	3.2(1.8-4.6)	0.90(0.89-0.92)
Bay St. Louis, Miss.	2	33(27-44)	0.41(0.17-1.08)	2(2-2)	8.0(1.4-14.6)	0.05(0.02-0.09)
Chandeleur Sound, La.	2	39(32-43)	0.42(0.25-0.82)	1(1-1)	4.7(1.8-7.7)	0.09(0.09-0.09)
California scorpionfish						
Inside LA Harbor	1	22(17-30)	0.26(0.14-0.48)	4(3-5)	1.9(1.9-1.9)	0.03(0.03-0.03)
Outside LA Harbor	2	21(16-34)	0.29(0.14-0.52)	3(2-5)	1.3(1.2-1.5)	0.11(0.11-0.12)
Backside Catalina	1	22(18-38)	0.42(0.23-0.88)	3(2-5)	1.4(1.4-1.4)	0.07(0.07-0.07)
Winter flounder						
Sandy Hook Bay	4	19(15-31)	0.09(0.03-0.40)	2(2-3)	1.5(1.3-1.6)	0.07(0.05-0.13)
New York Bight	13				2.2(1.7-3.1)	0.23(0.06-0.56)
Summer Flounder						
Sandy Hook Bay	2	33(28-37)	0.40(0.20-0.63)	6(5-7)	1.3(1.1-1.6)	0.04(0.04-0.04)
Cape May Peninsula	2	34(29-30)	0.40(0.24-0.57)	8(7-9)	0.8(0.7-1.0)	0.02(0.02-0.02)
Windowpane flounder						
New York Bight	10				2.0(1.4-2.9)	0.21(0.04-0.63)
Hogchoker						
Hudson River	2	12(10-14)	0.03(0.01-0.05)	3(2-3)	2.1(1.7-2.5)	0.11(0.10-0.12)
Pacific sanddab						
Frontside Catalina	2	20(13-27)	0.14(0.04-0.28)	3(2-6)	1.2(1.1-1.2)	0.02(0.02-0.02)
Backside Catalina	2	20(16-26)	0.14(0.01-0.25)	3(2-6)	1.4(1.3-1.5)	0.04(0.03-0.06)
Southern flounder						
Galveston Bay, Tex.	2	34(21-42)	0.54(0.31-1.02)	1(1-3)	1.31(1.2-1.5)	0.02(0.02-0.02)
San Luis Pass, Tex.	2	29(20-42)	0.29(0.08-0.46)	1(0+-3)	1.3(1.3-1.3)	0.02(0.02-0.02)

[1]YOY = young of a year

TABLE 3.—National PCB survey of targeted finfishes.

Family	Species	No. of samples	PCB levels (ppm) Mean	Range
Bluefish	Bluefish	1	1.2	1.2 -1.2
Cod	Atlantic tomcod	1	0.10	0.10-0.10
	Red hake	8	0.10	0.03-0.34
	Whiting	1	0.03	0.03-0.03
Drum	Atlantic croaker	3	0.18	0.09-0.31
	Black drum	6	0.05	0.02-0.10
	Red drum	5	0.03	0.02-0.04
	Silver perch	4	0.14	0.08-0.23
	Southern kingfish	2	0.09	0.04-0.14
	Speckled trout	17	0.16	0.02-0.43
	Spot	4	0.16	0.03-0.35
	Weakfish	9	0.20	0.11-0.35
	White croaker	4	0.73	0.50-0.95
Flatfish	Hogchoker	2	0.11	0.10-0.16
	Pacific sanddab	5	0.03	0.02-0.06
	Southern flounder	4	0.02	0.02-0.02
	Summer flounder	4	0.03	0.02-0.04
	Windowpane flounder	10	0.21	0.04-0.63
	Winter flounder	17	0.15	0.05-0.56
Herring	Gulf menhaden	9	0.34	0.10-0.54
Mackerel	Pacific mackerel	5	0.16	0.06-0.31
	Spanish mackerel	6	0.11	0.02-0.92
Mullet	Striped mullet	26	0.13	0.01-0.85
Porgy	Sheepshead	3	0.07	0.02-0.14
Scorpion-fish	California scorpionfish	4	0.07	0.03-0.12
Sea bass	Kelp bass	4	0.04	0.02-0.06
Sea cat-fish	Gafftopsail catfish	4	0.10	0.04-0.17
Sea chub	Halfmoon	7	0.03	0.01-0.07
	Opaleye	3	0.01	0.01-0.01
Surfperch	Surfperch	1	0.13	0.13-0.13
Temperate bass	Striped bass	88	0.56	0.01-4.00
	White perch	8	5.13	0.04-22.00

Species indigenous to the Galveston Bay and Los Angeles Harbor areas had slightly higher PCB values than those species sampled from their pristine counterparts—namely, San Luis Pass and Catalina Island.

Apparent trends from the limited number of samples per species collected were: Flounders from the New York Bight Apex had higher PCB values than those flounders sampled from Cape May Peninsula and Sandy Hook Bay; striped mullets collected from Chandeleur Sound, La., and San Luis Pass, Tex., had lower PCB values than striped mullets sampled from other sites of the Gulf; seatrouts had slightly higher PCB values in the northeast than in the eastern part of the Gulf of Mexico; and species with high fat content sampled from contaminated sites had higher PCB values, e.g., Spanish mackerel, Gulf menhaden, than those species sampled from pristine sites.

Discussion

The lack of a consistent pattern of higher body burdens in selected contaminated areas may be related to the mobility of the species sampled. It is possible, though conjectural, that a large proportion of the

measured PCB body burdens is acquired in estuarine or other contaminated areas but that the migratory nature of most megafauna (and/or of their prey) yields the observed pattern of low body burdens across large areas of the continental shelf. Several authors have reported PCB results of a broader scale and have similarly noted low-level contamination throughout a region but no strikingly high PCB values in contaminated areas or elsewhere (Sims et al. 1977; McDermott-Ehrlich et al. 1978; Stout 1980; Stout and Beezhold 1981; Stout et al. 1981).

A condition factor could also be obscuring any tendency of fish from contaminated areas to show higher PCB body burdens. PCB's have an affinity for fats, so composites with a greater fat content might be expected to accumulate more PCB's. The average lipid content of white perch in the flesh sampled from the Hudson River was 6.1% versus 1.5% from Cape May. Striped bass from the Hudson River had an average lipid content of 1.5%. This may account for the higher PCB levels found in the flesh of white perch from the estuaries of the Hudson River. If fat content of the species examined is somehow inversely related to environmental stress, this will tend to confuse any direct relationship between environmental contamination and PCB body burdens and could contribute to the observed absence of dramatically elevated muscle burdens in targeted species.

Conclusions

The current proposed FDA tolerance or "action level" for PCB's in foodfish is 2 ppm. The FDA tolerance now being considered is 1 ppm. PCB's in edible fishes remain far below existing or proposed maximum permissible levels for the majority of species investigated. Also, estuarine and coastal regions of the world are increasingly subjected to a wide range of environmental alterations. Degradation ensues through the action of man's activities, energy needs, and increasing population. Such degradation may be gradual, but eventually results in rivers, estuaries, and coasts with greatly depleted natural resources. For example, the pollution of the Hudson and Delaware Rivers in the eastern United States is extremely high. Degradation of rivers on the east coast with the loss of striped bass and other species has already occurred. Striped bass is recognized as being one of the most important anadromous and coastal commercial and recreational fishes in the United States.

The New York Bight is the ultimate repository for wastes from over 20 million people as well as a host of major industries. Mutagens in bight waters may be associated with higher than normal incidences of developmental problems and mortalities in fish eggs and larvae. The New York Bight Apex is also a spawning and nursing area for some commercial species. The Hudson River valley is a conduit for New York Bight Apex contaminants. Presently, there is insufficient information on the long-term effects of pollution. The first step is to recognize the present or potential sources of pollutants. This should be followed by intensive efforts to determine the fate and effects of the pollutants over both short- and long-exposure periods. Unless curtailed, pollution could ultimately deplete marine resources, including fisheries.

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FOODS OF COASTAL FISHES DURING BROWN SHRIMP, *PENAEUS AZTECUS*, MIGRATION FROM TEXAS ESTUARIES (JUNE-JULY 1981)

During May, June, and July, brown shrimp, *Penaeus aztecus*, migrate from Texas bays and estuaries to offshore waters. These shrimp are, for the most part, smaller than the 114 mm total length (TL) legal fishing limit. To prevent overfishing of these juvenile and subadult (60-130 mm TL) shrimps and to allow them to move farther offshore during this period, the Gulf of Mexico Fishery Management Council and the State of Texas simultaneously prohibited nocturnal shrimping from the shoreline out to 370 km. The closure remained in effect over the period 22 May through 15 July 1981. The rationale for the closure was an expected increase in yield from additional growth of the protected brown shrimp and from elimination of waste due to discarding of undersized brown shrimp (Gulf of Mexico Fishery Management Council 1980; Caillouet and Koi 1981).

NOAA's RV *Oregon II* conducted a trawl survey of shrimp size distribution and abundance by depth in the closure area from 4 June through 3 July 1981. The survey provided us the opportunity to describe the foods of Texas coastal fishes while evaluating the natural mortality of brown shrimp due to predation. This paper examines the foods of 81 species of fishes collected during the shrimp survey. We present size- and depth-related changes in diet for the more abundant fishes, and further examine predation on penaeid shrimps.

Materials and Methods

Fish samples were taken from trawl catches by the RV *Oregon II* on 100 stations in 9-64 m waters off the Texas coast (Fig. 1). The survey was conducted from 4 June through 3 July 1981. All trawls were made at night (brown shrimp are nocturnally active) with a 12.2 m semiballoon trawl rigged with a tickler chain and 2.4 m × 1.0 m wooden doors towed at 3 kn. Four stations south of Galveston Bay were repeated at 2-wk intervals; thus, a total of 108 trawl tows were made over the entire coastline. Details of the sampling strategy are given by Matthews (1982). Species composition, abundance, and biomass data for fishes and invertebrates were recorded and standardized to catch per 30-min tow for 89 of the 108 trawl catches. Only penaeid shrimp data were recorded for the other 19 catches. All fishes from each catch (up to a 45 kg maximum) were labelled and frozen for stomach contents analysis.

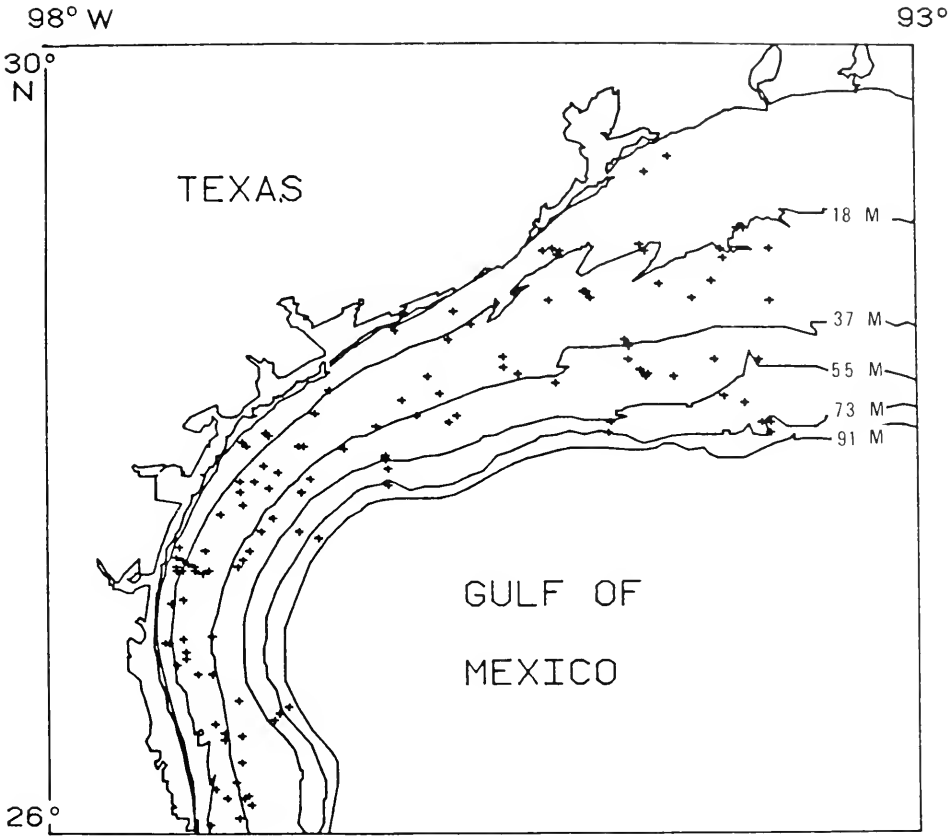

FIGURE 1.—RV *Oregon II* shrimp survey sites off the Texas coast, June-July 1981.

In the laboratory, each sample was thawed and the fishes were sorted and measured to the nearest millimeter (standard length for most genera; disc width or total length for others). In most cases, fishes <150 mm in length or width were discarded, since they were unlikely shrimp predators. However, in samples consisting of at least 75% potentially carnivorous fishes of <150 mm, a minimum of 50% of these fishes was examined. All discards were recorded.

Each fish was examined by opening the abdomen and removing the stomach. Empty stomachs were recorded. Stomach contents were identified visually, in some cases with a dissecting microscope, to 10 broad taxonomic categories: polychaetes, molluscs, holothurians, mysids, stomatopods, shrimps, crabs, squids, fishes, and octopi. Detritus was also recorded as a discrete category. Penaeid shrimps and fishes were further identified to genus and species when possible. Tail lengths of *Trachypenaeus* and *Sicyonia* were recorded as falling into one of a series of 5 mm size classes, while those of *Penaeus aztecus* were measured to the nearest millimeter. Fishes were subsequently grouped into about 25, 50, or 100 mm size classes to examine size- and depth-related differences in diet. However, many species were represented by too few individuals to justify comparison or showed no size-related diet changes; thus, data from only a few species are presented with size-class information. Results are presented as frequency of occurrence of the various food items in stomachs containing food. Food categories having a 30% or greater frequency of occurrence are referred to as "major," while those having <30% frequencies are referred to as "minor."

Results and Discussion

We examined the stomachs of 7,374 fishes of 81 species (11% of the total individuals collected). The frequency of occurrence of food items in stomachs is summarized in Appendix Table 1. A total of 61,385 fishes, including 17 more species, were discarded without examination for reasons presented in the previous section (Appendix Table 2). Shoal flounder,

Syacium gunteri, was discarded most frequently (10,725 individuals; 17% of total discards). Other frequently discarded fishes included longspine porgy, *Stenotomus caprinus;* Atlantic croaker, *Micropogonias undulatus;* Atlantic bumper, *Chloroscombrus chrysurus;* blackfin searobin, *Prionotus rubio*; and dwarf sand perch, *Diplectrum bivittatum.*

Fish stomach contents were examined according to six depth ranges: 9-17 m (18 stations), 18-26 m (31 stations), 27-36 m (27 stations), 37-45 m (15 stations), 46-54 m (6 stations), and 55-64 m (3 stations) (Tables 1-6). In all six depth ranges, detritus was the most frequently observed category, when data from all species were pooled. Among the 81 species examined from all depths, detritus was found in the stomachs of 62 species and was the most frequently observed category for 55 species. In contrast, Rogers (1977) listed detritus as occurring in stomachs of

TABLE 1.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 9 to 17 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Sh = shrimp, Ho = holothurians, Cr = crabs, Fi = fishes, Ms = other taxa such as molluscs, mysids, octopi, and polychaetes. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T (*Trachypenaeus*), S (*Sicyonia*), or P (*Penaeus aztecus*), followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence De	Sh	Ho	Cr	Fi	Ms	Prey fishes	Prey shrimps
Micropogonias undulatus	95-124	602	33	81	11	8	1	1	4		T(21):10-25, 35, 45; S(2):15
	125-163	1,236	25	82	10	5	3	1	2	eel (2), *Ophichthus*	T(41):5-35, S(1):10, P(1):45
Cynoscion nothus	76-124	275	75	62	26		1	12	1		T(5) 10, 20, 35
	125-149	95	77	55	18	5		27		*Anchoa, Prionotus*	T(2):20, 25
	150-219	25	52	25	42		8	25			T(2):30, 35
Menticirrhus americanus	112-149	60	85	44	22	11	22	11	11		T(1):5
	150-199	88	69	41	37		15	4	4		T(5):10, 15, 30; S(1):20
	200-282	24	50	42	25		33	17	33	*Prionotus*	T(2):10, 15
Leiostomus xanthurus	86-164	64	62	100							
Arius felis	132-199	17	6	31	13	19	38		25		T(1):45
	200-293	13	0	38	15	38	31	8	15		T(2):10, 40
Synodus foetens	125-199	30	87	25	25			50			T(1):40
Stellifer lanceolatus	72-112	30	33	45	35			25		*Anchoa*	T(3):5, 10, 20
Cynoscion arenarius	134-239	26	38		88		6	12			T(9):20-45; P(3):57, 62, 62
Other species (31)	65-662	241	34	85	8	1	2	4	2	*Lutjanus*	T(5):5-25, 35; S(2):15, 25, P(1):60
Total		2,762	39	76	13	5	4	5	3		T(100):5-45, S(6):10-25; P(5):45-62

TABLE 2.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 18 to 26 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL, except * = mm total length. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Sh = shrimp, Fi = fish, Cr = crabs, Sq = squid, Ms = other taxa including molluscs, mysids, octopi, polychaetes, and holothurians. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T (*Trachypenaeus*), S (*Sicyonia*), or P (*Penaeus aztecus*), followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence De	Sh	Fi	Cr	Sq	Ms	Prey fishes	Prey shrimps
Micropogonias undulatus	95-124	352	37	91	4		1		3		T(3):5,10,30; S(1):15
	125-149	582	55	87	7	3	3		2	*Anchoa, Saurida*, eel	T(13):5-15, 25-30, 45
	150-163	14	79	67	33						T(1):5
Cynoscion nothus	76-124	88	65	61	13	23		3		*Anchoa*	T(2):35, 40
	125-149	89	45	71	18	16	2	2	4	*Anchoa* (4)	T(3):10, 20, 35
	150-219	192	55	63	40	13		1		*Anchoa, Centropristis*, eel, *Monacanthus*	T(19):10-45; S(2):20
Leiostomus xanthurus	100-164	250	14	100							
Lepophidium graellsi	100-149*	15	40	89	22						T(1):15
	150-199*	79	54	78	28		3				T(3):10, 30, 40
	200-240*	46	61	83	11		17				T(1):10
Synodus foetens	100-149	23	48	25	16	58					T(1):20
	150-199	77	62	17	38	48			10	*Anchoa* (2)	T(6):15-25, 40-45; P(3):40, 46, 53
	200-244	20	50	40	10	50				*Anchoa, Citharichthys*	P(1):44
Centropristis philadelphica	85-124	71	51	66	29	6	6				T(6):5-15, 35, 40; S(2):20
	125-199	17	53	50	50		13				T(2):5, 20; S(1):15
Cynoscion arenarius	135-239	78	88	11	77	22	11			*Centropristis, Cynoscion*	T(6):15, 30, 40; P(1):60
Menticirrhus americanus	112-199	52	63	37	42	11	16		11	*Saurida*	T(6):20, 25, 40; S(2):20-25
	200-249	20	40	42	42	8	17		8		5(2):30, 45
Larimus fasciatus	78-135	70	36	98		2					
Lutjanus campechanus	65-149	50	52	46	17	17	17	17	8		
Other species (40)	48-450	253	49	70	22	5	5		2	*Anchoa* (2)	T(14):10, 20, 35; S(3):15
Total		2,436	48	79	15	6	3	1	2		T(87):5-45; S(13):15-25; P(5):40-60

only 5 of the 26 species he examined from Texas and Louisiana shelf waters. Of the 17 species held in common, we found detritus in the stomachs of 15 species, while rogers found detritus in only 4 species. We believe such differences are derived from differing methodologies (visual identification of stomach contents by us and microscopic examination by Rogers), but we suggest that ingestion of detrital matter by fishes remains widespread.

Fishes were found in stomachs of 30 species from all

TABLE 3.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 27 to 36 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL, except * = mm total length. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Fi = fish, Sq = squid, Sh = shrimp, St = stomatopods, Cr = crabs, Ho = holothurians, Po = polychaetes. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T (*Trachypenaeus*), S (*Sicyonia*), or P (*Penaeus aztecus*), followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence								Prey fishes	Prey shrimps
				De	Fi	Sq	Sh	St	Cr	Ho	Po		
Synodus foetens	125-149	37	65	31	62		15					*Saurida*[2], *Anchoa*, eel	T(2):15,45
	150-199	139	67	22	52	4	20					*Saurida*(4), *Anchoa*	T(8):5, 20-35, 50
	200-299	28	64	20	60	10	10						T(1):15
Centropristis philadelphica	85-124	99	42	54	5		37	2	4			*Bollmannia*	T(8):10-20, 35; S(2):15-20; P(1):20
	125-199	23	43	54			46						T(1):15; S(3):10, 35
Lepophidium graellsi	95-149*	12	42	86				14					
	150-199*	49	67	56	13		25		25				T(3):5-10; S(1):5
	200-240*	21	76	60	20			20					
Diplectrum bivittatum	87-99	23	74	50			50						T(3):10, 25, 40
	100-115	53	68	35			59	6	6				T(6):10-20
Micropogonias undulatus	95-124	51	73	43			29			36	7		T(4):10, 30
	125-163	24	62	44						33	22		
Cynoscion nothus	100-149	31	87	50	50	25						*Stenotomus*	
	150-219	23	70	14	14		71						T(3):20, 30, P(1):45
Urophycis floridana	114-124	7	28	20			60	40					T(1):5, S(1):10
	125-149	28	29	15	30		55	5			5	*Ophicthus*, eel	T(5):5, 15, 25, 40, S(3):10-15
	150-199	5	40		33		67						T(3):5-15
Lutjanus synagris	82-124	6	100										
	125-190	11	73	67			33						T(2):35
Calamus nodosus	121-162	13	100										
Menticirrhus americanus	112-249	13	92							100			
Other species (33)	48-655	84	48	66	5	2	32			2		*Saurida*	T(12):5,20-45
Total		780	61	44	19	2	32	2	2	4	1		T(62):5-45; S(10):5-35; P(2):20, 45

TABLE 4.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 37 to 45 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL, except * = mm total length. *N* = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Fi = fish, Sq = squid, Cr = crabs, Sh = shrimp, St = stomatopods, Ms = other taxa including polychaetes, mysids, and molluscs. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T (*Trachypenaeus*), S (*Sicyonia*), or P (*Penaeus aztecus*), followed by frequency and size range (mm tail length).

Fish species	Size class	*N*	%E	% frequency of occurrence							Prey fishes	Prey shrimps
				De	Fi	Sq	Cr	Sh	St	Ms		
Synodus foetens	100-149	14	50	43	57						*Saurida, Stenotomus*	
	150-199	151	66	37	53	2		8			*Saurida*(6), *Anchoa, Mullus, Serranus*	T(3):20, 40
	200-249	81	73	5	64	14		18			*Saurida, Trachurus, Scomber*	T(2):40, 50, P(1):53
	250-444	17	53	50	50						*Serranus*, Bothid	
Centropristis philadelphica	85-124	78	38	67	6	2	2	27		4		T(5):5-15, 30, 40, S(9):10, 20-30
	125-149	21	43	58	17		8	17	2		*Antennarius, Serranus*	T(1):10; S(2):20, 30
	150-224	5	60	50					50			
Lepophidium graellsi	125-199*	50	24	92				8				T(2):10-15
	200-240*	11	55	80	20							
Urophycis floridana	100-149	25	4	38	17		8	42			*Bollmannia*, eel	T(4):15-40; S(1)
	150-199	8	25		50		17	50	17		*Ophichthus*	T(1):40; S(1):10
Cynoscion nothus	125-149	9	22	57	43							
	150-219	12	25	33	33			33			*Saurida*(2), *Trachurus*	T(3):15, 40
Lutjanus synagris	82-124	19	58	88				12				T(1):15
Centropristis ocyurus	92-175	12	42		29		57	14		29		
Cyclopsetta chittendeni	150-224	12	67	50	50						*Saurida*, Bothid	
Diplectrum bivittatum	100-115	12	58	60				40				T(1):5; S(1)
Other species (27)	75-527	87	47	63	15		7	24	4	4	*Saurida*	T(4):5, 20, 30; S(4):15, 40
Total		624	50	53	26	2	4	19	2	2		T(27):5-50; S(18):10-40; P(1):53

TABLE 5.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 46 to 54 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL, except* = mm total length. N = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Cr = crabs, Fi = fish, St = stomatopods, Sh = shrimp, Sq = squid. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps denoted by T (*Trachypenaeus*) or S (*Sicyonia*), followed by frequency and size range (mm tail length).

Fish species	Size class	N	%E	% frequency of occurrence De	Cr	Fi	St	Sh	Sq	Prey fishes	Prey shrimps
Synodus foetens	100-149	7	71			100					
	150-199	43	60	53		35		12	18	*Saurida*	T(2):20, 35
	200-249	45	80	22		67		11			T(1):30
	250-299	10	80			100					
Centropristis philadelphica	85-99	7	57	33	33		33				
	100-124	32	34	33	14	5	5	48			T(5):5, 20-25, 40, S(2):20
	125-149	27	26	65	10	5		25			T(3):10, 30, 40; S(2):20
	150-199	11	0	55	27	9	9				
Urophycis floridana	125-149	20	15	76		18		35			T(3):20, 45
	150-249	21	10	63	5	26		11		*Prionotus*	S(1):25
Prionotus rubio	100-149	24	96					100			
Micropogonias undulatus	100-149	23	96	100							
Lutjanus campechanus	100-200	20	95					100			T(1):10
Lutjanus synagris	82-149	17	65	50				50			T(3):10, 20, 45
Lepophidium graellsi	150-240*	17	29	100							
Saurida brasiliensis	78-125	16	19	15		54		15	15	*Saurida* (2)	T(2):15, 25
Other species (19)	75-400	76	70	78		17		13		*Saurida, Ophichthus*	T(1):20
Total		416	57	56	6	21	2	20	3		T(21):5-45; S(5):20-25

TABLE 6.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected from 55 to 64 m water depths between 4 June and 3 July 1981. Fish sizes in mm SL. N = total stomachs examined, %E = percentage of empty stomachs, De = detritus, Fi = fish, Sh = shrimp, Cr = crabs, Sq = squid, Ms = other taxa including polychaetes, molluscs, and mysids. Frequency of occurrence of prey fishes and shrimps in parentheses. Prey shrimps indicated by T (*Trachypenaeus*) followed by frequency and size range (mm tail length).

Fish species	Size class	N	%E	% frequency of occurrence De	Fi	Sh	Cr	Sq	Ms	Prey fishes	Prey shrimps
Synodus foetens	100-149	8	75		100					*Saurida* (2)	
	150-199	17	76	25	75						
	200-249	108	69	30	67			12		*Saurida* (12)	
	250-400	38	66	23	69			8		*Saurida* (3)	
Centropristis philadelphica	100-124	9	89	100					100		
	125-149	15	67	40		20	60		20		
	150-199	11	27	13	25		63	25			
Prionotus rubio	100-149	21	62	75		25					T(2):20, 25
Micropogonias undulatus	125-160	18	0	100							
Lutjanus campechanus	125-199	14	71	75	25					*Halieutichthys*	
Lagodon rhomboides	91-147	13	69	100							
Centropristis ocyurus	92-149	11	27	88			12				
Priacanthus arenatus	150-205	11	73	67	33	33	33				T(1):10
Prionotus salmonicolor	98-155	11	18	78	11	11			11		T(1):15
Other species(17)	100-279	51	31	91	3	3			3		T(1):10
Total		356	58	65	28	4	7	5	1		T(5):10-25

water depths and were classified as major prey of 9 species, including inshore lizardfish, *Synodus foetens;* largescale lizardfish, *Saurida brasiliensis;* bigeye, *Priacanthus arenatus;* Atlantic cutlassfish, *Trichiurus lepturus;* Mexican flounder, *Cyclopsetta chittendeni;* knobbed porgy, *Calamus nodosus;* blackedge moray, *Gymnothorax nigromarginatus;* bonnethead, *Sphyrna tiburo;* and Atlantic sharpnose shark, *Rhizoprionodon terraenovae.* Fishes were a major food category for all size classes of *Synodus foetens* in all six depth ranges. For all species examined, predation on fishes was more frequent in the four offshore depth ranges (19-28% occurrence) than in the two inshore depth ranges (5 and 6% occurrence). Nineteen taxa of prey fishes were identified, with anchovies, *Anchoa* spp., the primary target in 9-26 m waters and *Saurida* the most frequent in 27-64 m waters. Rogers (1977) found fish in the stomachs of 23 out of 26 fish species from Texas and Louisiana shelf waters. Prey fish comprised at least 48% by volume of the diets of eight of those species: *Saurida brasiliensis* and *Synodus foetens* (as we found); Atlantic midshipman, *Porichthys plectrodon,* sand seatrout, *Cynoscion arenarius,* and silver seatrout, *C.*

nothus (we found 12-18% occurrence in these species); and roughback batfish, *Ogcocephalus parvus*, shortwing searobin, *Prionotus stearnsi*, and sash flounder, *Trichopsetta ventralis* (which we did not examine). Rogers also identified *Saurida* and *Anchoa* as primary prey species.

Crabs occurred in the stomachs of 21 fish species and, over all depths, were categorized as a major food of bank sea bass, *Centropristis ocyurus;* smooth dogfish, *Mustelis canis;* sharksucker, *Echeneis naucrates;* and barred grunt, *Conodon nobilis*, though few individuals of the latter three species were examined. In 9-17 m waters, crabs were a major food of hardhead catfish, *Arius felis*, and large (≥200 mm SL) southern kingfish, *Menticirrhus americanus*. No major crab predators were found in 18-45 m waters, but crabs were a major food of rock sea bass, *Centropristis philadelphica*, and *Priacanthus arenatus* in 46-64 m waters. Rogers (1977) noted that crabs occurred in stomachs of 20 of the 26 fish species he examined but comprised at least 20% by volume of the diets of only 3 species: *Centropristis philadelphica;* blackear bass, *Serranus atrobranchus;* and ragged goby, *Bollmannia communis*

Among other prey types, stomatopods were eaten by 11 species, squid by 6 species, and holothurians by 5 species. These taxa were occasionally major foods of one or two species in a given depth range. Polychaetes, molluscs, mysids, and octopi were also found in fish stomachs, though only rarely.

We found 38 species of shrimp predators from all depths. Seventeen species were classified as having shrimp as a major prey, but 9 of these were represented by data from fewer than 20 individuals. The 8 remaining species, in decreasing order of shrimp occurrence in stomachs from all depths, included *Cynoscion arenarius;* bighead searobin, *Prionotus tribulus; Diplectrum bivittatum; Prionotus rubio;* southern hake, *Urophycis floridana;* star drum, *Stellifer lanceolatus*; *Priacanthus arenatus*; and *Centropristis philadelphica*. Shrimp were major foods of *Cyonscion nothus*, *C. arenarius*, and *Menticirrhus americanus* from the two shallower depth ranges (9-26 m) and of *Cynoscion nothus*, *Centropristis philadelphica*, *Diplectrum bivittatum*, *Urophycis floridana*, and lane snapper, *Lutjanus synagris*, from 27 to 64 m depths. The overall frequency of occurrence of shrimps in fish stomachs increased from 13% in 9-17 m waters to 32% in 27-36 m waters, then declined to 4% in 55-64 m waters. Penaeid shrimps were identified in stomachs of 31 fish species. The penaeids included *Trachypenaeus* spp. (302 occurrences in 28 species), *Sicyonia* spp. (52 occurrences in 13 species), and *Penaeus aztecus* (13 occurrences in 6 species). Rogers (1977) found shrimp in stomachs from all 26 species examined, of which 8 species contained at least 20% by volume of shrimps in their diets. These included *Prionotus rubio, Diplectrum bivittatum*, and *Centropristis philadelphica* (classified as major shrimp predators by us); *Serranus atrobranchus* and blackedge cusk-eel, *Lepophidium graellsi* (classified as minor shrimp predators by us); bay whiff, *Citharichthys spilopterus* (in which we found no shrimp); and *Syacium gunteri* and speckled trout, *Cynoscion nebulosus* (which we did not examine). Rogers frequently identified *Trachypenaeus* spp. and *Sicyonia* spp., but did not find any *Penaeus aztecus* in the 4,550 stomachs he examined.

Species composition, abundance, and biomass data for all fishes and invertebrates were recorded from 89 of the 108 trawl catches collected during the shrimp survey. We compared the observed abundances and distributions of fishes and penaeid shrimps with our data on the occurrence of penaeids in fish stomachs (Table 7). Fishes were most abundant in the 9-17 m depth range (mean: 1,424/30-min

TABLE 7.—Comparison of catch per 30-min tow and size of fishes and penaeid shrimps by depth range with frequency of occurrence of shrimps in fish stomachs from collections off the Texas coast between 4 June and 3 July 1981. N = number of trawl-tows in each depth range.

	Depth range (m)					
	9-17 (N = 16)	18-26 (N = 27)	27-36 (N = 22)	37-45 (N = 17)	46-54 (N = 5)	55-64 (N = 2)
Density (#/tow) ($\bar{x}$ ± SE):						
Fishes	1,424±1,755	588±428	510±336	708±478	951±329	600±343
Trachypenaeus	65±123	608±536	872±651	481±469	125±206	0
Sicyonia	12±23	62±128	95±170	126±181	201±220	74±104
Penaeus aztecus	472±486	1,254±799	1,134±699	284±260	37±26	4±3
Wet weight (G) ($\bar{x}$ ±SE):						
Fishes	29.7±10.2	23.2±11.8	19.3±6.4	24.2±6.9	30.5±10.4	49.9±13.6
Trachypenaeus	3.8±3.7	3.9±2.0	4.4±1.6	4.8±4.0	5.5±5.2	—
Sicyonia	9.0±3.7	7.4±7.5	4.5±3.4	5.7±3.1	6.3±5.4	21.1
P. aztecus	9.7±5.3	11.5±2.5	11.7±2.9	14.2±8.2	36.5±3.6	63.5
Total fish stomachs examined:	1,663	1,733	550	573	418	164
% with *Trachypenaeus*	3.13	3.87	11.45	4.89	4.07	1.02
% with *Sicyonia*	0.36	0.52	2.18	2.97	0.48	0.00
% with *P. aztecus*	0.18	0.17	0.18	0.17	0.00	0.00

tow) and second most abundant in 46-54 m waters (mean: 951/tow). Largest fishes were collected in deepest waters. *Trachypenaeus* spp. and *P. aztecus* catches were highest in 18-36 m waters, and both species increased in size with increasing depth. *Sicyonia* spp. catches were highest in 46-54 m waters and lowest in 27-36 m waters. We found the highest frequency of occurrence of *Trachypenaeus* spp. in fish stomachs occurred in the same depth range (27-36 m) as their maximum catch per tow. Predation upon *Sicyonia* spp. was highest where these penaeids were smallest and moderately abundant (27-45 m depths). Predation upon *P. aztecus* was similar (low to none) in all depth ranges. We also examined data from 30 individual stations where relatively high catches (exceeding 1,000 individuals/tow) of fishes or penaeids were made. We postulated that if the fishes were actively seeking penaeid prey, the frequency of shrimps in fish stomachs from such stations would be higher than the average frequency for all stations in the corresponding depth range. However, we found no indication that locally high abundances of shrimps elicited greater predation by fishes nor any indication that concentrations of fishes at a given location were preying more frequently on penaeids as compared with the average predation frequency of a given depth range. Apparently, the trawl-susceptible fishes preyed in a nondirected, opportunistic manner upon *Trachypenaeus* spp. and *Sicyonia* spp. which were smaller and generally less abundant than *P. aztecus*.

A literature review revealed that the foods of 51 of the 81 fish species examined here have been reported previously to some degree, mainly from inshore and estuarine studies. The major exception is the work of Rogers (1977), as discussed in previous paragraphs. Thirteen of the species we examined yielded no data due to empty stomachs. Forty-seven species were represented in our study by 25 or fewer individuals, and we categorize these data as preliminary until more specimens are analyzed. However, this paper presents new information on the foods of 21 abundant Gulf of Mexico continental shelf fish species by depth range and size class whenever possible.

The analysis of fish stomach contents reported here indicates that brown shrimp stocks are not subjected to heavy predation pressure as the juveniles and subadults migrate offshore. Fifty of the 81 species of trawl-susceptible fishes we examined did not feed on penaeid shrimps, and only 6 species had eaten brown shrimp. The shrimp predators instead preferred smaller penaeids, in part due to the small sizes of the fishes, themselves. Future stomach contents studies, in addition to analyses of trawl-susceptible fishes, should include larger fishes captured by methods such as long lines, gill nets, and fish trawls.

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REGINA DIVITA
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APPENDIX TABLE 1.—Frequency of occurrence of food items (from stomachs containing food) in fishes from the Texas coast collected between 4 June and 3 July 1981. Depth range in meters. N = total stomachs examined. Size in mm SL except where indicated by * (mm total length) or ** (mm disc width). %E = percentage of empty stomachs, De = detritus, Fi = fish, Sh = shrimp, Cr = crabs, St = stomatopods, Sq = squid, Ms = other foods including polychaetes, molluscs, mysids, holothurians, and octopi. Prey shrimps denoted by T (*Trachypenaeus*), S (*Sicyonia*), or P (*Penaeus aztecus*), followed by frequency of occurrence in parentheses and size range (mm tail length).

Fish species	Depth range	N	Size		%E	% frequency of occurrence of food items							Prey shrimps
			Mean	Range		De	Fi	Sh	Cr	St	Sq	Ms	
Micropogonias undulatus	9-64	2,903	127	95-163	36	86	1	9	2	1	1	6	T(84) 5-45, S(4) 15, P(1) 45
Synodus foetens	9-64	893	192	48-444	73	33	69	16			7		T(27) 5-50, P(5) 40-53
Cynoscion nothus	9-46	839	135	76-219	65	53	18	28	1		1	1	T(42) 10-45, S(2) 20, P(1) 45
Centropristis philadelphica	9-64	437	120	85-224	43	59	6	30	11	3	1	2	T(32) 5-40; S(25) 10-30, P(1) 20
Lepophidium graellsi	9-64	317	183*	95-240	52	83	3	13	5	1			T(10) 5-15, 30, 40, S(1) 5
Leiostomus xanthurus	9-54	316	134	86-164	23	100							
Menticirrhus americanus	9-36	257	174	112-282	75	40	9	20	20	6		8	T(14) 5-30, 45, S(5) 20-30, 45
Diplectrum bivittatum	9-45	134	101	87-115	66	49		44	4	2			T(13) 5-25, 40, S(1) 10
Urophycis floridana	18-64	128	143	114-277	21	41	22	41	4	4		1	T(19) 5-20, 35-45, S(7) 10-15, 25
Lutjanus campechanus	9-64	118	107	65-200	59	60	13	13	10	2	8	6	T(2) 10, 20
Cynoscion arenarius	9-26	105	177	134-239	76	4	16	84	8				T(16) 15-45, P(4) 57-62
Larimus fasciatus	9-36	84	116	78-135	44	94	4	2					
Prionotus rubio	9-64	73	124	72-163	67	54		42	4				T(8) 10-45
Lutjanus synagris	9-54	66	114	82-190	67	68	5	27	5				T(6) 10-20, 35, 45, P(1) 60
Arius felis	9-36	43	192	132-293	16	44	3	17	28	11		17	T(4) 10, 40, 45, S(1) 10
Polydactylus octonemus	9-36	42	110	72-130	31	79	7	14					
Prionotus salmonicolor	9-64	33	130	98-155	39	70	5	20	5			5	T(1) 15
Chloroscombrus chrysurus	18-26	32	126	99-172	78	100							
Stellifer lanceolatus	9-17	30	86	72-112	33	45	25	35					T(3) 5, 10, 20
Saurida brasiliensis	18-54	28	99	78-125	21	36	50	9			9		T(2) 15, 25
Centropristis ocyurus	27-64	27	125	92-175	41	50	12	6	31			13	
Lagodon rhomboides	18-64	23	120	91-147	74	100							
Stenotomus caprinus	18-26	23	69	54-122	0	100							
Prionotus tribulus	18-64	21	122	100-145	57	33		67					T(4) 20, S(2) 15
Decapterus punctatus	18-64	20	151	133-170	85	100							
Orthopristis chrysoptera	9-54	20	136	112-176	50	100							
Priacanthus arenatus	27-64	20	183	150-205	55	44	33	33	11				T(2) 10-15
Cyclopsetta chittendeni	37-54	20	179	100-224	60	63	37						
Ophidion welshi	9-26	19	200*	174-236	42	100							
Porichthys plectrodon	9-64	17	134	109-161	53	100	12						
Scomber japonicus	9-64	17	159	130-326	18	93	7						
Ophidion holbrooki	18-54	16	204*	173-235	69	100							
Calamus nodosus	27-64	15	138	121-162	87	33	33					33	
Paralichthys lethostigma	9-45	14	217	138-265	36	56		44					T(3) 20, 30, 40
Serranus atrobranchus	37-64	13	80	71-88	15	91		9	9				S(1) 15
Prionotus paralatus	46-54	12	121	113-133	100								
Gymnothorax nigromarginatus	18-54	11	374*	240-463	82	50	50						
Brotula barbata	9-64	11	149*	120-170	55	40		60					T(3) 5, 20
Trichiurus lepturus	9-36	11	446*	372-560	55	20	60	20					T(1) 35
Citharichthys spilopterus	18-45	10	91	70-119	0	100							
Cyclopsetta fimbriata	37-64	10	184	118-227	20	75	12	12					
Mullus auratus	9-64	10	116	92-146	10	78		22					T(2) 10
Chaetodipterus faber	9-17	9	128	118-140	78	100							
Equetus umbrosus	9-17	8	124	114-134	0	100							
Trachurus lathami	37-45	8	150	142-156	75	100							
Prionotus roseus	27-64	7	122	112-144	0	71		43					T(2) 20, 30
Raja texana	27-45	7	348**	260-527	14	50		50					T(1) 44
Rhizoprionodon terraenovae	9-36	7	268	140-600	0	57	29	14					
Sardinella anchovia	18-36	7	177	173-186	86	100							
Scorpaena calcarata	18-36	7	62	48-111	29	100			20				
Peprilus burti	18-26	6	89	72-136	0	83		17					
Urophycis cirratus	37-45	6	125	111-140	17		20	60		40			T(2) 5, 20, S(1) 15
Odontoscion dentex	9-17	5	109	105-117	0	60	20	20					T(1) 5
Ancylopsetta quadrocellata	18-64	4	176	123-197	75	100							
Balistes capriscus	9-45	4	197	189-210	100								
Mustelis canis	9-45	4	359	342-375	0	25		25	75	25			S(1) 40
Opisthonema oglinum	18-26	4	164	162-166	100								
Sphyraena guachancho	27-36	4	230	220-234	50	50		50					T(1) 20
Sphyrna tiburo	9-26	4	471	343-662	0		50		25	50		25	
Trachinocephalus myops	18-45	4	124	118-130	50	100							
Bairdiella chrysoura	9-17	3	114	109-119	67	100							
Echeneis naucrates	27-45	3	467	189-655	33	50			50			50	
Haemulon aurolineatum	46-54	3	138	136-140	100								
Congrina flava	27-45	2	238*	175-300	50	100							
Conodon nobilis	9-17	2	140	128-152	50				100				
Diplectrum formosum	27-36	2	164	163-166	0	100							
Prionotus scitulus	27-36	2	108	100-115	0			100					T(1) 30, S(1) 20
Ancylopsetta dilecta	55-64	1	174		100								
Archosargus probatocephalus	9-17	1	191		0	100							
Brevoortia gunteri	9-17	1	160		0	100							
Carcharhinus limbatus	18-26	1	133		100								
Carcharhinus porosus	18-26	1	330		100								
Caulolatilus microps	46-54	1	190		100								
Chilomycterus schoepfi	18-26	1	141		100								

APPENDIX TABLE 1.—*Continued.*

Fish species	Depth range	N	Size Mean	Range	%E	% frequency of occurrence of food items De	Fi	Sh	Cr	St	Sq	Ms	Prey shrimps
Dasyatis sabina	9-17	1	245**		0			100					
Lagocephalus laevigatus	18-26	1	103		100								
Myrophis punctatus	18-26	1	400*		100								
Rypticus maculatus	9-17	1	116		0	100							
Scomberomorus maculatus	27-36	1	345		100								
Syacium papillosum	37-45	1	206		0		100	100				100	
Symphurus plagiusa	18-26	1	114		100								
TOTAL		7,374											T(302):5-50; S(52):5-45, P(13):20-62

APPENDIX TABLE 2.—Fishes collected from the Texas coast between 4 June and 3 July 1981 which were excluded from stomach analyses because of small size (<150 mm in length).

Species	Number	Species	Number
Syacium gunteri	10,756	*Ancylopsetta dilecta*	65
Stenotomus caprinus	8,563	*Priacanthus arenatus*	53
Micropogonias undulatus	6,787	*Brotula barbata*	50
Chloroscombrus chrysurus	4,352	*Centropristis ocyurus*	48
Prionotus rubio	2,895	*Antennarius radiosus*	44
Diplectrum bivittatum	2,699	*Brevoortia patronus*	43
Peprilus burti	2 631	*Scomber japonicus*	42
Cynoscion nothus	2,206	*Selene setapinnis*	40
Sphoeroides parvus	1,662	*Prionotus carolinus*	35
Citharichthys spilopterus	1,621	*Upeneus parvus*	31
Halieutichthys aculeatus	1,315	*Urophycis floridana*	31
Porichthys plectrodon	1,307	*Menticirrhus americanus*	28
Lutjanus synagris	1,161	*Prionotus ophryas*	28
Serranus atrobranchus	1,123	*Prionotus scitulus*	26
Etropus crossotus	1,106	*Etropus microstomus*	19
Saurida brasiliensis	1,088	*Synodus foetens*	19
Centropristis philadelphica	993	*Equetus umbrosus*	18
Lutjanus campechanus	739	*Caulolatilus intermedius*	16
Prionotus paralatus	665	*Decapterus punctatus*	15
Prionotus tribulus	629	*Peprilus paru*	15
Prionotus salmonicolor	595	*Hoplunnis tenuis*	14
Trachurus lathami	587	*Sardinella anchovia*	14
Cyclopsetta chittendeni	570	*Neomerinthe hemingwayi*	13
Stellifer lanceolatus	531	*Paralichthys squamilentus*	11
Larimus fasciatus	458	*Serraniculus pumilio*	11
Mullus auratus	446	*Syacium papillosum*	11
Bollmannia communis	422	*Balistes capriscus*	10
Lepophidium graellsi	362	*Histrio histrio*	9
Scorpaena calcarata	357	*Raja texana*	9
Polydactylus octonemus	328	*Trichiurus lepturus*	9
Prionotus stearnsi	319	*Anchoa mitchilli*	8
Leiostomus xanthurus	318	*Congrina flava*	8
Cynoscion arenarius	291	*Engyophrys senta*	7
Ogcocephalus radiatus	266	*Brevoortia gunteri*	5
Lagocephalus laevigatus	209	*Etrumeus teres*	5
Synodus poeyi	203	*Cyclopsetta fimbriata*	4
Prionotus roseus	187	*Eucinostomus gula*	4
Opisthonema oglinum	183	*Aluterus schoepfi*	3
Symphurus plagiusa	156	*Bairdiella chrysoura*	3
Monacanthus hispidus	128	*Paralichthys lethostigma*	3
Hoplunnis macrurus	111	*Serranus subligarius*	3
Lagodon rhomboides	108	*Calamus nodosus*	2
Harengula jaguana	106	*Sphoeroides dorsalis*	2
Gymnachirus texae	98	*Lactophrys quadricornis*	1
Anchoa hepsetus	96	*Epinephelus flavolimbatus*	1
Orthopristis chrysoptera	89	*Kathetostoma albigutta*	1
Urophycis cirratus	80	*Myrophis punctatus*	1
Bellator militaris	76	*Antennarius scaber*	1
Ancylopsetta quadrocellata	67	*Scomberomorus maculatus*	1
		Total	61,385

THE OCCURRENCE OF SPOT, *LEIOSTOMUS XANTHURUS*, AND ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, LARVAE IN ONSLOW BAY AND NEWPORT RIVER ESTUARY, NORTH CAROLINA[1]

Past studies indicate that spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, spawn offshore in autumn and probably in winter (Hildebrand and Schroeder 1928; Hildebrand and Cable 1930; Dawson 1958). Peak spawning times and specific spawning areas have been deduced from sightings of large numbers of recently spawned larvae at specific locations nearshore or offshore. Weinstein et al. (1980) reported on the upstream distribution of postlarval spot and Atlantic croaker within the Cape Fear River estuary, N.C., above a steam electric power plant.

Extensive studies have been conducted in the Cape Fear River estuary[2] in the southern portion of Onslow Bay. Some of these studies dealt with recruitment of sciaenids into the Cape Fear River estuary. However, the hydrographic conditions of this estuary[3] are markedly different from those of other estuaries along the North Carolina coast and from most other estuaries along the east coast of the United States; therefore, any comparisons made with the Cape Fear findings will result in some differences.

In our current study which extended from October 1972 through April 1974, ichthyoplankton was systematically sampled monthly in northern Onslow Bay and Newport River estuary, N.C. The goal of the study was to determine the abundance and distribution of Atlantic menhaden, *Brevoortia tyrannus*, larvae (Nelson[4]), but spot and Atlantic croaker larvae were also caught in large numbers. Our study is based on the findings from these sciaenid samples. We present data on the occurrence, size, and abundance of spot and Atlantic croaker larvae from offshore to inshore and relate these findings to spawning time and area, as well as timing and duration of recruitment of these larvae into the Newport River estuary. Little has been previously published concerning the recruitment of larvae of these two species into estuaries, particularly in North Carolina waters.

Methods

Larval fish were collected monthly aboard the RV *Onslow Bay* by towing paired 60 cm bongo plankton nets of 0.333 and 0.505 mm mesh. Oblique tows were conducted from surface to near bottom at each station at a speed of 2.8 km/h (1.5 kn). Minimum duration of tows was 5 min, and the number of oblique tows (normally 2-4) made at each station depended on the water depth. This procedure was followed to insure similarity of water volumes sampled at each station. Bongo nets were weighted with a 45.4 kg (100-lb) lead weight, and depth of tow was recorded with a bathykymograph attached just above the bongo nets. Flow rates were estimated from torpedo-shaped digital flowmeters (made by General Oceanics, Inc., Miami, Fla.[5]) that were placed in the center of the mouth of each bongo net. A calibration factor, based on the length of tow, was determined for each flowmeter; average volume of water strained, per station per month, ranged from 63.3 to 78.1 m^3.

Collection stations were grouped among three areas: Offshore, inshore, and estuarine. The two ocean areas were each divided into three zones, while the estuarine area was considered one zone (Fig. 1). The approximate distances from shore, depths of water, and number of stations for each zone are described in Table 1.

The number and location of stations varied between the 1972-73 and the 1973-74 sampling periods. Nineteen stations were sampled each month, except April, from October 1972 to September 1973. In October 1973, three inshore stations, two in zone 1 and one in zone 2, and all offshore stations in zone 4 were deleted, and three stations in zone 6 were added,

[1]Contribution No. 83-20B, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[2]Brunswick Steam Electric Plant, Cape Fear Studies, Sections 1-10. Reports to Carolina Power and Light Co., Raleigh, N.C., January 1980, 428 p.

[3]Brunswick Steam Electric Plant, Cape Fear Studies. Ocean larval fish, November 1976-1978. Environmental Technology Section, Vol. V, 1979. Report to Carolina Power and Light Co., Raleigh, N.C., 305 p.

[4]Nelson, W. R. 1977. Onslow Bay studies. Unpubl. manuscr., 64 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, N.C.

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

TABLE 1.—Number, offshore distance, and depth of collection stations in Zones 0-6, Onslow Bay and Newport River estuary, N. C., 1972-73 and 1973-74.

Area	Zone no.	No. stations 1972-73	No. stations 1973-74	Distance offshore (km)	Depth (m)
Offshore	6	0	3	74-79	32.9-40.2
	5	3	3	44-50	27.4-31.1
	4	3	0	32-36	21.9-27.4
Inshore	3	3	3	17-22	16.5-20.1
	2	3	2	8-13	14.6-16.5
	1	3	1	3-6	14.6-14.6
Newport River estuary	0	4	4	0	1.8-12.8

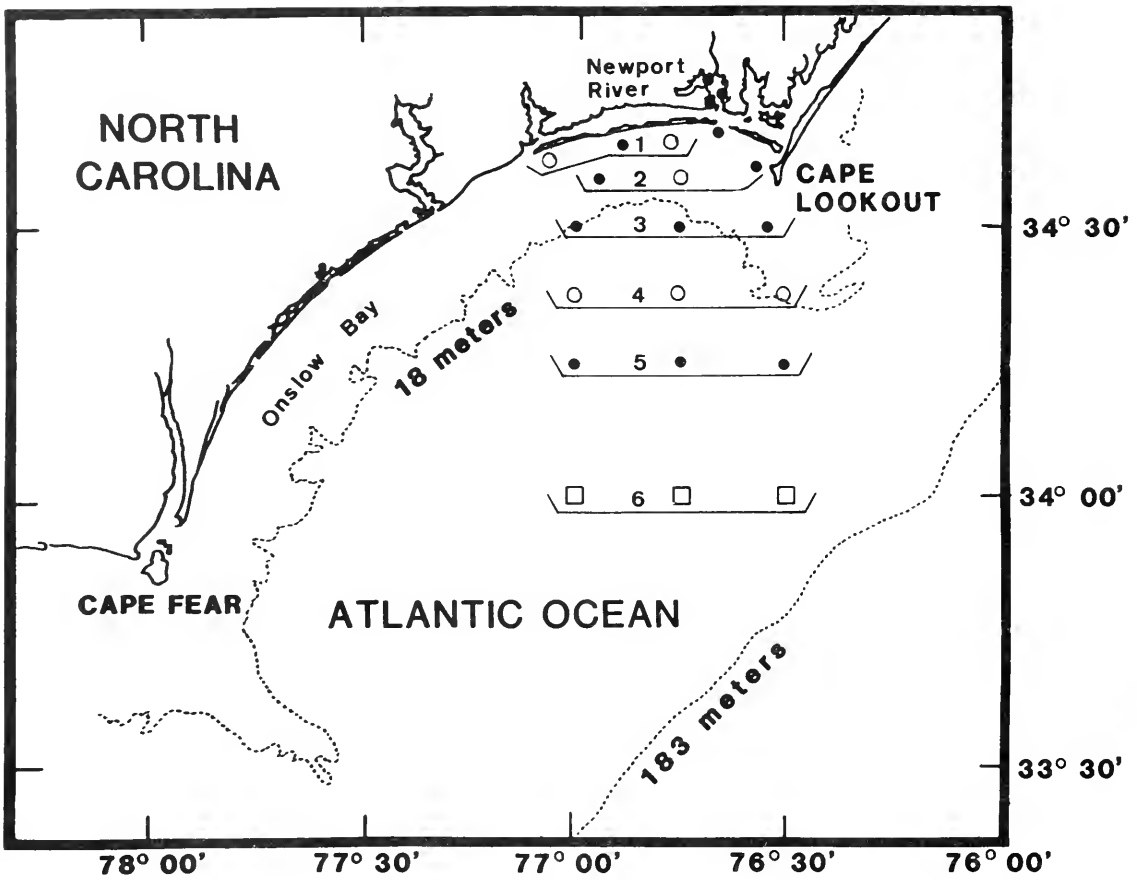

FIGURE 1.—Location of ichthyoplankton stations in Onslow Bay and Newport River estuary, N.C., sampled October 1972-April 1974 (dots), October 1972-September 1973 (circles), and October 1973-April 1974 (squares). Sampling stations are grouped according to offshore distance and water depth: Zone 0, Newport River estuary; zones 1-3, inshore to ocean; zones 4-6, offshore to ocean.

leaving 16 stations to be sampled the second year. Because the *Onslow Bay* had limited range and had to be returned to port each night, about 5 d/mo were required to run all stations. Samples were taken between 0800 and 1700 h. Tows were not stratified by tidal cycle; all collections were assumed completely random. During the 19 mo, sampling was missed completely for 1 mo and was only partially completed during six other months, due either to mechanical failure of the vessel or winch or to adverse weather.

Samples were preserved in 5% buffered Formalin. Larvae and eggs were removed with the aid of a dissecting microscope. Larvae were identified to the lowest determinable taxon, counted, and measured to the nearest 0.1 mm standard length (SL) or notochord length, depending on stage of development. All measurements denote larval length. For large catches, 50 larvae/subsample were measured. Larvae were categorized by length groups according to the developmental stages as defined by Fruge and Truesdale (1978) and Powell and Gordy (1980). Preflexion larvae measured 2.0-4.0 mm SL, flexion 4.1-5.0 mm, and postflexion >5.0 mm. Larval data from the 0.333 and 0.505 mm mesh nets were combined for each station within a month to provide a better synoptic profile of each station, since there is less extrusion of larvae <4 mm from the 0.333 mm mesh net and higher catches of larvae >10 mm in the 0.505 mm mesh net. Counts were adjusted to a standard catch (Smith and Richardson 1977:36) at each station by the following formula:

$$SHF = \frac{100D}{V}$$

where SHF = standard haul factor
V = volume of water strained (m^3)

D = depth of sample (m)
100 = number of square meters of surface area.

For example, a tow which strains 60 m^3 of water through a depth of 12 m provides a SHF of 20. Multiplying the number of larvae in the catch by the SHF gives an estimate of the number of larvae in the entire water column under a surface area of 100 m^2. Thus the calculated number is dependent on both density (number per m^3) and depth.

Results

We compared mean standard lengths and larval abundance for each species by month, station, and year to show spawning time and movement.

Spot, 1972-73 Season

Limited spawning may have occurred in September, since only one spot larva was caught in October, when sampling began (Table 2). A few larvae were caught at three offshore and two inshore stations in November and at all offshore and four inshore stations in December. Preflexion larvae (2.0-4.0 mm), which denote recent spawning and were present at all of those stations, increased markedly in abundance in December, especially at offshore stations. Mean length of larvae increased from November to December by about 1 mm at offshore stations, but decreased by slightly <1 mm at inshore stations. No larvae were captured at estuarine stations until January. In January, larvae were caught at all offshore, five inshore, and three estuarine stations. Preflexion larvae were caught at two offshore stations, but none were caught at inshore stations. This was the last month that preflexion larvae were present, indicating that spawning had ceased or at least diminished. Mean lengths were 7.9 mm at offshore and 9.2 mm at inshore stations, an increase over December of 4.4 and 5.8 mm, respectively. This was the largest increase recorded and reflects the decline of preflexion larvae at offshore stations and their absence at inshore stations. Mean length of larvae caught at estuarine stations was 13.3 mm. In February, as in the previous 2 mo, larvae were caught in relatively large numbers at all offshore stations, but in relatively low numbers at inshore stations. The number of larvae in the estuary during February increased fivefold over those caught in January. Larval mean lengths had increased only slightly in each area (offshore, inshore, and estuarine). In March, larvae were caught at one offshore, seven inshore, and three estuarine stations. Fewer larvae were caught in March than in February, but mean lengths had increased in each area.

From October through March, an average of 28.2 and 2.2 spot larvae/station sampled were caught offshore and inshore, respectively. Number of larvae per station peaked at offshore (81.7) and inshore (4.3) stations in December and at estuarine stations (367.0) in February. Mean lengths of larvae from offshore to inshore increased in November (no larvae were caught in the estuary) and progressively increased from offshore to the estuary during January-March. The large number and relatively small size of larvae caught offshore, as compared with the number

TABLE 2.—Number of sampling stations, and number and length of spot larvae collected in Onslow Bay and Newport River estuary, N.C., October-March 1972-73 and 1973-74.

		1972-73				1973-74			
		No.	Total	Length (mm SL)		No.	Total	Length (mm SL)	
Month	Area	stn.	larvae	Range	Mean	stn.	larvae	Range	Mean
October	Offshore	4	0	—	—	0	0	—	—
	Inshore	7	1	4 4	4.4	6	0	—	—
	Estuary	4	0	—	—	4	0	—	—
November	Offshore	6	15	2.6-3.0	2.8	6	1	7.6	7.6
	Inshore	9	3	3.2-4.2	3.8	6	5	2.0-3.2	2.5
	Estuary	4	0	—	—	4	0	—	—
December	Offshore	6	490	2.4-5.6	3.5	2	17	2.7-4.6	3.4
	Inshore	9	39	2.6-5.2	3.4	6	15	3.0-6.6	4.8
	Estuary	4	0	—	—	4	0	—	—
January	Offshore	6	252	2.4-12.0	7.9	6	554	2.4-9.6	5.0
	Inshore	9	7	4.4-11.2	9.2	6	40	3.6-13.2	9.4
	Estuary	4	310	11.2-16.4	13.3	4	6	11.6-16.0	13.3
February	Offshore	6	198	4.4-12.8	8.3	3	3	3.3-7.4	5.5
	Inshore	9	31	5.2-12.8	9.5	6	5	7.2-11.7	8.9
	Estuary	4	1,468	8.8-18.8	13.7	3	2	12.9-14.6	13.8
March	Offshore	6	5	6.4-12.0	9.0	3	1	7.2	7.2
	Inshore	9	31	7.6-16.0	13.4	6	1	10.8	10.8
	Estuary	4	84	10.4-18.0	14.5	4	2	12.0-14.8	13 4
Totals	Offshore	34	960			20	576		
	Inshore	52	112			36	56		
	Estuary	24	1,862			23	10		

and length of those caught inshore, indicated that more spawning occurs offshore than inshore.

Spot, 1973-74 Season

Although samples were taken from May 1973 through April 1974, not all stations were sampled each month, and no spot larvae were caught until November. In November, one larva (7.6 mm) was caught at an offshore station, none were caught at estuarine stations, and only five (all preflexion larvae, 2.0-4.0 mm) were caught at inshore stations (Table 2). The presence of preflexion larvae indicated that spot had spawned recently, and the presence of the postflexion larva (7.6 mm) denoted that some spot had spawned as early as October. However, low abundance of larvae in October samples, taken over two spawning seasons, indicated only limited early-season spawning. In December, larvae were caught at the only two offshore stations sampled and at four inshore stations, but none were caught at any estuarine stations. Preflexion larvae were caught at both offshore stations and at one inshore station. In January, more spot larvae were caught in each of the three sampling areas than at any other time of the current season. Larvae were caught at all offshore and four inshore stations. Preflexion larvae, captured at five offshore stations and one inshore station, indicated that spot had recently spawned and that spawning was widespread within and probably outside the sampling area. Other larvae ranged up to 9.5 mm offshore and up to 13.2 mm inshore. A few larvae, ranging from 11.6 to 16.0 mm, were caught at estuarine stations. In February, the number of larvae showed a marked decline; only three were caught at offshore, five at inshore, and two at estuarine stations. Preflexion larvae were caught at one offshore station. The remaining larvae ranged from 7.2 to 11.7 mm at other offshore and inshore stations. Larvae caught at estuarine stations measured 12.9 and 14.6 mm. In March, only four larvae were caught, all postflexion, ranging from 7.2 mm at offshore stations to 14.8 mm at estuarine stations. In April, one 4 mm larva was caught at an offshore station, and none were caught at inshore or estuarine stations.

From October through March an average of 28.8 and 1.6 spot larvae/station sampled were caught at offshore and inshore stations, respectively. Larval abundance peaked at offshore and inshore stations in January, as compared with December of the previous season. Abundance at estuarine stations was very low; six larvae were caught in January, two in February, and two in March. In December, mean lengths increased from offshore to inshore (no larvae were caught in the estuary), and from January through March mean lengths progressively increased from offshore to the estuary. As during the 1972-73 spawning season, the large number and relatively small size of larvae caught offshore, compared with those caught inshore, indicated that more spawning occurs offshore than inshore.

Atlantic Croaker, 1972-73 Season

No samples were taken prior to October 1972, but number and size of larvae collected in October indicated that Atlantic croaker had spawned in September. In October, larvae were caught at three offshore, six inshore, and two estuarine stations (Table 3). Preflexion larvae (2.0-4.0 mm), indicative of recent spawning, were caught at three offshore stations and at five inshore stations. Larvae caught at estuarine stations ranged from 4.3 to 9.9 mm and included both flexion and postflexion larvae. These Atlantic croaker larvae were recruited into the estuary at a much smaller size and about 3 mo earlier than spot larvae. In November, Atlantic croaker larvae were caught at all offshore and inshore stations, but were not caught at any estuarine stations. The presence of preflexion larvae, caught at five offshore and five inshore stations, indicated that spawning was widespread within and probably outside our sampling area. In December, larvae were caught at all offshore and four inshore stations. Preflexion larvae continued to be quite abundant and occurred at three offshore and four inshore stations. Only postflexion larvae were caught at estuarine stations. Preflexion larvae were not caught after December, indicating that spawning had probably ended or at least diminished. In January, larval abundance declined in each area, but larvae were caught at all offshore, three inshore, and two estuarine stations. In February, larval abundance increased slightly at offshore and inshore stations and showed a marked increase at estuarine stations. Larvae were caught at four offshore, three inshore, and all estuarine stations. In March, mean length and number of larvae caught in each area declined from the previous month. Larvae were caught at two offshore, four inshore, and three estuarine stations. No samples were taken in April, and no larvae were caught after March.

From October through March, an average of 10.6 and 5.0 Atlantic croaker larvae/station sampled were caught offshore and inshore, respectively. Abundance peaked at offshore stations in November (1 mo earlier than spot larvae), at inshore stations in December (same as spot), and at estuarine stations in Feb-

TABLE 3.—Number of sampling stations, and number and length of Atlantic croaker larvae collected in Onslow Bay and Newport River estuary, N.C., October-March 1972-73 and 1973-74.

		1972-73				1973-74			
		No.	Total	Length (mm SL)		No.	Total	Length (mm SL)	
Month	Area	stn.	larvae	Range	Mean	stn.	larvae	Range	Mean
October	Offshore	4	41	2.3-6.5	4.1	0	0	—	—
	Inshore	7	61	2.6-8.2	4.4	6	25	2.4-8.0	5.1
	Estuary	4	84	4.3-9.9	7.1	4	15	4.4-8.0	5.8
November	Offshore	6	211	2.2-10.6	3.5	6	1	3.0	3.0
	Inshore	9	62	2.2-11.6	5.0	6	21	2.4-7.6	3.8
	Estuary	4	0	—	—	4	3	7.2-9.6	8.3
December	Offshore	6	60	3.0-7.7	5.4	2	0	—	—
	Inshore	9	104	2.8-9.0	5.5	6	13	4.8-10.0	7.3
	Estuary	4	25	8.8-11.6	10.0	4	9	9.4-11.8	10.5
January	Offshore	6	13	4.8-9.0	7.3	6	6	4.0-5.6	4.7
	Inshore	9	4	8.0-10.4	9.4	6	5	8.4-10.0	9.2
	Estuary	4	10	10.0-12.8	10.9	4	0	—	—
February	Offshore	6	31	4.8-10.4	7.8	3	0	—	—
	Inshore	9	16	7.6-11.6	9.2	6	0	—	—
	Estuary	4	440	7.6-22.8	10.5	3	31	9.0-12.9	11.2
March	Offshore	6	3	5.2- 7.2	6.1	3	0	—	—
	Inshore	9	12	7.6-10.0	8.6	6	0	—	—
	Estuary	4	25	7.2-12.0	10.1	4	8	9.6-12.0	10.8
Totals	Offshore	34	359			20	7		
	Inshore	52	259			36	64		
	Estuary	24	584			23	66		

ruary (same as spot). In November, mean length increased from offshore to inshore (no larvae were caught in the estuary). During each of the other months, mean lengths progressively increased from offshore to the estuary. Larval distribution and size indicated a greater frequency of spawning closer to shore by Atlantic croaker than by spot. Also, the Atlantic croaker larvae were recruited into the estuary earlier in the season and at a smaller size than were spot larvae.

Atlantic Croaker, 1973-74 Season

Samples were taken from May 1973 through April 1974, but not all stations were sampled each month (Table 3). Eight Atlantic croaker larvae, ranging in length from 3.3 to 5.2 mm, were caught at estuarine stations in September and were the smallest caught in the estuary (not included in Table 2). In October, no samples were taken at offshore stations but larvae were caught at four inshore and two estuarine stations. Preflexion larvae (2.0-4.0 mm), which denote recent spawning, were caught at one inshore station. Larvae caught at estuarine stations were either flexion (4.1-5.0 mm) or postflexion (>5.0 mm). In November, larvae were caught at one offshore, four inshore, and two estuarine stations. Preflexion larvae were caught at one offshore and three inshore stations. This was the last month that preflexion larvae were present, except for one caught in January. Larvae caught in the estuary were all postflexion. In December, no Atlantic croaker larvae were caught at offshore stations, but they were caught at four inshore stations and at two estuarine stations. Size ranged from 4.8 mm inshore to 11.8 mm in the estuary. In January, larvae were caught at three offshore and two inshore stations, but none were caught at any estuarine stations. Larvae caught offshore ranged from 4.0 to 5.6 mm, indicating that spawning had probably occurred between our December and January collections. Larvae caught inshore were all postflexion. In February and March, larvae were not caught at any offshore and inshore stations, but were caught at two estuarine stations in February and three in March. All larvae were postflexion. In April, two offshore, seven inshore, and four estuarine stations were sampled, but only one larva was caught, a 6.0 mm larva at an inshore station.

Certain similarities were noted between the 1972-73 and 1973-74 spawning seasons, even though only a limited number of Atlantic croaker larvae were caught during the latter period, and not enough were caught during any month to determine the time of peak abundance. From October through March, an average of only 0.4 and 1.9 mm larvae/station sampled were caught offshore and inshore, respectively. When larvae were caught in each of the three areas, mean lengths progressively increased from offshore to the estuary. When larvae were caught in only two areas, mean length increased either from offshore to inshore or from inshore to the estuary. Distribution and size of larvae indicated a greater frequency of spawning closer to shore by the Atlantic croaker than by spot, as with larvae caught during 1972-73. Also, as in 1972-73, Atlantic croaker larvae were recruited into the estuary earlier in the season and at a smaller size than were spot larvae.

Discussion

The distribution and abundance of sciaenid larvae differed between the two spawning seasons studied. The estimated numbers of spot and Atlantic croaker larvae present at selected stations (those that were sampled each month and could be compared between the two years) in each of the three sampling areas indicated that during the 1973-74 season the numbers of spot and Atlantic croaker larvae were 34 and 87% less, respectively, than during the previous year, and that the combined number of larvae for both species was down 55%. This decline could have resulted from a higher mortality of eggs or early-stage larvae, from stations being missed (other than selected stations), from peaks of abundance being missed, or from a true decline in numbers present.

Nelson et al. (1978) found that inshore and offshore Ekman transport mechanisms affected the abundance of Atlantic menhaden larvae in the surface waters of Onslow Bay. Since no comparable studies[6] have been conducted for spot and Atlantic croaker larvae in these offshore areas, we must infer movement and drift patterns of these species from studies within the estuaries, and by relating egg and larval stages to their likely position in the water column as they move from offshore towards an inlet.

Eggs and preflexion sciaenid larvae are buoyant and would be near the surface waters where they would respond to the forces of Ekman transport; however, larvae probably become demersal during the flexion and postflexion stages. As this "settling out" phenomenon occurs, they would be less affected by the Ekman transport of surface waters and more affected by other forces (inertia and Coriolis) that occur at greater depths.

Within the estuary, young spot and Atlantic croaker larvae are abundant in the middle and lower layers of the water column during the day, while at night they tend to accumulate near the surface (Wallace 1941; Haven 1957; Lewis and Wilkens 1971; Weinstein et al. 1980). Most sciaenid larvae, except for the earlier stages, are probably within these layers in Onslow Bay. Stefánsson et al. (1971) found that the circulation pattern of water in Onslow Bay was progressively changing seasonally, but that there was always an indication of a general counterclockwise eddy. Unpublished field and experimental observations at the Southeast Fisheries Center Beaufort Laboratory of the National Marine Fisheries Service indicate that small sciaenid larvae are able to swim against the current for brief periods of time. Sciaenid larvae probably are able to move into the estuaries from offshore by a combination of swimming, resting on or near the bottom, and drifting with the current or water mass.

Even though spot and Atlantic croaker larvae were taken over the same general time period each year, some differences between the two species occurred in spawning time, movement, abundance, and larval size. Atlantic croaker spawned before October of each year, since larvae were captured in relatively large numbers in the ocean in October, about 2 mo earlier than spot larvae (Tables 2, 3). Atlantic croaker larvae were first captured in the estuary in either September or October of each year, whereas no spot larva was caught in the estuary until January, about 4 mo later than the Atlantic croaker.

Atlantic croaker larvae caught in October and November at offshore and inshore stations were generally larger than spot larvae caught in November and December (Tables 2, 3). This larger size, however, was not maintained. After the initial 2 mo, mean lengths of the Atlantic croaker were usually less than those of spot in comparable time periods and sampling areas. Also, Atlantic croaker larvae caught in inside waters were noticeably smaller than spot larvae. This size difference between the two species, and the fact that Atlantic croaker larvae were captured in the estuary much earlier in the season than spot, indicate that Atlantic croaker spawn earlier in the season and/or closer to shore than spot, and that their larvae usually move into the estuary at a smaller size and probably at an earlier age. Warlen (1982) and Warlen and Chester[7] generally agreed that larval size and age are related. However, during winter months with water temperatures relatively low, they found more age variations in larvae of similar lengths than with water temperatures relatively high.

Hildebrand and Cable (1930) believed that spot and Atlantic croaker spawned relatively nearshore in the Beaufort, N.C., area and that the principal spawning months were December-January for spot and October-March for Atlantic croaker. Powles and Stender (1978) reported that spot and Atlantic croaker spawn over the continental shelf in the South Atlantic Bight. We found that spot spawn more heavily offshore than inshore, whereas Atlantic croaker spawn with about equal intensity in both

[6]Cape Fear River Estuary studies in southern Onslow Bay were done under different hydrographic conditions than we encountered in the current study.

[7]Warlen, S. M., and A. J. Chester. 1982. Age, growth and distribution of larval/early juvenile spot, *Leiostomus xanthurus*, off North Carolina. Unpubl. manuscr., 25 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, N.C.

areas. Although spawning occurs over several months for both species, the principal spawning months are December-January for spot and October-December for Atlantic croaker. Some Atlantic croaker were collected each month until mid-April; spot were caught through March.

Preflexion larvae, indicative of recent spawning, were present generally during the first half of each season at many offshore stations and at a lesser number of inshore stations, but the size variation of larvae between the two areas suggests that the primary spawning area was offshore (Figs. 2, 3). The 1972-73 data show that small, recently hatched larvae were more predominant offshore than inshore and that larvae generally were progressively larger as they moved into the estuary, as was also found by Warlen (1982). Size increased with passage of time as the larvae moved from the major offshore spawning area, through the transitory inshore area, to the estuarine nursery area.

With some exceptions, larvae were more abundant offshore than inshore. During the 1972-73 season, as larvae moved to inshore waters, their numbers (available to our gear) usually showed a marked decline, probably the result of natural mortality, predation, and the ability to avoid capture because of their increased mobility at a larger size. In the estuary, availability again increased as numbers built up in a much smaller area (Table 4).

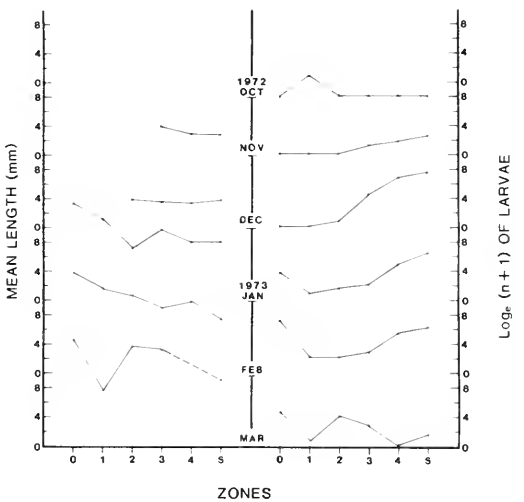

FIGURE 2.—Mean length and relative abundance of spot larvae collected October 1972-March 1973 in Onslow Bay and Newport River estuary, N.C. Sampling stations are grouped according to offshore distance and water depth: Zone 0, Newport River estuary; zones 1-3, inshore to ocean; zones 4-6, offshore to ocean. The mean length (mm) scale is 0-10 for each month. Some plots extend into adjacent months when a point exceeds 10 mm (i.e., the first point plotted in February is 14 mm).

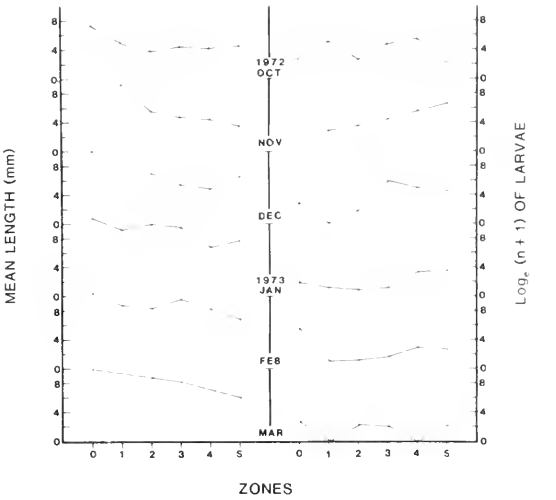

FIGURE 3.—Mean length and relative abundance of Atlantic croaker larvae collected October 1972-March 1973 in Onslow Bay and Newport River estuary, N.C. Sampling stations are grouped according to offshore distance and water depth: Zone 0, Newport River estuary; zones 1-3, inshore to ocean; zones 4-6, offshore to ocean. Some plots extend into adjacent months as in Figure 2.

TABLE 4.—Estimated numbers and percentages of spot and croaker larvae (adjusted by standard haul factor) collected in Onslow Bay and Newport River estuary, N.C., October-April 1972-73 and 1973-74.

Area and species	1972-73 No. larvae	1972-73 No./stn	1972-73 % by area	1973-74 No. larvae	1973-74 No./stn	1973-74 % by area
Offshore						
Spot	16,436	483	55.5	10,812	491	93.5
Croaker	5,398	159	43.1	111	5	8.8
Total	21,834	642	51.8	10,923	496	85.1
Inshore						
Spot	1,206	23	4.1	681	16	5.9
Croaker	2,822	54	22.6	665	16	52.6
Total	4,028	77	9.6	1,346	32	10.5
Estuary						
Spot	11,954	498	40.4	74	3	0.6
Croaker	4,294	179	34.3	488	18	38.6
Total	16,243	677	38.6	562	21	4.4
Totals						
Spot	29,596	269		11,567	127	
Croaker	12,514	114		1,264	14	
Total	42,110	383		12,831	141	

We were unable to relate the mean length and relative abundance of spot and Atlantic croaker larvae to different sampling areas for the 1973-74 season, to the same degree as for the 1972-73 season, because of the low availability of larvae.

The conclusions derived from our Onslow Bay study show a general offshore-to-inshore gradient for spot and Atlantic croaker larvae. This gradient for both mean numbers and size of larvae appears to be a function of distance from shore and time of year.

Generally, protracted spawning occurs offshore, and larvae of these two species continue to grow as

they move toward shore and into the estuary. Two primary factors that seem to affect growth are water temperature and the amount of plankton "blooms" present (Williams et al. 1968). Therefore, in February and March, with some exceptions, as water temperatures start to rise, collections will have larger individuals by area than during colder months. By considering a specific point along this route as larvae move from offshore areas to the estuary and then by looking at the monthly means, we note that size increases seasonally.

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SURVIVAL AND HOMING OF JUVENILE COHO SALMON, *ONCORHYNCHUS KISUTCH*, TRANSPORTED BY BARGE

During the winter and spring of 1976-77 the Pacific Northwest experienced its worst drought in recent times. Flow in the Columbia River, which is dammed extensively for hydroelectric generation and irrigation, was extremely low during the spring of 1977 (averaging $<4{,}245$ m^3/s). In low flow years, very little water is diverted over spillways at the hydroelectric projects. Consequently, many migrating juvenile Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, were destined in 1977 to pass through the turbines, where substantial numbers would be killed (Chaney and Perry 1976[1]) unless remedial steps were taken. Realizing that the losses of juvenile salmonids could be catastrophic, the National Marine Fisheries Service (NMFS) and the U.S. Army Corps of Engineers (CofE) prepared two barges to supplement trucking as a means of transporting juvenile salmonids around dams on the Columbia and Snake Rivers (McCabe et al. 1979).

To assess the effectiveness of barging, various experiments were conducted. One, a joint activity by NMFS, the U.S. Fish and Wildlife Service (FWS), and CofE, involved transporting tagged coho salmon, *Oncorhynchus kisutch*, from Willard National Fish Hatchery (Little White Salmon River), Wash., to a release site on the Columbia River downstream from Bonneville Dam (Fig. 1). Objectives of the experi-

[1]Chaney, E., and L. E. Perry. 1976. Columbia Basin salmon and steelhead analysis: Summary report; 1 September 1976. Pac. Northwest Reg. Comm., Vancouver, Wash., 74 p.

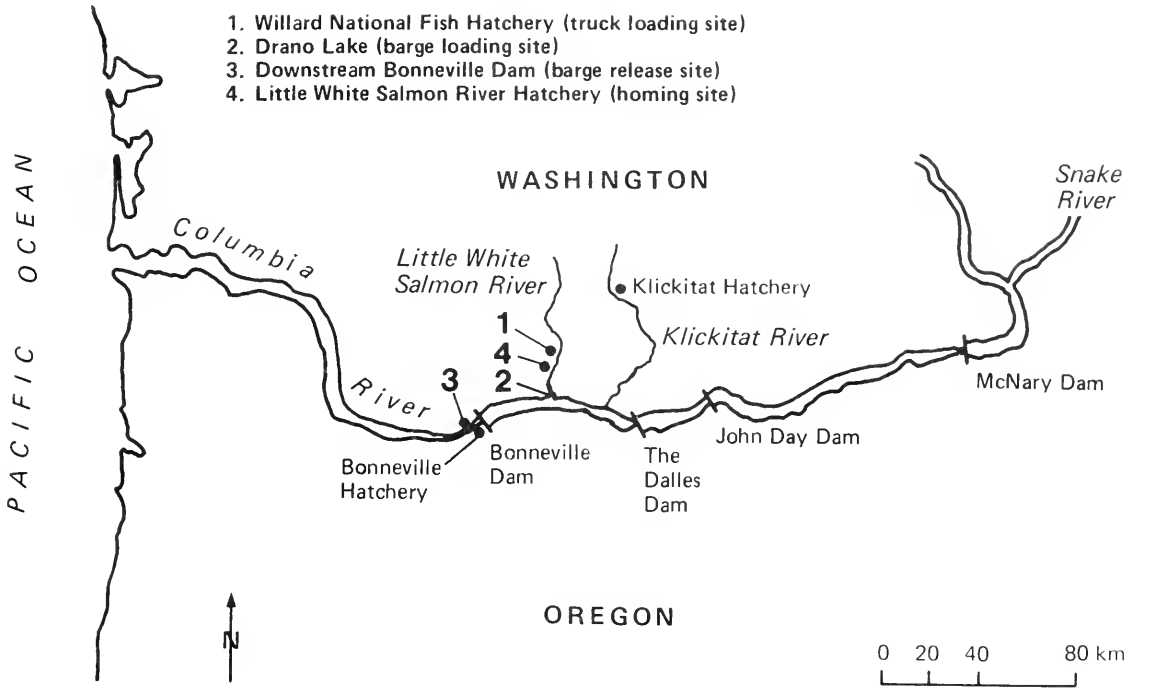

FIGURE 1.—Lower Columbia River and features of the study on transported coho salmon.

ment were to 1) determine if juvenile coho salmon transported by barge around Bonneville Dam would return as adults to the Little White Salmon River Hatchery and 2) determine if survival to the adult stage could be enhanced by barging the fish around Bonneville Dam.

Methods

Two lots of coho salmon from Willard Hatchery were identified by tagging with magnetic microwire tags (Ebel 1974), and adipose fins were excised from fish in both lots to identify them as wire-tagged. A control lot (20,625 fish) was released at the hatchery on 18 April 1977. On 22 April 1977 the test lot (19,785 fish) was transported by tanker truck about 9 km to Drano Lake on the Columbia River, where the fish were loaded via flexible hose onto a waiting barge. Shortly after loading, the barge departed; about 4 h later the coho salmon were released into the river downstream from Bonneville Dam.

The barge, with a steel cargo tank 33.2 m long × 8.5 m wide, was essentially a floating raceway (McCabe et al. 1979). One or two stern pumps supplied river water to a bow spray bar. After exiting the spray bar, water flowed through eight screened compartments and exited via four stern overflow scuppers. One complete turnover of water took about 20 min with both pumps operating.

Evaluation of the effectiveness of barging was based on a comparison of the percentage of fish from control (hatchery-released) and test (barged) lots that either 1) returned to the Willard Hatchery in the fall of 1977 (these early-arriving fish were precocious males), 2) returned to the hatchery in 1978 as full-term adults, or 3) were intercepted by commercial or sport fisheries. Adult fish returning to the Willard Hatchery were collected in a trap at the Little White Salmon National Fish Hatchery, located about 7 km downstream from Willard Hatchery. All coho salmon collected in this trap in 1977 and 1978 were examined for the wire tags used in this experiment. Tag information on coho salmon caught in sport and commercial fisheries was provided by fish and wildlife agencies in Washington, Oregon, California, and Canada.

Results And Discussion

Returns of coho salmon to the trap at Little White Salmon Hatchery and to the fisheries (both sport and commercial) are presented in Table 1. Total recoveries of tagged releases were 0.19% for the control group and 0.39% for the test group. There was no dif-

TABLE 1.—Summary of test and control releases of coho salmon from Willard National Fish Hatchery and returns to the hatchery and fisheries.

Category	Releases and returns	
	Control	Test
Release date	18 Apr. 1977	22 Apr. 1977
No. tagged juveniles released	20,625	19,785
Weight at release (no. fish/kg)	10.2	10.9
Total no. returns	40	77
to Willard Hatchery		
precocious males	1	4
full-term adults	13	10
to Bonneville Hatchery[1]	2	1
to sport and commercial fisheries	[2]24	[3]62
Total percent returns	0.19	0.39
to Willard Hatchery	0.07	0.07
to fisheries	0.12	0.32

[1]Only precocious males were recovered at Bonneville Hatchery.
[2]Numbers of fish landed in the following areas: Washington 5; Oregon 16; California 3
[3]Numbers of fish landed in the following areas: Washington 20; Oregon 34, California 7; Canada 1.

ference in hatchery returns between the control and test groups; however, there was a highly significant difference between the two groups in returns to the fisheries (Table 2). The overall contribution to the fisheries was 170% greater (adjusted for the difference in numbers released) from the test group than from the control group.

Although it was expected that both groups of fish (controls were released 4 d earlier) would mix below Bonneville Dam and encounter the same environmental conditions, we do not know for certain that this occurred. However, when the catches were separated by fisheries in Washington, Oregon, and California and compared, the proportion of test to control fish did not differ significantly from one fishery to another (chi-square, $df = 2$, $P>0.05$), indicating that the test and control groups were mixed as adults. Consequently, we believe the two groups were adequately mixed as juveniles.

The degree to which the trucking of coho salmon from Willard Hatchery to the barge contributed to their increased survival is unknown; no information is available on juvenile mortality of the control group during its migration from Willard Hatchery to Drano Lake. Although coho salmon from the test group did return to the Little White Salmon River (the homing site), the number of returns was smaller than expected, based on returns to the fisheries. This seems to indicate that the homing ability of the test group was impaired.

TABLE 2.—Chi-square tests of null hypotheses regarding catch and return data on coho salmon in the Columbia River.

Hypothesis	Chi-square[1]
Returns of adult coho salmon to the Little White Salmon River Hatchery are the same for transported (test) as for nontransported (control)	0.00
Coho salmon from the transport and control groups contribute equally to sport and commercial fisheries.	17.55***
Total returns of coho salmon (to fisheries and hatcheries) are the same for both transport and control groups.	12.64***

[1]Adjusted chi-square, using Yates correction for continuity.
*** = $P<0.001$.

Columbia River flow was unusually low (averaging $<4{,}245$ m^3/s) in the spring of 1977, and there was essentially no water passing over the spillways at Bonneville Dam during the experimental release. Consequently, fish released from the hatchery had to pass Bonneville Dam via the turbines. These unusual conditions no doubt contributed to the significantly lower survival of the hatchery release. However, with the completion of the second powerhouse at Bonneville Dam in the early 1980's, reduction or elimination of spills will become an increasing reality. Therefore, transportation may be a practical way to enhance survival of salmonids reared in hatcheries above Bonneville Dam.

Other researchers have studied the effect of transportation on the survival and homing ability of Pacific salmon and steelhead in the Columbia River system. Ebel et al. (1973) collected migrating juvenile chinook salmon, *O. tshawytscha*, and steelhead trout at a lower Snake River dam and transported them via tanker truck to a release site downstream from Bonneville Dam. Based on the number of returning adults, they concluded that survival of the transport group was higher than that of the control group; in addition, the homing ability of the transported fish was not impaired. Slatick et al. (1975) also concluded that the homing process of chinook salmon and steelhead trout transported from the same lower Snake River dam had not been impaired. Ellis and Noble (1960) were unable to increase adult returns to the Klickitat Hatchery (Fig. 1) by transporting juvenile fall chinook salmon; both trucks and a screened barge were used in their tests. In the barge test, fall chinook salmon from the Klickitat Hatchery were loaded into the barge (from a truck) at the confluence of the Klickitat and Columbia Rivers, transported 265.5 km downstream, and released. Returns to the Klickitat River were less for fall chinook salmon barged as juveniles than for hatchery-released controls; also there was considerable straying among returning transported adults. Adult returns were less for fall chinook salmon transported as juveniles in trucks from the Klickitat Hatchery and released in the lower Columbia River than were returns from hatchery-released controls. Ebel et al. (1973) and Slatick et al. (1975) transported juvenile salmonids that were actively migrating and had completed part of their seaward journey, whereas Ellis and Noble's (1960)

test groups of fall chinook salmon were transported directly from the Klickitat Hatchery.

Transporting hatchery fish by barge around the Columbia River dams to avoid mortality remains a viable management option. In spite of an impaired homing ability, barged fish in this study returned to the hatchery at a rate equal to that of the controls. Barging not only increased survival, which benefited the sports and commercial fisheries, but also provided an adequate number of fish returns to the hatchery for reproduction purposes.

Acknowledgments

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MOVEMENT OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, IN THE NORTHEASTERN PACIFIC OCEAN AS DETERMINED BY TAGGING EXPERIMENTS (1971-80)

The sablefish, *Anoplopoma fimbria*, is a North Pacific species distributed along the North American coast from Mexico to the Bering Sea and on the Asian coast east to Kamchatka and south to northeastern Japan. The maximum life span of sablefish appears to be near 40 yr (Beamish and Chilton in press). At 3 yr of age, sablefish reach a weight of about 1 kg and an average length of 47 cm. By 8 yr of age, sablefish have grown to about 3 kg and average 64 cm in length (Low et al.[1]).

The sablefish fishery in the northeastern Pacific Ocean and Bering Sea developed rapidly in the past 15-20 yr, growing from small United States and Canadian fisheries to large-scale multinational fisheries by Japan, the U.S.S.R., and the Republic of Korea (ROK). The increased exploitation of sablefish was followed by declines in catch per unit effort (CPUE) in many areas (Low et al. footnote 1). Because of this decline in CPUE, a tagging program was instituted to identify management areas and determine migration patterns.

Some studies of sablefish migration had been conducted in the 1950's and 1960's (Holmberg and Jones 1954; Edson 1954; Pruter 1959; Pasquale 1962; Novikov 1968; Pattie 1970). In these studies, most of the tagged fish were recovered near the area tagged. However, some fish were recovered over 1,000 km away (Holmberg and Jones 1954; Pruter 1959). Some fish tagged in the Gulf of Alaska were recovered off the California coast (Edson 1954) while other fish, tagged off the Washington coast, were recovered in the Bering Sea (Pasquale 1962; Pattie 1970). The results of these studies provided direct evidence of the occurrence of some long-range movement. The degree of long-range movement within the population could not be evaluated, since, in most of the studies, the number of fish tagged and recovered was small and each tagging project covered only a portion of the known range of sablefish.

Methods

To tag sablefish, over as much of its range as pos-

[1]Low, L. L., G. K. Tanonaka, and H. H. Shippen. 1976. Sablefish of the northeastern Pacific Ocean and Bering Sea. Processed rep., 115 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

sible, a cooperative tagging program was established involving the National Marine Fisheries Service, California Department of Fish and Game, Oregon Department of Fish and Wildlife, and research vessels from the U.S.S.R. and the ROK. A total of 34,640 sablefish were tagged from 1971 through 1976 from off southern California to the Kodiak Island area in the Gulf of Alaska. The number of sablefish tagged varied along the coast with the greatest number released in International North Pacific Fisheries Commission (INPFC) area, Columbia (Fig. 1). No fish were tagged in the western Gulf of Alaska or British Columbia (INPFC areas, Charlotte and Vancouver, north of lat. 48°30′); only a small number were tagged in the central Gulf of Alaska.

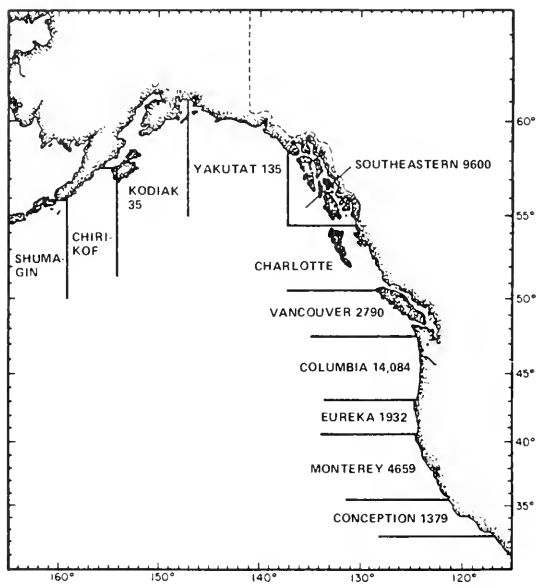

FIGURE 1.—Number of sablefish tagged in each International North Pacific Fisheries Commission area, 1971-76.

Five types of gear were used to capture sablefish in the cooperative research program: Trawl, trap, longline, rod and reel, and troll. Trawl, trap, and longline were the predominant gear types accounting for almost 99% of the captures. After capture, the sablefish were placed in tanks continuously supplied with seawater. The fish to be tagged were dipped from the tank, placed in a padded tagging cradle, and measured for fork length to the nearest centimeter. Those fish not seriously injured at capture were tagged and released. Most of the trawl-caught fish tagged during the study were taken in 400-mesh Eastern trawls equipped with 3.8 cm mesh liner. The traps used had either one or two tunnels and were 0.86 m wide by 0.86 m high by 2.44 m long (Hipkins 1974).

Three types of tags were used in the cooperative research program: Anchor, spaghetti, and an experimental tag. Spaghetti tags (yellow-colored, size #20 vinyl tubing) were applied to 636 fish in 1971 and another 100 by 1972 to provide a standard for evaluating the recovery rate of the anchor tags. Some experimental tags similar to standard spaghetti tags, but applied with a hollow needle and secured by interlocking plastic terminals, were tested in 1973. Only 76 fish were tagged with this method, which proved to be too time consuming for general use. The primary tag, a Floy FD68[2] anchor tag, was used on the remainder of the fish. Tagging information recorded included the tagging agency, vessel name, cruise number, fishing set, gear used, fishing depth, position in degrees and minutes, date, fish length, and the relative condition of the fish.

Tag recovery data were recorded in the same way as the release data, although the information reported was more variable. The most consistent recovery data reported were tag number, recovery date, fish length, and recovery location. Other data occasionally reported for recoveries include the capture gear, depth of capture, sex, weight, and state of maturity.

In some instances, the tag recovery information was treated as more detailed than actually reported. For example, the recovery location, recorded in degrees and minutes, may have been derived from other information, such as a recovery location lying between two reported loran base lines in a given depth strata or a location reported as lying at a given bearing and distance from a prominent landmark. The dates may represent the midpoint of periods ranging from 3 to 30 d, or may also be the day of delivery of a sablefish catch which contained the tagged sablefish. However, the errors introduced by such interpolation were very small in terms of the distances traveled or time the tagged fish were at large.

Distance traveled between release and recovery locations was the shortest distance between the two points calculated by great circle distance.

Sablefish tagging and recovery data were transformed into SPSS (Statistical Package for the Social Sciences) files. SPSS programs (Nie et al. 1975) were used to produce both the descriptive and analytical statistics presented in this report.

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

Results

As of 31 December 1980, there were 1,362 tag recoveries for an overall recovery rate of 3.9%. The INPFC area of recovery was known for 1,334 of the 1,362 recoveries. Recoveries by INPFC area are shown in Figure 2 where it can be seen that most sablefish were recovered in the same area as tagged and that only a limited amount of long-range movement occurred.

More precise analysis of movement was possible for 969 sablefish for which recovery was reported by position rather than general geographic area. Grouping these recoveries by distance from release site revealed that 65% of all recoveries occurred within 100 km of the release site, 24% were recovered within

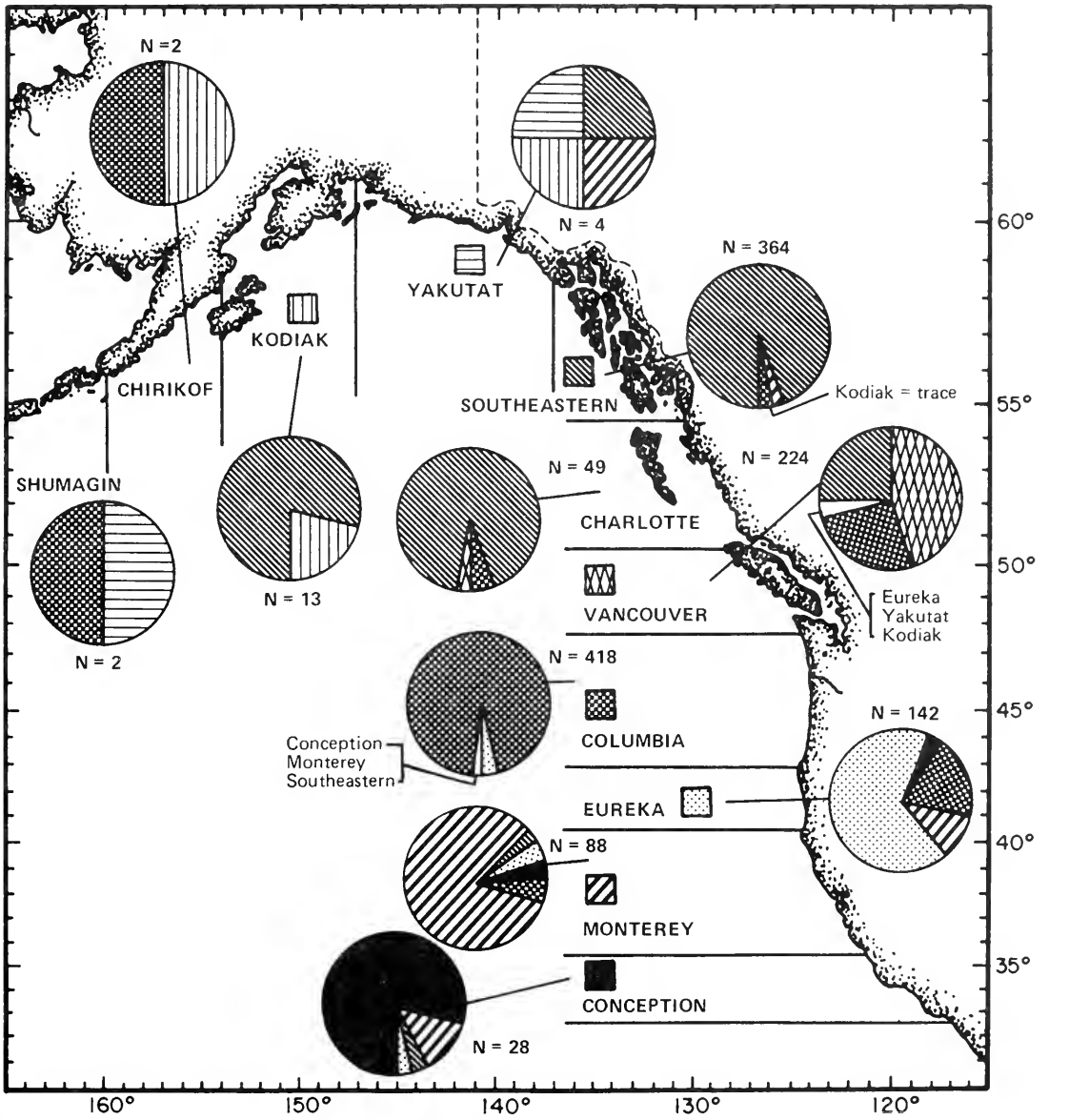

FIGURE 2.—Number of sablefish recovered in each International North Pacific Fisheries Commission (INPFC) area and the percentage of recoveries by INPFC area of tagging.

100-500 km, 8% within 500-1,000 km, and only 3% were recovered at distances >1,000 km from the release site (Table 1). Regression analysis (Table 2) revealed a slight, but significant increase in distance traveled in relation to the number of days at liberty.

Analysis of variance tests of movement relative to area released was significant, indicating that the amount of movement differed between areas (Table 3). Least significant range tests (Sokal and Rohlf 1969) showed fish recovered from Yakutat releases were significantly different ($P = 0.05$) from other recoveries. Only two tagged fish were recovered from releases made in the Yakutat area, both at long distance from the release site.

TABLE 1.—Distance traveled between release and recovery sites by tagged sablefish in the northeastern Pacific Ocean.

Distance (km)	Percent
<100	65.3
100-500	23.9
501-1,000	7.6
1,001-2,000	2.8
>2,000	0.3
$N = 969$	

TABLE 2.—Regression analysis of kilometers traveled by tagged sablefish on the number of days at liberty.

$\beta = 0.0876$ SE = 0.0131
$\alpha = 97.63$ $R^2 = 0.044$

ANOVA

Source	df	Mean squares	F
Regression	1	4,079,421.425	44.653**
Residual	967	91,358.267	

**$P<0.05$.

An analysis was performed to determine if there was any seasonal variation in movement such as movement between spawning and feeding grounds or winter and summer grounds. Releases and recoveries were fairly evenly distributed throughout the year, although more were recovered during the spring and summer months when the fisheries were more active. It was assumed that if seasonal movement occurred, fish would be recovered near the release site in the same season and in other areas in other seasons; however, for fish tagged in January-March and October-December the opposite occurred (Table 4). Recoveries tagged in the spring (April-June) and winter (October-December) months exhibited the greatest amount of movement, which suggests that fish may be more active in these months. Using chi-square statistics, significant differences were detected between seasons ($\chi^2 = 42.42$,9 df), but not in any discernible pattern.

TABLE 3.—Movement of sablefish in relation to INPFC area of release.

Area of release	N	Mean	SD	95% C.I.	Min.	Max
Conception	23	150.8	289.1	25.8-275.8	5	1,010
Monterey	94	240.3	415.6	155.2-325.4	0	2,172
Eureka	92	60.2	102.5	39.0- 81.4	0	576
Columbia	315	108.5	246.5	81.2-135.8	0	2,373
Vancouver	85	75.5	88.7	56.3- 94.6	0	531
Southeast	352	249.8	352.9	212.8-286.8	0	1,866
Yakutat	2	1,510.3	281.1	0-4035.6	1,311	1,709
Kodiak	6	375.5	285.0	76.4-674.6	30	779
Total	969	170.7	293.5	152.2-189.2	0	2,373

ANOVA

Source	df	Mean squares	F
Between areas	7	1,373,994.5	15.946**
Within areas	961	86,165.4	

**$P<0.05$.

TABLE 4.—Seasonal variation in sablefish movement in the northeastern Pacific Ocean.

Release	Time of recovery				Total
	Jan.-Mar.	Apr.-June	July-Sept.	Oct.-Dec.	
Jan.-Mar.					
Mean (km)	196.33	67.09	54.83	78.51	78.44
Sample size	24	106	69	28	227
SD	392.58	166.95	64.05	142.97	184.44
Apr.-June					
Mean (km)	317.37	380.12	175.87	228.71	254.29
Sample size	29	89	141	77	336
SD	314.48	431.75	267.96	329.30	345.16
July-Sept.					
Mean (km)	92.04	117.98	74.19	128.23	95.64
Sample size	21	48	89	28	186
SD	126.68	188.08	239.45	265.66	220.92
Oct.-Dec.					
Mean (km)	196.68	159.56	131.20	293.08	175.57
Sample size	28	61	84	35	208
Total					
Mean (km)	209.37	185.32	120.64	200.34	164.63
Sample size	102	304	383	168	957
SD	292.43	328.62	233.40	376.89	301.98

It was hypothesized that movement was related to size-at-tagging. To test this, recoveries were grouped into three divisions: <40 cm, 40-60 cm, and >60 cm. These divisions were derived from data presented by Low et al. (footnote 1), and correspond to juvenile, juvenile-maturing, and mature fish, respectively. No significant differences were found among the three groups (Table 5).

One difficulty in evaluating the recovery information is the lack of area specific catch and effort data with which to weight recoveries. For example, in 1973 the sablefish fisheries off Oregon and Washington were at a low level, while those off California were active. Releases made off Oregon in 1972 were recovered off California in 1973. In 1974, fisheries off Oregon became active and most of the fish tagged off Oregon were recovered at or near release locations, and many sablefish tagged off California were recovered off Oregon as well.

Catch data are available by INPFC area for all nations harvesting sablefish. These data can be utilized to provide a rough weighting to tag returns if it is assumed that catch is proportional to effort. Table 6 contains the percent of total catch, recoveries, and tagged sablefish for each INPFC area. It can be seen that recoveries for each area were generally proportional to releases except for the Monterey, Eureka, and Vancouver areas in which higher or lower recoveries occurred due to movement between adjacent areas. Neither the releases nor recoveries of tagged sablefish was proportional to area sablefish catches. A high percentage of the catch came from the Yakutat and Kodiak areas (30%) while only 0.5% of the tagged fish and 1.3% of the recoveries occurred in these areas. Conversely, the Columbia and Vancouver areas accounted for 13% of the catch, but 49% of releases and 48% of the recoveries. The Chirikof and Shumagin regions accounted for 15% of the catch (nearly equal to Columbia-Vancouver), but no fish were released in these areas, and only 0.2% of the recoveries occurred in these areas. While general catch data is not a substitute for more detailed catch and effort data, it does indicate that on a gross level estimates of movement did not appear to be influenced by the level of fishing as measured by catch.

TABLE 5.—Analysis of variance of distance traveled (km) by sablefish in relation to size at tagging.

Size Group (cm)	Mean	SD	n
<40	134.9	298.8	106
40-60	118.7	273.4	687
>60	117.2	260.3	560
All sizes	119.3	270.0	1,353

ANOVA

Source	df	Mean squares	F
Between groups	2	9,259.95	0.098
Within groups	957	94,493.38	

Discussion

The results of this study indicate that for the study period, sablefish are primarily nonmigratory and that most movement is limited to relatively short distances. Long-distance movement was found to occur in only a small portion of the population. These results suggest that the amount of interchange decreases with distance and movement has little effect on abundance over long distances. Beamish et al. (1980) reported similar results for sablefish tagging studies performed in the waters of British Columbia.

The results also provide indications that the northeastern Pacific sablefish population can be subdivided into "stocks" or management units. It does appear that sablefish off southern California are independent of those off Oregon and Washington and these are independent of stocks in the eastern Gulf of Alaska, since very little movement occurs over long distances. Finer divisions are suggested by the data,

TABLE 6.—Total sablefish catch for 1971-79, the number of sablefish released and recovered (1971-80), and the percentage of total catch, releases, and recoveries with each INPFC area.

INPFC area	Total catch (t) (1971-79)	Number of		Percent of total in area		
		Releases	Recoveries	Catch	Releases	Recoveries
Conception	7,886	1,379	28	3	4.0	2
Monterey	30,563	4,659	88	10	13.0	7
Eureka	12,557	1,938	142	4	6.0	11
Columbia	28,067	14,084	418	9	41.0	31
Vancouver	12,273	2,790	224	4	8.0	17
Charlotte	20,386	0	49	7	0.0	4
Southeastern	54,628	9,600	364	18	28.0	27
Yakutat	53,060	155	4	18	0.4	0.3
Kodiak	37,240	35	13	12	0.1	1.0
Chirikof	18,223	0	2	6	0.0	0.1
Shumagin	25,866	0	2	9	0.0	0.1
Total	300,749	34,640	1,334			

but definite conclusions cannot be reached in the absence of fisheries data to weight the results.

The net distance traveled was not related to size, time at liberty, or season. During the period of this study, the abundance of sablefish was believed to have been decreasing from overfishing (International North Pacific Fisheries Commission 1980). It is possible that behavior and migration tendencies could be different when the population is stable or increasing. Recently, a relatively strong year class of sablefish has been noted in most areas (International North Pacific Fisheries Commission 1980). Some of these fish had been tagged in 1979 and 1980 (Hughes 1980[3]). It will be interesting to see if movement patterns of adults alter in response to the presence of a large year class.

Acknowledgments

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WINTER AND ALTERED SPRING MOVEMENTS OF STRIPED BASS IN THE SAVANNAH RIVER, GEORGIA

The striped bass, *Morone saxatilis*, population of the Savannah River supports a small sport fishery and provides all the brood fish for the Richmond Hill, Ga., striped bass hatchery. Information on the biology and management of Savannah River striped bass also has application for management of similar populations in coastal rivers of Georgia, South Carolina, and Florida.

Previous studies of striped bass in the Savannah River have shown that the population is primarily

riverine rather than anadromous. Spawning takes place in the freshwater, tidally influenced zone 30-40 km upstream from the river mouth during late March through early May, normally at water temperatures of 16°-20°C (Dudley and Black 1978). After spawning, striped bass in the Savannah River move upstream and remain in the river until the following autumn (Dudley et al. 1977). The fish may then move downstream to overwinter in estuarine areas, although, until now, no direct evidence for this assumption has been available except for the existence of a small and unpredictable sport fishery in the estuary during November through January. This note summarizes additional information about striped bass movements during the winter and during the spring spawning season.

Study Area

The study area extends from the mouth of the Savannah River to the Augusta city dam 370 km upstream and has been described by Dudley et al. (1977). The tidally influenced section of the river is composed of three branches. Front River, the main shipping channel, flows through the industrial part of Savannah, Ga., and is 10-12 m deep downstream from Highway 17. Back River and Middle River flow through the Savannah National Wildlife Refuge, are bordered by cypress forest and extensive grassy marshlands, and are 1-3 m deep at mean low water (Fig. 1).

The tide gate, completed by the U.S. Army Corps of Engineers in 1977, was built to control sedimentation in the shipping channel. The gate allows the incoming tide to flow upstream in Back River but closes when the tide starts to drop, preventing downstream flow. Tidal brackish water and freshwater flowing down upper Back River pass through the diversion canal and increase water velocities in Front River. The gate has changed flow patterns and has increased salinity in parts of Back and Front Rivers. Salinity in Back River from the tide gate to Highway 17 is 1-3‰ higher than without tide gate operation, when salinity upstream from the diversion canal is usually zero. With gate operation, salinity in Back River at Highway 17 can reach 3‰ (Dudley and Black[1]).

During studies conducted in 1973-75 (Dudley et al. 1977), Back River was blocked at the site of tide gate construction. During the present study the tide gate was operating.

Methods

In freshwater a boom-type electrofishing boat with alternating or pulsed direct current was used to capture striped bass. During November through March, attempts were made to capture striped bass with gill nets of 24.3 and 15 cm stretch mesh 30-100 m long. These nets were fished primarily in the Savannah Back River, especially near the tide gate, and in other areas of the downstream 80 km of the river. A 10 cm mesh net was also used but caught mostly smaller fish. Gill nets were checked for fish every 30 min.

Both ultrasonic and radio transmitters were used. The ultrasonic transmitters (manufactured by Smith-Root[2] of Vancouver, Wash.) are easily detected in the estuary, but difficult to track in upstream areas due to noise generated by water currents and by sand moving along the bottom. Ultrasonic transmitters used in the spring of 1979 weighed 54 g, measured 20 mm in diameter and 100 mm long, and had a life expectancy of 6 mo. Those used in the winter of 1979-80 and in the spring of 1980 weighed 40 g, measured 20 mm in diameter and 110 mm long, and had a 1-yr life expectancy.

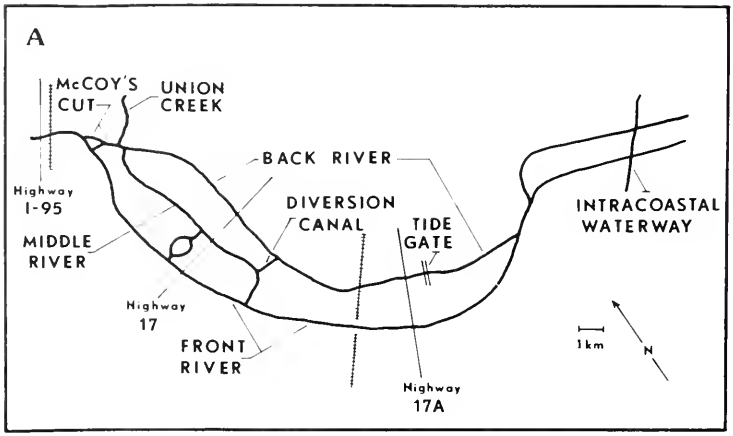
Radio transmitters (manufactured by AVM Electronics of Champaign, Ill.) are easily detected in freshwater but not in saline water. Radio tags measure 70 × 25 × 20 mm, weigh 23 g, and transmit for more than 1 yr. The surgical tagging procedure followed that of Dudley et al. (1977).

In our studies of winter movements, the downstream 100 km of the river was searched for tagged striped bass at about weekly intervals. During this time we also tried to capture and tag additional fish. In our studies of spring movements, the downstream 60 km, including most side channels, was searched about five times per week. The river in the vicinity of the spawning grounds was divided into nine sections to facilitate comparison of 1980 movements with those observed in earlier studies (Dudley et al. 1977) (Fig. 1B).

We used a chi-square test of independence to compare sections used by striped bass in 1980 with sections frequented by striped bass tracked in the earlier, pretide gate study. In that test, river sections E through H were combined, because of the small number of sightings made in them.

[1]Dudley, R. G., and K. N. Black. 1979. Effect of the Savannah River tide gate on striped bass eggs and larvae. Final report to the U.S. Army Corps of Engineers on contract DACW21-78-C-0073, 46 p. + app.

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



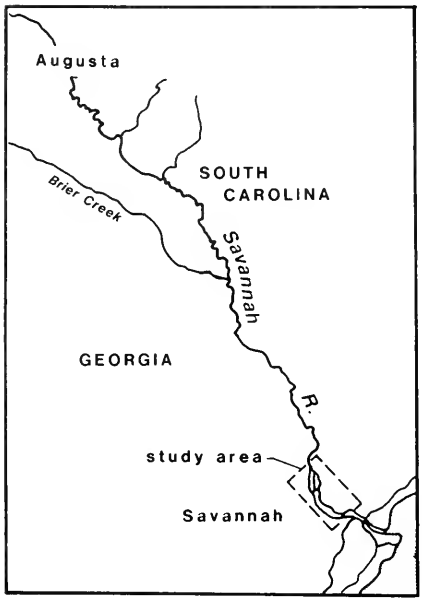
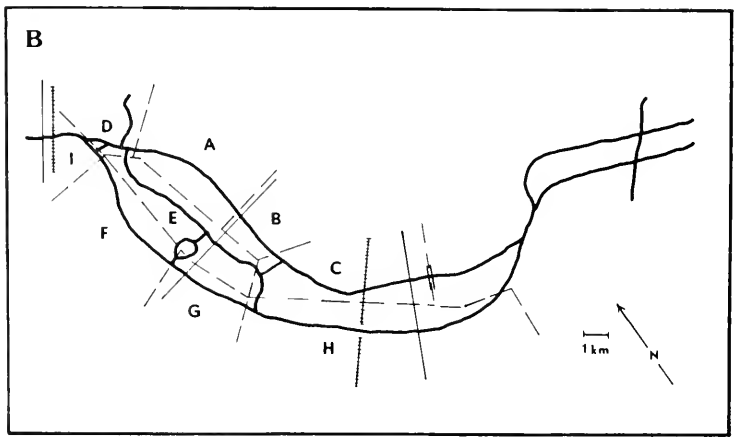


FIGURE 1.—A) Schematic of the Savannah River near Savannah, Ga., from Interstate 95 (km 45) to the Intracoastal Waterway (km 10). Meanders, small islands, etc., are not shown. The river mouth is approximately 10 km southeast of the Intracoastal Waterway. B) Savannah River near Savannah, Ga., showing river segments (A through I) used in analyzing striped bass distribution patterns during the spawning season.



A Hydrolap Surveyor was used to measure temperature, dissolved oxygen, pH, conductivity, and redox potential at each site where a tagged fish was located. Additional sites were sampled on a regular basis during March through May of 1980. No unusual water chemistry readings were noted, and only temperature and salinity are cited in the text as needed.

Results

Thirteen fish were successfully tagged with transmitters and tracked. Six of these were found periodically for more than 100 d, while two were found for more than 1 yr.

Three fish tagged during March and April 1979 provided useful information during the following fall, winter, and spring. During a single search of the entire study area in July 1979, fish F1, F2, and F3 were found at km 257, 222, and 246, respectively. Fish F2 never moved from km 222 and was presumed dead. On 26 September only fish F1 was found (km 234) although only areas upstream from km 107 were searched. Neither fish F1 nor F3 could be found during the winter, but both were found on the spawning grounds the following spring. There is considerable question regarding the whereabouts of these two fish during the winter. Since neither fish had an operating ultrasonic transmitter, they could not have been found in saline waters. If these fish remained in freshwater sections of the river, they would have been detected. The whole river extending to Augusta was searched twice in October, and numerous searches to km 75 were made between October and March. The apparent absence of these fish from the river, and their sudden reappearance in March (fish F3) and early April (fish F1) when they were found without difficulty, indicate that they probably were in saline water during the winter.

Three fish (F4, F5, and F6) were tagged with ultrasonic transmitters in mid-December in saline water (5‰) immediately upstream from the tide gate. Fish F5 was also tagged with a radio transmitter. These fish remained within a few kilometers upstream from the tagging site for 2, 25, and 100 d, respectively. They subsequently left that area and could not be found for extended periods (117, 89, and 19 d, respectively) in spite of numerous searches which reached to the river mouth. They all were later found in upper Back River in April. None of the three fish used freshwater segments of the river during winter.

Seven additional fish were tagged in April 1980. Four were tagged on 4 April with ultrasonic transmitters and three on 17 April with radio transmitters. Thus a total of 12 fish (all except fish F2) yielded movement data during the 1980 spawning season (Table 1).

There was considerable variation among the movement patterns of individual fish (Table 2). Fish F4, F8, and F9 exhibited abnormal patterns. Fish F4 remained at the mouth of Union Creek at the end of the study. Prior to 6 May it shifted its position on occasion but later it apparently died. Fish F8 and F9

TABLE 1.—Striped bass successfully tagged and tracked in the Savannah River, Ga., during 1979 and 1980. Tag type: R = radio; U = ultrasonic. Capture method: G = gill net; DC = direct current; AC = alternating current. Track duration indicates time period during which useful data were obtained. In upstream areas, fish tagged with ultrasonic transmitters were not tracked.

Fish			Tagging			Found on spawning grounds 1980		Upstream location late May 1980 (river km)	Track duration (d)
ID	Weight (kg)	Sex	Date	Tag type	Capture method	First date	Last date		
				Back River, Spring 1979					
F1	7	M	4 Mar 79	R	G	3 Apr	7 May	Not found[1]	429
F2	9	M	10 Mar 79	RU	DC	([2])	—	—	120
F3	10	M	28 Apr 79	RU	AC	21 Apr	29 Apr	196	396
				Tide Gate, December 1979					
F4	6	—	16 Dec 79	U	G	14 Apr	([3])	—	156
F5	8	—	17 Dec 79	RU	G	10 Apr	11 Apr	227	163
F6	6	—	17 Dec 79	U	G	21 Mar	25 Apr	—	129
				Back River, Spring 1980					
F7	15	F	4 Apr 80	U	AC	—	15 Apr	—	11
F8	12	F	4 Apr 80	U	AC	—	9 May	—	35
F9	11	M	4 Apr 80	U	AC	—	9 May	—	35
F10	13	F	4 Apr 80	U	AC	—	11 Apr	—	7
F11	5	M	17 Apr 80	R	DC	—	23 Apr	301	42
F12	8	F	17 Apr 80	R	DC	—	25 Apr	Not found	8
F13	7	M	17 Apr 80	R	DC	—	2 May	241	41

[1]Radio transmitter of fish F1 may have stopped working by late May 1980.
[2]Fish F2 apparently died at km 222, summer 1979.
[3]Fish F4 apparently died in Back River, April 1980.

TABLE 2.—Movement patterns of individual tagged striped bass during spring 1980 in the Savannah River, Ga., as compared with a pretide gate study (Dudley et al. 1977). Fish observed more than once in a given section on a given day are counted as one observation.

Fish	No. days observed/river section									
	A	B	C	D	E	F	G	H	I[1]	Total
F1				14	1				2	15
F3	4			6		1			10	11
[2](F4)	(1)			(18+)						(19+)
F5				3						3
F6	1		2	3		1	1			8
F7	2			1			1			4
[2](F8)	(2)							(12)		(14)
[2](F9)	(1)		(4)					(11)		(16)
F10	1			4						5
F11				3					5	3
F12	1		1							2
F13	12			1						13
Totals excl. fish F4, F8, F9	21	0	3	35	1	2	2	0		64
	32%	0%	5%	55%	2%	3%	3%	0%		
Totals incl. fish F4, F8, F9	25	0	7	53+	1	2	2	23		113+
	22%	0%	6%	47%	1%	2%	2%	20%		
Totals previous study	90	67	19	24	5	1	0	1		207
	43%	32%	9%	12%	2%	0.5%	0%	0.5%		

[1]This river section was not used in calculating totals or percents since it was not used in the pretide gate study.

[2]These fish exhibited unusual movement patterns which may have been caused by tagging.

remained in river segment H from 22 April until 9 May. These fish continued to move about in that segment and later left. Only one other fish in our earlier study (Dudley et al. 1977) entered that area.

Eighty-seven percent of our observations of striped bass were in river segments A and D during the 1980 spawning season. None were found in segment B, although in our previous study (Dudley et al. 1977) 32% of our observations of fish were in that segment. The distribution of our observations among river segments in 1980 differed significantly ($P = 0.005$) from that found in 1973, 1974, and 1975 (Dudley et al. 1977). The difference is due to the increased use by 1980 of segment D by striped bass, and a decreased use of segment B. In 1980, with the tide gate in operation, striped bass were more likely to be found further upstream in Back River.

Five striped bass (F1, F3, F4, F5, F6) tagged prior to the start of the 1980 spawning season gave an indication of the first arrival of the fish on the spawning grounds. Although gill nets set in upper Back River captured some smaller striped bass as early as mid-February, our tagged fish did not enter upper Back River until late March. Four of our five fish first entered this area between 21 March and 14 April when the river temperature was between 17° and 18°C. The other fish (F6) did not enter this area until 22 April after residing in segments C and G.

Each of the 12 tagged fish (all except fish F2) left the spawning area between 11 April and 9 May. The mean date of departure was 26 April (±10 d), similar to the mean date of departure (25 April ±5 d) found in our earlier work. As expected, the fish moved upstream after spawning. Four of the six striped bass carrying radio transmitters were subsequently found as far upstream as km 301, even though only one incomplete search of the river was made in late May (Table 1).

Discussion

The Savannah tide gate has caused significant alterations in both flow and salinity regimes. Our data regarding the location of adult striped bass during the spawning season showed that these fish are found farther upstream when the gate is in operation. This observation is consistent with that of an earlier study (Dudley and Black footnote 1) that striped bass eggs occur farther upstream when the tide gate is operating. Thus the tide gate apparently causes an upstream shift in striped bass spawning. This shift possibly reflects an alteration in salinity patterns. Savannah River striped bass spawn in freshwater and would thus move farther upstream to avoid increased salinity. The overall effect on spawning success from this upstream shift is probably minimal, although in combination with altered flow patterns its ultimate effect on striped bass eggs and larvae is unclear.

Our data concerning movements at other times of the year supplement earlier finds (Dudley et al. 1977). Savannah River striped bass are primarily

riverine, ascending the river following spawning. Movements of fish F1 and F3 revealed that fish residing upstream during the summer will return to the spawning grounds the following spring, and then reascend the river after spawning. Factors responsible for this behavior, quite different from that in northern populations, are not positively known.

Dudley et al. (1977) suggested temperature preference may be a reason for riverine behavior, and recent studies by Coutant and Carroll (1980) and Coutant et al.[3] further support this idea. Cooler, more preferable temperatures are likely to be found upstream in the Savannah River in late spring and summer. In late May 1980 the temperature at km 301 was 16°C, while the river temperature at Savannah (km 35) was 24°C. Four striped bass were found upstream on 28 and 29 May in waters of between 16° and 19°C. While Coutant and Carroll (1980) found that small (3.1 kg) striped bass preferred temperatures of 20°-24°C, striped bass of 5 kg or greater preferred temperatures of 16°-22°C (Coutant et al. footnote 3). All our tagged fish exceeded 5 kg. Both Orsi (1971), working in California, and Nichols and Miller (1967), working in Chesapeake Bay, found that larger striped bass were more likely to move to cooler ocean waters.

Available evidence suggests that striped bass use the saline portions of the Savannah River estuary and adjacent waters during the winter. Of five fish known to have working transmitters during the winter, only one could be regularly located and it was in saline water. The other four could not be found in freshwater or saline reaches of the river. These fish likely moved to nearby marine or estuarine waters during January and February. Fish known to be in the river in summer had already departed by October.

Although our tagged fish probably inhabited the lower estuary or marine waters during the winter of 1980, Savannah River striped bass sometimes remain in areas 250-330 km from the river mouth during the winter (Dudley et al. 1977). The differences in these findings could reflect variations among individual fish or among years, caused, perhaps, by winter temperature or flow regimes. The small number of fish tagged during the winter precludes investigating this problem, but observations made during attempts to collect striped bass suggest that year-to-year variations in wintering areas do occur. In some years (e.g., 1974) large striped bass were commonly sighted in upstream areas (Dudley et al. 1977). In other years (1979, 1980) none were seen there in spite of intensive efforts to collect them.

[3]Coutant, C. C., H. R. Waddle, and B. A. Schaich. 1980. Temperature and habitat selection by striped bass. Underwater Telem. Newsletter 10(1):1-4. Available from Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37830.

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INTERTIDAL FEEDING AND REFUGING BY CUNNERS, *TAUTOGOLABRUS ADSPERSUS* (LABRIDAE).

The cunner, *Tautogolabrus adspersus,* is the northernmost representative of the wrasses (Labridae) in the western North Atlantic (Bigelow and Schroeder 1953). While its food habits have been studied (Olla et al. 1975; Shumway and Stickney 1975), there is only one report of feeding behavior (Olla et al. 1975). During the summer of 1981, I studied the foraging behavior of cunners in an intertidal habitat and found a feeding pattern which may be an adaptation to predators.

Methods

The study site was a rocky intertidal area at Scituate, about 25 km south of Boston, Mass. Boulder density ranged from 1 to 4 per m^2 in the area. Observation sites were completely exposed at low water and submerged to a depth of 1.8 m during high tides. Water temperature was 15°-21°C during the study period.

From 5 July to 21 August 1981, I spent 57 h in underwater observations, primarily at three refuges in the intertidal zone where cunners were seen during each high tide. On three occasions I followed the initial occupancy (first fish in) and final desertion (last fish to leave) of the largest refuge during flood and ebb tides, respectively. On 9 d I followed 69 feeding forays by individual fish from the three refuges, recording the estimated size of the fish, the duration of the foray, the number of feeding acts per foray (these consisted of pecks at items on the bottom or rare rises to strike at objects in the water column), the prey at which the feeding was directed, the maximum distance ventured from the refuge on a foray, and fidelity of return to the starting point. On two occasions the same fish was followed on consecutive forays (two and three forays each, respectively); otherwise, each observation was made on different fish. A 9 m × 9 m grid marked every 30 cm was laid out over the bottom to help in determining the distance covered per foray and to aid in the estimation of fish size.

Other underwater observations included three high and two low tide dives with scuba on the seaward side of the intertidal zone in areas which remained permanently submerged (minimum depth 2 m), and two 100 m snorkel transects swum over the intertidal area during the high tide for 9 d (18 transects total). The dives were to determine qualitatively if a portion of the cunner population stayed in the subtidal region throughout the tidal cycle (high tide dives were made after confirming the refuges were occupied). The subtidal habitat consisted of patches of small (20 cm diameter), substrate-embedded rocks, interspersed with sand bar areas. These rocks were typically covered with Irish moss, *Chondrus crispus.* Larger rocks (≥2 m diameter) were scattered within the area and provided shelter for cunners in hollows and macroalgal (principally *Laminaria* sp.) growth. Water depth was 2-6 m. The snorkel transects served to identify other fish species, which moved into the intertidal zone with high tide, especially potential predators of cunners.

Available foods for cunners in the rock range were measured by randomly placing a 0.25 m^2 hoop in the area where the fish fed during low tide and by enumerating the animals found on the surface within the hoop.

Finally, the species and the number of potential bird predators in the study area during high tide were recorded.

Results

Cunner activity in the intertidal zone centered about the refuges where 2-8 fish were seen at a given time. The refuges were boulders from 0.5 to 1.0 m in diameter with hollows underneath in which the cunners remained when not foraging. Similar boulders with hollows were present in the study area but were not used as refuges. The only difference I noticed between the occupied and unoccupied sites was that the occupied refuges had two entrances while unoccupied hollows had only one. Both entrances were used in the occupied sites.

Cunners moved into the refuges an average of 107.2 min (SE = 64; range 64-150; $n = 17$) before peak high tide. Water depth at the time the refuges were first occupied was 126 cm (SD = 5; $n = 3$). The fish approached singly from a seaward direction. Feeding forays could start immediately, but up to 20 min might pass between first occupancy and the observation of the first foraging activity.

On the average, forays by 10-20 cm fish lasted 106 s, included 6 feeding acts, and took fish 3.7 m from the refuge ($n = 69$; Table 1). The cunners showed a remarkable fidelity to their refuges. In 69 observed

TABLE 1.—Feeding behavior of cunners in the intertidal zone.

	Mean	SE	Range	*n*
Duration of foray (s)	106	16	5-840	69
Maximum foraging distance from refuge (m)	3.7	0.3	0.6-12.2	58
No. of feeding acts per foray	6	1	0-65	67

forays only four fish (6%) did not return to the home refuge upon termination of the foray.

The fish generally fed on the bottom and were seen taking mussels, barnacles, and, on occasion, littorinid snails. All of these were abundant (Table 2). If the prey was not taken on the first strike, the cunner often repeatedly struck at the object until it was dislodged. In some cases a cunner gripped a food item that was firmly anchored, bent its body into a U, and then made a series of violent flexing motions which continued until the prey was freed. On 3 of the 69 forays, cunners rose and struck at free-floating plants (*Ceramium* sp.). Amphipods were concealed within some of these plants, and were probably the targets of the strikes.

Cunners abandoned the refuges and retreated seaward an average of 61.5 min (SE = 8.6; range 14-108; $n = 11$) after high tide peaked. Water depth at the time the last fish left the refuge was 71 cm (SD = 10; $n = 3$). Again the movements were made by individuals, not groups.

I made one observation as sunset fell during the high tide. The seven cunners that were foraging retreated from the refuge within 17 min after the sun dipped below the horizon. The timing of this retreat was 66.9 min (SE = 4.6) after peak flood tide with a water depth at the refuge of 122 cm. The timing was similar to the normal retreats, but the water was considerably deeper than during the other last fish retreats.

Cunners similar in size to those which foraged intertidally were found in the subtidal site during both high and low tides. I counted 43 cunners here, but no feeding behavior was observed. In three random 0.25 m^2 hoop drops, all fell on sand areas, turning up no potential food organisms. I found no mussels or barnacles during the dives, perhaps because sediment load owing to wave action renders the habitat unsuitable. Some littorinids were present.

Since the refuges were occupied during the high tide dives, this suggests that only part of the local cunner population makes the intertidal movement.

During the eighteen 100 m snorkel transects I saw pollock, *Pollachius virens*; tautogs, *Tautoga onitis*; one American eel, *Anguilla rostrata*; one ocean pout, *Marcrozoarces americanus*; and one winter flounder, *Pseudopleuronectes americanus*, as well as cunners. Pollock and tautogs were both rare, and I never saw more than three per transect. In the same distance 10-20 cunners were typically counted.

The only birds observed in or slightly seaward of the study site during high tides were double-crested cormorants, *Phalacrocorax auritus*. From 2 to 25 individuals were seen during high tide on 8 of 9 d.

TABLE 2.—Potential food resources for cunners in the intertidal zone. Values are means from three 0.25 m^2 surface samples taken on low tide on 9 August.

Taxon	No. of individuals per 0.25 m^2	SE	Range
Crustacea			
Balanus balanoides	1,475	651	546-2,730
Neopanope texana	2	1	0-5
Mollusca			
Mytilus edulis			
alive[1]	40	11	57-18
dead[1]	31	17	5-64
spat[2]	7,726	4,554	585-16,192
Littorina littorea	691	101	489-792
Thais lapillus	1	1	0-1
Anthozoa	4	4	0-12

[1]Valve length 2.5-4.4 cm
[2]Valve length 1 cm or less

None were present during low tides of the same dates. They appeared wary of divers, and I was able to make only one observation of a foraging cormorant. Surface visibility was only 5 m due to fog so I did not see the bird when it dived; but when viewed, it was swimming along the bottom poking its head into the hollows under rocks. It did not capture a fish before it noticed me and fled.

Discussion

Olla et al. (1975, 1979) have described the dependance of subtidal cunners on home shelters, from which they seldom ventured more than a few meters. Yet in this study I found that part of the cunner population abandoned subtidal sites to forage in the intertidal zone during high tides. These fish moved individually to specific refuges in which they congregated and from which individuals conducted rhythmic feeding forays over the surrounding area (Table 1). The cunners appeared to choose as refuges only sites with two entrances. A possible reason for this is that two entrances provide quicker access (or exit) during times of danger. During the ebb tide fish abandoned the refuges and moved off, again singly.

It is generally assumed that temperate wrasses use cover as an antipredator strategy (Olla et al. 1979; Hobson et al. 1981), though these threats have not been documented. The adoption of refuges in the intertidal area, similar to the pattern in the subtidal zone, is presumably also in response to a predator threat. During the snorkel transects I saw no piscine predators of cunners. In previous work at the study site I observed striped bass, *Marone saxatilis*; blue fish, *Pomatomus saltatrix*; and spiny dogfish, *Squalus acanthias*, all of which could eat cunners (Bigelow and Schroeder 1953), but these sightings were rare events. In contrast, bird predation may be more important. During eight of nine observations I saw double-crested cormorants, known fish eaters

(Godfrey 1979), more near to or into the intertidal zone as the tide rose. My one observation of a foraging cormorant found it poking its head into the hollows under rocks. This searching pattern, and the paucity of other fish in the area, suggests that the birds were hunting cunners. Though I have not demonstrated that the double-crested cormorant is a predator of cunners, it is of some interest to note that the closely related European cormorant, *Phalacrocorax carbo*, forages successfully on labrids similar to the cunner in habits and habitat preference (Steven 1933; Dipper et al. 1977).

In making the movement from the subtidal area to the intertidal zone, the cunners expend energy and may face an increased predation threat (Olla et al. 1979). Presumably the advantage gained by having access to the rich intertidal food supply (Table 2) offsets the costs and risks. In this study, intertidal cunners were observed striking at mussels, barnacles, and littorinids, items which are important components of the cunners' diet in other sites (Olla et al. 1975; Shumway and Stickney 1975). The cunners may be driven to the intertidal resources by a shortage of food in the subtidal area. The mussels,barnacles, and littorinids common in the intertidal area were not found (mussels and barnacles), or appeared rare (littorinids), subtidally. However, alternative prey may have been present and used. Conversely the high density of food items might permit more efficient foraging and make the intertidal area quite attractive to cunners. In this case a lack of suitable refuges might limit the numbers of individuals able to forage intertidally.

Access to the intertidal food supply is limited to high tide and daylight hours (Olla et al. 1975; Dew 1976). Based on initial refuge occupancy and final abandonment times, cunners could forage for about 169 min before retreating. While I know each refuge was occupied during high tide, I have no evidence of recurring use of a given refuge by an individual on more than one tide. Hobson (1972) found low specificity to nocturnal refuges in tropical labrids, but Olla et al. (1975, 1979) demonstrated a high specificity to subtidal home shelters in the cunner. Determining whether individual fish are specific to the intertidal refuges would contribute greatly to an understanding of the system.

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RELATIVE EFFICIENCY OF TWO CLAM RAKES AND THEIR CONTRASTING IMPACTS ON SEAGRASS BIOMASS

Fishing gear and techniques are continually being developed and modified as alternatives to traditional fishing methodologies. As new equipment becomes available, most individual fishermen carry out their own field trials and peer interviews to determine which gear best meets their needs. Nevertheless, both quantitative comparisons of the relative efficiencies of alternative methodologies (e.g., Medcof and MacPhail 1964; Caddy 1973) and controlled scientific tests of the environmental impacts of contrasting techniques (e.g., Glude and Landers 1953; Caddy 1973; Fonseca et al.[1]) are necessary to provide the biological basis for resource managers to develop sound management policies. Quantitative data on the relative costs and benefits of alternative fishing methodologies are especially important in the estuaries, where fishing intensity often brings the demands of different fisheries into conflict.

Here we provide relative cost and benefit data for two different clam rakes, both available to hard clam (*Mercenaria mercenaria*) fishermen along the east and gulf coasts of the United States. At a study site in coastal North Carolina, we estimated the efficiency of hard clam capture by each rake in two habitats—a seagrass bed and a sand flat. We also employed replicate trials of both clam rakes within the seagrass bed to estimate relative impacts of raking on seagrass biomass. We chose damage to seagrass as a measure of important environmental impact because most coastal resource managers now recognize the direct and indirect contributions of seagrass beds to coastal zone fisheries production (e.g., Thayer et al. 1975).

Materials and Methods

The Contrasting Gear

We compared two clam rakes, known in North Carolina as the pea digger and the bull rake (Fig. 1). The pea digger (also called the potato rake in New England) is a traditional implement of hand rakers in North Carolina. It resembles a garden rake, having a wooden shaft (handle) about 1.2 m long, leading to a steel head with 3-6 prongs, each about 14 cm long, with 3.5 cm gaps. It is used by making forward and/or backward strokes which penetrate the sediments to a shallow depth (3-8 cm, depending upon substrate compaction and habitat). Whenever a rake prong encounters a clam, a distinctive scraping noise signals the clammer to excavate more deeply and to unearth the catch. The pea digger used in this study weighed 1.2 kg, had a wooden shaft 1.3 m long, and prongs 14 cm long.

The bull rake (also known as the shinnecock rake) has been introduced recently to North Carolina from Long Island Sound (see description in Glude and Landers 1953). It is a heavier, more robust implement, usually weighing from 8 to 11 kg. The rake consists of a steel basket attached to a metal (steel or aluminum) shaft which ends in a t-shaped handle. The basket has a rectangular opening (usually 18 × 48 cm) with teeth extending outward along the lower lip of the basket. The basket is formed by a grate of steel bars spread about 2-3 cm apart. The rake is used by pushing the teeth to a 14 cm depth into the sediments and then pulling it with short, quick jerks. The depth of penetration varies only slightly with substrate type. As the rake is pulled along through the sediments, clams, shells, and (if present) seagrass and debris are forced into the basket. When the rake seems heavy enough to suggest a full basket, it is removed from the water where the clams can be sorted. Because of its longer (and extendable) handle, the bull rake is often used from boats and can extend the depth at which hand clammers can work effectively. The bull rake used in this study (Fig. 1) weighed 8.6 kg, had a 1.8 m steel shaft and teeth 4 cm long, extending from a basket made of 0.7 cm steel rods 2.2 cm apart.

Although other hand rakes are used by clammers along the east and gulf coasts (including especially the "Jersey" rake), we chose to test the pea digger and bull rake because they fall at opposite ends of a size spectrum. Of all commonly used clam rakes, the pea digger is the lightest implement, has the fewest teeth, and digs to the shallowest depths in the sediments, whereas the bull rake falls at the opposite extreme for each of those three criteria.

The Study Site

Gear trials were conducted during June 1981 in two habitats along the southern (barrier island) margin of Back Sound, near Beaufort, N.C. This general study area and its physical environment are described in several previous publications (Sutherland and Karlson 1977; Nelson 1979; Peterson 1982). Water temperature was about 22°C during our study. Specific sites were chosen in an unvegetated sand flat and a

[1] Fonseca, M.S., G. W. Thayer, A. J. Chester, and C. Foltz. 1981. The impact of scallop harvesting on eelgrass (*Zostera marina* L.) meadows. Unpubl. manuscr., 15 p. Southeast Fish. Cent. Beaufort Lab., Natl. Mar. Fish. Serv., NOAA, Beaufort, NC 28516.

FIGURE 1.—Differences between the bull rake (left) and pea digger (right) in number and spacing of teeth, and head size and mass.

nearby seagrass bed (about 80% *Zostera marina* and 20% *Halodule wrightii*). Three replicate sediment cores, taken in April 1981 at each site to a depth of 20 cm and analyzed by standard sieving techniques (Ingram 1971; Folk 1974), revealed that sediments in both habitats were predominantly medium, fine, and very fine sands. In the seagrass bed, however, the sediment size distribution shifted substantially towards finer size classes: Average percent dry weights in the three decreasing size classes (medium, fine, and very fine sands) were 13.9, 44.7, and 18.3%, respectively, as compared with 28.8, 64.1, and 2.9% in the sand flat. Furthermore, the seagrass sediments contained 20.6% silt and clay, whereas the sand-flat sediments contained only 2.3% by weight within these mud size classes. The sand flat held relatively little shell debris, whereas buried empty clam shells were common in the seagrass bed. Average density of seagrass shoots in the seagrass habitat was 496 (± 1 SD of 165) M^{-2},, based on eight 0.5 m^{-2} samples. We selected all specific study plots in water <1 m deep at low tide, for ease of access. Our study plots were located at about midrange of the depth occupied by seagrasses in the Beaufort area.

Sand-Flat Methods

We chose 2×4 m plots in pairs, matching plots in space, water depth, and surface appearance of the substrate. We marked each plot by inserting a 1.6 m stake at each corner. One plot (chosen at random) of each of the 14 selected pairs was raked systematically for 6 min using a bull rake, while the other matching plot in each pair was raked systematically for 6 min with a pea digger. Prior to our use of the two rakes, we had carefully observed the usage of each rake by several professional clammers in the field so that we could employ each device in a way that closely resembled its customary usage. We used only backward strokes in deploying the pea digger, which penetrated 3-6 cm into the sediments in both habitats. During the 6-min raking period, variable proportions of the 2×4 m plots were raked (including occasional larger areas). In each plot the actual area raked was marked in the field and recorded. We also recorded the numbers of hard clams, collected from each trial,

broken down into legal (≥2.54 cm thickness) and illegal sizes. The actual area raked inside 5 pairs of plots was then systematically sieved by hand through 6 mm mesh to a depth of 12 cm to estimate the numbers of legal- and illegal-sized clams missed during raking. These observations permit a quantitative comparison of the two rakes: 1) Rate of hard clam capture and 2) efficiency of hard clam capture for both size classes of clams in the sand-flat habitat.

Seagrass Bed Methods

We chose matched 2 × 2 m plots, which we then marked with 1.6 m stakes. Plots used here were smaller than in the sand flat, because the presence of seagrasses and higher clam densities slowed the raking and reduced the area covered in 6 min. We selected 5 groups of 3 plots each, two for application of each rake and a third as a control to estimate initial seagrass biomass. Raking, sieving, and data recording were carried out in the same fashion as in the sand flat. In addition to measuring the area covered by each rake in 6 min for each plot and counting the numbers of hard clams (in the two size classes) collected, we also excavated by hand and placed into buckets all fresh seagrass material left behind in each raked area and from a 1 m^2 area within each control plot. We returned all seagrass material to the laboratory where we washed away salt and sediments, separated by clipping aboveground components (blades and shoots) from belowground components (roots and rhizomes), and weighed each separately after drying to constant weight at 105°C. These data permit a quantitative comparison of the two rakes in 1) rate of hard clam capture and 2) efficiency of hard clam capture for both legal- and illegal-sized clams in the seagrass habitat, analogous to the sand-flat contrasts. By subtracting the dry weight of seagrass remaining in raked areas from the dry weight in the matched controls, we were also able to estimate the mass of above- and belowground seagrass removed by each rake. We then used these figures to estimate the relative environmental impact of each rake in the form of estimated dry weight of seagrass removed 1) per unit time, 2) per unit area raked, and 3) per legal-sized clam captured in the seagrass habitat.

Results

Sand-Flat Habitat

The pea digger produced significantly more legal-sized hard clams per unit time of use in the sand-flat habitat, with a mean catch more than 50% higher than that of the bull rake (Table 1). The rate of capture of illegal-sized clams was equally low for both rakes in this habitat. Although both rakes were 100% efficient in their capture of legal-sized clams inside the areas raked in this environment, the pea digger covered significantly more area during a fixed period of time (Table 1) and, therefore, was able to catch more clams than the bull rake. Because of equal capture efficiency, the average numbers of legal-sized and illegal-sized clams caught per unit area raked did not differ significantly between rakes in the sand-flat environment (Table 1).

TABLE 1.—Hard clam capture rate per unit time, per unit area raked, and capture efficiency of two clam rakes from 14 paired replicate plots of a sand flat. Complete excavation to estimate capture efficiency was done for only 5 of the 14 pairs. *F*-tests revealed no significant difference between treatments in variance, except for area raked which required a log transformation prior to performing the *t*-test.

	Sand flat		
	Average ±1 SD		
Statistic	Bull rake	Pea digger	*t*-test[1]
1) No. clams caught/6 min			
legal-sized[2]	3.9 (±3.3)	6.1 (±2.1)	*
illegal-sized	0.2 (±0.4)	0.2 (±0.4)	ns
2) Area raked (m^2/6 min)	5.66(±0.37)	6.67(±0.90)	**
3) No. clams caught/m^2			
legal-sized	0.70(±0.59)	0.93(±0.34)	ns
illegal-sized	0.04(±0.08)	0.03(±0.06)	ns
4) Efficiency of capture[3]			
legal-sized	100% (±0.0)	100% (±0.0)	ns
illegal-sized[4]	25%	33%	ns

[1]* = $P < 0.05$;** = $P < 0.01$; ns = $P > 0.05$, in a two-tailed paired *t*-test.
[2]≥2.54 cm thick.
[3]Back-transformed mean of arcsin-transformed percents of clams captured.
[4]Insufficient densities of small clams prohibited replicate estimates of capture efficiency, thus these percents are based on pooled totals (4 and 3, respectively) and were tested by Fisher's exact test.

Seagrass Habitat

In the seagrass bed, the two rakes again differed significantly in average catch of legal-sized clams per 6 min of raking; however, in contrast to the sand-flat results, the bull rake was the more productive implement (Table 2). The bull rake also tended to catch more small clams per unit time, although the numbers of clams caught in this size class were small and the differences between rakes not statistically significant (Table 2). The greater return from use of the bull rake was mainly a consequence of the significantly greater area raked per unit time. The number of clams captured per unit area actually raked and the efficiency of clam capture in areas actually raked did not differ significantly between rakes for either size class of hard clam (Table 2).

A 6-min application of the bull rake in the seagrass habitat caused an estimated loss of seagrass biomass

that was more than double the estimated loss caused by 6 min of pea digger use (Table 3). Both aboveground and belowground components of the seagrass demonstrated this statistically significant difference between rakes. The bull rake also produced a greater estimated loss of seagrass biomass per unit area raked, an effect that was also significant for both aboveground and belowground components (Table 3). An estimated 87% of the initially present seagrass dry weight was removed by the bull rake in a 1 m^2 area that was completely raked. The magnitude of this effect was similar for components both above (89%) and below (83%) ground. In contrast, the pea digger removed only an estimated 47% of seagrass dry weight per unit area completely raked, with the impact falling less heavily on roots and rhizomes (37% decline) than on shoots (55% decline). The two rakes did not differ significantly in estimated seagrass biomass removed per legal-sized clam collected, although the estimated loss of belowground dry weight per clam collected by the bull rake was almost double the estimated loss caused by the pea digger (Table 3).

Discussion

By use of replicated field trials, we compared the effectiveness of two clam rakes in two contrasting ways. We estimated in each of two habitats the rate of hard clam capture per unit time, as would be appropriate if harvest time were limiting. We also converted our data into estimates of harvest per unit area raked, as would be appropriate if suitable clamming habitat—rather than time—were limited. We view these measures as endpoints in a spectrum of possibilities with the first more appropriate for managers of clam resources that are abundant relative to the intensity of harvest, and the second more relevant to clam resources subjected to very intense harvest pressure. By examining both endpoints, we hope to bracket actual prevailing conditions.

Our harvest data imply that habitat strongly influences the relative effectiveness of these two clam rakes. In unvegetated sandy sediments, the pea digger captured significantly more legal-sized hard clams per unit time than the bull rake (Table 1). In a seagrass bed, the relative effectiveness was reversed (Table 2). The difference between rake effectiveness was not a consequence of greatly differing efficiencies of clam capture within raked areas, but rather of differing rates of areal coverage. Because of approximately equal efficiencies of clam capture, the rakes did not differ significantly in hard clam capture per unit area raked in either habitat.

We suspect that the pea digger's advantage in unvegetated sandy sediments was dependent upon two confounded factors: 1) The relatively low densities of both living and dead hard clams, and 2) the absence of living seagrass. In areas with low hard clam densities, the pea digger will glide over unproductive bottom without creating frequent contacts that require excavation. Thus, more area can be covered than with a bull rake, which must be pulled more deeply through the sediments regardless of the scarcity of clams. Entanglements with roots of living seagrasses may tend to slow the progress of the pea digger which must plow through mats of seagrass, whereas the greater inertia of the moving bull rake is less influenced by encountering a small obstacle. Because these two factors (clam abundance and sea-grasses

TABLE 2.—Hard clam capture rate per unit time, per unit area raked, and capture efficiency of two clam rakes from six paired replicate plots in a seagrass bed. *F*-tests revealed no significant difference between treatments in variance, except for area raked which required a log transformation prior to performing the *t*-test.

Statistic	Seagrass bed, Average ±1 SD: Bull rake	Pea digger	*t*-test[1]
1) No. clams caught/6 min			
legal-sized[2]	9.2 (±3.1)	5.8 (±2.6)	*
illegal-sized	1.2 (±1.2)	0.5 (±0.8)	ns
2) Area raked (m^2/6 min)	1.95(±0.06)	1.53(±0.32)	*
3) No. clams caught/m^2			
legal-sized	4.70(±1.54)	4.06(±2.01)	ns
illegal-sized	0.60(±0.61)	0.29(±0.46)	ns
4) Efficiency of capture[3]			
legal-sized	83%(±6)	69%(±12)	ns
illegal-sized[4]	20%(±20)	18%(±40)	ns

[1] * = $P<0.05$; ns = $P>0.05$, in a two-tailed paired *t*-test.
[2] ≥2.54 cm thick.
[3] Back-transformed mean of arcsin-transformed percents of clams captured.
[4] $n = 5$ for this comparison, because one plot had no illegal-sized clams.

TABLE 3.—Comparison of environmental impacts on seagrass of two different clam rakes used in seven paired replicate plots. *F*-tests revealed no significant difference between treatments in variance for any comparison.

Estimated impact	Seagrass bed, Average ±1 SD: Bull rake	Pea digger	*t*-test[1]
1) Dry wt removed (g/6 min)			
shoots	121.6(±43.1)	54.2(±39.8)	**
roots and rhizomes	81.2(±31.9)	26.3(±21.9)	*
total	202.8(±69.3)	80.5(±58.3)	**
2) Dry wt removed [2] (g/m^2 raked)			
shoots	60.3(±17.5)	37.4(±24.0)	**
roots and rhizomes	40.2(±13.2)	17.6(±11.4)	*
total	100.5(±26.9)	54.9(±31.5)	**
3) Dry wt removed (g/6 min) per legal clam caught			
shoots	21.2(±21.6)	15.5(±22.4)	ns
roots and rhizomes	14.1(±15.2)	7.5(±11.0)	ns
total	35.3(±36.7)	23.0(±33.3)	ns

[1] * = $P<0.05$; ** = $P<0.01$; ns = $P>0.05$ in a two-tailed paired *t*-test.
[2] Average seagrass dry weight (g/m^2 ±1 SD) in the 7 control (1 m^2) plots: shoots - 67.7 (±19.8); roots - 48.2 (±15.7); total - 116.0 (±32.4).

cover) are confounded in our study, we cannot distinguish between them. However, because most studies have consistently demonstrated higher densities of marine benthic infauna, including hard clams, in seagrass meadows than in nearby unvegetated bottom (e.g., O'Gower and Wacasey 1967; Santos and Simon 1974; Orth 1977; Brook 1978; Stoner 1980; Peterson 1982), we suspect that our habitat-specific differences in rake effectiveness can be generalized. Nevertheless, exceptions are likely to exist, implying that our results on relative catch efficiency should be applied only where hard clam abundances are known to be greater in the seagrass habitat.

We chose to estimate the dry weight of seagrass removed as a measure of environmental damage because many studies have identified, and most coastal resource managers now recognize, the value of preserving meadows of seagrass. For instance, seagrasses have been identified as locally significant producers of fixed carbon to fuel estuarine and coastal food chains and as providers of nursery habitat for juvenile finfishes and shellfishes, many of which are either commercially harvested or else serve as significant food items for commercially harvested species (e.g., Thayer et al. 1975). Our raking and seagrass harvest results demonstrate that the bull rake removed more seagrass than the pea digger per unit time of use and per unit area raked. Furthermore, differences between rakes in estimated seagrass removal tended to be greater for the belowground than the aboveground components of the seagrass. Because roots and rhizomes probably provide the source of vegetative propagation, a potentially important mode of spread in seagrasses, the bull rake may have more long-lasting effects on seagrass cover than the pea digger, as well as a greater immediate impact. Seagrass that is removed by raking probably enters the detrital pool and thus continues to fulfill one of its important functions. However, the loss of seagrass may reduce the value of the grass bed as a nursery habitat. We did not collect any data to test this possibility, but the dependence of bay scallops on seagrass surface area for juvenile attachment sites and the dependence of various juvenile fishes on seagrass cover for predator protection and on seagrass surface for foraging habitat (e.g., Thayer et al. 1975) imply that the value of a seagrass bed is diminished by uprooting significant amounts of seagrass.

This study was designed to provide estuarine resource managers with some of the biological information needed to manage and regulate clamming in shallow estuarine habitats. We have demonstrated that the superior effectiveness of the more massive bull rake in a seagrass habitat is accompanied by substantially more uprooting of seagrass than is caused by raking with a pea digger. However, environmental planners and resource managers must apply these results with caution in their attempts to weigh the benefits of permitting bull rake usage in seagrass beds against the potential costs associated with increased uprooting of seagrasses. Our experiments were restricted to a single seagrass system; changing the seagrass type or the sediment grade may yield different results. More importantly, we made no direct measurements of the cost of seagrass removal. It is likely that, because the amount of uprooted seagrass appears to be an increasing function of clamming intensity, the impact of removal could be negligible in some areas where clamming intensity is low relative to the areal extent of the seagrass habitat. Thinning of seagrass may even be beneficial under some conditions by stimulating growth of the plants left behind. Recovery by growth may be rapid enough at certain seasons to render the impact of seagrass removal insignificant to the production of associated vertebrate and invertebrate species.

Although we calculate the seagrass removal per unit resource harvested (Table 3), quantitative estimates of the cost of seagrass removal are necessary to convert these biological data into a management criterion. Even if resource managers choose to prohibit the use of bull rakes inside seagrass beds on the basis of the enhanced loss of seagrass biomass per unit time, per unit area, and per unit resource (clam) collected (Table 3), this prohibition should probably be restricted to seagrass meadows. Even though the bull rake is not as effective as the pea digger in harvesting clams on an unvegetated sand flat (Table 1), it may well be a superior implement in other habitats, such as soft muds. It is also used in deeper waters (Glude and Landers 1953), where short-handled rakes without baskets are ineffective and where seagrass is sparse or absent. We are aware that any habitat-specific regulation of a fishery requires more intense enforcement to be effective than an outright prohibition of certain gear, but the deeper water and unvegetated mud-bottom usages of bull rakes (Glude and Landers 1953) suggest that the bull rake deserves a place in the repertoire of legal clamming gear, despite its threat to seagrass.

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HETEROCARPUS LONGIROSTRIS MACGILCHRIST FROM THE NORTHERN MARIANA ISLANDS

In March and April 1981 the National Marine Fisheries Service Honolulu Laboratory chartered the FV *Typhoon* to conduct a fisheries resource survey in the waters of the Commonwealth of the Northern Mariana Islands. One of the major objectives of this survey was the investigation of deepwater pandalid shrimp stocks. Although not previously recognized as a species of commercial interest (Holthuis 1980), *Heterocarpus longirostris* MacGilchrist 1905 was caught in sufficient numbers on this cruise to suggest a commercial potential.

Heterocarpus longirostris has been recorded in the literature from a few specimens caught in the Indian Ocean. MacGilchrist (1905) reported taking two male specimens at 1,754 m in the Bay of Bengal; Balss (1925), one female specimen taken at 1,143 m off Nias Island, Sumatra; and Calman (1939), one female specimen taken at 914-1,463 m in the Maldive area. Catches from this cruise constitute a first record of this species from the Pacific Ocean. *Heterocarpus longirostris* is very similar to *H. laevigatus* in general morphology. *Heterocarpus longirostris* differs from *H. laevigatus* in that the preorbital dorsal surface of the rostrum is multidentate and there is a blunt point posteriorly on the carina of the third abdominal somite. In *H. laevigatus* the dorsal surface of the rostrum is edentate in advance of the orbit and the posterior portion of the third abdominal somite is rounded. Further differences are discussed in MacGilchrist (1905).

The FV *Typhoon* fished for shrimp in the Saipan-Tinian area using traps baited with chopped fish, usually skipjack tuna, *Katsuwonus pelamis*. The traps consisted of half-round frames of iron rebar (91 × 72 × 42 cm) wrapped with 13 × 25 mm or 13 × 13

mm wire mesh and covered by either burlap or canvas over the arched upper surface. On each sampling day one string of three traps was set at each of three sampling depths, 366, 732, and 1,097 m (200, 400, and 600 fathoms). Strings were set in the afternoon and recovered the next morning with a normal soaking time of between 16 and 20 h. Three species of *Heterocarpus*—*H. ensifer, H. laevigatus,* and *H. longirostris*—accounted for the majority of the catch. Shrimp referable to both *H. laevigatus* and *H. longirostris* were present in the catches throughout the cruise, but during the major part of the cruise they were considered to be the same species and recorded as "*H. laevigatus.*" These two species were recorded separately only on the last two series of sets (two strings at each of the three experimental depths). Information on the catch for these six strings is presented in Table 1.

The species with the highest catch rate (kilograms per trap) was *H. laevigatus; H. ensifer* and *H. longirostris* followed with catch rates about half that of *H. laevigatus. Heterocarpus laevigatus* was also the largest species caught, averaging 25 individuals/kg. *Heterocarpus longirostris* was next, averaging 47/kg, and *H. ensifer* was the smallest, averaging 146/kg. Differences in the reproductive biology of these species are suggested by the differing proportion of egg-bearing females present in the catch for each species. The percentage of berried females was highest for *H. ensifer* at 33% whereas that for *H. longirostris* was only 19%, and no berried *H. laevigatus* were caught. It is quite likely that these values change on a seasonal basis. Vertical separation of the three species was complete for the last six strings set. *Heterocarpus ensifer* was caught only at 366 m, *H. laevigatus* only at 737 m, and *H. longirostris* only at 1,097 m.

Though not documented due to confusion in the species identification of *H. laevigatus* and *H. longirostris* during most of the cruise, there is reason to believe that species separation by depth was essentially complete for the entire cruise. Table 2 lists the catch of the three species of *Heterocarpus* for the entire cruise excluding the last six strings. *Heterocarpus ensifer* was found almost exclusively at 366 m with a few being caught at 732 m. Mean size and percentage of berried female values for the entire cruise (Table 2) are very similar to those obtained from the last six strings (Table 1) for *H. ensifer* (112/kg compared with 146/kg and 31% compared with 33%, respectively). Similarly, values of mean size and percent berried for *H. laevigatus* in Table 1 match closely those for the *H. laevigatus/H. longirostris* group at 732 m (and the few at 366 m) in Table 2 as do the values for *H. longirostris* (Table 1) with those at 1,097 m (Table 2). This supports the assumption of vertical separation of these three species.

Both *H. laevigatus* and *H. ensifer* are considered to be commercially important species and have supported small local fisheries in some Pacific areas (Hawaii State 1979). Based on the results of this cruise, *H. longirostris* compares favorably with these two species as one with commercial potential. It is very close to *H. ensifer* in relative abundance (mean catch in weight per trap) and second, to *H. laevigatus*, in mean size. *Heterocarpus laevigatus* is first in both

TABLE 1.—Catch of *Heterocarpus ensifer, H. laevigatus,* and *H. longirostris* for the last six strings of the cruise.

Depth (m)	No. of traps fished	Catch			Mean catch/ trap (kg)	Mean size of shrimp (No./kg)	Percent berried
		Species	Number	Weight (kg)			
366	6	*H. ensifer*	542	3.7	0.6	146	33
732	6	*H. laevigatus*	172	7.0	1.2	25	0
1,097	6	*H. longirostris*	170	3.6	0.6	47	19

TABLE 2.—Catch of *Heterocarpus ensifer, H. laevigatus,* and *H. longirostris* for the entire cruise excluding the last six strings.

Depth (m)	No. of traps fished	Catch			Mean catch/ trap (kg)	Mean size of shrimp (No./kg)	Percent berried
		Species	Number	Weight (kg)			
366	34	*H. ensifer*	1,580	14.05	0.4	112	31
366	34	*H. laevigatus/H. longirostris*	67	3.5	0.1	19	1.5
732	56	*H. ensifer*	35	0.3	0.01	117	17
732	56	*H. laevigatus/H. longirostris*	2,654	90.75	1.6	29	1.6
1,097	57	*H. laevigatus/H. longirostris*	1,920	35.9	0.6	53	21

categories. Although further survey work is needed to determine the depth of maximum abundance for *H. longirostris*, the apparent greater depth of habitat for this species (1,097 m as compared with 766 m for *H. laevigatus* and 366 m for *H. ensifer)* is the major undesirable characteristic for development of any proposed fishery. Fishing at these greater depths would require greater capital investment not only in a more powerful depth recorder but also in expensive line which would need to be replaced after any gear loss.

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NOTICES

NOAA Technical Reports NMFS published during last 6 months of 1982.

Circulars

444. Whales, dolphins, and porpoises of the eastern North Pacific and adjacent Arctic waters, a guide to their identification. By Stephen Leatherwood, Randall R. Reeves, William F. Perrin, and William E. Evans. July 1982, v + 245 p., 267 figs., 2 tables, Append. A-F.

446. Marine flora and fauna of the northeastern United States. Lichens (Ascomycetes) of the intertidal region. By Ronald M. Taylor. August 1982, iii + 26 p., 43 figs.

447. Proceedings of the Eighth U.S.-Japan Meeting on Aquaculture at Bellingham, Washington, October 17-18,1979. By William N. Shaw (editor). November 1982, iii + p. [Six articles are published in this paper.]

Special Scientific Report—Fisheries

758. Equipment and techniques for handling northern fur seals. By Roger L. Gentry and John R. Holt. July 1982, iii + 15 p., 10 figs., 1 table.

759. Catch temperatures for some important marine species off California. By James L. Squire, Jr. August 1982, iii + 19 p., 23 figs., 3 tables.

760. Parasite-host records of Alaska fishes. By Adam Moles. September 1982, iii + 41 p.

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DEPARTMENT OF COMMERCE * UNITED STATES OF AMERICA *

Fishery Bulletin

Vol. 81, No. 3 July 1983

(Continued on back cover)

Seattle, Washington

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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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The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 1 April 1985.

Fishery Bulletin

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Notes

STOMACH CONTENTS OF SILVER HAKE, *MERLUCCIUS BILINEARIS*, AND ATLANTIC COD, *GADUS MORHUA*, AND ESTIMATION OF THEIR DAILY RATIONS

E. G. DURBIN,[1] A. G. DURBIN,[1] R. W. LANGTON,[2] AND R. E. BOWMAN[3]

ABSTRACT

The model of Elliott and Persson was used to estimate the daily ration of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, collected in the western North Atlantic between Cape Hatteras and Nova Scotia during the years 1973-76. The model required field measurements of the weight of food in the stomachs during consecutive 3-h periods over 24 h, and laboratory estimates of the exponential gastric evacuation rate. The silver hake and Atlantic cod were each grouped into two size classes for analysis (≤20 cm and >20 cm, and ≤30 cm and >30 cm, respectively). Upper and lower daily ration estimates were 3.2 and 2.9% body weight (BW) per day for hake ≤20 cm, 2.2 and 0.8% BW per day for hake >20 cm, and 1.5 and 0.9% BW per day for cod >30 cm. There were insufficient small cod to estimate daily ration. These ration estimates are intermediate between two previous estimates for silver hake and Atlantic cod on Georges Bank obtained by different methods.

With the increasing interest in multispecies management and total ecosystem management, it is essential to understand the role of fish predators within the ecosystem. As a part of this, it is necessary to determine the feeding habits and the daily ration of the major species. Here we estimate the daily ration of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, in the northwest Atlantic, based on stomach samples collected by the Northeast Fisheries Center, National Marine Fisheries Service. The model of Elliott and Persson (1978) was used to investigate diel feeding periodicity and to estimate the daily ration, based on field measurements of stomach contents, and laboratory estimates of the exponential evacuation rate R.

METHODS

Method of Estimating Daily Food Consumption

Most recent studies have concluded that gastric evacuation is best described by a curvilinear function such as an exponential curve (Tyler 1970; Brett and Higgs 1970; Elliott 1972; Kiørboe 1978; Persson 1979; but see Jobling 1981). In an evaluation of different models to estimate daily ration in fishes, Elliott and Persson (1978) demonstrated that their model, which assumes exponential evacuation, provided accurate estimates of ingestion, whereas models which assumed a constant (linear) gastric evacuation rate (Bajkov 1935 and derivations thereof) significantly underestimated ingestion. Since recent comments support the validity of the exponential model for the field estimation of daily ration on the basis of stomach contents (Cochran 1979; Elliott 1979; Eggers 1979), this approach has been adopted for the present analysis.

In the Elliott and Persson model, the consumption of food (C_t) by a fish over the time interval t_0 to t_t is calculated from the amount of food in the stomach at time t_0 (S_0), the amount in the stomach at time t_t (S_t), and the instantaneous evacuation rate R:

$$C_t = \frac{(S_t - S_0 e^{-Rt})\, Rt}{1 - e^{-Rt}}. \quad (1)$$

To apply the model, a sample of fish is collected from the field at intervals of t hours for at least 24 h, and the mean stomach content weight is used to estimate S_0 and S_t for each time interval. The estimates of C_t calculated for each time interval t are then summed to give the total daily ration.

The model assumes that the fish feed continuously, at a constant rate, during time interval t. The cumulative amount of food consumed (C_t) therefore increases linearly during time t. However, Elliott and Persson (1978) showed that even if feeding is not

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continuous, the estimates of C_t will not be seriously biased, provided that stomach samples are collected at intervals of 3 h or less.

The total daily ration can also be calculated in a single step from

$$C_t = 24\,R\,\bar{S} \qquad (2)$$

where $\bar{S}$ equals the mean stomach content weight over the 24-h period (Elliott and Persson 1978). However, in order to investigate diel feeding periodicity, it is necessary to calculate ingestion during time intervals <24 h, using Equation (1). For the present analysis the 24-h day was divided into eight consecutive 3-h time periods; data collected within each of these periods were arbitrarily assigned to the midpoint of that time period. Ingestion between that time and the midpoint of the next time interval was then calculated using Equation (1), where $t = 3$ h.

In the Elliott and Persson model, R is assumed to be exponential (i.e., a constant proportion of the stomach content is evacuated per unit time), and unaffected by fish size, food size, meal size, and the frequency of feeding. R is affected by food type, however, and increases with increasing temperature, usually following an exponential or power curve. Gastric evacuation is assumed to begin immediately after the food is ingested, without an appreciable time lag.

The most appropriate values of R to be used in this analysis were determined from a literature review (Appendix 1). The general relationship between R and temperature (t) is that $R = ae^{bt}$ (Elliott 1972), where a and b are constants. The slope (b) of this relationship appears to be fairly constant for different prey types and fish species ($\bar{b} = 0.115$, App. Table 1) but the intercept (a) may change significantly according to the type of food.

For several marine fishes that were fed small prey, the relationship between R and temperature (°C) was

$$R = 0.0406\,e^{0.111t} \qquad (3)$$

(App. Fig. 1). The data indicated that fish prey are digested more slowly than small prey types, however. This effect has not been clearly defined, but the maximum range in R that has been observed within a single fish species was in the Atlantic cod, where the exponential evacuation rate for fish flesh (based on our calculation of data from Bagge 1977) was about 10% of that for a crustacean prey, shrimp tails (Tyler 1970) (App. Fig. 1). A complicating factor is that the food particle sizes in those studies using fish as prey were much larger than in studies using other prey types, and the effect of large particle size on the evacuation rate is poorly known. Thus we are not presently able to determine whether the reduced evacuation rates observed for fish prey are principally due to the prey type (fish flesh) or to the comparatively large particle sizes used in these studies. A further problem is that we lack information on digestive rates for many important prey species of marine fishes.

Because of these limitations to our knowledge of the rates at which different prey species are evacuated, the stomach contents of the Atlantic cod and silver hake have been grouped into two categories in the present study: "fish prey" and "all other prey." Most of the "other prey" were small organisms, and we used Equation (3) to estimate R for these prey. Because of the uncertainty concerning the value of a for fish prey, we made two estimates of R for this food type: first, where a in Equation (3) = 0.0406, and second where a was 10% of this value, i.e., a = 0.00406. These estimates should represent upper and lower limits to the true value of R for fish prey. The temperature for which R was calculated was the mean temperature at which each fish species and size class was collected (see Tables 1, 6, 7).

Description of the Data Set

The survey area from which stomach samples were taken extends from the offshore waters of Cape Hatteras to western Nova Scotia, and is divided into five geographic regions (Fig. 1). Stomach content data gathered during spring and fall cruises (Table 1) during the years 1973-76 were analyzed. Details of the sampling procedure and methods of stomach content analysis are given in Langton et al. (1980). Sampling continued throughout the 24-h day and was designed to provide broad coverage over a wide geographic area rather than intensive surveys within small regions. In order to define the food web, 100 stomachs (50 young-of-the-year and 50 adult fish) were to be collected per geographic region per cruise from each of 17 selected fish species. At each station no more than 10 stomachs per species were to be sampled. The same species was not to be sampled from consecutive stations unless it appeared that, because of low abundance, the desired number of fish could not be collected using the normal sampling scheme. In this case the fish were collected as needed to fill the quota for the geographic area. Young-of-the-year fish were preserved whole in 10% Formalin,[4] after slitting the gut cavity to ensure quick penetra-

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

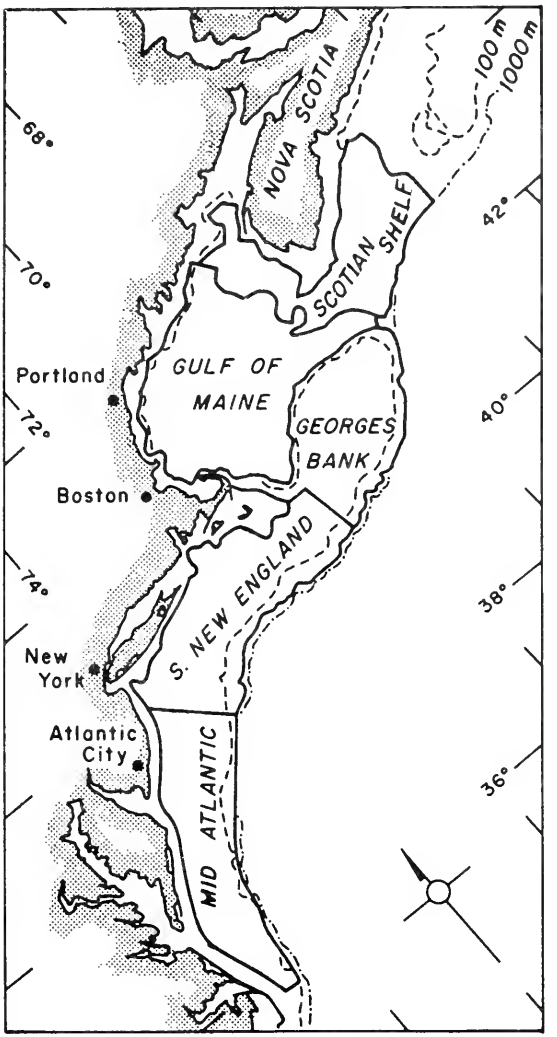


FIGURE 1.—Five geographic areas of the northwest Atlantic composing the sampling area for fish food studies.

tion by the preservative. With the larger fish the length, sex, and maturity were determined at sea, and the stomach was then removed, individually labeled, and preserved in 10% Formalin for later analysis. Fish showing signs of regurgitation (everted stomach, food present in mouth or esophagus) were not included in the samples. In the laboratory the stomach contents were identified to the lowest possible taxon and weighed (wet weight). For the present study, the weight of sand and gravel were subtracted from the total stomach content weight, and stomachs that contained recognizable food in amounts too small to be weighed (<0.01 g) were considered empty.

The weight of each fish was calculated from its total length and length-weight relationships (Wilk et al. 1978) where

$$\text{Wet wt (g)} = 0.3555 \times 10^{-5} \text{ length (mm)}^{3.1109} \quad \text{(silver hake)}$$

$$\text{Wet wt (g)} = 0.6031 \times 10^{-5} \text{ length (mm)}^{3.0979} \quad \text{(Atlantic cod).}$$

Combining all cruises, 1,159 silver hake were collected during the spring, and 1,555 during the fall; the number of fish sampled per tow averaged 8.0 and 8.6, respectively (Table 1). Silver hake were collected almost exclusively in the southern three geographic regions (Middle Atlantic, Southern New England, and Georges Bank), where a total of 2,625 fish were taken in 304 tows. Mean temperatures during spring cruises were several degrees colder than during the fall; however, the mean depth at which the fish were collected was not greatly different during the two seasons (Table 1).

In all cruises combined, 775 Atlantic cod were sampled during spring, and 922 during fall; the average number of fish sampled per tow (5.0 and 4.5, respectively) was lower than for silver hake. Atlantic cod were collected mainly from the northern three geographic regions (Georges Bank, Gulf of Maine, and Western Nova Scotia), where a total of 1,661 fish were sampled from 351 tows. The temperatures at which cod were collected in the spring were colder than those at which they were taken in the fall. Because of the more northerly distribution of the cod, they were taken from colder water temperatures than the silver hake (Table 1). The depths at which hake and cod were taken during the spring were similar (Table 1). However, during fall, the cod were found at somewhat greater depths than hake.

Because of the considerable size range of each species (Fig. 2), and changes in food habits which occurred with increasing size (discussed below), the silver hake and Atlantic cod were divided into two size-classes for further analysis: ≤20 cm (small) and >20 cm (large) for hake, and ≤30 cm (small) and >30cm (large) for cod. Mean lengths and weights of each size class during spring and fall are presented in Table 2.

For the present study, the data from the four spring cruises were combined to provide a composite picture of diel changes in stomach contents of each species over the entire study area. Data from the four fall cruises were similarly combined. Possible differences in diel feeding patterns or feeding rate that may have existed in different regions or years are not

TABLE 1.—Total number of tows from which silver hake and Atlantic cod were sampled, total number of fish sampled, mean number of fish sampled per tow, and mean temperature and depth of capture. Cruise dates were: (Spring) 3/3 to 15/5 1973; 12/3 to 4/5 1974; 4/3 to 12/5 1975; 4/3 to 8/5 1976; (Fall) 26/9 to 20/11 1973; 20/9 to 14/11 1974; 15/10 to 18/11 1975; 20/10 to 23/11 1976.

	Total no of tows	Total no of fish sampled	No. of fish per tow $\bar{x}$	Temperature of capture (°C) $\bar{x} \pm$ 95% C.L.	Depth of capture (m) $\bar{x} \pm$ 95% C.L.
Silver hake					
Spring					
All fish	144	1,159	8.0	8.08 ± 0.17	88.4 ± 3.8
≤20 cm				7.63 ± 0.23	64.1 ± 3.7
>20 cm				8.45 ± 0.23	106.6 ± 5.7
Fall					
All fish	180	1,555	8.6	11.86 ± 0.10	82.6 ± 2.3
≤20 cm				11.94 ± 0.15	75.5 ± 3.2
>20 cm				11.76 ± 0.13	90.1 ± 3.3
Atlantic cod					
Spring					
All fish	155	775	5.0	5.76 ± 0.16	90.3 ± 2.9
≤30 cm				5.72 ± 0.48	89.6 ± 5.9
>30 cm				5.77 ± 0.17	90.4 ± 3.2
Fall					
All fish	204	922	4.5	9.15 ± 0.15	104.8 ± 3.1
≤30 cm				8.46 ± 0.30	87.1 ± 4.6
>30 cm				9.30 ± 0.17	108.6 ± 3.5

TABLE 2.—Mean length and estimated wet weight of silver hake and Atlantic cod.

		Total length (cm)			Wet weight (g)		
	n	$\bar{x} \pm$ 95% C.L.	Minimum	Maximum	$\bar{x} \pm$ 95% C.L.	Minimum	Maximum
Silver hake							
Overall	2,714	20.3 ± 0.5	3	64	125.8 ± 6.6	0.1	1,908
Spring	1,159	23.0 ± 0.7	3	64	156.0 ± 11.4	0.1	1,908
≤20 cm	496	10.2 ± 0.4	3	20	9.9 ± 1.0	0.1	51.2
>20 cm	663	32.6 ± 0.5	21	64	265.3 ± 15.4	59.6	1,908
Fall	1,555	18.3 ± 0.6	3	55	103.3 ± 7.5	0.1	1,191
≤20 cm	797	7.2 ± 0.2	3	20	4.1 ± 0.6	0.1	51.2
>20 cm	758	30.1 ± 0.4	21	55	207.7 ± 11.3	59.6	1,191
Atlantic cod							
Overall	1,697	53.2 ± 1.2	4	150	2,861 ± 170	0.6	41,649
Spring	775	54.5 ± 1.8	4	133	3,062 ± 259	0.6	28,693
≤30 cm	143	18.8 ± 1.3	4	30	104.5 ± 16.5	0.6	285
>30 cm	632	62.6 ± 1.5	31	133	3,732 ± 293	315	28,693
Fall	922	52.2 ± 1.5	5	150	2,692 ± 225	1.1	41,649
≤30 cm	161	17.9 ± 1.2	5	30	90.5 ± 13.6	1.1	285
>30 cm	761	59.5 ± 1.4	31	150	3,243 ± 256	315	41,649

considered; evaluation of such differences would require a separate study, with additional, more intensive field surveys designed to investigate these problems (see Pennington et al. (in press) for a discussion of the required sampling design).

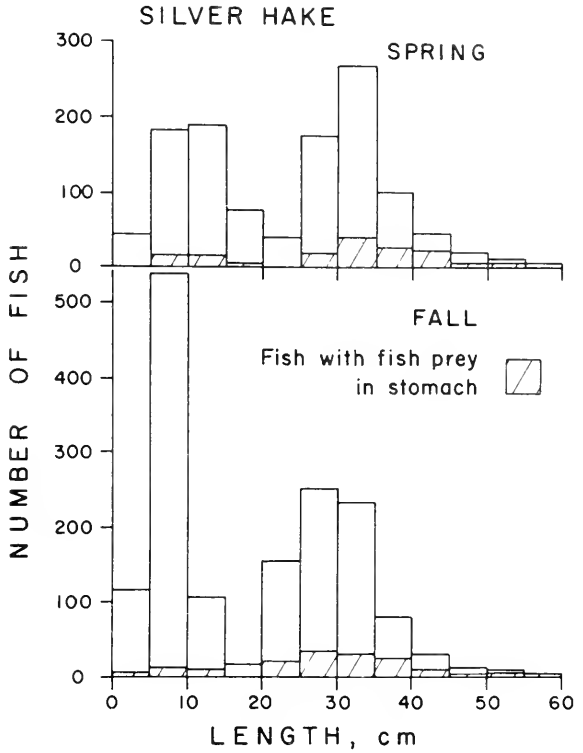
As stated above, for the analysis of diel changes in stomach contents and the calculation of daily ration, data from tows within each successive 3-h period of the day were grouped together and arbitrarily assigned to the midpoint of the time period. The number of tows taken during each period is shown for each species by season and size class in Tables 6 and 7. Large silver hake and large Atlantic cod were fairly evenly sampled throughout the day. Small hake were caught in larger numbers by night, however. Small cod were few, and generally the sample sizes for each time period were very small (<10 individuals).

In order to compare mean values from different subsets of the data, an F-test for the equality of variances was first performed. If the variances were not significantly different ($P < 0.05$), a Student's t-test was applied to test for the significance of the difference in the mean values of the two subsets. If the variances were unequal, Satterthwaite's approximation (Steel and Torrie 1960) was used to compute the degrees of freedom associated with the approximate t value, using a computer program which is available in the Statistical Analysis System (SAS 79) statistical package (SAS Institute, Inc.).

RESULTS

Stomach Contents

In both Atlantic cod and silver hake, the food habits and the mean amount of food in the stomachs changed with increasing fish length (Tables 3, 4). The



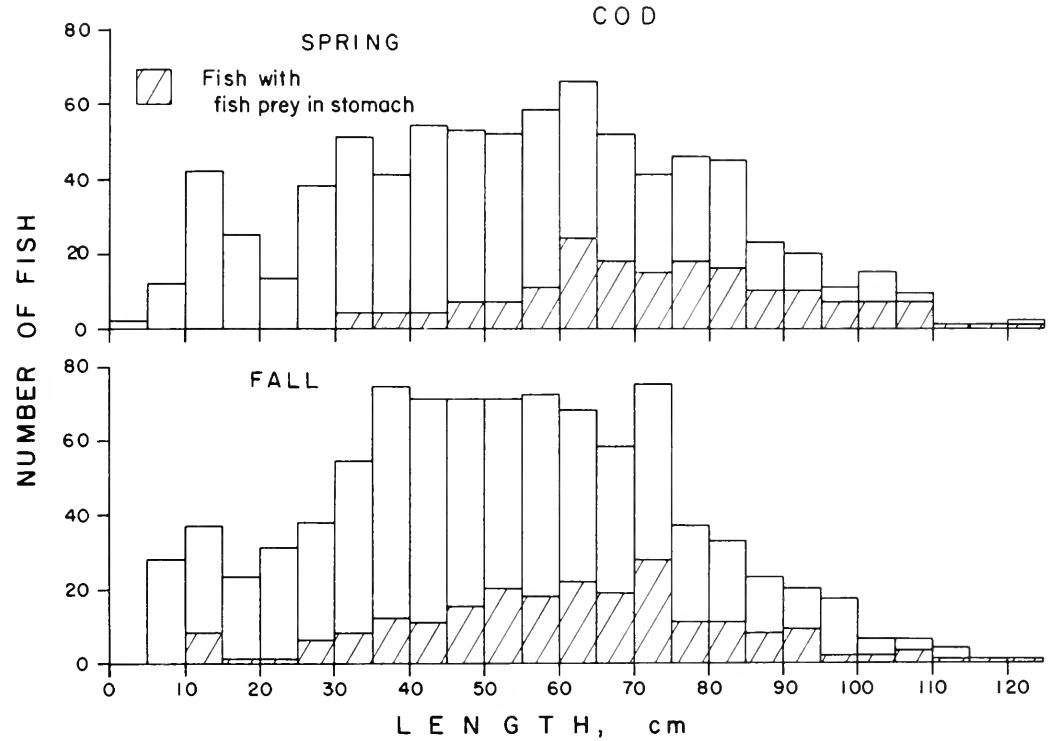


FIGURE 2.—Size-frequency distribution of silver hake and Atlantic cod collected during the spring and fall in the study area. The number of fish in each size class containing fish prey in their stomachs is also shown.

proportion of fish prey in the diet increased as the fish grew larger. This change in food habits was accompanied by an increase in the mean weight of stomach contents as a percent of body weight (Tables 3, 4). Thus, on the average, the stomachs of large fish contained more food, as a percent of body weight, than the stomachs of small fish (see especially the mean values for fish with nonempty stomachs, last three columns in Tables 3 and 4).

In silver hake, the "other prey" category was im-

TABLE 3.—Mean weight of stomach contents of silver hake, in 10 cm length classes, during spring and fall. BW = body weight.

Size class (cm)	Total no. of fish examined (No. of empty stomachs)	Mean stomach contents of all fish, including those with empty stomachs						Stomach contents, excluding fish with empty stomachs		
		Total wet wt per fish (g)	Fish prey wt per fish (g)	Other prey wt per fish (g)	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish
Spring										
1-10	283(79)	0.022	0.005	0.017	0.73	0.15	0.58	1.01	0.21	0.80
11-20	213(42)	0.19	0.024	0.16	0.86	0.14	0.72	1.08	0.18	0.90
21-30	264(95)	0.84	0.30	0.54	0.63	0.22	0.41	0.98	0.35	0.64
31-40	332(147)	3.15	2.19	0.95	1.00	0.67	0.33	1.79	1.20	0.59
41-50	53(18)	21.99	19.82	2.17	3.10	2.80	0.30	4.70	4.24	0.46
51-60	13(6)	24.54	24.51	0.027	2.29	2.29	0	4.26	4.25	0.00
61-70	1(1)	0	0	0	0	0	0	0	0	0
All Fish	1,159(388)	2.41	1.88 (78.0%)	0.53 (22.0%)	0.93	0.46 (49.2%)	0.47 (50.8%)	1.40	0.69 (49.3%)	0.71 (50.7%)
Fall										
1-10	697(144)	0.016	0.001	0.015	1.08	0.08	1.00	1.36	0.10	1.26
11-20	100(28)	0.17	0.046	0.12	0.92	0.19	0.73	1.28	0.27	1.01
21-30	448(218)	0.32	0.18	0.14	0.29	0.17	0.13	0.57	0.33	0.24
31-40	264(113)	2.66	2.25	0.41	0.83	0.68	0.15	1.45	1.19	0.27
41-50	38(22)	10.07	10.04	0.032	1.71	1.70	0.01	4.06	4.04	0.01
51-60	8(3)	15.84	15.80	0.047	1.59	1.58	0	2.54	2.53	0.01
61-70	0							0		
All fish	1,555(528)	0.89	0.76 (85.4%)	0.13 (14.6%)	0.82	0.26 (31.4%)	0.56 (68.6%)	1.24	0.39 (31.5%)	0.84 (67.7%)

TABLE 4.—Mean weight of stomach contents of Atlantic cod, in 10 cm length classes, during spring and fall. BW = body weight.

Size class (cm)	Total no. of fish examined (No. of empty stomachs)	Mean stomach contents of all fish, including those with empty stomachs						Stomach contents, excluding fish with empty stomachs		
		Total wet wt per fish (g)	Fish prey wt per fish (g)	Other prey wt per fish (g)	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish
Spring										
1-10	13(1)	0.0064	0	0.0064	0.59	0	0.59	0.64	0.00	0.64
11-20	71(11)	0.11	0	0.11	0.39	0	0.39	0.46	0.00	0.46
21-30	59(5)	1.15	0.0017	1.15	0.52	0	0.52	0.57	0.00	0.57
31-40	92(7)	2.63	0.28	2.35	0.57	0.07	0.50	0.61	0.07	0.54
41-50	107(6)	5.31	0.43	4.87	0.49	0.04	0.45	0.52	0.04	0.48
51-60	114(11)	13.12	0.87	12.25	0.66	0.04	0.62	0.73	0.05	0.69
61-70	110(5)	34.42	13.42	21.00	1.09	0.42	0.68	1.15	0.44	0.71
71-80	86(5)	45.52	25.38	20.14	0.90	0.50	0.40	0.96	0.53	0.43
81-90	66(1)	38.53	25.85	12.68	0.55	0.36	0.19	0.55	0.37	0.19
91-100	28(2)	99.02	58.21	40.82	0.99	0.59	0.40	1.06	0.63	0.43
101-110	23(3)	190.02	160.80	29.22	1.39	1.18	0.21	1.59	1.36	0.24
111-120	2(0)	27.30	12.70	14.60	0.13	0.06	0.07	0.13	0.06	0.07
121-130	3(0)	627.96	575.92	52.04	2.50	2.28	0.22	2.50	2.28	0.22
131-140	1(0)	658.00	658.00	0	2.29	2.29	0	2.29	2.29	0.00
All fish	775(57)	28.86	17.13 (59.4%)	11.73 (40.6%)	0.71	0.23 (32.6%)	0.48 (67.4%)	0.77	0.25 (32.5%)	0.51 (66.2%)
Fall										
1-10	35(10)	0.034	0.002	0.032	0.75	0.02	0.73	1.05	0.03	1.02
11-20	63(14)	0.095	0.008	0.087	0.28	0.04	0.24	0.36	0.05	0.31
21-30	63(9)	1.14	0.53	0.61	0.72	0.40	0.31	0.84	0.47	0.37
31-40	144(12)	2.15	0.44	1.72	0.42	0.08	0.34	0.46	0.09	0.37
41-50	149(8)	6.82	2.98	3.84	0.62	0.27	0.34	0.65	0.29	0.36
51-60	128(16)	11.96	6.75	5.22	0.64	0.37	0.27	0.73	0.42	0.31
61-70	129(14)	17.92	11.39	6.53	0.56	0.35	0.20	0.62	0.39	0.23
71-80	109(13)	23.39	16.79	6.60	0.48	0.34	0.14	0.55	0.39	0.16
81-90	49(7)	62.39	54.23	8.16	0.83	0.72	0.11	0.97	0.84	0.13
91-100	34(4)	113.95	63.65	50.30	1.08	0.61	0.46	1.22	0.69	0.53
101-110	11(3)	48.12	39.21	8.91	0.36	0.30	0.06	0.50	0.42	0.08
111-120	4(0)	399.86	96.17	303.70	2.36	0.56	1.80	2.36	0.56	1.80
121-130	3(0)	709.41	709.41	0	2.82	2.82	0	2.81	2.81	0.00
131-140	0							0		
141-150	1(0)	98.02	0	98.02	0.24	0	0.24	0.24	0.00	0.24
All fish	922(110)	20.70	13.52 (65.3%)	7.17 (34.6%)	0.59	0.30 (51.4%)	0.29 (48.6%)	0.67	0.35 (52.2%)	0.33 (49.3%)

portant in the diet up to a size of about 40 cm; hake >40 cm fed almost exclusively on fish. The mean weight of "fish prey" exceeded that of "other prey" in all silver hake size classes >30 cm during spring, and >20 cm during fall (Table 3).

In contrast to silver hake, Atlantic cod in all size classes fed on "other prey" to a significant degree. Fish prey was absent from the diet of cod ≤30 cm during the spring, but was observed in all size classes in the fall (Table 4). Fish prey constituted a significant portion of the diet in cod >60 cm during spring, and >30 cm during fall, but the mean weight of fish prey did not exceed that of other prey except in cod >70 cm (spring) or >50 cm (fall).

The total weight of food as a percentage of body weight was significantly greater ($P < 0.05$) in the hake than in the cod during both the spring and the fall (Table 5). During spring, hake contained significantly more fish prey (% BW) than cod, but the amount of "other" prey was not significantly different ($P < 0.05$) (Table 5). During the fall, the amount of fish prey was not significantly different, but hake contained significantly more "other" prey than cod.

The mean stomach content weight as a percentage of body weight of the large silver hake was significantly greater ($P < 0.05$) than the small silver hake during spring, while during the fall the stomach content weight of the small hake was greater. During both seasons, large hake contained significantly ($P < 0.05$) more fish prey than the small hake (Table 5); the large hake contained 66.2 and 77.3% fish prey as a percentage of body weight during spring and fall, respectively, and the small hake 18.7 and 8.5%, respectively.

Fish prey constituted 0 and 32.1% of the stomach contents of small Atlantic cod, and 37.4 and 55.1% of the stomach contents of large Atlantic cod during spring and fall, respectively. During spring, small cod contained a lower mean stomach content, as a percentage of body weight, than large cod (Table 5). This was due to the lack of fish prey in the diet of small cod, since the amount of food in the "other" category did not differ significantly between the two size classes. During fall, the mean stomach contents (total, fish and "other" prey) as a percentage of body weight did not differ ($P < 0.05$) between the two size classes of cod.

The mean weight of food in the stomachs of each group of fish did not exceed 1.0% BW (body weight), but the range of values observed in individual fish extended from 0 to 23.7% (Table 5). In general, the maximum observed values for the fish prey category were larger than those for the other prey category (especially in Atlantic cod). Among silver hake, the maximum values for large fish were greater than for small

TABLE 5.—Overall mean and 95% confidence limits, minimum and maximum values, and median stomach contents of the different categories of silver hake and Atlantic cod. BW = body weight.

		Stomach contents, all fish including those with empty stomachs					Stomach contents, excluding fish with empty stomachs		
		No. of fish	Mean ± 95% C.L. (% BW)	Min (% BW)	Max (% BW)	Median (% BW)	No. of fish	Mean ± 95% C.L. (% BW)	Median (% BW)
Silver hake									
≤20 cm									
Spring	Total food	496	0.785 ± 0.104	0	12.86	0.439	375	1.039 ± 0.127	0.741
	Fish prey	496	0.147 ± 0.083	0	12.86	0	375	0.195 ± 0.110	0
	Other prey	496	0.638 ± 0.071	0	4.55	0.374	375	0.844 ± 0.083	0.586
Fall	Total food	797	1.056 ± 0.094	0	10.37	0.583	625	1.346 ± 0.110	0.891
	Fish prey	797	0.090 ± 0.046	0	10.37	0	625	0.115 ± 0.058	0
	Other prey	797	0.966 ± 0.084	0	9.63	0.498	625	1.232 ± 0.098	0.866
>20 cm									
Spring	Total food	663	1.044 ± 0.216	0	22.05	0.035	396	1.747 ± 0.345	0.309
	Fish prey	663	0.691 ± 0.194	0	20.07	0	396	1.157 ± 0.318	0
	Other prey	663	0.353 ± 0.106	0	22.05	0	396	0.590 ± 0.174	0.107
Fall	Total food	758	0.565 ± 0.152	0	20.08	0.005	402	1.066 ± 0.276	0.116
	Fish prey	758	0.437 ± 0.138	0	20.08	0	402	0.825 ± 0.255	0
	Other prey	758	0.128 ± 0.065	0	17.13	0	402	0.241 ± 0.121	0.039
Atlantic cod									
≤30 cm									
Spring	Total food	143	0.462 ± 0.087	0	3.66	0.340	126	0.525 ± 0.094	0.397
	Fish prey	143	0.000 ± 0.000	0	0.00	0	126	0.000 ± 0.000	0
	Other prey	143	0.462 ± 0.087	0	3.66	0.340	126	0.525 ± 0.094	0.397
Fall	Total food	161	0.554 ± 0.313	0	23.65	0.178	128	0.697 ± 0.390	0.270
	Fish prey	161	0.178 ± 0.288	0	23.65	0	128	0.224 ± 0.363	0
	Other prey	161	0.376 ± 0.133	0	9.57	0.112	128	0.473 ± 0.164	0.214
>30 cm									
Spring	Total food	632	0.765 ± 0.097	0	9.66	0.342	592	0.817 ± 0.102	0.385
	Fish prey	632	0.286 ± 0.083	0	9.66	0	592	0.305 ± 0.088	0
	Other prey	632	0.479 ± 0.058	0	7.77	0.185	592	0.511 ± 0.061	0.209
Fall	Total food	761	0.601 ± 0.102	0	14.12	0.149	684	0.669 ± 0.113	0.201
	Fish prey	761	0.331 ± 0.094	0	12.45	0	684	0.369 ± 0.104	0
	Other prey	761	0.270 ± 0.042	0	7.21	0.073	684	0.300 ± 0.046	0.105

fish, whereas no consistent pattern emerged between large and small Atlantic cod.

A significant proportion of the stomachs in the samples was empty, especially among silver hake (Tables 3, 4). Moreover, among those fish containing measurable amounts of food in their stomachs, the distribution of stomach content weight was strongly skewed towards small values. For these two reasons, the median stomach content weight was always considerably less than the mean weight (Table 5).

The mean and median stomach content weights within the entire population, which includes fish that had empty stomachs, were less than the corresponding values when only those fish containing measurable quantities of food were considered (last three columns of Tables 3 and 4; last two columns of Table 5). The differences were greater for silver hake than Atlantic cod, because of the large percentage of hake with empty stomachs. These data show that, even when the analysis is restricted to the fish that have recently fed (i.e., the fish with nonempty stomachs), the amount of food in the stomachs is, on the average, very much less than the maximum amount that the fish are physically capable of ingesting (as indicated by the maximum observed values, Table 5).

The mean stomach contents by season for each species, all sizes combined, are presented in grams and as a percentage of body weight in Tables 3 and 4. When the stomach contents are expressed in terms of weight (grams), the apparent importance of fish prey in the diet is greater than when the stomach contents are expressed as a percentage of body weight. This disparity occurs because the large, more piscivorous, fish contain a much greater weight of food in their stomachs, and have a disproportionate effect compared with the more numerous, but less piscivorous, small fish. This bias is eliminated if the stomach content weight is normalized to the weight of the fish (percent body weight) for the calculation of mean stomach contents. This also allows intercomparison of samples with different size-distributions of fish. We have, therefore, expressed the stomach content data as percent body weight for the analysis of diel changes in stomach fullness and daily ration.

Diel Changes in Stomach Contents

The diel feeding patterns of large and small silver hake appeared to differ. The weight of the stomach contents of small hake fluctuated over the 24-h day, but did not show any trends indicative of diel periodicity in feeding intensity during either spring or fall (Fig. 3). However, large hake exhibited a strong

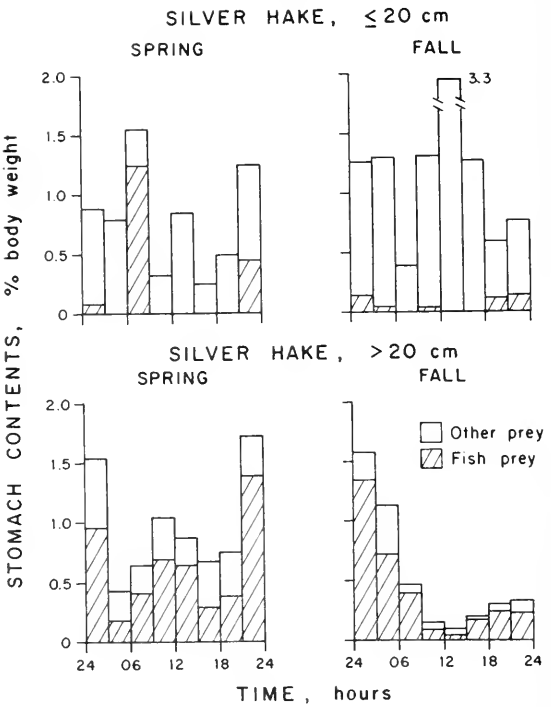


FIGURE 3.—Diel changes in "total stomach content weight," "fish prey," and "other prey" in the stomachs of small and large silver hake during spring and fall.

pattern of nocturnal feeding during the fall (Fig. 3). This pattern was less clear during spring, when comparatively large amounts of food were observed in the stomachs during the daytime. However, maximum amounts of food occurred at night, between 2100 and 0300.

Among small silver hake, the number of empty stomachs averaged 23.4% during spring over the 24-h day, with highest values observed between 1500 and 2400 (see Fig. 5). During the fall, the mean number of empty stomachs was 21.9%, with no apparent diel pattern. Among large hake, the number of empty stomachs averaged 40.4% during spring and 47.8% during fall. The percentage remained fairly constant throughout the day except for peaks between 1500 and 2100 during spring and 0900 and 1500 during fall. These peaks corresponded to the periods when the minimum mean weight of stomach content was observed (Fig. 3).

In contrast to silver hake, there were no apparent diel trends in the stomach contents of Atlantic cod (Fig. 4). The percentage of empty stomachs was lower in cod than in hake, and there was no diel pattern (Fig. 5). Among large cod, the percentage of empty stomachs over the day averaged 6.4% during spring

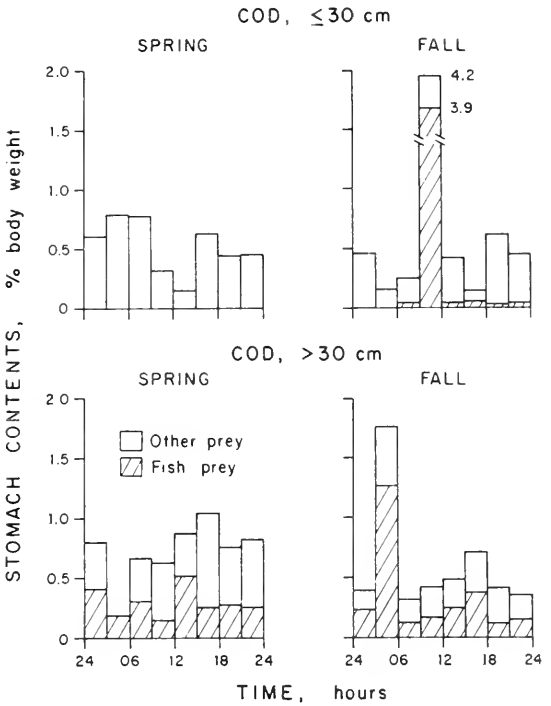


FIGURE 4.—Diel changes in "total stomach content weight," "fish prey," and "other prey" in the stomachs of small and large Atlantic cod during spring and fall.

and 10.2% during fall. Among small cod, the respective percentages were 10.6 and 14.7%.

Daily Ration

In order to describe the average feeding behavior of all fish in the samples, the mean stomach content weights, which included fish with empty stomachs, were used to estimate the mean feeding rate for each 3-h period during the day (Tables 6, 7). Ingestion estimates fluctuated considerably, and negative as well as positive values occurred. The negative ingestion estimates resulted when the decline in amount of food in the stomach from one period to the next was greater than predicted from the evacuation rate used in the calculation. Daily rations were obtained by summing the amount of food ingested during each 3-h period.

With the exception of small silver hake in the fall, the daily ration estimates for the two species were not greatly different: small hake, 1.82 and 4.65% BW during spring and fall, respectively; large hake, 2.40 and 1.92%; and large Atlantic cod 1.42 and 1.66% BW (Tables 6, 7). Overall, hake consumed more than large cod; the daily ration of small cod was not estimated because of the small sample size. The daily ration of small hake and large cod was higher, and of large hake was lower, during the fall than during

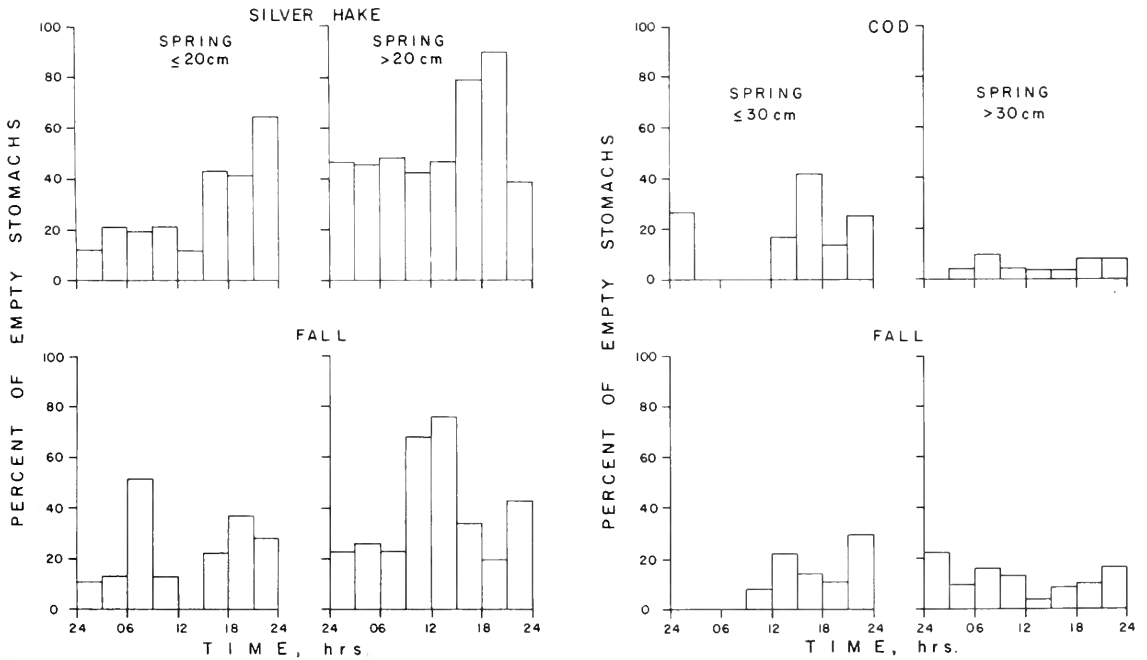


FIGURE 5.—Diel changes in the percentage of empty stomachs of silver hake and Atlantic cod collected during each 3 h time period.

TABLE 6.—Number of fish caught, amount (% BW) of food in the silver hake stomachs ($\bar{x}$ ± standard error of mean), and estimated mean amount of food ingested during each 3-h period. BW = body weight.

	Time	Total no. of fish (No. of tows)	Total food		Fish prey		Other prey	
			Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)
Silver hake ≤20 cm								
Spring								
Temp = 7.63°C	24-3	136 (13)	0.888 ± 0.079	0.145	0.083 ± 0.024	−0.061	0.805 ± 0.078	0.207
R = 0.0947	3-6	101 (7)	0.795 ± 0.093	1.101	0.009 ± 0.007	1.430	0.786 ± 0.092	−0.329
	6-9	36 (4)	1.557 ± 0.400	−0.973	1.252 ± 0.412	−1.083	0.305 ± 0.078	0.110
	9-12	14 (4)	0.325 ± 0.135	0.693	0 ± 0.0	0	0.325 ± 0.135	0.693
	12-15	17 (2)	0.848 ± 0.124	−0.453	0 ± 0.0	0.008	0.848 ± 0.124	−0.461
	15-18	30 (5)	0.244 ± 0.089	0.360	0.007 ± 0.005	−0.001	0.237 ± 0.089	0.361
	18-21	128 (7)	0.497 ± 0.057	1.005	0.004 ± 0.004	0.505	0.493 ± 0.056	0.500
	21-24	34 (7)	1.249 ± 0.390	−0.060	0.443 ± 0.382	−0.288	0.806 ± 0.156	0.228
			$\bar{x}$ = 0.800	Σ = 1.818	$\bar{x}$ = 0.225	Σ = 0.510	$\bar{x}$ = 0.576	Σ = 1.309
Fall								
Temp = 11.94°C	24-3	145 (15)	1.262 ± 0.116	0.625	0.143 ± 0.062	−0.055	1.118 ± 0.095	0.682
R = 0.153	3-6	204 (16)	1.299 ± 0.106	−0.544	0.046 ± 0.033	−0.036	1.253 ± 0.102	−0.507
	6-9	35 (4)	0.385 ± 0.105	1.329	0 ± 0.0	0.037	0.385 ± 0.105	1.290
	9-12	31 (6)	1.309 ± 0.183	2.991	0.030 ± 0.030	−0.024	1.278 ± 0.187	3.016
	12-15	6 (3)	3.226 ± 0.692	−0.952	0 ± 0.0	0.012	3.226 ± 0.692	−0.963
	15-18	86 (8)	1.275 ± 0.168	−0.255	0.010 ± 0.007	0.138	1.266 ± 0.169	−0.394
	18-21	76 (11)	0.601 ± 0.102	0.487	0.117 ± 0.063	0.087	0.484 ± 0.086	0.399
	21-24	214 (17)	0.770 ± 0.079	0.967	0.144 ± 0.065	0.065	0.626 ± 0.053	0.901
			$\bar{x}$ = 1.266	Σ = 4.648	$\bar{x}$ = 0.061	Σ = 0.224	$\bar{x}$ = 1.205	Σ = 4.424
Silver hake >20 cm								
Spring								
Temp = 8.45°C	24-3	99 (16)	1.542 ± 0.408	−0.813	0.963 ± 0.319	−0.612	0.579 ± 0.274	−0.201
R = 0.104	3-6	46 (7)	0.430 ± 0.170	0.377	0.179 ± 0.153	0.321	0.251 ± 0.084	0.056
	6-9	60 (11)	0.639 ± 0.254	0.670	0.407 ± 0.246	0.460	0.232 ± 0.082	0.210
	9-12	92 (17)	1.043 ± 0.300	0.130	0.693 ± 0.275	0.153	0.350 ± 0.141	−0.024
	12-15	102 (15)	0.875 ± 0.227	0.038	0.639 ± 0.225	−0.210	0.236 ± 0.065	0.248
	15-18	79 (18)	0.673 ± 0.163	0.296	0.287 ± 0.128	0.201	0.386 ± 0.113	0.095
	18-21	78 (12)	0.747 ± 0.228	1.373	0.383 ± 0.171	1.292	0.364 ± 0.158	0.081
	21-24	107 (14)	1.726 ± 0.369	0.324	1.390 ± 0.369	−0.063	0.336 ± 0.083	0.388
			$\bar{x}$ = 0.959	Σ = 2.395	$\bar{x}$ = 0.618	Σ = 1.542	$\bar{x}$ = 0.342	Σ = 0.853
Fall								
Temp = 11.76°C	24-3	115 (19)	1.575 ± 0.359	0.161	1.340 ± 0.335	−0.162	0.235 ± 0.149	0.324
R = 0.150	3-6	85 (14)	1.134 ± 0.310	−0.317	0.724 ± 0.240	−0.086	0.411 ± 0.205	−0.231
	6-9	84 (13)	0.468 ± 0.234	−0.192	0.392 ± 0.235	−0.191	0.076 ± 0.023	−0.0006
	9-12	71 (9)	0.144 ± 0.070	0.009	0.096 ± 0.069	−0.023	0.048 ± 0.015	0.030
	12-15	70 (13)	0.099 ± 0.031	0.171	0.043 ± 0.025	0.178	0.055 ± 0.020	−0.007
	15-18	94 (18)	0.201 ± 0.122	0.218	0.171 ± 0.121	0.169	0.029 ± 0.014	0.052
	18-21	155 (23)	0.304 ± 0.090	0.178	0.245 ± 0.090	0.088	0.060 ± 0.013	0.089
	21-24	84 (18)	0.337 ± 0.132	1.689	0.227 ± 0.127	1.484	0.110 ± 0.031	0.205
			$\bar{x}$ = 0.533	Σ = 1.917	$\bar{x}$ = 0.405	Σ = 1.457	$\bar{x}$ = 0.128	Σ = 0.461

spring.

When the daily ration was estimated using an R value for fish prey derived from Equation (3) (Tables (6-8), then fish prey constituted 28.1 and 4.8% of the daily ration of small hake during spring and fall, respectively. In large cod, fish prey constituted 38.2 and 55.1% of the daily ration, whereas in large silver hake, fish prey constituted 64.4 and 76.0% (Tables 6-8). However, if the lower estimate of the evacuation rate for fish prey items is used in the calculation, the importance of fish prey in the diet of all groups was sharply reduced (Table 8). The effect on the total estimated daily ration was small for hake ≤20 cm, because this size class did not feed heavily upon fish prey. However, since large hake and large cod feed extensively upon fish prey, a change in the R value for this prey type significantly affected the total estimated daily ration (Table 8).

DISCUSSION

Application of the Elliott and Persson Model

The Elliott and Persson model was originally described for field samples collected in a restricted area from the same population over time. Present data were obtained from extensive surveys over large areas rather than intensive surveys of single populations. As applied here, the model provides a broad overview of ingestion by fish located over a very large geographic area. Resolution of this composite picture to include possible differences in fish behavior in different years or areas would have required additional intensive field surveys and was beyond the scope of the present study.

Daily ration estimates, which are based on field

TABLE 7.—Number of fish caught, amount (% BW) of food in the Atlantic cod stomachs ($\bar{x}$ ± standard error of mean), and estimated mean amount of food ingested during each 3-h period. BW = body weight.

	Time	Total no. of fish (No. of tows)	Total food		Fish prey		Other prey	
			Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)
Atlantic cod ≤30 cm								
Spring								
Temp = 5.72°C	24-3	5 (2)	0.603 ± 0.241		0 ± 0.0		0.603 ± 0.241	
	3-6	14 (4)	0.790 ± 0.262		0 ± 0.0		0.790 ± 0.262	
	6-9	4 (1)	0.785 ± 0.235		0 ± 0.0		0.785 ± 0.235	
	9-12	24 (6)	0.316 ± 0.042		0.001 ± 0.001		0.314 ± 0.041	
	12-15	9 (3)	0.154 ± 0.103		0 ± 0.0		0.154 ± 0.103	
	15-18	7 (2)	0.635 ± 0.282		0 ± 0.0		0.635 ± 0.282	
	18-21	63 (10)	0.442 ± 0.053		0 ± 0.0		0.442 ± 0.053	
	21-24	17 (9)	0.451 ± 0.152		0 ± 0.0		0.451 ± 0.152	
			$\bar{x}$ = 0.522		$\bar{x}$ = 0		$\bar{x}$ = 0.522	
Fall								
Temp = 8.46°C	24-3	30 (11)	0.461 ± 0.113		0 ± 0.0		0.461 ± 0.113	
	3-6	6 (5)	0.151 ± 0.076		0.006 ± 0.006		0.145 ± 0.076	
	6-9	7 (5)	0.252 ± 0.083		0.040 ± 0.040		0.212 ± 0.090	
	9-12	6 (6)	4.213 ± 3.889		3.942 ± 3.942		0.271 ± 0.124	
	12-15	12 (7)	0.418 ± 0.150		0.039 ± 0.030		0.379 ± 0.126	
	15-18	24 (5)	0.140 ± 0.044		0.053 ± 0.026		0.087 ± 0.038	
	18-21	30 (7)	0.615 ± 0.111		0.028 ± 0.028		0.587 ± 0.108	
	21-24	46 (6)	0.448 ± 0.208		0.045 ± 0.021		0.403 ± 0.208	
			$\bar{x}$ = 0.837		$\bar{x}$ = 0.519		$\bar{x}$ = 0.318	
Atlantic cod >30 cm								
Spring								
Temp = 5.77°C	24-3	58 (16)	0.795 ± 0.125		0.406 ± 0.126		0.389 ± 0.061	
R = 0.0769	3-6	64 (17)	0.575 ± 0.089	−0.063	0.191 ± 0.075	−0.147	0.384 ± 0.054	0.084
	6-9	81 (18)	0.660 ± 0.146	0.228	0.300 ± 0.122	0.166	0.360 ± 0.066	0.062
	9-12	116 (20)	0.628 ± 0.086	0.116	0.147 ± 0.066	−0.102	0.481 ± 0.059	0.219
	12-15	88 (17)	0.865 ± 0.168	0.410	0.509 ± 0.170	0.439	0.356 ± 0.052	−0.029
	15-18	80 (16)	1.039 ± 0.183	0.394	0.255 ± 0.135	−0.167	0.784 ± 0.134	0.561
	18-21	60 (20)	0.757 ± 0.121	−0.076	0.270 ± 0.087	0.076	0.487 ± 0.100	−0.152
	21-24	85 (22)	0.820 ± 0.151	0.245	0.261 ± 0.126	0.052	0.558 ± 0.096	0.192
				0.161		0.223		−0.061
			$\bar{x}$ = 0.767	Σ = 1.415	$\bar{x}$ = 0.292	Σ = 0.540	$\bar{x}$ = 0.475	Σ = 0.876
Fall								
Temp = 9.30°C	24-3	91 (28)	0.398 ± 0.087		0.234 ± 0.084		0.164 ± 0.032	
R = 0.114	3-6	94 (24)	1.763 ± 0.323	1.748	1.271 ± 0.298	1.304	0.492 ± 0.128	0.443
	6-9	103 (25)	0.314 ± 0.060	−1.108	0.119 ± 0.055	−0.926	0.195 ± 0.029	−0.182
	9-12	95 (24)	0.418 ± 0.092	0.230	0.168 ± 0.083	0.099	0.249 ± 0.047	0.130
	12-15	111 (31)	0.483 ± 0.085	0.220	0.245 ± 0.070	0.148	0.238 ± 0.050	0.072
	15-18	84 (22)	0.714 ± 0.158	0.438	0.373 ± 0.158	0.235	0.341 ± 0.048	0.203
	18-21	87 (20)	0.415 ± 0.061	−0.109	0.119 ± 0.058	−0.172	0.296 ± 0.034	0.063
	21-24	96 (21)	0.355 ± 0.076	0.071	0.149 ± 0.066	0.076	0.206 ± 0.046	−0.005
				0.172		0.151		0.021
			$\bar{x}$ = 0.608	Σ = 1.662	$\bar{x}$ = 0.335	Σ = 0.915	$\bar{x}$ = 0.273	Σ = 0.745

TABLE 8.—Upper and lower estimates of R for fish prey, and the effect upon the estimated daily ration, where: $R_{\text{fish, max}} = 0.0406\ e^{0.111t}$; $R_{\text{fish, min}} = 0.00406\ e^{0.111t}$, and $R_{\text{other}} = 0.0406\ e^{0.111t}$. Basic data from Tables 6 and 7. BW = body weight.

	Fish prey (% BW)	Other prey (% BW)	Total (% BW)	Fish prey % of total
Silver hake ≤20 cm				
Spring				
$R_{\text{fish, max}}$	0.510	1.309	1.818	28.1
$R_{\text{fish, min}}$	0.051	1.309	1.360	3.8
Fall				
$R_{\text{fish, max}}$	0.224	4.424	4.648	4.8
$R_{\text{fish, min}}$	0.022	4.424	4.446	0.5
Silver hake >20 cm				
Spring				
$R_{\text{fish, max}}$	1.542	0.853	2.395	64.4
$R_{\text{fish, min}}$	0.154	0.853	1.007	15.3
Fall				
$R_{\text{fish, max}}$	1.457	0.461	1.917	76.0
$R_{\text{fish, min}}$	0.146	0.461	0.607	24.1
Atlantic cod >30 cm				
Spring				
$R_{\text{fish, max}}$	0.540	0.876	1.415	38.2
$R_{\text{fish, min}}$	0.054	0.876	0.930	5.8
Fall				
$R_{\text{fish, max}}$	0.915	0.745	1.662	55.1
$R_{\text{fish, min}}$	0.092	0.745	0.837	11.0

stomach content data, require information on digestion rate of the various prey types. Equation (3) is based on maximum evacuation rates observed in the laboratory for small, easily digested food items. Evacuation rates determined from this equation should provide an upper limit to estimates of ingestion rates (Table 8). Since there are indications that fish prey may be digested more slowly, the daily ration was also estimated using the lowest observed values of evacuation rate for fish prey (Table 8). This reduced the estimate of ingestion of fish prey by a factor of 10, and provided a lower limit for the probable ingestion rates. The potential significance of this 10-fold range in the R value is well illustrated by the case of silver hake >20 cm, where during the spring, for example, fish prey constituted 66.2% of the stomach contents by weight, yet the calculated ingestion of fish ranged from as much as 64% to as little as 15% of the diet, depending on the R value used.

This illustrates the need for additional information on the digestion rates of a variety of different prey items, particularly fish prey. If different prey types are digested at different rates, then the static picture of the food web as provided by stomach content analysis may not truly indicate the relative rates of flow of the different elements through the food web.

Food Habits and Stomach Content Weight

The food habits and stomach content weight of silver hake and Atlantic cod in the present study are in general agreement with the results of other studies (Rae 1967, 1968 a, b; Tyler 1971; Vinogradov 1972; Daan 1973; Langton and Bowman 1980).

Rae (1967, 1968a, b) provided a detailed description of the food habits of Atlantic cod in the North Sea, the Faroes, and Iceland, and Vinogradov (1972) described the food habits of silver hake in the North Atlantic. These studies are not directly comparable with the present study because they presented the diet by the frequency of occurrence of prey, not by weight. However, Rae reported that in general, fish prey were seldom eaten by cod <21 cm, but became increasingly important in the diet as the cod grew larger. Cod >50 cm fed mostly on fish. Vinogradov also found that hake became increasingly piscivorous with increasing size, and that hake >40 cm fed almost entirely on fish. These results are consistent with the present study.

Langton and Bowman (1980) have described the food habits of silver hake and Atlantic cod (>20 cm in length) that were caught during 1969-72 in the same area as the present study. Silver hake averaged 27.5 cm in length, their mean stomach content weight was 2.5 g, and the proportion of fish in the diet was 70.9% by weight. Atlantic cod averaged 54.7 cm in length, their mean stomach content weight was 27.9 g, and fish prey constituted 64.0% of the diet by weight. These are very close to our present results with hake >20 cm [mean length = 31.2 cm, mean weight of stomach contents = 2.9 g (0.79% BW), proportion of fish in the diet = 81.7% by weight], and cod >30 cm [mean length = 60.9 cm, mean weight of stomach contents = 29.6 g (0.68% BW), and mean proportion of fish in the diet = 62.3% by weight]. These results imply that no large-scale changes in the mean weight of stomach contents in the two species occurred in the study area between 1969 and 1976. Possible changes in factors such as prey species or prey size, however, are not evaluated in this report.

The weight of the stomach contents of 15-40 cm Atlantic cod from Passamaquoddy Bay, New Brunswick, was reported by Tyler (1970: figure 7). During spring, the stomach content weights were very similar to those of 15-40 cm cod reported here. However, during late summer-fall, cod in Tyler's study generally had more food in their stomachs (usually >1% BW; range 0.4-2.7% BW) than fish in this study.

Daan (1973) investigated the food habits of Atlantic cod from the northern and southern portions of the North Sea. In general, the weights of the stomach contents of cod (divided into 10 cm size classes) in his study were considerably higher than in the present study (compare Daan's table XI with our Table 4). Daan's samples were collected principally during the daytime, but he considered that diel feeding periodicity was not significant in his study area. In addition, Daan's cod were more piscivorous than the cod collected during the present study (compare his figure 2 with our Table 4). He found that fish prey became increasingly important in the diet with increasing size of cod. These results are in agreement with the present study.

The percentage of empty stomachs observed during our study is in agreement with those reported by Tyler (1971), Daan (1973), and Langton and Bowman (1980).

Diel Changes in Stomach Contents

Edwards and Bowman (1979) and Bowman and Bowman (1980) concluded that silver hake >20 cm were principally nocturnal feeders. Results of the present study also indicate that hake >20 cm feed more intensively at night. However, the lack of significant diel changes in the stomach content weight of hake ≤20 cm indicates that these small fish may feed continuously throughout the day.

The lack of evident feeding periodicity in Atlantic cod was consistent with an extensive study by Rae (1967) and with observations by Daan (1973). Sattersdal (1967) reviewed several studies on feeding periodicity in gadoids, and also concluded that with cod, feeding may take place at any time during the night or day.

Daily Ration

Daan (1973) estimated the daily ration of Atlantic cod from the North Sea, where the mean temperature (5°-9°C) was similar to that experienced by Atlantic cod in the present study. Although these fish, on the average, contained more food in their stomachs, the estimates of the daily food intake were relatively

lower than in the present study, declining from 1.3% BW/d in a 40 cm cod to 0.8% BW/d in a 60 cm fish, to 0.5% BW/d in a 100 cm fish.

Grosslein et al. (1980) used energy budget calculations to estimate the daily ration of six major fishes (Atlantic cod, silver hake, yellowtail flounder, haddock, herring, and mackerel) in the northwest Atlantic during 1963-72. The mean daily ration of silver hake was calculated to be 1.3% BW/d; the daily ration of Atlantic cod was 0.9% BW/d. During 1963-72, the daily food consumption by hake averaged 24.2% of the total consumption by the six species; the daily ration of the cod was 3.7% of the total.

A study by Edwards and Bowman (1979) estimated the daily ration of silver hake to be 3.1% BW/d, and Atlantic cod to be 2.3% BW/d. These authors also concluded that the hake is a major consumer in the food web of the northwest Atlantic.

These daily ration estimates compare with mean upper and lower estimates of 3.2 and 2.9% BW/d for silver hake $\leq$20 cm, 2.2 and 0.8% BW/d for hake $>$20 cm, and 1.5 and 0.9% BW/d for Atlantic cod $>$30 cm in the present study (Table 8, assigning spring and fall estimates equal weight for the determination of mean ingestion).

Differences in the estimates of daily ration in the above studies reflect differences in the mean stomach content weight of the fish, as well as differences in the methods used to estimate daily ration. However, estimates of daily ration in silver hake were consistently found to be greater than in the Atlantic cod.

The high proportion of empty stomachs among silver hake, and the fact that the average amount of food in the stomachs of both silver hake and Atlantic cod were small, is intriguing from an ecological viewpoint. For example, the results may simply reflect the innate feeding behavior of these two predators, i.e., they feed at a modest rate even when food is plentiful and easily obtained. On the other hand, the results could mean that food is either scarce, or if abundant, difficult for the fish to locate or capture. It would be of interest, in future work, to explore the question of whether the major fish predators in the northwestern Atlantic are food limited, since this will greatly affect the importance of different predator-prey links in the food web and the intensity of competition among different fishes for food.

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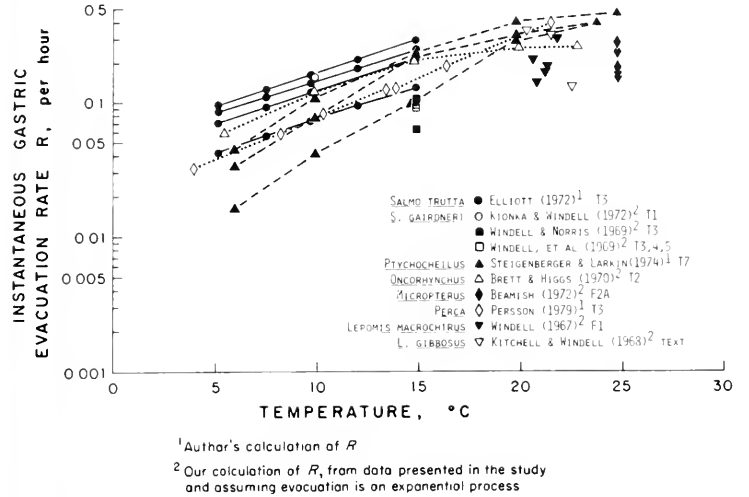
APPENDIX 1

Estimation of the Instantaneous Gastric Evacuation Rate, *R*

A number of factors may affect the instantaneous rate of gastric evacuation, *R*. These include temperature, food type, food particle size, meal size, fish size, autolysis of food in the stomach, swimming activity, prestarvation, experimental stress, experimental error, and time lags between ingestion and the beginning of gastric evacuation.

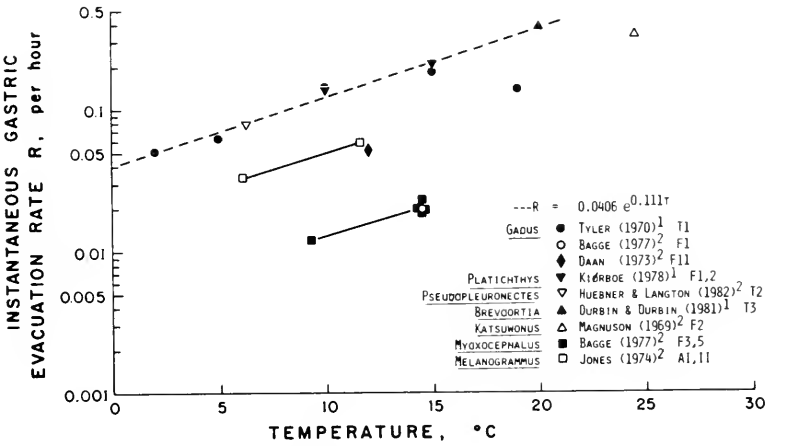
R values from the more complete studies of marine and freshwater fishes are presented as a function of temperature in Appendix Figures 1 and 2.



[1] Author's calculation of *R*

[2] Our calculation of *R*, from data presented in the study and assuming evacuation is an exponential process

APPENDIX FIGURE 1.—The relationship between the instantaneous gastric evacuation rate (R, per hour) and temperature in several marine fishes. Note that the body temperature of *Katsuwonus* was probably greater than that of the water temperature shown here. Dashed line and equation based on data from Tyler (1970, 2 -15 C), Kiørboe (1978), Durbin and Durbin (1981), and Huebner and Langton (1982). Source of data, where T = Table, F = Figure, and A = Appendix is shown.



[1] Author's calculation of *R*.

[2] Our calculation of *R*, from data presented in the study and assuming eve evacuation is an exponential process.

APPENDIX FIGURE 2.—The relationship between the instantaneous gastric evacuation rate (R, per hour) and temperature in several freshwater fishes. Sources of data as in Appendix Figure 1.

TEMPERATURE

The gastric evacuation rate R appears to follow an exponential or power curve relationship with temperature t (Elliott 1972):

$$R = ae^{bt}. \quad (1)$$

Evacuation rates of brown trout that were fed small, rapidly digested prey (*Gammarus*, *Baetis*, Oligochaetes, chironomids), were described by the relationship

$$R = 0.053\ e^{0.112\,t}. \quad (2)$$

In further experiments with other foods (*Protonemura*, *Hydropsyche*, *Tenebrio*) Elliott (1972) found that the intercept (a) in Equation (2) was dependent on prey type, but that the slope (b) was constant and independent of prey type. Data from other freshwater and marine fishes (within their preferred temperature range) indicate that the value of b is fairly close to that found by Elliott for the brown trout (Appendix Table 1; $\bar{b} = 0.115$). At temperatures outside the preferred range, evacuation rates were depressed (i.e., Atlantic cod at 19°C, Tyler 1970). The value of a varies widely in different studies, apparently because of the different prey types used.

The fastest evacuation rates have been reported for a variety of small food organisms. These rates, when adjusted for differences in experimental temperature, were fairly similar among several marine and freshwater fishes: Atlantic cod, fed 0.5 g chunks of shrimp (*Pandalus*) tails (Tyler 1970); the flounder *Platichthys*, fed 0.1 g polychaetes (Kiørboe 1978); winter flounder *Pseudopleuronectes*, fed 0.5-1.0 cm pieces of squid (Huebner and Langton 1982); Atlantic menhaden, fed 80 μm diatoms (Durbin and Durbin 1981)[1]; brown trout, fed 1 and 15.7 mg *Gammarus*, 0.9 and 7.8 mg *Baetis*, 0.33 and 3.3 mg chironomids, and 29 mg oligochaetes (Elliott 1972); sockeye salmon, fed small commercial pellets (Brett and Higgs 1970); pumpkinseed sunfish fed damselfly larvae (Kitchell and Windell 1968); and bluegill sunfish fed 180 mg crayfish (Windell 1967) (App. Figs. 1, 2).

The marine species ingesting these readily digested foods followed a common R-temperature relationship (App. Fig. 1):

$$R = 0.0406\ e^{0.111t}. \quad (3)$$

The a and b values are similar to those observed by Elliott (1972) for the brown trout feeding on easily digested foods (0.053 and 0.112, respectively); b is also similar to the overall mean value in Appendix Table 1.

APPENDIX TABLE 1.—Slope (b) of the relationship between the instantaneous evacuation rate (R, per hour) and temperature (°C) for several freshwater and marine fishes, where: $R = ae^{bt}$. The intercept (a) varies with food type.

Species	Slope (b)	Experimental temp. range (°C)	Author
Brown trout, *Salmo trutta*	0.112	5.2-15.0	Elliott (1972)[1]
Northern squawfish, *Ptychocheilus oregonesis*	0.131	6.0-24.0	Steigenberger and Larkin (1974)[1]
Perch, *Perca fluviatilis*	0.140	4.0-21.7	Persson (1979)[1]
Cod, *Gadus morhua*	0.106	2.0-15.0	Tyler (1970)[1]
Ophiocephalus punctatus	0.137	2.0-28.0	Gerald (1973)[2]
Haddock, *Melanogrammus aeglefinus*	0.095	6.1-11.6	Jones (1974)[2]
Flounder, *Platichthys flesus*	0.081	10.0-15.0	Kiørboe (1978)[1]
$\bar{x} \pm \sigma = 0.115 \pm 0.022$			

[1]Based on author's calculations of R.
[2]Based on our calculation of R from data in study, and assuming that evacuation is an exponential process.

FOOD TYPE

Studies have shown that there are differences in evacuation rates with different food types. While these results may reflect inherent differences in the digestibility of the food, they may also indicate an interaction between food type, particle size, and meal size. In practice, these factors may be difficult to resolve, particularly when the results of different studies are being compared.

However, certain small prey organisms were digested significantly more slowly than those cited above. This may reflect the chemical composition of the prey. For example, slower digestion of *Tenebrio* and *Hydropsyche* by bluegill and brown trout was attributed to the high fat content of these organisms (Kitchell and Windell 1968; Elliott 1972). Pure fat retards

[1]Gastric evacuation rate R in menhaden was estimated from the feces elimination rate R'.

evacuation in rainbow trout (Windell et al. 1969) as well as in vertebrates other than fishes (Quigley and Meschan 1941). Artificial pelleted food, which is high in organic content, is also digested more slowly than natural food (Windell and Norris 1969; Windell et al. 1969). The degree of external protection of the prey can also affect the digestion rate. For example, rainbow trout digested the caddisfly *Arctopsyche*, and the cottid *Enophrys* digested *Calliphora* larvae, more slowly than other prey types, evidently because the integument of the prey was resistant to the penetration of the gastric juices (Reimers 1957; Western 1971). MacDonald et al. (1982) also reported that the shell in *Yoldia* retarded the evacuation rate in several marine fishes.

The lowest evacuation rates which have been observed were from fish feeding on fish flesh, usually in fairly large particle and meal sizes [Atlantic cod, fed whole 14 g sprats, meal sizes about 3.7% BW (Daan 1973), Atlantic cod, fed to satiation on 2-3 g pieces of greater weever (Bagge 1977); haddock *Melanogrammus aeglefinus*, fed saithe, 1-7% BW (Jones 1974); skipjack tuna, fed 10.2 g osmerids, 8.6% BW (Magnuson 1969); *Ophiocephalus*, fed small fish 7.9% BW (Gerald 1973); sea scorpion fed to satiation on 5 g pieces of greater weever (Bagge 1977); northern squawfish, fed small *Salmo* (Steigenberger and Larkin 1974); largemouth bass, fed 1.22 g emerald shiners, 2-8% BW (Beamish 1972) (App. Figs. 1, 2)]. These reductions in R may be significant: for example, with Atlantic cod and sea scorpion, the instantaneous evacuation rates for fish flesh were only about one-tenth those predicted by Equation (3) for easily digested foods.

Whether these reduced evacuation rates were due primarily to the food type (fish), or to the large particle sizes, compared with those of the small prey which were digested more rapidly, cannot be determined from the data.

Additionally, in a few studies, after several food types were tested individually and found to have similar evacuation rates, meals composed of mixtures of these food types were given (Windell 1967; Elliott 1972). The evacuation rate of the mixed meal was not significantly different from that of the individual food types. However, evacuation rate of mixed meals containing food types which have individually different R values does not appear to have been investigated.

FOOD PARTICLE SIZE

The exponential model predicts that the evacuation rate, R, depends only on the weight of food in the stomach, i.e., $dW/dt = -RW$. Thus R should be independent of food particle size. A meal of a given weight, composed of a number of small particles, should be evacuated at the same rate as a meal of equal weight, but composed of a single large particle. However, if digestion occurs at the surface of particles, then the surface area as well as the weight or volume of the food may influence digestion. A surface-area dependent model predicts that small particles should be digested more rapidly than large particles because of their greater surface area per unit volume, i.e., $dW/dt = -RW^{2/3}$.

Few studies have considered the effect of particle size on R.

Elliott (1972) found no effect of food particle size on the gastric evacuation rates of brown trout fed small invertebrates. However, the particle sizes tested were quite small and may have been below some critical size which has a measurable effect on R.

The evacuation rates of Atlantic cod that were fed whole fish or large pieces of fish flesh (Daan 1973; Bagge 1977) were lower than those of Atlantic cod fed small pieces of shrimp (Tyler 1970). However, it is not clear whether this difference is an effect of food particle size or food type.

Swenson and Smith (1973) examined gastric evacuation of walleye and sauger fed 0.8, 1.1-1.9, and 3.1-5.0 g minnows. The two smallest size classes were evacuated at a significantly faster rate than the 3.1-5.0 g fish. However, the difference between the evacuation rates was small, and the different food particle sizes therefore did not have a major effect on the evacuation rate.

MEAL SIZE

Experimental data on the effect of meal size on the gastric evacuation rate is conflicting.

The exponential model predicts that gastric evacuation is not affected by meal size. Studies using small prey as the food have confirmed this prediction: Brown trout, fed 0.06-0.5% BW meals of *Gammarus* and 0.35-1.4% BW of *Tenebrio* (Elliott 1972); pumpkinseed sunfish, fed 1.2 and 2.7% BW of damselfly naiads (Kitchell and Windell 1968); Atlantic cod fed 0.25-0.78% BW on shrimp tails (Tyler 1970); flounder, fed variable meal sizes of polychaetes (Kiørboe 1978); and Atlantic menhaden, fed 0.7-7.0% BW on the diatom *Ditylum* (Durbin and Durbin 1981). Some studies using fish flesh as the food also indicated that meal size did not affect R: Sea scorpion, fed 5.5-11.1% BW on greater weever (Bagge 1977); skipjack tuna, fed various meal sizes averaging 8.6% BW on fish (Magnuson 1969).

However, some authors have suggested that in their studies (where fish flesh was the food), evacuation was slower for large meals than for small (Steigenberger and Larkin 1974; Jones 1974). These authors found that significant time lags, on the order of hours, elapsed between ingestion and the onset of gastric evacuation. Similar lags have been reported by other investigators who used fish as the prey type (Daan 1973; Gerald 1973). Some question therefore remains as to whether meal size had a direct effect on R in these studies, or whether the primary effect of increasing meal size was to cause a progressive increase in the time lag before the onset of gastric evacuation.

EFFECT OF MULTIPLE MEALS

Most digestion rate studies have examined stomach evacuation rates following a single meal. However, in nature most fish do not normally feed in this manner, but rather feed on a more or less continuous, or a periodic, basis. In this situation the time for food to pass through the stomach and the relation between the amount of food in the stomach and evacuation rates will be more complex.

Elliott (1972) fed brown trout three meals, 6 h apart. He then determined the stomach contents 4 h after the last meal. This amount was in good agreement with that calculated from the exponential model, and Elliott concluded that multiple meals, and the presence of food already in the stomach, did not affect R or the exponential model of gastric evacuation.

Tyler (1970) fed Atlantic cod three meals, 24 h apart at 5° C. He too used an exponential model to predict the amount of food remaining in the stomach after the third meal. The actual amount was slightly, but significantly, lower (by about 7%) than the predicted. He concluded that, overall, the fit was adequate.

In the studies of Kiørboe (1978) and Huebner and Langton (1982), individual fish were fed a number of meals in sequence. Although the data showed a significant degree of variability, reflecting differences in the voluntary food intake of the fish, the mean values followed a common exponential relationship, which implies that multiple meals did not affect R.

CONCLUSIONS

In summarizing this brief discussion, several conclusions can be drawn:

1) The exponential model of gastric evacuation provides a good fit to most experimental data, and also provides good estimates of ingestion rate when used in the Elliott and Persson (1978) model.

2) The two factors which are known to most strongly influence the instantaneous gastric evacuation rate R are temperature and food type. Multiple meals do not affect the value of R. The available evidence indicates that particle size and meal size probably do not affect R (at least with small prey items), but these questions need further investigation.

3) The slopes (b) of the R-temperature relationships among several marine and freshwater fishes were similar, although the intercepts (a) varied according to the type of food.

FACTORS AFFECTING THE DISTRIBUTION, ABUNDANCE, AND SURVIVAL OF *PANDALUS JORDANI* (DECAPODA, PANDALIDAE) LARVAE OFF THE OREGON COAST

PETER C. ROTHLISBERG[1] AND CHARLES B. MILLER[2]

ABSTRACT

Abundance, distribution, and survival of larval pink shrimp, *Pandalus jordani*, differed between 1971 and 1972. Consistent southwest winds in the February-March spawning season of 1972 kept surface flow onshore and larvae closer to the coast than did the mixed winds of 1971. The early season of 1972 was warmer than that of 1971, and development was faster: Zoea V were prevalent at the end of April 1972, compared with median advancement to Zoea III by early May in 1971. Corresponding to the lesser dispersal and faster development of 1972, survival was substantially better than in 1971.

Overall larval survival at settlement time appears from analysis of long-term fishery data and upwelling indices to have some dependence upon the strength of June to August upwelling. Extrapolation from laboratory studies suggests that is because survival is enhanced by the temperatures consistently 12°C and below maintained by strong upwelling. Timing of spawning and development interacts with timing of the flow regime. Summer upwelling generally keeps the habitat suitably cold for optimal development and survival and returns larvae to seaward for settlement roughly at the beds from which they were spawned.

Hjort (1914, 1926) was the first to suggest the importance of larval mortality in establishing year class strength of marine fish. This concept has been useful generally, and, in particular, larval mortality most fully explains fluctuations of stocks in species both short-lived and fecund. However, larval mortality per se is only one component of total mortality. Factors affecting parental stock size, fecundity, spawning and hatching rates, larval dispersal, metamorphosis, and postlarval and prerecruitment mortality will also generate year-to-year variation in population size. In many marine animals these life history phases are in totally different habitats and have very different durations.

Given the complexity of the life cycle and the variety of habitat features which can therefore act importantly, it is not surprising that sound explanations of year class variations have begun to emerge only now. Long time series of catch data and well-developed understanding of oceanographic processes are both required. Interesting recent examples include Southward et al. (1975), Boudreault et al. (1977), Driver (1978), and Dow (1978). Creation of indices of coastal upwelling strength (Bakun 1973) has given us an important variable for study of factors influencing year class strength in marine populations. Upwelling acts in several ecologically significant ways, affecting temperature, salinity, nutrient concentrations, and current patterns. Enhancement of productivity in nearshore regions is well documented (Steemann Nielsen and Jensen 1957; Ryther and Menzel 1965; Ryther 1969). However, not only enhancement of productivity, but the specific changes in flow caused by upwelling can have important effects. Success of life stages is likely to be related to the time of onset of seasonal upwelling, intensity and duration of upwelling, and even to details of its intermittency. Effects can be negative. Lasker (1978) found that upwelling dispersed the food of larval northern anchovy, *Engraulis mordax*, reducing food availability below levels established in the laboratory (Lasker 1975) as minimal. Coe (1956), Winnor (1966), Lough (1976), and Nelson et al. (1976) have all shown that upwelling can both improve and reduce survival by transport of larvae toward or away from favorable habitat.

We report here an attempt to evaluate the importance of larval survival to the year class strength of the pink shrimp, *Pandalus jordani*, and to determine which aspects of ocean dynamics affect larval survival. First, larval distribution and abundance of *P. jordani* were ascertained by field sampling. Second, apparent survival in several spawning seasons was compared with laboratory studies of the effects of habitat factors (Rothlisberg 1979) and with the hydrographic regime during sampling to estimate the degree to which environmental factors determined

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larval survival in the field. Finally, an attempt was made to examine the contribution of year-to-year variation in ocean conditions during the postspawning season to variation in year class strength. Ocean conditions were primarily characterized by Bakun's upwelling indices.

MATERIALS AND METHODS

Sampling for *Pandalus jordani* larvae was carried out during 32 cruises from January 1971 to August 1972 along a transect extending 60 nmi from the coast off Newport, Oreg., U.S.A. (Newport Hydroline; stations designated NH-1, etc. according to distance from coast; Fig. 1). Sampling was at approximately fortnightly intervals (Fig. 2). On all but one cruise the 24.4 m RV *Cayuse* was used. In March and April 1972 a more extensive grid sampling was conducted on two cruises along a series of seven transects from Tillamook Head (I, Fig. 1) south almost to the Siuslaw River (VII). These transects extended 30 mi from the coast.

Temperature and a salinity sample were taken at the surface at each station, and temperatures at lower depths were obtained by bathythermograph (BT) cast to the bottom or a maximum of 150 m. Bottom salinity was obtained from a bottle sample collected at the greatest extent of the BT cast. On 9 of the 11 cruises in 1972 (C7205D and C7207E excluded), drift bottles were released. Plankton was collected by stepped oblique tows to near the bottom or to a maximum of 150 m with a 0.7 m diameter bongo net (cylinder-cone nets 5.1 m long of 0.571 mm Nitex[3] with effective filtering area to mouth area ratio of 8:1). The tows with three to five steps lasted 10 to 25 min, depending on depth. At towing speeds of 2 to 3 kn the nets filtered 600 to 1,000 m^3; specific amounts were determined from TSK flowmeters in the mouth of each net. Depths were maintained by a 40 kg kite-otter depressor (Colton 1959) and recorded by time-depth recorder. Samples were preserved at sea with formaldehyde. Only the port side sample was analyzed from each pair, a total of 367 from the two years. Because of their relatively low density, the entire sample was sorted for shrimp larvae.

The National Weather Service gathers hourly wind data at a recording anemometer located at the base of the south jetty at Newport, Oreg. We used this data in their stored form (north-south and east-west vector components; m/s) to generate progressive vector diagrams.

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

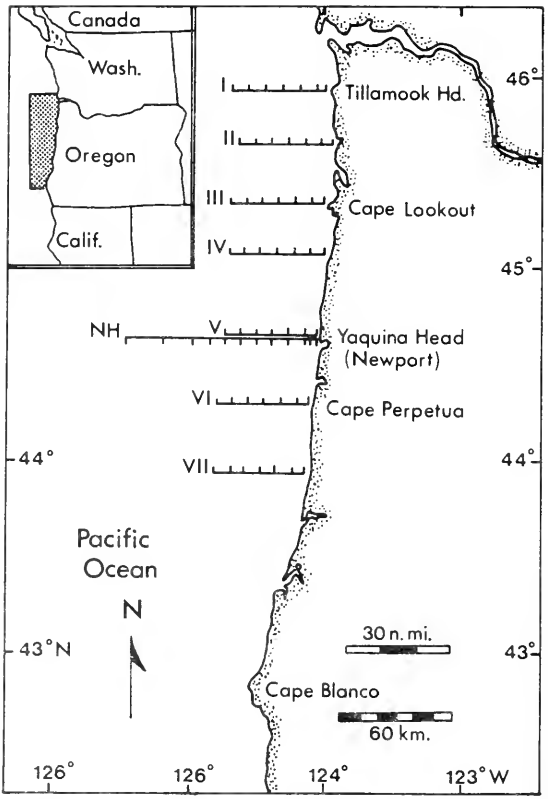

FIGURE 1.—Sampling transects off the Oregon coast. Newport Hydro (NH) line with stations: 1, 3, 5, 10, 15, 20, 25, 30, 35, 40, 50, and 60 nmi from the coast. Transects I-VII with stations 1, 5, 10, 15, 20, 25, and 30 nmi from coast. Transect V and NH line overlap.

RESULTS

Seasonal Wind, Current, and Temperature Regimes, 1971 and 1972

Progressive vector diagrams for wind from January through July in 1971 and 1972 (Fig. 3) show that the two years differed in several respects. In February 1971 winds were mixed, while in 1972 the southwest winds typical of winter were consistent. Southwest winds dominated in March 1971, except for a spell of northwest wind from the 15th to the 21st. March winds in 1972 were mostly from the southwest, but less intense. There were a few 1-d reversals to northwest wind. April in both years was transitional, and a short spell of northwest wind initiated the upwelling season. Winds of the upwelling season, May through August, were stronger in 1972 than in 1971.

Comparison of upwelling indices for 1971 and 1972 with the 25-yr average for 1946-71 puts them in long-

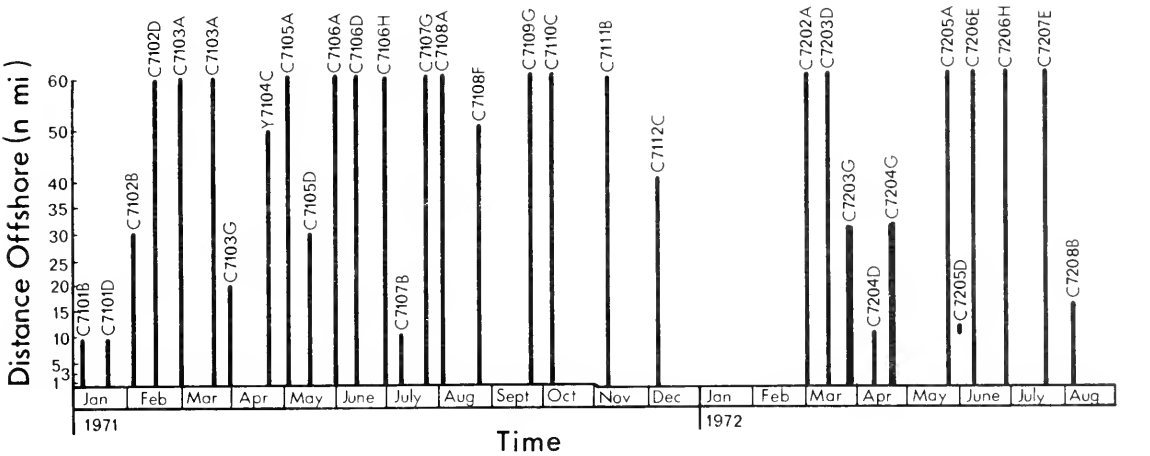

FIGURE 2.—Date and offshore extent of 32 cruises sampling larval *Pandalus jordani* from January 1971 to August 1972.

term perspective. These monthly indices (Bakun 1973, footnote 4) estimate the magnitude of the offshore component of Ekman transport mtons/s per 100 m coast) from mean monthly sea surface, geostrophic winds based on pressure fields. Deviations from the long-term mean (Table 1) imply that surface flow onshore in the first quarter of 1971 was below average, while that of 1972 was near normal. Upwelling in 1971 was less than normal, while that of 1972 was close to the long-term mean.

The northward Davidson Current was well demonstrated by the drift of bottles released in March and early April. There was also an onshore component which produced high return rates in those months (mean for March and early April = 47%; Fig. 4). By late April currents acquired a large southward component, and an offshore component reduced return rates (19.8% for late April through August; Fig. 4). Surprisingly, a considerable northward component remained in all months in the zone very close to the coast, as implied by returns from the 1 to 5 nmi stations in all periods except late May and early August.

In February through April 1971, temperatures varied between 8° and 10°C inside 20 nmi (Fig. 5). From late April through July they increased to between 14° and 15°C due to increased sunshine and lack of strong upwelling. The sharp, temporary decrease of early June corresponded to a pulse of upwelling in late May 1971 (Fig. 3). Nearshore temperatures in 1972 were more constant and warmer in the early part of the larval season than in 1971, ranging between 10° and 12°C. We attribute that to the strong onshore flow of late winter in that year. Temperatures rose slightly in spring but were held below the highs reached in late June of 1971 by the stronger upwelling conditions of 1972.

TABLE 1.—Upwelling indices by year and quarter for 1971 and 1972 along with the anomalies from a 25-yr average (from Bakun 1973, see text footnote 4).

	1973		1972	
	Index	Anomaly	Index	Anomaly
Entire year	1	10	−2	7
First quarter (Jan.-Mar.)	−33	20	−49	3
Second quarter (Apr.-June)	26	−5	29	−2
Third quarter (July-Sept.)	33	−15	42	−5

Larval Distribution and Abundance of *Pandalus jordani* in 1971

Zoeae I, II, and III were found first on 16 February. They were widely distributed but most abundant at 5, 10, and 15 nmi (Fig. 6). In early March all larvae were within 20 nmi with highest density at 5 nmi; most were recently hatched, but there were some Zoeae II's, III's, and IV's. The cruise of 20 March appeared to coincide with the peak of larval hatching, Zoea I predominating and most abundant within 20 nmi of shore. The late March cruise was abbreviated because of bad weather. However, all larvae found at the 3 and 5 nmi stations were Zoea I. By 22 April the *P. jordani* were dispersed as far as 50 nmi offshore, but the peak of abundance was still at 5 nmi and consisted mostly of Zoeae II's and III's. A few

[4]A. Bakun, Pacific Environmental Group, Southwest Fisheries Center, NMFS, NOAA, c/o Fleet Numerical Oceanography Center, Monterey, Calif., pers. commun. February 1982.

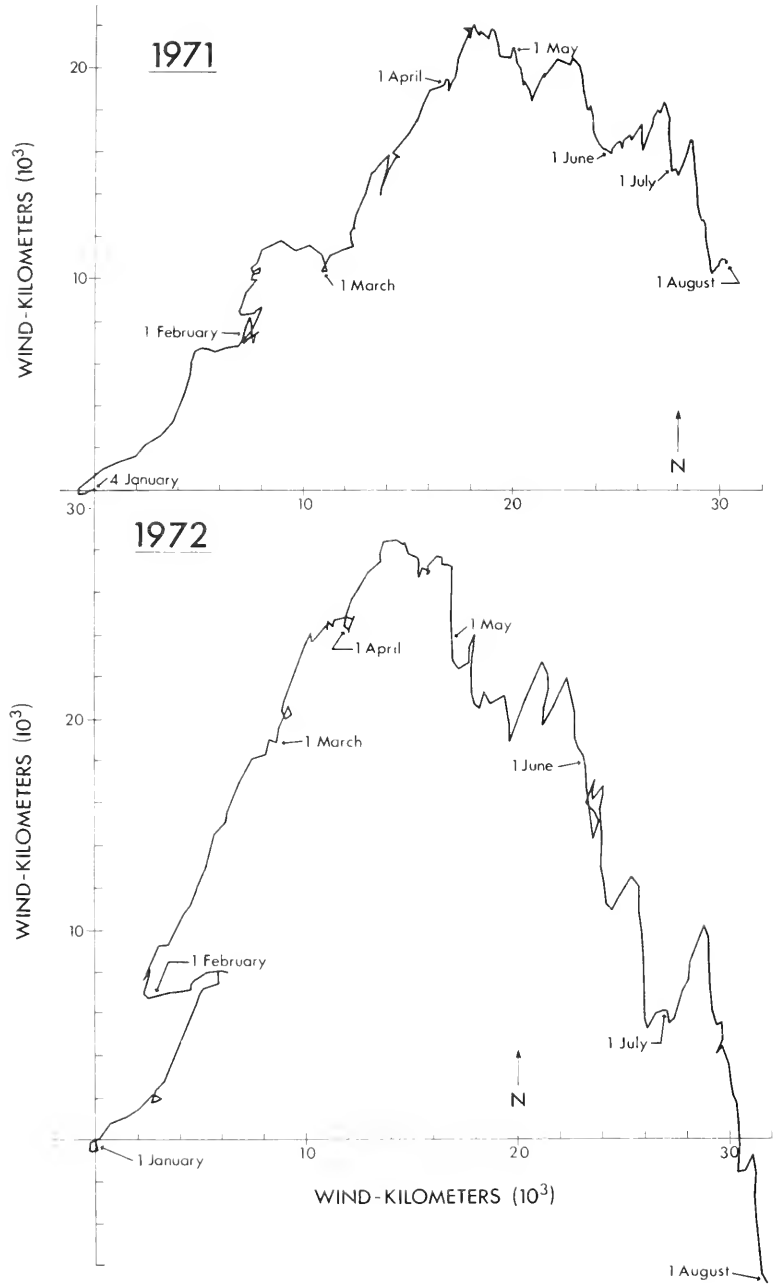

FIGURE 3.—Progressive vector diagrams for wind at Newport, Oreg., 1 January-1 August 1971 and 1972.

Zoeae VI's and VII's were caught at the 15 nmi station. On the early May cruise there were two centers at 5 and 50 nmi with young stages predominant at both. Samples collected 14 May contained a few intermediate and later larvae between 5 and 30 nmi. On 1 June, larvae were widely distributed between 10 and 60 nmi and were Zoeae VI to XIII. Larval abundance, though greater than in mid-May, was still low. Even greater dispersion was seen on 12 June (3 to 60 nmi), but there was a peak at 25 nmi. The cruise of 28 June produced the only two juveniles of the season at 5 and 15 nmi. Other larvae in late zoeal stages (X to XIII) were found between 10 and 40 nmi. No larvae or juveniles were found on 6 or 21 July.

To simplify the depiction of distribution of specific larval stages, abundances (no./1,000 m^3) were

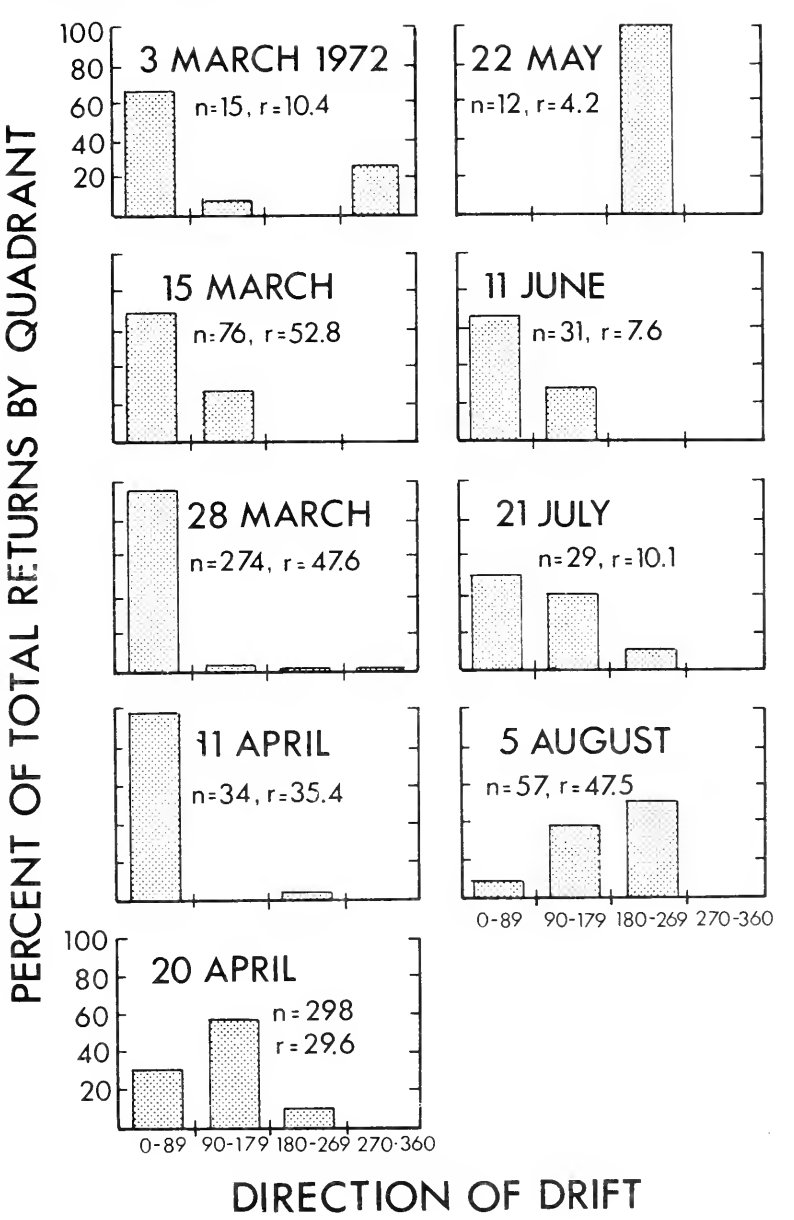

FIGURE 4.—Drift bottle-returns, 1972. Number, rate of return, and direction of drift summarized by quarterly components (from data supplied by M. J. Hosie, Fish Commission of Oregon, and W. Gilbert, Oregon State University School of Oceanography).

summed for each station over all cruises (Fig. 7). In 1971, Zoea I, though most abundant inshore, was spread over the entire 60 nmi of the transect. This trend continued to Zoea V, but increasing numbers appeared in the two seaward stations for II through V. By Zoea VI numbers were much diminished and most larvae were outside 15 nmi. This trend persisted through Zoea XIII. Small captures of late larvae and juveniles make generalizations for them difficult.

Larval Distribution and Abundance of *Pandalus jordani* in 1972

No cruises were made in 1972 until 4 March, when small numbers of young larvae (I and II) were found between 3 and 15 nmi (Fig. 6). On 16 March there were many Zoea I at 3 and 5 nmi and lower numbers farther out. Small numbers of Zoeae II and III were also present. A 30-mi transect in late March showed the center of abundance was at 10 nmi; mostly they

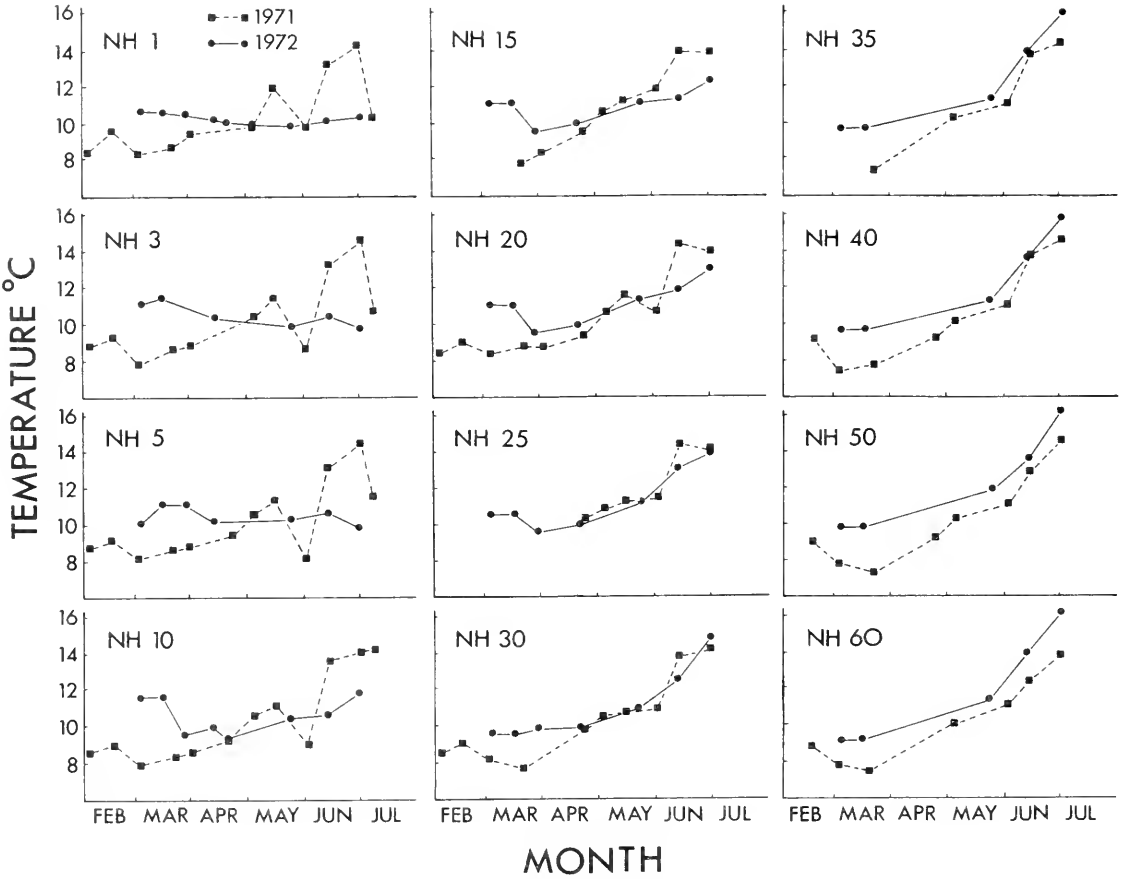

FIGURE 5.—Surface seawater temperatures at 12 sampling stations (NH-1 to NH-60) for February-July 1971 and 1972.

were Zoea III. The peak of larval hatching had apparently passed by that date. Larvae were present at the 1 nmi station for the first time and were present at all stations to 20 nmi. This contrasts to 1971, when *P. jordani* larvae were never found so close to shore. The 11 April cruise was curtailed for rough seas at 10 nmi. The most abundant stages were III's and IV's, but all stages from I to VIII were present. On 20 April stages I to XI were scattered between 5 and 30 nmi with VI to VIII most common. The distribution on 22 May was displaced offshore and spread between 10 and 45 nmi. Development was well advanced, and the first juveniles of the season were found at 25 and 30 nmi. Zoeae X to XII were dominant. Larvae on 11 June were advanced, older than XI, and distributed from 5 to 60 nmi with a peak between 10 and 20 nmi. Many juveniles were caught in a night tow at 15 nmi.

Figure 7 shows that early stages were generally less dispersed seaward in 1972 than in 1971. Zoeae I to IV were found only inside 15 nmi. Older larvae were found farther offshore, but rarely extended beyond 40 nmi. Late larvae (XIII) and early juveniles, though present in small numbers, were more abundant than in 1971 and were most abundant between 15 and 30 nmi.

Coastal Distribution and Abundance

All seven 30-nmi transects from Tillamook Head to the Siuslaw River were completed in late March 1972, but, due to bad weather, only the northern six were sampled in late April. As on the Newport line (Transect V), early larvae were most numerous inside 15 nmi, extending in to the 1 nmi stations in March (Fig. 8) over the whole grid. Larvae were most numerous at the 1 and 5 nmi stations, significantly more so than elsewhere as indicated by analysis of concordance of rank order of the stations according to larval density ($W = 0.62$; df = 7,7; $P<0.01$; see

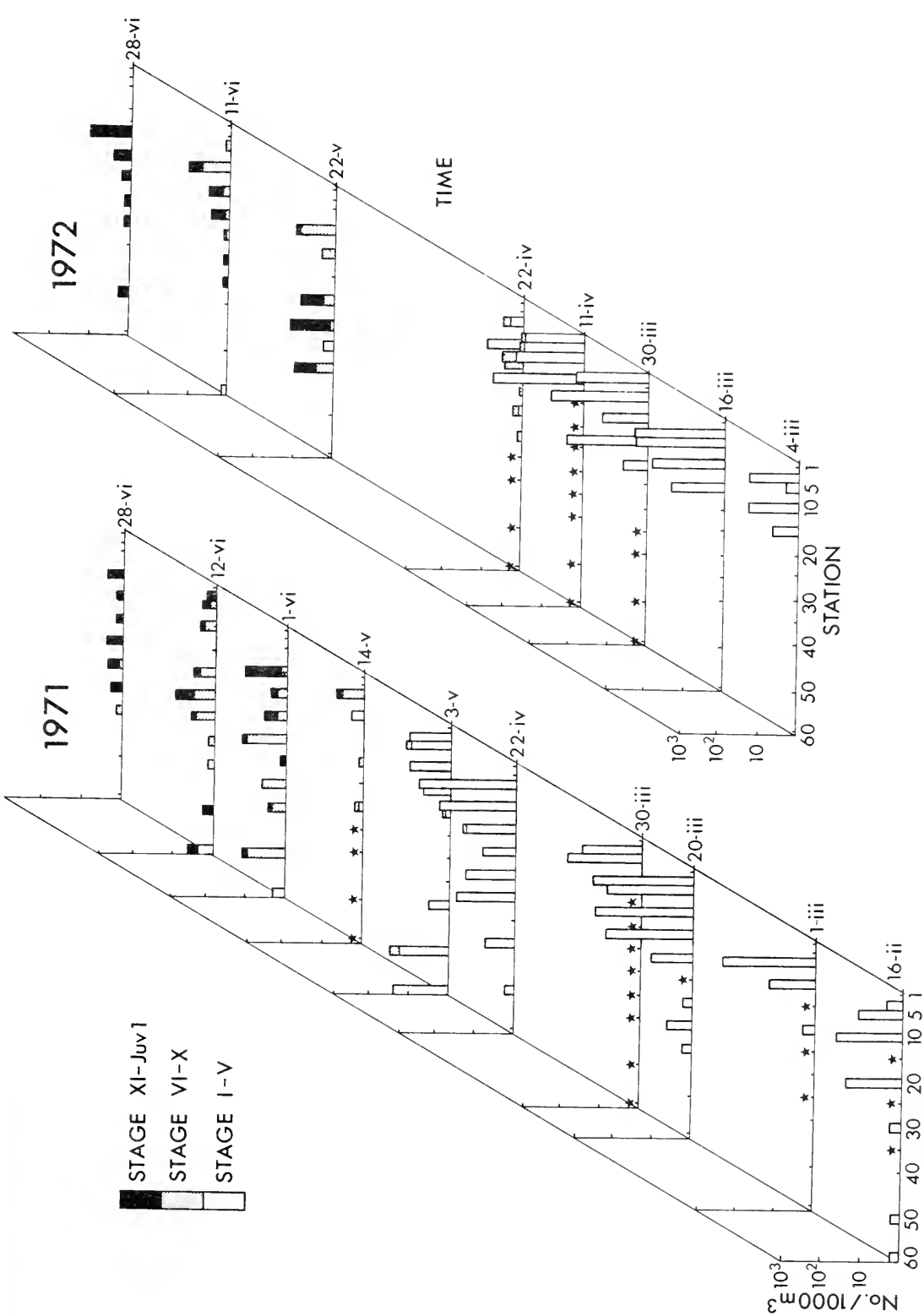

FIGURE 6.—Three dimensional display of larval distribution and abundance with time in 1971 and 1972.

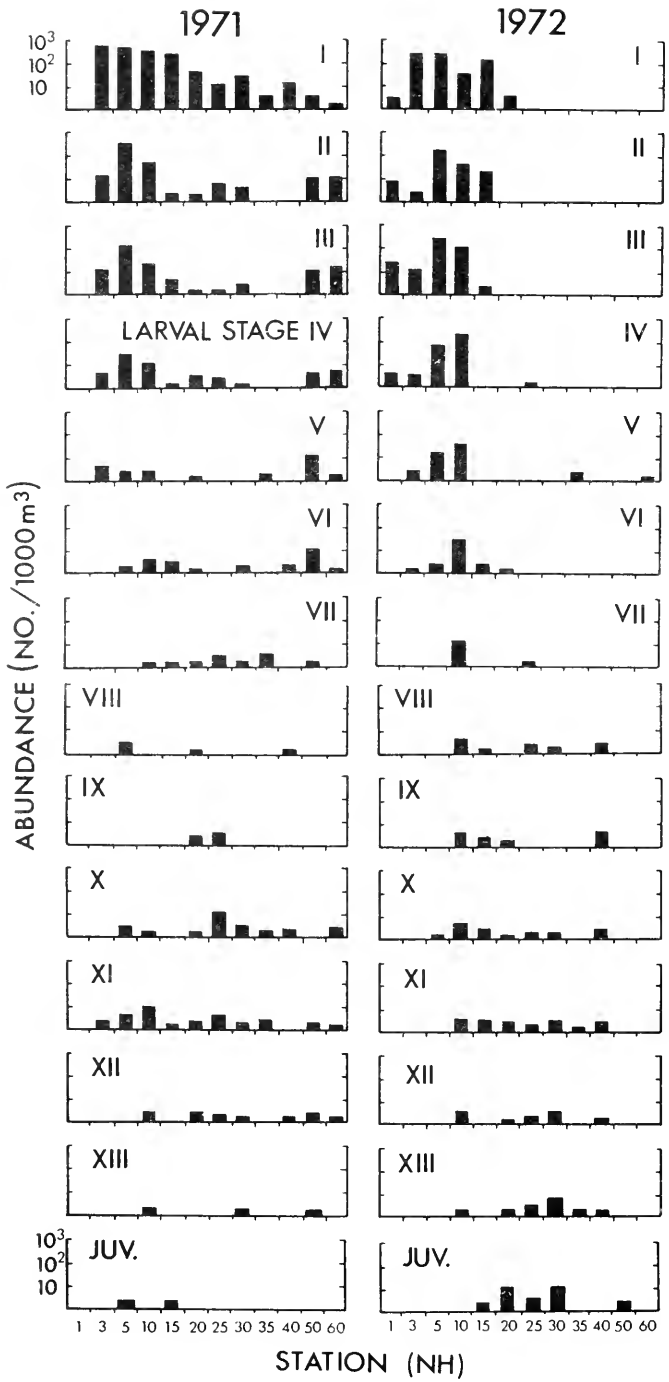

FIGURE 7.—Stage-specific larval distribution and abundance over all cruises in 1971 and 1972.

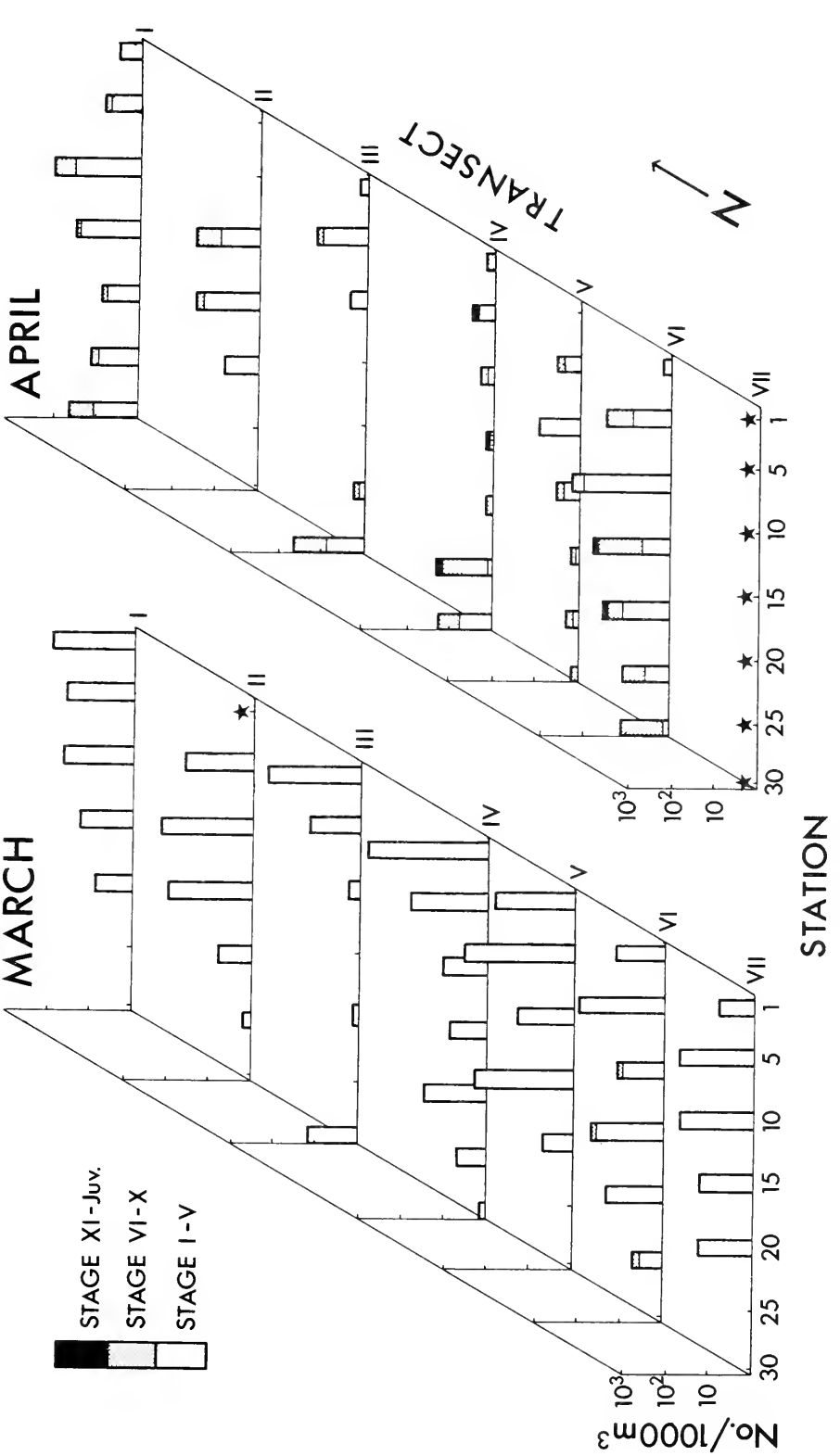

FIGURE 8.—Alongshore and offshore larval distribution and abundance in March and April 1972.

Tate and Clelland 1957). Overall larval abundance also varied between transects, IV and V having higher total numbers of larvae than the rest (1,093 and 718/1,000 m^3 compared with ca. 250). Offshore displacement and dispersion of larvae had occurred by late April. Larvae were most numerous at the 10 nmi station, and many were collected out to 30 nmi. Concordance among transects with respect to rank order of stations was less than in March but still significant ($W = 0.43$; df = 7,6; $P < 0.01$). Larval numbers were reduced from March. Transects VI and I had the most larvae (418 and 232/1,000 m^3 compared with <100 in the others).

The gradient of larval age along the coast was evaluated by summing abundance of each stage within transects (Fig. 9). March showed no consistent gradient, but there were considerable differences in median stage among transects. Medians for transects V and VI were 3.28 and 3.43, respectively. Others averaged 2.0. By April transects were more uniform in this respect. Median stage was 4.9 with a low of 4.2 and high of 5.8. The median increased 2.4 stages from March to April. While transects were more uniform, there was a wider range of stages in April with a slight increase in occurrence of older larvae in more southerly transects (IV to VI).

Onshore-offshore distribution was characterized by summing stage abundance at equivalent stations between transects for each cruise (Fig. 10). Zoeae I to IV predominated in March and were most abundant within 15 to 20 nmi. By April older larvae were dispersed outside 5 nmi.

Field Estimates of Larval Growth Rates

The two years differed in the rate of change of developmental stage frequency. Development can be followed roughly by successive estimates of the median stage in the pooled samples for each cruise (arrows in Fig. 11). In early cruises of 1971 larvae already were widely dispersed and subject to temperatures below 9°C in the whole region (Fig. 5). Cold persisted until late April, and median stage only in-

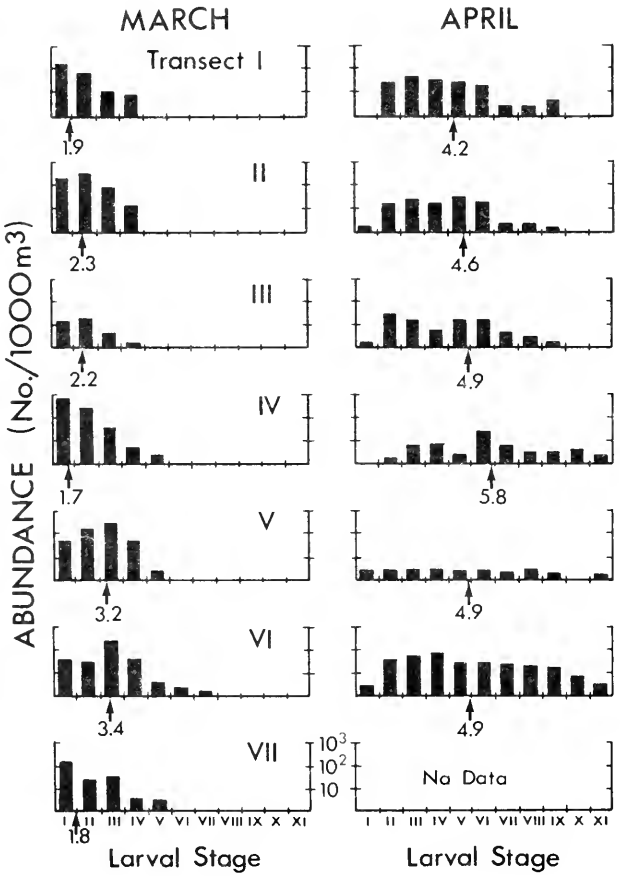

FIGURE 9.—Stage-specific larval distributions and abundance in March and April 1972. Larval abundance summed by stage within transects.

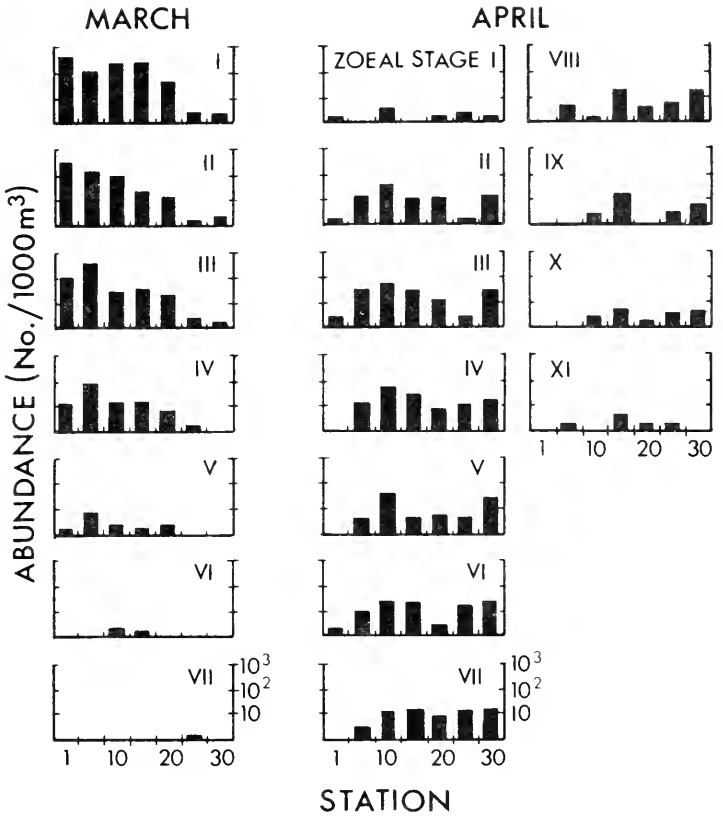

FIGURE 10.—Stage-specific larval distribution in March and April 1972. Larval abundance summed by stage over all transects.

creased to III by 4 May. There was rapid increase in median stage between 22 April and 1 June 1971, coinciding with rapid increase in surface temperature through May. In early cruises of 1972, larvae were confined to stations inshore of 20 nmi. Temperatures at those stations were about 2°C warmer than in 1971, and development was greater through 22 April, when median stage was V. Individuals up to Zoea XI were already present, which did not occur in 1971 until after the May spurt in development. Faster development in 1972 corresponded to water temperatures consistently higher than in 1971 from mid-March until June. By May of both years larvae were mostly dispersed between 10 and 50 nmi. Over that range temperatures were about the same and increasing from early May through June. Despite this, the increase in median stage slowed through June in both years. The median stage on 29 June was nearly XII in 1971 and XIII in 1972. The difference is not significant, and Zoea X through juvenile stages were present on that date in both years.

Larval Survival—Estimates from Field Sampling, 1971 and 1972

To assess larval survival in the field, total abundance was calculated for each larval stage over all cruises and stations (no./1,000 m^3 × sampled depth = no./1,000 m^2). In each year the total number of Zoea I was taken to be 100% of the larval hatch, and the number of each successive stage was expressed as a percent of that hatch (Fig. 12). Sampling effort was very similar between the two years in respect to timing and total number of cubic meters of water filtered (72,246 m^3 in 1971; 67,979 m^3 in 1972), so that the difference in survival probably was not an artifact.

We caught 1,653 Zoea I in 1971 and 530 in 1972. There is a reversal in this estimate from the order of the years in respect to hatch as estimated from egg counts in the commercial catch. Table 2 shows that the latter estimate was quite close in the two years: 1.75×10^{12} and 2.20×10^{12} in 1971 and 1972, respec-

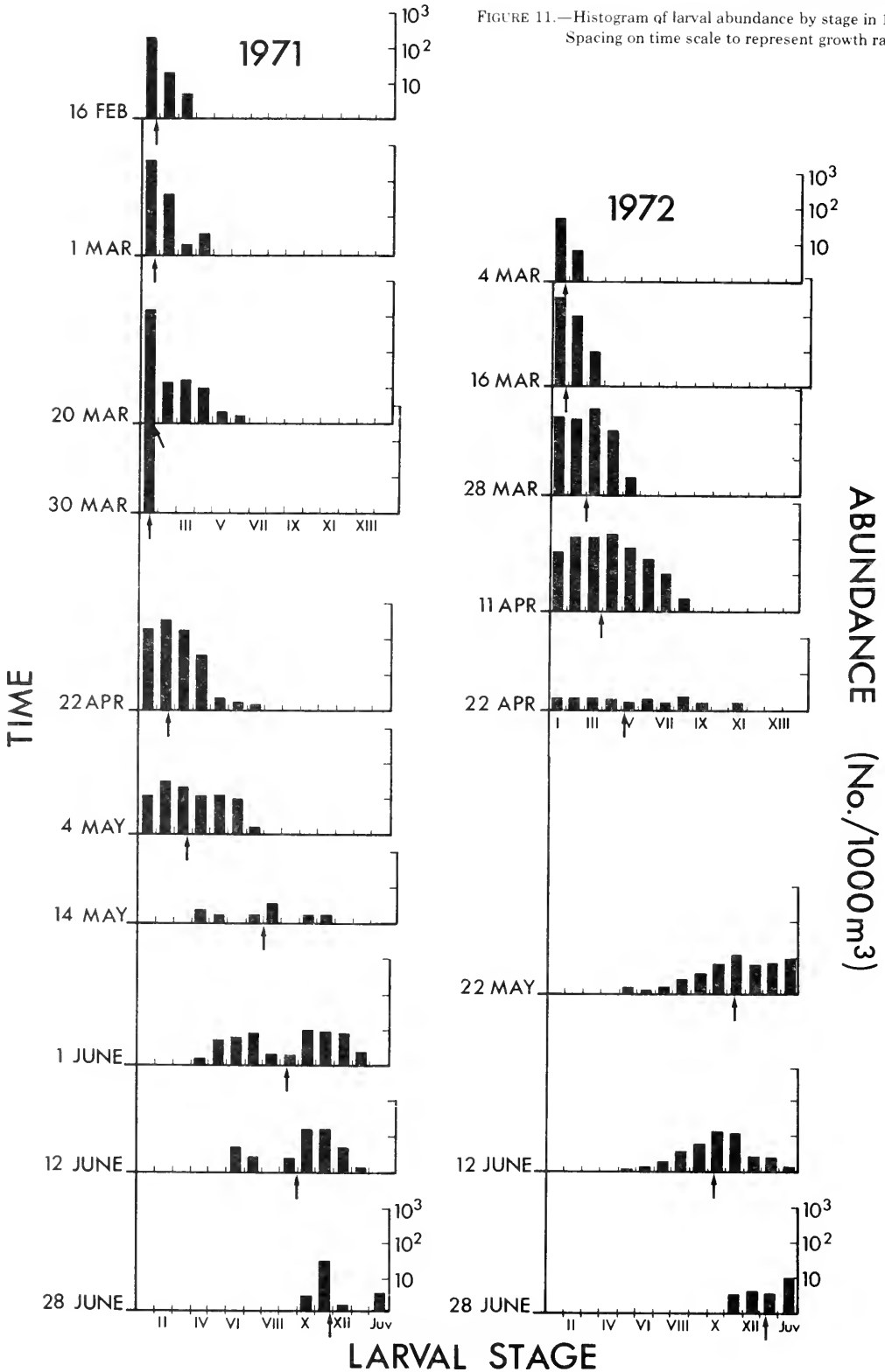

FIGURE 11.—Histogram of larval abundance by stage in 1971 and 1972. Spacing on time scale to represent growth rate.

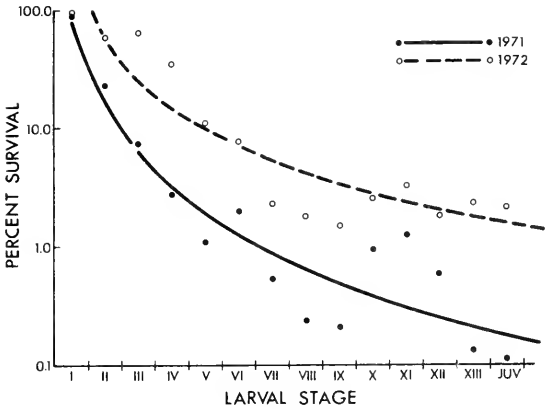

FIGURE 12.—Larval survival (percent) based on total numbers at each stage caught in the plankton sampling along NH line.

tively. Compared with the long-term variation in the commercial estimate of egg number, 1971 and 1972 were both close to average (mean 1961-80 = 1.93). In 1971, only 26.9% survived to Zoea II and <1% survived past Zoea VII. Only two Stage I juveniles (Rothlisberg 1980) were found in 1971, representing 0.17% of the hatch. In 1972 over 64% survived through Zoea III, with numbers and percentages decreasing gradually with age. Five Stage I juveniles were caught, 1.06% of the hatch. Percent surviving to the juvenile phase in 1972 was an order of magnitude higher than in 1971. This is not, of course, simply a comparison of two versus five survivors. There was a consistent difference between the years throughout the developmental sequence. Some survival estimates from the decreasing abundance at successive stages are shown at the bottom of Table 2. Such estimates depend on the assumption that reproduction is relatively synchronous (Mullin and Brooks 1970; Fager 1973). In both years the main pulse of hatching of *P. jordani* occurred within a relatively limited period, essentially synchronously.

Some of the variability of percent survival at individual stages (Fig. 12) can be due to the relationship between sampling frequency and molting frequency (mean intercruise period was 14.5 d, while mean intermolt period is 6.8 d, a ratio of 2.1:1). Stages can effectively be passed by the bulk of the population between two samplings. A simulation model of survival through stages of development and time was developed to illustrate this effect. The model imposed an intermolt period of 6 d over the entire

TABLE 2.—Estimates of larval survival (e^{-it}) from fishery data supplied by Fish Commission of Oregon (J. Robinson, see text footnote 5) and from field estimates of larval abundance $i = \ln (N_t/N_0)/t$ where $t = 1.5$ yr, the interval from hatching to recruitment to the commercial gear, i_{juv} = calculation for first year instantaneous mortality after recruitment to the bottom, from stomach analysis of hake, *Merluccius productus*, by Gotshall (1969, 1972); i_{larval} = instantaneous larval mortality as a proportion of the total instantaneous mortality (i) with instantaneous juvenile mortality (i_{juv}) held constant, see text. $t = 1.274$ yr (100 d), estimated time of larval period in plankton; $t = 0.364$, period between calculations of N_0 and N_t in 1971; $t = 0.263$, period between calculation of N_0 and N_t in 1972.

Year	$N_0 \times 10^{12}$	$N_t \times 10^9$	$N_t/N_0 \times 10^4$	$-\ln N_t/N_0$	i	i_{juv}	i_{larval}	$e^{-it} \times 10^4$
1961	2.45	0.50	2.04	8.50	5.66	1.50	24.30	12.8
1962	1.25	1.10	8.80	7.04	4.69	1.50	18.96	55.4
1963	2.30	0.33	1.43	8.85	5.90	1.50	25.58	9.0
1964	4.20	2.60	6.19	7.39	4.93	1.50	20.26	38.8
1965	0.75	0.75	10.00	6.91	4.61	1.50	18.51	62.7
1966	2.95	1.20	4.07	7.81	5.20	1.50	21.78	25.6
1967	0.80	1.25	15.62	6.46	4.31	1.50	16.87	98.3
1968	2.25	1.30	5.78	7.46	4.97	1.50	20.50	36.3
1969	1.00	0.75	7.50	7.20	4.80	1.50	19.55	47.2
1970	2.15	3.00	13.95	6.58	4.38	1.50	17.28	87.8
1971	1.75	0.25	1.43	8.85	5.90	1.50	25.60	9.0
1972	2.20	1.95	8.86	7.03	4.69	1.50	18.94	55.7
1973	1.85	1.66	8.97	7.02	4.68	1.50	18.89	56.5
1974	3.14	2.70	8.60	7.06	4.71	1.50	19.05	54.1
1975	3.24	1.98	6.11	7.40	4.93	1.50	20.30	38.4
1976	1.51	0.88	5.83	7.45	4.96	1.50	20.47	36.7
1977	1.50	0.64	4.27	7.76	5.17	1.50	21.61	26.8
1978	2.28	0.22	0.96	9.25	6.16	1.50	27.03	6.1
1979	0.72	0.30	4.17	7.78	5.19	1.50	21.69	26.2
1980	0.47	0.50	10.64	6.85	4.56	1.50	18.27	66.9
Mean								42.52
Estimation of larval survival, from larval abundance (no./1000 m²)								
1971	140,040	236	16.85	6.38	—	—	17.51	8.25
1972	40,146	475	118.32	4.44	—	—	16.88	98.02

length of the development and an instantaneous daily mortality rate (i) of 0.0788, the mean observed, overall rate of the two sampling years. This mortality was constant over all stages and constant within the molt cycle. The mortality rate was incorporated in a simple exponential decay formula to estimate survival rate over time ($N_t=N_0e^{-it}$). Two hatching-time distributions were used: 1) A standard Normal distribution with 10^6 individuals released over 20 d, and 2) a severely peaked distribution with 850,000 of the 10^6 released over 5 d around median hatch time. We feel the latter distribution most accurately reflects hatching of *P. jordani* in the field.

The population was sampled in the model at various intervals, and the sequence of abundance of successive stages was determined by summing the abundance of each over all samples, just as we have done with the field estimates. These model stage abundances were presented in Figure 13. As would be expected, sampling more than once within an intermolt period (every 4 d) tends to overestimate survival to each larval stage. Sampling every 9 d (1.5 times the intermolt period) consistently underestimated larval numbers and survival. The severely peaked distribution of larval hatching times resulted in an oscillating estimate of larval survival. Magnitude of the oscillation was related to the degree of phase agreement between the sampling and molting. In all cases, however, whether the number of larvae was over- or underestimated at any particular stage, the survival rate based on sums of estimates of abundance paralleled the "actual" rate.

Table 3 summarizes the time between cruises, the estimated surface temperatures for each intercruise period (taken from Fig. 5), and an estimated intermolt period based on larval rearing experiments (Rothlisberg 1979). The shortest period between two cruises over the 2-yr sampling period was 8 d (22-30 May 1972), while the average was 14.5 d. Surface temperature for the larval period was rarely below 8°C (expected intermolt period = 8.08 d) and was 10° between 22 and 30 May 1972 (expectation = 7.0 d). The mean ratio of interval between cruises to intermolt period was 2.1, indicating that the survival estimates of this study would be low to an extent. Larvae could progress more than two stages between some cruises.

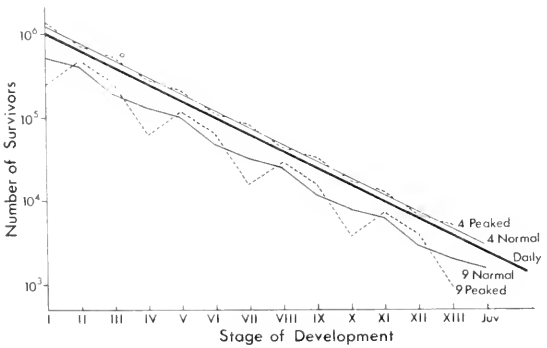

FIGURE 13.—The effect of sampling interval and larval hatching distribution on estimates of larval abundance and survival rate. Heavy line indicates "actual" survival rate; 4-normal, sampling standard normal distribution of larval hatch every 4 d; 9-normal, sampling every 9 d; 4-peaked, sampling peaked distribution of larval hatch every 4 d; 9-peaked, sampling peaked distribution every 9 d (see text for further explanation).

TABLE 3.—Period between cruises (days), estimated temperature for the period (from Fig.5), intermolt period at the temperature (from Rothlisberg 1979), and the ratio between intercruise (IC) period and intermolt (IM) period.

Sampling date	Intercruise period (days)	Temperature (°C)	Intermolt period (days)	Ratio IC/IM
1971				
16 Feb.	13	9	7.3	1.8
1 Mar.	19	9	7.3	2.6
20 Mar.	10	8	8.1	1.2
30 Mar	23	9	7.3	3.2
22 Apr.	12	10	7.0	1.7
4 May	10	11	6.6	1.5
14 May	16	11	6.6	2.4
1 June	11	12	6.4	1.7
12 June	16	14	6.3	2.5
28 June				
Mean				2.1
1972				
4 Mar	12	11	6.6	1.8
16 Mar.	12	11	6.6	1.8
28 Mar.	14	10	7.0	2.0
11 Apr.	11	10	7.0	1.6
22 Apr.	30	10	7.0	4.3
22 May	8	10	7.0	1.1
30 May	13	10	7.0	1.9
12 June	16	10	7.0	2.3
28 June				
Mean				2.1
Overall Mean				2.1

Estimates of Larval Survival from Commercial Landings

Long-range trends in larval survival of *P. jordani* were sought from Oregon fishery statistics to put the apparent differences in larval survival between 1971 and 1972 into perspective. Data on number of ova and of age 1 shrimp were provided by J. Robinson[5]. He estimated ova from adjusted estimates of numbers of females in samples of the April commercial landings and an empirical length to fecundity relationship (Robinson 1971). Numbers of age 1

[5]J. Robinson, Oregon Department of Fisheries and Wildlife, Marine Science Drive, Newport, OR 97365, pers. commun. February 1982.

shrimp were estimated from commercial landings 1.5 yr later (November) when they were fully recruited to the fishing gear. Figure 14 shows the fluctuations in these data from 1961 to 1980. Instantaneous rate of total mortality, i, was calculated from the data according to formulae of Ricker (1958). Results are shown in Table 2.

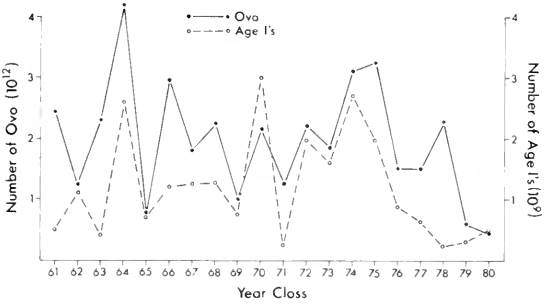

FIGURE 14.—Number of ova and number of age I shrimp recruited to the commercial fishery 1.5 yr later, by year class (Robinson unpubl. data).

Separation of the planktonic larval mortality from total mortality required an estimate of juvenile mortality. Gotshall (1969,1972), using an analysis of stomach contents of Pacific hake, *Merluccius productus*, which has been shown to prey on *P. jordani* without respect to age, has calculated that juvenile mortality rate, i_{juv}, is 1.50/yr. Proportioning total instantaneous mortality within the 18 mo from hatching to first harvest was done according to:

$$i = \frac{0.274\ (i_{larval}) + 1.226\ (i_{juv})}{1.5},$$

where $i = \ln(N_t/N_0)/t$, with $t = 1.5$ yr

$i_{juv} = 1.50$ (Gotshall 1969, 1972)

i_{larval} = instantaneous rate of larval mortality.

$$\text{Solving } i_{larval} = \frac{1.5(i) - 1.226(i_{juv})}{0.274}$$

Computed values of i_{larval}, along with overall larval survival (e^{-it}), from commercial catch sample estimates for 1961 to 1980 are shown in Table 2 and compared with our results for 1971 and 1972. Both sets of estimates indicated that 1971 was a very poor year for larval survival, while 1972 was slightly above average.

Factors Affecting Larval Survival

Comparison of onshore-offshore distribution patterns and wind patterns between 1971 and 1972 suggested that Bakun's upwelling index (1973, footnote 4) might be a useful indicator of habitat quality for survival of larval *P. jordani*. A study of possible correlations was originally made with data from 1961 to 1973. Fortnightly, monthly, and quarterly indices were calculated and regressed against the apparent overall larval-juvenile survival ($e^{-it} \times 10^4$). The July index was the most highly correlated for a single month ($R = 0.599$), while the average for the June through August period gave the highest correlation found ($R = 0.749$). For those months the equation

$$\text{Larval survival} = e^{-it} \times 10^4 = 0.73\ (\text{upwelling index}) - 8.31$$

accounted for 56.2% of variability in larval survival. A new equation based on data from 1961 through 1980,

$$\text{Larval survival} = e^{-it} \times 10^4 = 0.889\ (\text{upwelling index}) - 9.652,$$

accounts for 54.9% of the 20 yr variability in larval survival. The slope is significantly different from zero ($t_{18} = 4.81, P<0.001$). The point for 1967 contributes strongly to the strength of the relationship, but the regression is significant without it ($t_{17} = 3.35$, $P<0.01$). The relationship between larval survival and upwelling index is shown in Figure 15.

This relationship of survival to upwelling strength

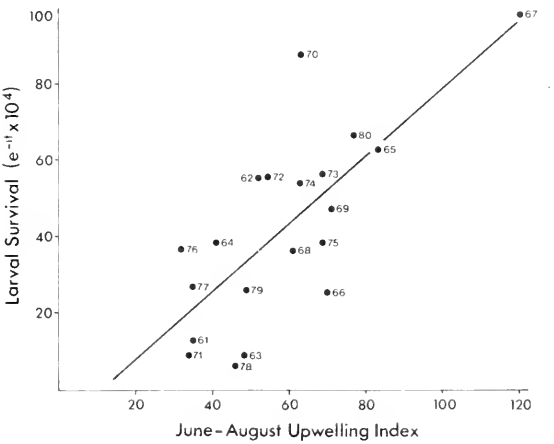

FIGURE 15.—Relationship between average upwelling in June through August 1961 to 1980 and estimated larval survival ($e^{-it} \times 10^4$) 1961 to 1980, with fitted regression line.

gives some insight into what factors may limit survival, and thus year class strength, in the *P. jordani* fishery. Surface seawater temperatures in 1971 and 1972 (Fig. 5) were different in several respects. The regression analysis draws attention to months from June through August. In these late months of larval development, temperatures were several degrees higher at nearshore stations in 1971 than in 1972. Evaluation of laboratory rearing experiments showed that survival was highest at 11° to 12°C, and it decreased rapidly above that range (Rothlisberg 1979).

DISCUSSION

Movements of adult *Pandalus jordani* associated with reproductive events have not been well defined. In contrast to other pandalids, e.g., *P. borealis* (Haynes and Wigley 1969; Horsted and Smidt 1956) and *P. montagui* (Lebour 1939, 1947; Mistakidis 1957; Allen 1963), there is no evidence of an inshore migration of female *P. jordani* prior to hatching of eggs they bear. Dahlstrom (1970) found that *P. jordani* at Morro Bay, Calif., moved 2 to 3 nmi farther offshore to spawn in the winter. Lukas and Hosie (1973) reported that female *P. jordani* left their study area 10 to 20 nmi off Tillamook Head, Oreg., in the fall. Numbers in March were greater at the south end of their grid than to the north, but there was no evidence of inshore or offshore movement associated with hatching. During the present study off Newport, Oreg., we found highest concentrations of adult *P. jordani* between 20 and 25 nmi offshore. While trawling was casual, and results are not reported here, there was no evidence of shoreward movement of ovigerous females during the period of hatching.

Prevailing wind and resultant currents could have transported larvae to the nearshore zone during the present study. Differences in wind and current between 1971 and 1972 are reflected in larval distributions for the two years. Furthermore, extended alongshore sampling in 1972 showed that shifts in distribution along the Newport line were representative of shifts along the whole coast. Shifts were not restricted to areas of high adult abundance.

Widespread distribution of early zoea in early and mid-March 1971 can probably be attributed to the mixed winds of February and to the spell of northwest wind in mid-March. More dramatic offshore displacement was seen in early May 1971, when larvae were found in abundance at 50 and 60 nmi. Numbers decreased markedly after May, probably through continued offshore displacement beyond the sampling area. More limited offshore displacement of early larvae in 1972 coincides with stronger, more consistent southwest winds in February and March of that year. Older larvae were generally closer to shore in 1972 than in 1971. Offshore displacement by upwelling probably was reduced in 1972 by the advanced larval development at the initiation of upwelling compared with 1971. Since older larvae live deeper in the water column (Rothlisberg and Pearcy 1977), late onset of upwelling with respect to the development sequence will produce less offshore displacement.

Year-to-year fluctuations in seasonal winds, upwelling, and surface advection in the northwest Pacific have been repeatedly described (e.g., Wickett 1967; Hubbard and Pearcy 1971; Peterson and Miller 1975). However, until the upwelling index was developed by Bakun (1973), it was difficult to correlate strength of upwelling in a long sequence of years with variations in productivity at any level. This now can be done, although specific processes involved may remain obscure. Several of the features of upwelling may act to change production of a given life stage or species. The correlation we found between upwelling index and larval survival is something of a surprise. Earlier studies (Winnor 1966; Wickett 1967; Hubbard and Pearcy 1971) stressed the advective nature of upwelling. Thus we expected greater larval "wastage" to seaward for years with early onset and greater strength of upwelling. The colder temperatures also might be supposed detrimental to *P. jordani* because they should slow development. The unexpected, high, positive correlation of larval survival and June to August upwelling can be explained by other knowledge of larval physiology in *P. jordani*. Laboratory rearing experiments have shown optimal larval survival at 11° to 12°C (Rothlisberg 1979). Upwelling maintains these relatively low temperatures through the summer months, whereas weaker upwelling allows summer warming (Patullo et al. 1969). Temperatures above 14°C in June 1971 would have been harmful and may have contributed directly to low larval survival in that year.

The reproductive strategy of *P. jordani* appears to rely on the complex advection of late winter and spring. Many demersal species of the Pacific northwest spawn in winter and spring, apparently to maximize onshore drift of larvae and retention in coastal nursery grounds (Parrish et al. 1981). *Pandalus jordani* larvae, on the other hand, hatch in late winter and have a planktonic phase extending through the transition from northward-onshore to southward-offshore currents. They should usually encounter 1) onshore retention in early stages and 2) offshore displacement of later stages during subse-

quent upwelling, reaching deeper water over habitat suitable to settling.

Application to all years uniformly of Gotshall's (1969, 1972) instantaneous mortality for juvenile *P. jordani* on the bottom ignores the certain variation in that mortality. Despite this limitation, the estimate of larval survival derived from the analysis was similar to estimates from our 2 yr of intensive plankton sampling. We are aware of the dangers of a comparison based on only two spawning seasons, but the comparison is in the correct direction, and it is all we have. Although there are limitations, comparison of egg numbers with numbers of first fishery recruits shows promise for identifying conditions critical in establishing year class strength. Higher resolution could be obtained if annual estimates of early benthic mortality were made, perhaps using the Pacific hake, *Merluccius productus*, as a biological sampler.

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EFFECTS OF BENZO(A)PYRENE ON THE EARLY DEVELOPMENT OF CALIFORNIA GRUNION, *LEURESTHES TENUIS* (PISCES, ATHERINIDAE)

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ABSTRACT

Benzo(a)pyrene (BaP), which is carcinogenic and mutagenic in mammals, exists worldwide in the marine environment. Sources of this polycyclic aromatic hydrocarbon include oil spills, industrial effluents, and atmospheric fallout. This study is the first to examine the effects of BaP on the embryonic development of a teleost, the California grunion. Gametes were stripped from spawning adults, and eggs were artificially fertilized. The fertilized eggs were then incubated for up to 14 days with initial concentrations of BaP ranging from 0 to 869 ppb. Steady-state tissue levels of BaP ranged from 0.46 to 19.92 ppm, which represented bioaccumulation factors of 146-437 times the steady-state BaP concentrations in seawater. When compared with controls, embryos exposed to initial BaP levels of 24 ppb or greater showed decreased hatchings, reduced notochord lengths, and increased morphological abnormalities. These results suggest that exposure of grunion embryos to BaP in contaminated areas may lead to their decreased survival.

Benzo(a)pyrene (BaP) is one oil constituent commonly found in marine sediments and organisms (ZoBell 1971; Neff 1979). This polycyclic aromatic hydrocarbon is introduced into the ocean via oil spillage, offshore drilling leaks, industrial effluents, runoff of asphalt roads, creosoted pilings, and atmospheric fallout (Andelman and Suess 1970; Dunn 1976; Puffer et al. 1979). Because BaP exhibits toxic, mutagenic, and carcinogenic properties in mammals, one might infer that it could also exert detrimental effects on fish populations (Heidelberger 1975; Miller 1978). Such effects could lead directly to a decrease in a valuable food source and pose a public health problem in the consumption of contaminated seafoods (Dunn and Fee 1979).

Awareness of significant BaP contamination in the marine biota has led to research on adult stages (Lee et al. 1972; Puffer et al. 1979) and, more recently, the sensitive embryonic-larval stages of fish (Hose et al. 1981, 1982). Grunion are particularly suitable for such a study because their embryonic development is well documented and they are easily reared in captivity (David 1939; Ehrlich and Farris 1971). Furthermore, grunion spawn on sandy beaches where developing eggs remain in the sand until the tide uncovers, agitates, and stimulates the eggs to hatch (Walker 1952). During this time, the developing eggs may be exposed to BaP. Therefore, we have undertaken this study to examine the effects of BaP on the early life history of California grunion, *Leuresthes tenuis*.

MATERIALS AND METHODS

Decontaminated seawater (sterilized, free of detectable BaP and particulate matter) was obtained by exposure of Los Angeles Harbor water to direct sunlight for 1 wk. Photooxidation by sunlight resulted in the breakdown of contaminating BaP to noncarcinogenic byproducts such as phenols and quinones (National Academy of Sciences 1972). Seawater exposed to sunlight was filtered through Whatman No. 5 filters to remove large, particulate matter and then sterilized by ultraviolet light. Water was maintained at a salinity of 31-32 ‰, a pH of 7.7-7.9, and a temperature of 20.0°-21.5°C.

BaP was dissolved in acetone, mixed with decontaminated seawater, and stirred for 24 h. The added concentrations of BaP in seawater were 5, 10, 100, 500, 1,000, and 5,000 ppb. The final concentration of acetone in the control and BaP-treated groups did not exceed 0.04%. Spawning California grunion were collected at Redondo Beach, Calif. Gametes were stripped and artificially fertilized in BaP-free, decon-

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taminated seawater. One hour after fertilization, three replicates of 25-35 eggs for each treatment level were placed in glass incubation jars (12.8 × 5.4 cm) which were wrapped with black tape and aerated with Pasteur pipettes connected to air pumps. Each jar contained 100 ml of decontaminated seawater to which various levels of BaP had been added as described above. In all cases, sand was excluded as an incubation medium. Dissolved BaP concentrations were measured when the California grunion eggs were introduced into the glass jars and on alternate days until day 15, using fluorescence spectroscopy (365 nm excitation, 405 nm emission) (Felton et al. 1982). Seawater samples (2 or 4 ml) were analyzed by Aminco-Bowman spectrophotofluorometer sensitive to 2 ng BaP.

Hatching and morphological abnormalities were observed and photographed at intervals over a 14-d period using a Wild M5 dissecting microscope and a Zeiss[5] photomicroscopy attachment. The significance of arc sin-transformed percentages of abnormalities was tested using analysis of variance followed by the Student-Newman-Keuls multiple range test (Sokal and Rohlf 1969). Notochord length of embryo and yolk-sac larvae was measured using a calibrated ocular micrometer. Notochord length was defined as the distance from the tip of the snout to the tip of the notochord before flexion and was always measured on the left side of the embryos and larvae. Deformed, circular-shaped embryos were measured from the posterior tip of the deformed notochord to the opposite side of the embryo, and this diameter was used to calculate the circumference which was considered to be equal to the notochord length. All values were recorded to the nearest 0.1 mm. Differences were tested using analyses of variance and the Student-Newman-Keuls test.

To measure accumulation of BaP by California grunion embryos, two additional series of incubation jars were prepared containing similar BaP concentrations and to which was added a small amount (6.7 nCi) of (α7, 10-^{14}C) benzo(a)pyrene (Amersham/Searle Corp., Arlington Heights, Ill.; 21.7 mCi/mmol, 99% chemical and radiochemical purity). On alternate days, three replicate samples of two eggs each were taken from the ^{14}C-BaP series to measure BaP accumulation using the method of Hose et al. (1981). Radioactivity was measured using a Beckman LS250 scintillation counter with an efficiency of 80% at 4°C. Total radioactivity was calculated using a series of solubilized embryos as the quenched standards.

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

RESULTS

BaP Determinations

Added BaP levels of 5, 10, 100, 500, 1,000, and 5,000 ppb to seawater yielded initial BaP concentrations in the incubation jars of 4, 7, 24, 297, 361, and 869 ppb, respectively, when measured at time "0" when the California grunion eggs were introduced into the jars. Dissolved BaP levels declined thereafter with a half-life of 3.0±0.1 d ($\bar{x}$±SD) until steady-state levels of 24 ppb (361 ppb initial), 9 ppb (297 ppb initial), 5 ppb (24 ppb initial), 3 ppb (7 ppb initial), and 2 ppb (ppb initial) were reached within 4-10 d (Fig. 1). Stable BaP levels occurred most rapidly at lowest doses, while BaP concentrations in jars receiving the highest initial dose of 869 ppb decreased throughout the experimental period and did not achieve steady-state.

Accumulation of ^{14}C-BaP

The amount of BaP plus its metabolites in each egg corresponding to measured ^{14}C increased from day 1

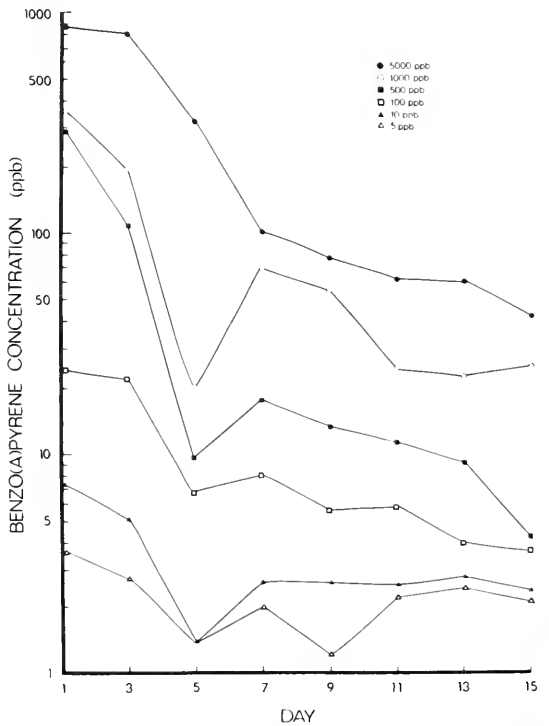


FIGURE 1.—Dissolved benzo(a)pyrene (BaP) concentrations following addition of 5-5,000 ppb BaP during the 14-d incubation period for the California grunion.

to day 3 in direct proportion to initial BaP concentrations and remained at steady-state levels thereafter for all groups except those exposed to an initial BaP dose of 297 ppb (Fig. 2). In embryos from this group, levels of BaP plus its metabolites increased throughout the exposure period ($R = 0.882$, 5 df, $P<0.01$). At day 15, BaP concentrations in treated embryos ranged from 0.459 (4 ppb initial) to 19.918 (869 ppb initial) ppm wet weight (Table 1). Tissue burdens from the initial BaP concentrations corresponded to bioaccumulation values of 127 to 23. Bioconcentration factors of 146-437 over steady-state BaP levels were measured.

Hatching

Hatching results are shown in Table 2. Low-level exposure to initial concentrations of BaP (4 and 7 ppb) had no significant effect ($P>0.05$) on the hatching abilities of exposed California grunion embryos, compared with the controls. However, with initial concentrations of 24 ppb and greater, significant differences ($P\leq0.05$) were observed between the control and experimental groups. At 24 ppb, 78% of the California grunion hatched, as compared with an average 95% hatching success in the controls. At 297 ppb only 6% of the California grunion hatched. After being exposed to 361 ppb BaP, only two of 95 larvae hatched, and both were abnormal. No eggs hatched after exposure to initial BaP concentrations of 869 ppb. Of those eggs which hatched on day 10, 99% had been exposed to 0 and 4 ppb initial BaP concentrations, 94% had been exposed to 7 ppb BaP, and 92% had been exposed to 24 ppb. All other hatchings occurred by day 13.

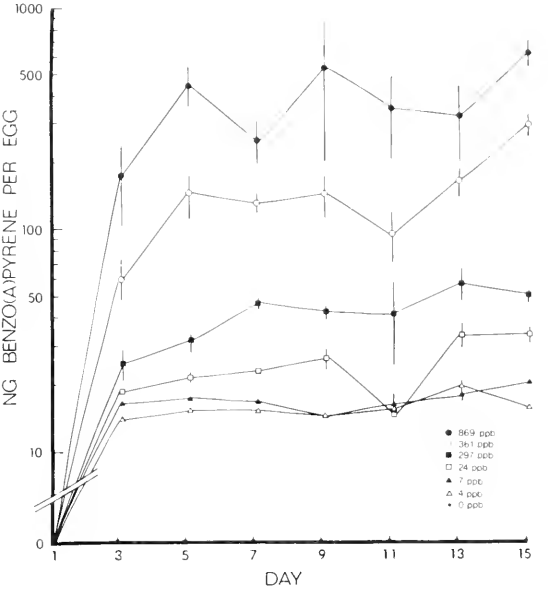


FIGURE 2.—Amount of benzo(a)pyrene (BaP) per California grunion egg corresponding to accumulated radioactivity (6.7 nCi ^{14}C-benzo(a)pyrene/ug BaP) during the 14-d incubation period. Initial dissolved BaP concentrations ranged from 0 to 869 ppb. Values shown are mean + standard deviation.

TABLE 1.—Tissue burdens of benzo(a)pyrene (BaP) and bioaccumulation factors in 15 d-old California grunion embryos.

Initial BaP concentration of seawater (ppb)	Embryo BaP concentration[1]		Bioconcentration factor	
	Wet weight (ppm)	Dry weight (ppm)	Initial BaP level in seawater	Steady-state BaP level in seawater
4	0.459±0.002	3.021±0.076	127±3	241±6
7	0.594±0.026	3.911±0.173	81±4	214±13
24	0.922±0.079	6.872±0.586	38±3	200±17
297	1.374±0.098	10.232±0.731	5±0	146±9
361	10.480±2.256	62.798±13.521	35±8	437±94
869	19.918±2.700	112.034±15.164	23±3	—[2]

[1] $\bar{x}$±SD, $n = 5$.
[2] Steady-state concentration not reached during study.

TABLE 2.—Percent hatching of California grunion eggs exposed to increasing BaP concentrations.

Initial BaP concentration (ppb)	Eggs		
	Total no.	No. hatched	% hatched[1]
0	88	84	95.4±5.5
4	87	81	93.3±2.8
7	92	83	90.3±11.2
24	84	65	78.1±8.2
297	81	5	6.2±6.0
361	95	2	2.1±1.8
869	90	0	0±0

[1] $\bar{x}$±SD, $n = 3$.

Abnormalities

There was significant difference ($P\leq0.05$) between percent of abnormalities in yolk-sac larvae in the control groups and those in groups exposed to initial BaP concentrations of 24 ppb or greater (Table 3). Of hatched larvae exposed to 24 ppb BaP, almost 20% were abnormal, over twice the number of abnormalities found in the control group. From solutions

TABLE 3.—Percent of California grunion yolk-sac larvae with developmental abnormalities when exposed to increasing concentrations of BaP.

Initial BaP concentrations (ppb)	Eggs hatched		
	No.	No. with developmental abnormalities	% with developmental abnormalities[1]
0	84	8	9.4±3.4 (3)
4	81	7	8.8±2.8 (3)
7	83	13	15.5±7.5 (3)
24	65	13	20.0±2.4 (3)
297	5	2	41.6±11 8 (2)[2]
361	2	2	100.0±0 (2)[2]
869	0	0	0

[1] $\bar{x}$±SD (n)
[2] No eggs hatched in one replicate of these series, therefore n = 2.

containing 297 ppb BaP, 42% of the yolk-sac larvae were abnormal.

Gross abnormalities observed in yolk-sac larvae exposed to 24 ppb BaP included lateral foldings of the posterior one-fourth of the tail, absence of caudal fin folds, and hemorrhagic lesions or congested vasculature in the caudal region (Table 4).

In contrast, development of embryos exposed to 24-361 ppb BaP for 14 d was retarded and resembled that of the normal embryo at 2.5 and 5.5 d of age (Fig. 3a, b) (David 1939). Abnormalities included 1) malformed tails with congested vessels or hemorrhage, 2) sporadic heartbeat resulting in intermittent blood flow, 3) head displacement in relation to the yolk sac, and 4) lack of melanophores near the lateral line above the intestinal tract.

Embryos exposed to 869 ppb BaP for 14 d resembled normal embryos at 1.2-2.5 d of age (David 1939). However, affected embryos had a lateral curvature midbody with occasional melanophores found on the trunk. In general, those embryos with shorter notochord lengths were observed to have yolk sacs much larger than those of the controls.

TABLE 4.—Abnormalities observed in California grunion yolk-sac larvae and embryos exposed to increasing concentrations of BaP.

	BaP exposure (ppb)	Abnormality
Yolk-sac larvae	24	Lateral folding of posterior fourth of tail. Absence of caudal finfold. Congested vasculature on caudal region.
Embryos	24-361	14-d-old embryo retarded in growth (resembled normal embryo growth at 1.5-5.5 d of age). Sporadic heart beat. Displacement of head in relation to yolk sac. Absence of melanophores near lateral lines. Absence of lens formation. Lesions as in larvae (above).
	869	14-d-old embryo retarded in growth (resembled normal embryo growth at 1 2-2.5 d of age). Lateral curvature midbody. Absence of melanophores (except in trunk region). Unused yolk sac. Lesions as in larvae (above).

Notochord Length

Notochord lengths (NL) of embryos and yolk-sac larvae are shown in Figure 4. Larvae which hatched after exposure to initial levels of BaP up to 361 ppb were not significantly different from controls in length ($P>0.05$). Shorter notochord lengths were observed in embryos exposed to BaP concentrations >7 ppb ($P<0.05$). Upon hatching, the mean notochord length of the control larval group was 5.8 mm, while embryos of the same age exposed to 24 ppb BaP averaged 4.0 mm NL.

DISCUSSION

Toxic and teratogenic effects of the carcinogen BaP on developing fish were studied by incubating embryonic stages of California grunion to increasing concentrations of BaP. Eggs were hatched in seawater alone, although California grunion eggs are normally incubated in sand. David (1939) concluded that there was probably no special adaptation of embryo metabolism to sand incubation, and speculated that spawning in the sand was a mechanism to protect eggs from predation. Incubation in seawater without sand permitted optimal observation of embryonic development with minimum disturbance. Also, exclusion of sand reduced the possibility of fungal and bacterial overgrowth and eliminated any possible contamination and influence by sand and/or sand-absorbed materials, as well as eliminating a large, potentially adsorptive surface for BaP. Preliminary trials resulted in a hatching rate of 90-100% in our laboratory, comparable to values previously reported (David 1939; Hubbs 1965).

Because of the low solubility of BaP in seawater, it was necessary to select a solubilizing or dispersing agent to create a uniform distribution (Davis et al. 1942; Wilk and Schwab 1968; Neff 1979). Such an agent could affect early development by acting in an additive or synergistic manner with BaP. Solvents examined in preliminary studies were benzene, Triton X-100, trioctanoin, and acetone, all of which caused observable alterations except for acetone in low concentrations. Triton X-100 and trioctanoin proved lethal, whereas the carcinogen benzene induced tail malformations. The validity of utilizing a solvent to distribute high levels of BaP in seawater can be compared with the not-uncommon situation in nature whereby lipophilic compounds are solubilized by contaminating substances such as detergents or oils. Also, certain solvents in which BaP is soluble, such as benzene, toluene, and xylene, are present in varying quantities in crude and refined oil. However,

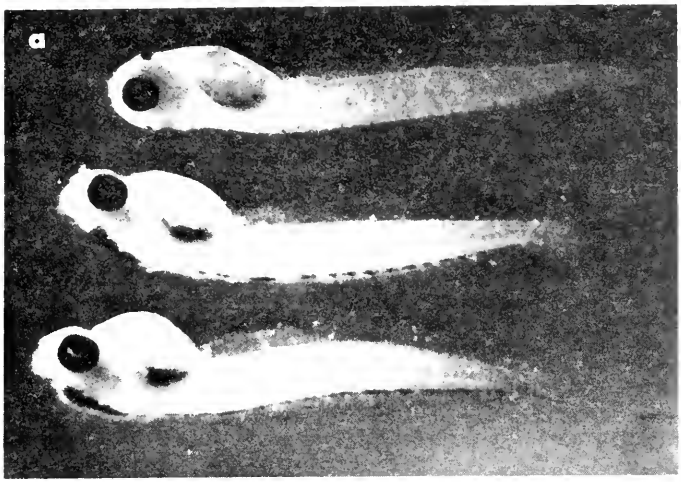
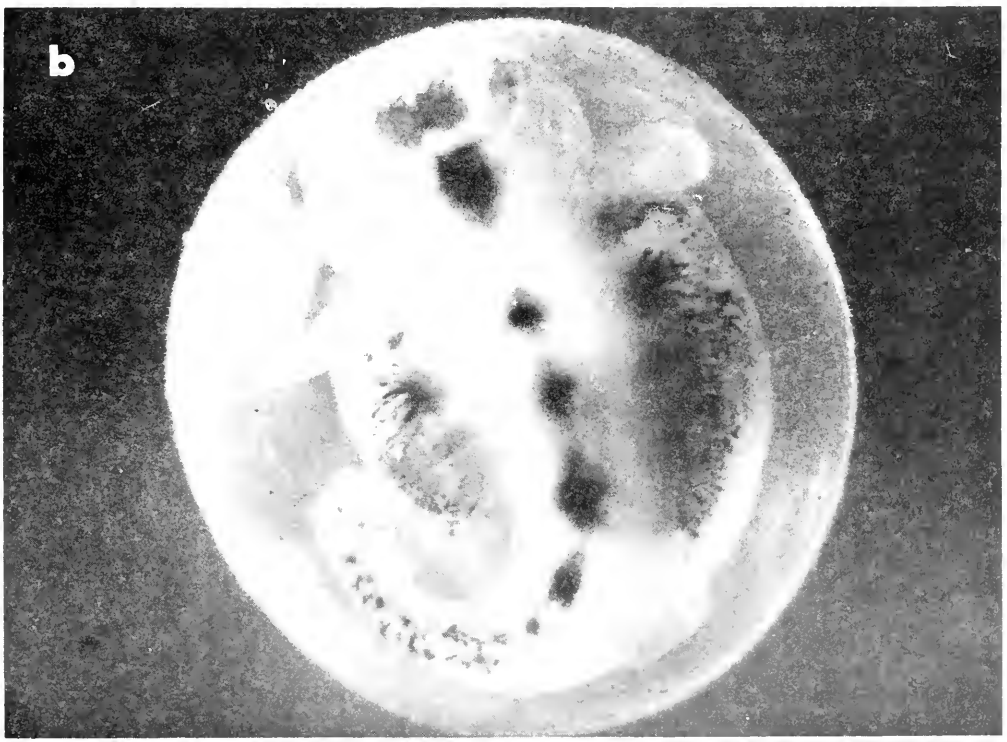


FIGURE 3.—California grunion incubated in decontaminated seawater, 14-d postfertilization: a) newly hatched larvae, with no benzo(a)pyrene (BaP) present (control) (90×); b) embryos, initially containing 24 ppb BaP (540×).



it should be emphasized that this study was not undertaken to duplicate field conditions of environmental exposure of California grunion eggs incubating in contaminated sands, although our results suggest that such studies are warranted.

Another difficulty was the decline of dissolved BaP over the 2-wk span in which the embryos were exposed (Fig. 1). This decline occurred despite precautions such as wrapping the jars to prevent photooxidation and opening the jars for daily inspection only under subdued light filtered free of ultraviolet wavelengths which degrade BaP. Loss of BaP could be caused, perhaps, by oxidation and adherence to glass, in addition to the uptake and metabolism of BaP by the embryos themselves. Felton et al. (1982) demonstrated that 16-20 ppb of crystalline BaP could be dissolved with agitation. This concentration could not be maintained,

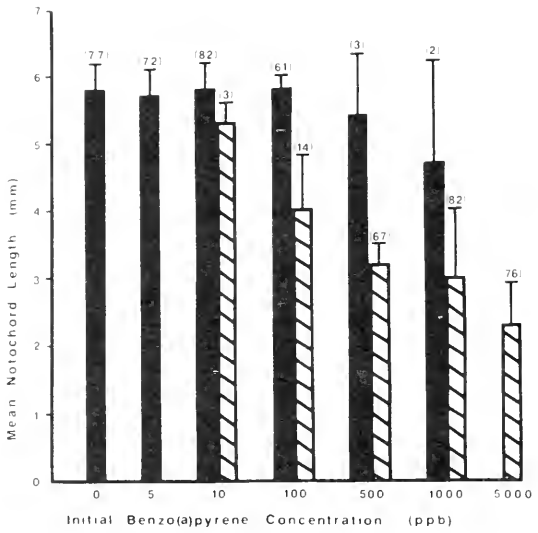


FIGURE 4.—Mean notochord length of California grunion embryos (slashed bars) and yolk-sac larvae (black bars) after 14-d incubation in seawater containing 0-5,000 ppb benzo(a)pyrene. Vertical lines = SD; numbers in parentheses = total no. embryos or larvae.

however, without continued addition of BaP; in fact, it decreased to about 1 ppb after several hours. Additional BaP dissolved in ethanol resulted in levels that decreased to near zero in 24 h. Struhsaker (1977) reported a similar difficulty in maintaining a stable concentration of benzene in seawater and attributed this to the volatility of benzene.

Because the uptake of polycyclic aromatic hydrocarbons occurs primarily via the aqueous BaP fraction, rather than by direct accumulation from surrounding sediment (Roesijadi et al. 1978), the exposure of grunion eggs to BaP in these experiments may simulate what occurs in the natural environment. For example, an oil spill may result in initially high concentrations of hydrocarbons, but photooxidation, adsorption into sediments and water-column particulates, and tidal action will decrease the concentrations of various oil constituents (such as BaP) over time. We have periodically monitored unfiltered waters of the Los Angeles Harbor for BaP concentration during the period 1977-81. Levels of BaP fluctuated from below the limit of detectability (<0.1 ppb) up to 5.4 ppb (Puffer et al. 1979). Niaussat and Auger (1970) have reported levels of 1.6 ppb BaP in seawater collected from a remote, isolated atoll in the eastern tropical Pacific Ocean. BaP levels in sand collected offshore of Cabrillo Beach in the Los Angeles Harbor ranged from 223 to 471 ppb (Duncan and Puffer 1982) and as high as 18,000 ppb in sediments from the inner Los Angeles Harbor (Gossett et al. 1983). Concentrations of BaP in sediments worldwide have ranged from nondetectable levels up to 15,000 ppb (Neff 1979). This suggests that embryos may be exposed to high levels of BaP in interstitial water during incubation in sand. As there were no prior studies regarding the effect of BaP on early grunion development, we utilized a wide range of BaP concentrations to achieve various tissue burdens. This not only reflects the broad range of exposure in nature, but also affords an opportunity to assess the sensitivity of eggs incubated under controlled conditions in seawater containing various concentrations of BaP and to correlate observed effects with known tissue BaP levels in embryos.

The extent of BaP uptake by California grunion embryos was directly proportional to initial and steady-state BaP concentration in seawater. By day 15, embryos accumulated BaP at levels 146-437 times the steady-state BaP concentration in seawater.

Comparative BaP bioaccumulation factors range from 5,142 to 21,000 for rainbow trout alevins and flatfish larvae, respectively (Hose et al. 1981; Hannah et al. 1982) and 861 for the clam *Macoma inquinata* (Roesijadi et al. 1978). While Hannah et al. (1982) noted an increase over time in BaP concentrations in embryonic rainbow trout, tissue BaP levels in California grunion remained essentially constant from day 3 to day 15. Eldridge et al. (1978) demonstrated that tissue levels of benzene in Pacific herring, *Clupea harengus pallasii*, reached equilibrium within 6-12 h at 11 times the initial water concentration. Steady-state tissue levels of BaP probably represent an equilibrium between pollutant absorption, embryonic metabolism, and excretion of the more hydrophilic metabolites (Binder and Stegeman 1980).

The observed alterations in development of California grunion exposed to BaP include 1) hatching, 2) abnormalities, and 3) reduction of notochord length. The earliest consequence of egg exposure to BaP was a reduction in hatching rate. Initial concentrations of BaP >24 ppb caused a significant mortality of yolk-sac larvae. These results are consistent with those reported by Ernst et al. (1977) who showed a 25/25 (100%) hatching rate of *Fundulus grandis* eggs exposed to 1.1 ppm water-soluble fraction of No. 2 fuel oil, a 4/25 (16%) hatching rate when exposed to 2.2 ppm, and 0/25 (0%) when exposed to 4.4 ppm. BaP has long been known to be embryo toxic in rodents (Rigdon and Rennels 1964) and more recently in sand sole, *Psettichthys melanostictus*, (Hose et al. 1982) and following maternal exposure in flathead sole, *Hippoglossoides elassodon*, (Hose et al. 1981). Furthermore, petroleum hydrocarbons, including

BaP, can alter the duration and time of teleost hatching (Ernst et al. 1977; Leung and Bulkley 1979; Hannah et al. 1982). Normally, hatching of California grunion eggs occurs in 10-14 d. Since most hatched eggs in this study did so on day 10 and no later than day 13, no effect was noted on duration and time of hatching of California grunion eggs. The dramatic and significant effect was on hatching rate.

The second effect noted was increased abnormalities of the developing yolk-sac larvae embryos. Of those yolk-sac larvae observed, 20% had a midbody lateral curvature when exposed to 24 ppb BaP or greater, as compared with 9% of the controls. Vascular abnormalities observed in embryos included stasis in yolk-sac vessels, apparent hemorrhages in the caudal regions, intermittant heart beat, and distinctly underdeveloped bodies with nonutilized yolk hydrocarbons (Ernst et al. 1977; Lonning 1977), particularly BaP (Hose et al. 1981, 1982; Hannah et al. 1982). Depressed heart rates of fish embryos treated with high levels of petroleum hydrocarbons have been attributed to inhibition of metabolism and/or neurotransmission (Whipple et al. 1981) and can result in partial or complete mortality (Anderson et al. 1977).

The third response observed in California grunion embryos exposed to BaP was reduction in notochord length. The notochord length of embryos exposed to 24 ppb BaP averaged 70% of that of controls. At 297 ppb BaP or greater, the notochord length of affected embryos was generally <50% of the notochord length of the control group. Retarded growth was also evident in rainbow trout alevins reared in 0.08-2.99 ppb BaP (Hannah et al. 1982) and may result from the inhibitory effects of polycyclic aromatic hydrocarbons on DNA synthesis (Santodonato et al. 1981) and, hence, mitosis (Bourne and Jones 1973; Kocan et al. 1981).

At the end of 14 d, embryos exposed to initial concentrations of 24-297 ppb BaP resembled normal embryos at 2.5-5.5 d of development. This retarded growth was characterized by a lack of lens formation, absence of caudal fin folds, and a reduced number of melanophores. However, there was one exception to this trend of slow development: The pectoral fins of embryos treated with 24-297 ppb BaP appeared to be of normal size and maturity, whereas all other aspects of embryo development seemed severely delayed. Irregular cleavage and retarded development in oil-treated fish embryos have been previously described (Lonning 1977), and assessment of the developmental effects of petroleum hydrocarbons on marine fish eggs has been reviewed by Kuhnhold (1977). These include sublethal effects such as chromosomal aberrations and morphological anomalies as well as direct toxicity (Rosenthal and Alderdice 1976). Toxic hydrocarbon levels reportedly correlated with mitotic errors in eggs of Atlantic mackerel, *Scomber scombrus*, (Longwell and Hughes 1980). Anderson et al. (1977) also noted lack of pigmentation in estuarine killifish, and a histological examination of *Fundulus grandis* embryos exposed to the water-soluble fraction of No. 2 fuel oil revealed pathological lens, liver, kidney, and epthelial tissues (Ernst et al. 1977).

In summary, the effects observed in California grunion embryos exposed to the carcinogen BaP were threefold: Decreased hatching rates, increased number of morphological abnormalities, and shortened notochord lengths. These grossly visible alterations would be detrimental to the potential growth and survival of fish in the wild (Rosenthal and Alderdice 1976). The number of fish reaching adulthood would decrease directly as a result of the lethal effects of BaP on embryos and indirectly as a result of decreased ability of affected fish to elude predators. Also, short-term observations such as these do not address the problem of carcinogenesis, although recent experiments have demonstrated that the polycyclic aromatic hydrocarbon, 7,12-dimethylbenz(a)anthracene, is tumorigenic in freshwater fish (Schultz and Schultz 1982).

It is predicted that BaP will increase in the environment unless restrictions can be imposed upon its production. However, reduced production of BaP is unlikely, as this compound is an unavoidable byproduct of incomplete combustion and petroleum usage (National Academy of Sciences 1972). Therefore, the results of our experiments indicate that the short- and long-term effects of BaP on the developmental stages of fish and other marine life warrant further investigation.

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SIMULATION OF THE NORTH ATLANTIC OCEAN DRIFT OF *ANGUILLA* LEPTOCEPHALI

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ABSTRACT

A numerical simulation model of surface current drift was developed in order to simulate the poorly understood drift migration of *Anguilla* leptocephali in the North Atlantic Ocean. The model was based upon the advection-diffusion equation, which was approximated by finite differences. Currents for the model were calculated from ships' drift data. Leptocephali were "started" at various points in the presumed American and European eel spawning areas, and the model produced spatiotemporal patterns of leptocephalus concentrations resulting from surface current drift and turbulent diffusion. In the American eel drift simulations the patterns followed a sequence of four phases: 1) Initial northwest drift on the presumed Antilles Current; 2) the formation of a "patch" of leptocephali offshore of Florida and the Gulf Stream; 3) dispersal along the North American coast resulting from the continued input of larvae into the Gulf Stream from the patch; and 4) transport eastward into the Atlantic on the Gulf Stream. In the European eel drift simulation, the leptocephali slowly spread throughout the Sargasso Sea region of the North Atlantic, and there was little Gulf Stream transport by the eighth month of drift. The patterns of distribution produced by the model correspond well with the limited collection data for both species, though it remains for future sampling efforts to verify whether the features present in the simulations actually occur.

Schmidt (1925) summarized over two decades of work to provide what has since become known as the "classical solution" to the Atlantic eel problem. Schmidt proposed that adult European eels, *Anguilla anguilla*, and American eels, *A. rostrata*, migrate in the fall from their freshwater habitats and travel to spawning areas in the Sargasso Sea. The adults spawn in the early months of the year and then die. The resulting larvae (termed leptocephali) are presumed to drift passively on surface currents toward their respective coasts. Schmidt stated that American eels, having a shorter distance to traverse, drift about a year as leptocephali before metamorphosing to the glass eel phase and commencing their migration toward freshwater. European eel leptocephali are presumed to take 3 yr to complete their journey. This scenario was challenged by Tucker (1959), who hypothesized that the two Atlantic anguillid eel species are in fact only one. Tucker proposed that all adult European eels die during their migration, that all anguillid leptocephali are the progeny of eels originating in North America, and that European eel stocks are replenished by leptocephali that simply drifted across the Atlantic after failing to land on the North American coast. Tucker felt that differences in the vertebral counts used to discriminate between the two species could be explained by a thermal shock suffered by developing embryos in part of the spawning area. Tucker's hypothesis has been largely discounted, and recent electrophoretic (Jamieson and Turner 1980; Comparini and Rodino 1980) and karyotypic (Passakas 1981) evidences indicate the existence of two anguillid eel species in the North Atlantic and associated freshwaters.

Nonetheless, there are persistent unanswered questions concerning the migrations of larval, juvenile, and adult eels (Vladykov 1964; McCleave and Harden-Jones 1979). One of these questions concerns the location and timing of American and European eel spawning. Schmidt (1925) identified the European eel spawning area as lying between lat. 22° to 30°N and long. 48° to 65°W, and stated that spawning "commences in late winter or early spring and lasts well on in summer." He based these limits on the distribution of the smallest leptocephali (<10 mm) he collected. To the present time no adult eel has been captured away from the continental shelves, and no identified anguillid eel eggs have been collected. Schmidt did not collect many small American eel leptocephali, and consequently his delineation of the American eel spawning area and time is much less precise. Recently there have been several systematic sampling efforts for small leptocephali with the ob-

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jective of defining the spawning areas of the European eel (Tesch et al. 1979; Schoth and Tesch 1981) and the American eel (McCleave and Kleckner[3]). Kleckner and McCleave[4] have obtained evidence that recently hatched American eel leptocephali are associated with a thermal front in the Sargasso Sea.

Also, little is known regarding the time course of the leptocephalus drift migration. Following Schmidt's (1925) summary, several authors have compiled information on the spatiotemporal distribution of anguillid leptocephali, including Smith (1968), Vladykov and March (1975), Tesch (1980), and Kleckner and McCleave (1980). These studies only provide a broad outline of the course of the leptocephalus drift migration, as the number of identified leptocephali collected is still small, considering the scale of the migration in terms of distance and probable numbers. The available data are difficult to interpret and may better represent the distribution of sampling effort than the distribution of leptocephali (Kleckner and McCleave 1980). Unless sampling at a particular location was done systematically, the absence of leptocephali from collections can only be interpreted as negative evidence concerning the presence of leptocephali at that location. It is still not known how leptocephali are transported in the Florida Current-Gulf Stream system. How do American eel leptocephali cross the Gulf Stream to approach the North American coast, and why are substantial numbers of these leptocephali not transported across the Atlantic to populate Europe? Are any behavioral components necessary in the leptocephalus drift migration? In summary, where and when are leptocephali most likely to be found, and what implications does this distribution have for the eel's life history and migration patterns?

To answer some of these questions a simulation model of leptocephali drift in the North Atlantic surface currents was developed. The intent was to implement the simulation so that leptocephali started at points in the presumed Sargasso Sea spawning area would be transported in a way realistically approximating actual surface current transport. The objectives of the research were to generate patterns of distribution representing the likely time course of a passive drift migration and to compare and interpret these distributional patterns with information about the actual leptocephalus distribution and the eel's life history. In this way the model serves an explanatory role, highlighting the factors important in generating a distribution of leptocephali, and also provides a framework for future research on the leptocephalus drift migration. Distributional patterns that developed during some of the simulations are presented here, with emphasis on the American eel; limited results for the European eel are also given.

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MATERIALS AND METHODS

Anguilla leptocephali are found in the top few hundred meters of the water column (Kleckner and McCleave 1980; Schoth and Tesch 1981), and therefore the model was developed with only two horizontal spatial dimensions. The model was based upon the time-dependent, two dimensional form of the advection-diffusion equation:

$$\frac{\partial P}{\partial t} + \frac{\partial}{\partial x}\left(uP - K_x \frac{\partial P}{\partial x}\right) + \frac{\partial}{\partial y}\left(vP - K_y \frac{\partial P}{\partial y}\right) = 0$$

where P = concentration of leptocephali;
u and v = velocities in the respective x and y directions; and
K_x and K_y = diffusivity coefficients for the respective directions.

Leptocephali were not assumed to have any directed swimming capability, so the velocities in the above equation represent simple water current velocities. The diffusivity coefficients express the dispersion of leptocephali by turbulence, eddies, and other phenomena not expressed by the advective terms (Okubo 1980).

The derivatives in the above continuous equation were approximated by finite differences. For example, to approximate the time derivative the following relation was used:

$$\frac{\partial P}{\partial t} \cong \frac{P^{t+1} - P^t}{\Delta t}$$

where P^t = concentration of leptocephali at the present time t;
P^{t+1} = concentration of leptocephali at time $t + \Delta t$; and
Δt = duration of the time step.

The derivatives with respect to the x and y directions were approximated by weighted finite differences. The method developed by Fiadeiro and Veronis

(1977) was followed for determining the weighting so as to provide increased numerical stability and to approximate more closely the solution to the continuous equation. Further details on the numerical methods used were presented elsewhere (Power 1982).

In approximating the advection-diffusion equation by finite differences, the region under study is partitioned by a grid, and a difference equation is derived for each cell formed by the grid. The difference equations express the concentration of the substance at the center of each cell formed by the grid in terms of fluxes between adjoining cells. The end result is a large system of simultaneous (difference) equations, which can be repeatedly solved to obtain the cell concentrations at successive time steps. The region included in this study was the Gulf of Mexico, Caribbean Sea, and the North Atlantic Ocean between lat. 10° and 50°N and west of long. 40°W (Fig. 1). Coastlines were approximated by cell boundaries, as were the Caribbean islands and shoal waters of the Bahamas. Flux of leptocephali across these boundaries was prohibited. Leptocephali approaching the Bay of Fundy, Gulf of St. Lawrence, and the long. 40°W boundary of the model were permitted to be transported out of the modeled area (dashed lines in Figures 2-9).

Currents for the model were calculated using ships' drift data obtained from the National Oceanographic Data Center (Fig. 2). A ship's drift observation is the inferred surface current calculated by comparing the ship's true position after a given period of steaming with the navigator's dead reckoning position. Surface current charts of the North Atlantic are derived from the same data base used in this study. Each ship's drift observation was resolved into an east and north component, and the current component at the interface between two cells was calculated as the mean of all the appropriate current components recorded in the 1° of latitude and longitude bisected by the cell interface. The means were calculated by calendar months, so for each month in the simulations a different current regime was used. Using June as a representative month, the median number of observations used to calculate a current component was 10, and 75% of the components were calculated using five or more observations. The number of observations was greatest within 5° of the North American coast, with sample sizes >100 commonly occurring. Sample sizes were poorest in the southeast portion of the modeled area. An average of 3% of the cell interfaces had no associated ships' drift observations. These points where data were completely missing were

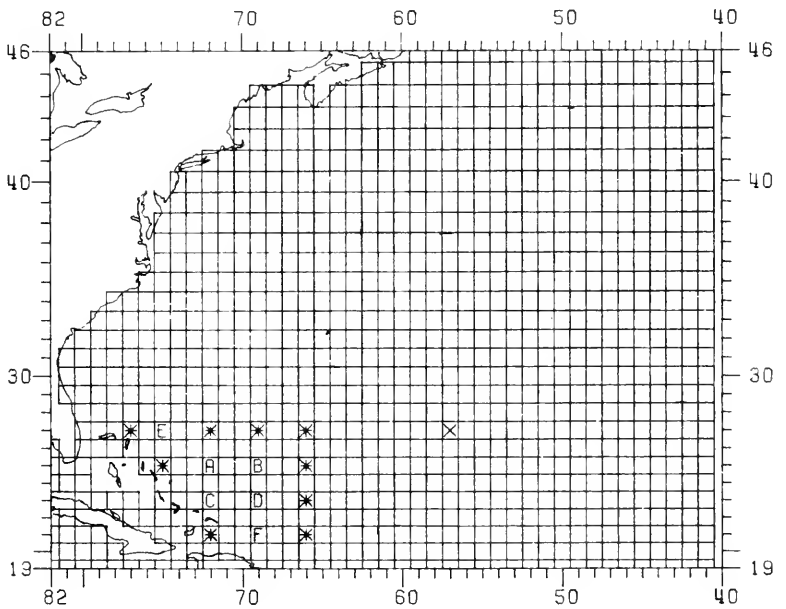

FIGURE 1.—Main portion of the geographic region included in the simulations, along with the 1° by 1° grid and coastline approximation. Lettered cells are the starting points for American eel leptocephalus drift simulations discussed in the text, and cells with stars are the starting points in other simulations not presented here. Note for comparative purposes that points A and C and points B, D, and F are the same meridians, while points A and B and points C and D share the same latitudes. Cell with an × is the starting point for the European eel drift simulation.

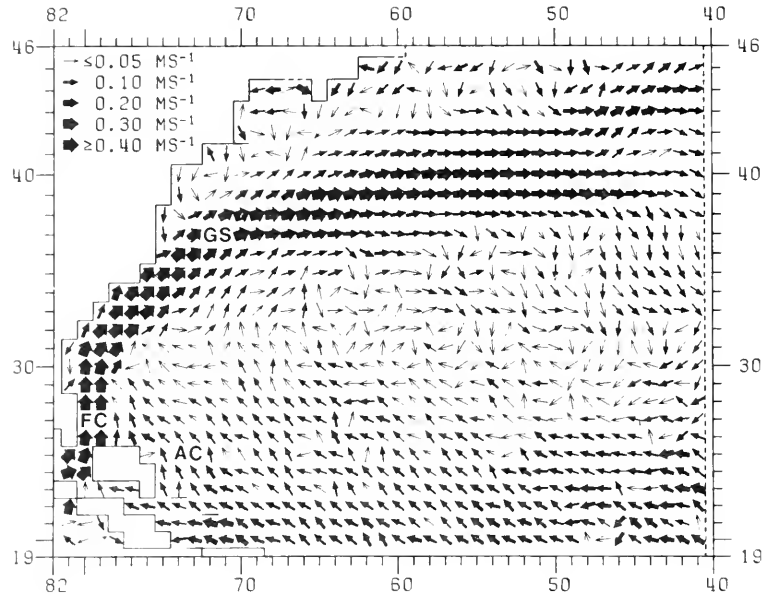

FIGURE 2.—Surface current vectors used in the simulations for the month of May. Vector in a cell was computed by taking the mean of the current components at the cell's edges and calculating the resultant vector. Key depicts representative current speeds. AC = Antilles Current; FC = Florida Current; GS = Gulf Stream.

irregularly spaced throughout the modeled area, so their components were calculated by interpolating between adjoining cells and months. Current velocities were necessarily taken as representative of the currents that occur throughout the depth range of *Anguilla* leptocephali. The leptocephali were assumed to maintain themselves continually in surface waters, so the finite differences were derived with no assumptions regarding fluid continuity. The effect of this is that leptocephali are concentrated in regions of net water convergence (downwelling) and dispersed from regions of divergence (upwelling).

The diffusivity coefficient (K) was calculated as a function of grid spacing. Data from numerous dye diffusion experiments reviewed by Okubo (1971) were used in a least squares regression analysis to compute the equation $K = (3 \times 10^{-4}) h^{1.1}$ relating the diffusivity parameter (in m^2/s) to the length scale (grid spacing) h in meters. No spatial variation in diffusivity, other than that due to meridional grid narrowing in more northerly latitudes, was assumed. Diffusivities used ranged from 68 to 110 m^2/s.

In carrying out the simulations, American eel leptocephali were considered to be "spawned" as point sources at the various locations designated by letters or stars in Figure 1. These starting locations cover most of the presumed geographic range of American eel spawning (Kleckner and McCleave 1980; Kleckner[5]). Locations designated by letters are in the area which, on the basis of collections of very small leptocephali, represent the principal spawning area. The distributional patterns of leptocephali started at these lettered locations are discussed in detail in this paper, and the various simulation runs are referred to by these letters. The date 1 March is representative of the peak American eel spawning period (Kleckner and McCleave 1980; Kleckner footnote 5). That point in time was used as the starting date for the American eel drift simulations, with no additional input of leptocephali after that date. The center of the estimated European eel spawning area (Schmidt 1925; Schoth and Tesch 1981) is marked in Figure 1 with an × at lat. 27°N, long. 57°W. The results of one simulation, in which leptocephali were started on 15 April at this point, are presented. The length of the time step in the simulations varied by month, but was always between 1.5 and 2.0 d. The simulation results are presented initially on a monthly basis and then later on a bimonthly basis.

There is little information regarding actual concentrations of leptocephali in the ocean. As the simulations progressed, individual cell concentrations were expressed as proportions of the start-

[5]R. C. Kleckner, Research Associate in Zoology, Department of Zoology, Murray Hall, University of Maine at Orono, Orono, ME 04469, pers. commun. July 1981.

ing concentration. No mortality of leptocephali was incorporated into the model, and the total number of leptocephali was conserved throughout the simulation except for the portion transported across the open boundaries discussed previously. A unitless number is given when referring to a concentration, so that reference to a concentration of 10^{-3} refers to a concentration of leptocephali that is three orders of magnitude below the starting concentration. The concentration contours presented in Figures 3-9 were determined by linearly interpolating between the concentrations at the centers of the cells. Each contour represents an order of magnitude change in concentration relative to neighboring contours. Only leptocephalus concentrations $>10^{-7}$ (proportion of the starting concentration) are shown. In Figures 3-9 the leptocephalus starting location is marked by a star.

The choice of contour intervals as orders of magnitude was arbitrary; in some cases, the display masked the spatial structure of the distributions. This can occur where the order of magnitude contours are widely spaced, and a discontinuity in the concentrations is between the contours. For this reason an agglomerative cluster analysis using a spatial autocorrelation coefficient, Moran's I (Cliff and Ord 1973), as the metric was carried out with cell concentrations as the variable. The weighting coefficient was the reciprocal of the distance between cells, and only immediately adjacent cells were linked (rook's moves). Examination of the equation for Moran's I indicates that when choosing among several coefficient values, the minimum I represents the most spatially uniform distribution. The clustering proceeded iteratively by examining all possible pairwise linkages of clusters of cells, and forming a new cluster from the pair that yielded the minimum value of I for the new cluster. Thus at any stage the clusters partition the distribution into "patches," i.e., regions in which the cells are most spatially uniform in concentration. The cell concentrations were logarithmically transformed for the analysis to minimize the effects of outliers on I. The results of these analyses are not explicitly presented, but are referred to when necessary to facilitate the interpretation of the contour plots.

RESULTS

Distribution of Leptocephali After 30 Days of Drift

The proximity of the starting point to the Gulf Stream, the Antilles Current northeast of the Bahamas, and the Bahamas themselves all influenced the distributional patterns of American eel leptocephali that developed 1 mo after the 1 March starting date (Fig. 3). Capture of leptocephali by the Gulf Stream was already evident, and larvae started east and northeast of the Bahamas showed northwesterly drift on the Antilles Current.

Leptocephali begun at F mostly moved away from that location during the first month (Fig. 3F). The larvae were somewhat dispersed even at this early date, as cluster analysis indicated a large patch east of the Bahamas between lat. 21° and 26°N. Concentrations declined sharply to the east and south, as they did in all runs, indicating little transport in those directions. To the west, leptocephali were split by the Bahamas, approaching the Gulf Stream by both the route north of the islands and through the channel between the Bahamas and Cuba. Some passed completely through this channel to be caught in the Florida Current and carried northward, so that the 10^{-7} contour extended to lat. 32°N.

There was gradual northwesterly dispersal of leptocephali started at more northerly (Fig. 3B, D) and northwesterly (Fig. 3A, C) locations than those at F. The larvae in these runs are more concentrated, with most remaining near the starting points. In runs A-D larvae are impinging upon the Bahamas, and in C the concentrations offshore of the Bahamas are particularly high. This is due to the clearly evident Antilles Current transport in run C, and this current also facilitated the entry of run C larvae into the Gulf Stream. Runs A and E also show Gulf Stream transport, but this is more by virtue of their starting point's proximity to the Gulf Stream. Gulf Stream transport is pronounced in E, with the 10^{-7} contour reaching north to lat. 39°N and east to long. 65°W.

Distribution of Leptocephali After 60 Days of Drift

By 30 April, 2 mo after the 1 March start, leptocephali had spread and most moved northwest of their starting locations (Fig. 4). There were now broader areas of more moderate concentration, typified by the area enclosed by the 10^{-2} contour east of the Bahamas. Gulf Stream transport was now evident in all runs A through F.

Run F is notable for the substantial distance traversed by the larvae, considering the position of point F (Fig. 4F). This was primarily caused by continued transport between the Bahamas and Cuba, entry into the Florida Current, and then rapid Gulf Stream transport. Antilles Current transport also contributed. Concentrations in run F fell into three

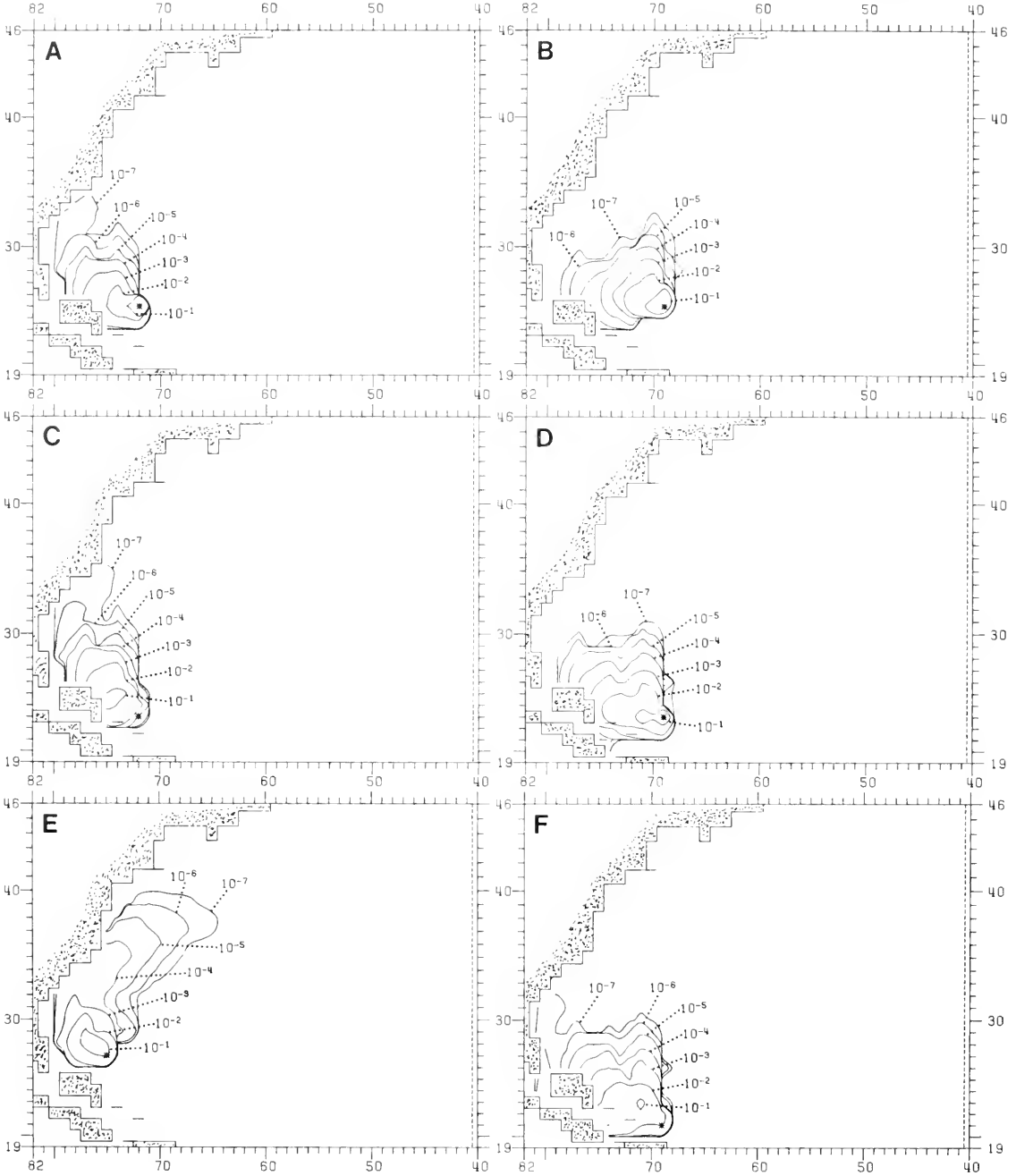

FIGURE 3.—Concentration contours of American eel leptocephali, expressed as a proportion of the starting concentration, for 30 March. Each lettered plot corresponds to the same lettered starting location in Figure 1. In this and subsequent figures stars mark the starting points. 30 March is 1 mo after the 1 March starting date.

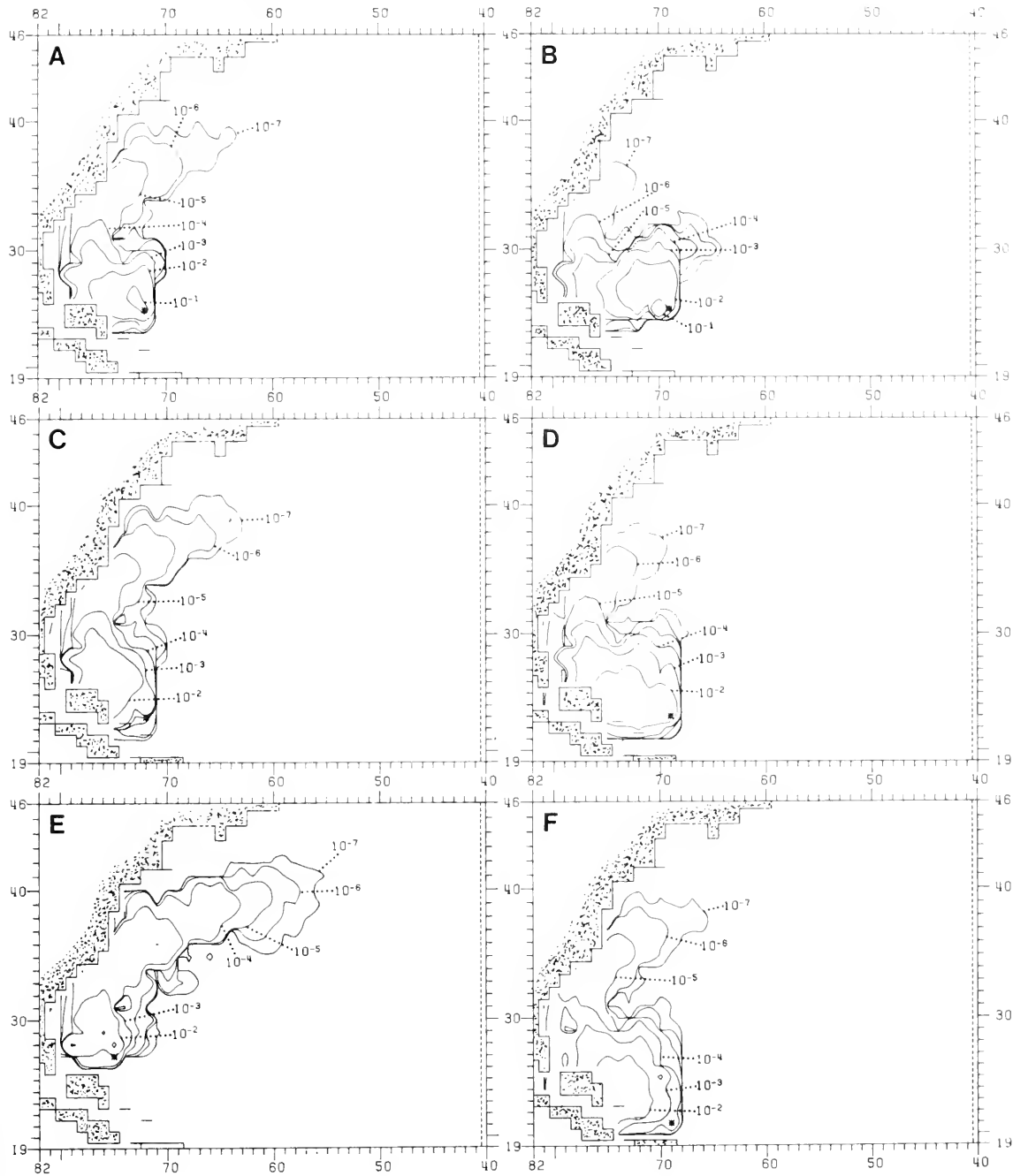

FIGURE 4.—Concentration contours after 60 d of American eel leptocephalus drift. Corresponding date is 30 April.

groupings: 1) High concentrations east of the Bahamas containing most leptocephali, 2) lower concentrations flanking this patch, and 3) Gulf Stream larvae.

Leptocephali started north and northwest of F (runs A through D) showed more uniform distributions than the previous month, although the sharp eastern and southern gradients were maintained. There was transport between the Bahamas and Cuba only in run D, and leptocephali in run B showed lesser dispersal when compared with other runs. Run C again showed most clearly the effects of Antilles Current transport, while run A showed a similar but less developed pattern. Leptocephali in runs A and C reached lat. 39°N and long. 65°W at concentrations $>10^{-7}$.

Run E continued to show the most widespread distribution, and while offshore of Florida there were still concentrations $>10^{-2}$, the 10^{-3} contour enclosed a considerable area offshore of the mid-Atlantic coast.

Distribution of Leptocephali After 90 Days of Drift

Runs A, C, D, and F became similar by the third month of drift (Fig. 5; 30 May). The cluster analyses for these simulations at day 90 are of interest, because in each a distinct geographic grouping of cells emerged consistently. These clusters did not combine with others until forced to do so at the final stages of clustering. This indicated that the cell groupings represented by the clusters had spatial distributions of leptocephali (as measured by Moran's I) which were internally more uniform than if cells external to the groupings had been included during clustering. This characterized (independently of concentration contour plots) an inportant feature in the spatial structure of the leptocephali at day 90. The clusters of cells in runs A, C, D, and F formed patches east of Florida and the Gulf Stream, north to northwest of the Bahamas, and northwest of the starting points (roughly between lat. 24° to 28°N and long. 71° to 77°W). These patches had mean cell concentrations of 0.015 to 0.025, and patch limits were approximated by the 10^{-2} contours (Fig. 5). The bulk of the starting concentrations was contained within these patches.

Another feature common to the A, D, and F runs was the large area of concentrations between 10^{-3} and 10^{-4} that paralleled the mid-Atlantic coast and then extended offshore at about lat. 38°N. Run C had an identical pattern, except that its concentrations in this area were an order of magnitude higher. This difference can be attributed to starting point C's location and the enhanced Antilles Current-Gulf Stream transport mentioned earlier.

Run B's pattern was similar to that of runs A, C, D, and F, but was not as fully developed. This is because run B leptocephali were started farther into the Sargasso Sea, where currents are weaker. The main patch of concentration was present, but it covered a broader area and had a slightly lower mean concentration of 0.01. The 10^{-5} contour along the North American coast in run B took the place of the 10^{-4} contour in runs A, D, and F. In B there were still high concentrations near the starting point.

Run E continued to exhibit the most extensive pattern of leptocephalus distribution (Fig. 5E). There was a patch offshore of Florida and the Gulf Stream with a mean cell concentration of 0.012, but it was smaller and farther north than the corresponding patch in other runs. More than half of the starting concentration lay north of lat. 31°N and within the 10^{-3} contour. Concentrations $>10^{-2}$ were well north of lat. 32°N in run E.

Distribution of Leptocephali After 150 Days of Drift

The patterns of distribution below lat 32°N persisted during the next several months in the simulations, while to the north there was an increase in the concentrations and continued Gulf Stream transport. The main patches of concentration offshore of the Gulf Stream and Florida remained in runs A, C, D, and F after 5 mo of drift (Fig. 6; 29 July). The patches moved slightly to the northwest, and lay between lat. 25° to 30°N and long. 70° to 78°W. This region still contained more than half of the total starting concentration in runs A, C, D, and F, and the mean cell concentration in this area was about 0.005.

The broad bands of concentration along the mid-Atlantic coast also persisted and increased in concentration to between 10^{-3} and 10^{-2}. This was a consequence of the patches offshore of Florida just mentioned. It appears the patches slowly introduced larvae into the Gulf Stream system. The subsequent transport in the Gulf Stream quickly spread larvae parallel to the coast, then offshore and out into the Atlantic. The patches in simulations A, C, D, and F formed in the same general location, so that for larvae carried north of lat. 30°N the starting location had a lesser effect on the distribution. This is illustrated by the fact that the 10^{-3} contours are virtually identical in position north of lat. 30°N in runs A, D, and F at 5 mo after starting. Run C formed the patch earlier, so more larvae had entered the Gulf Stream and were therefore more widely dispersed. Leptocephali at

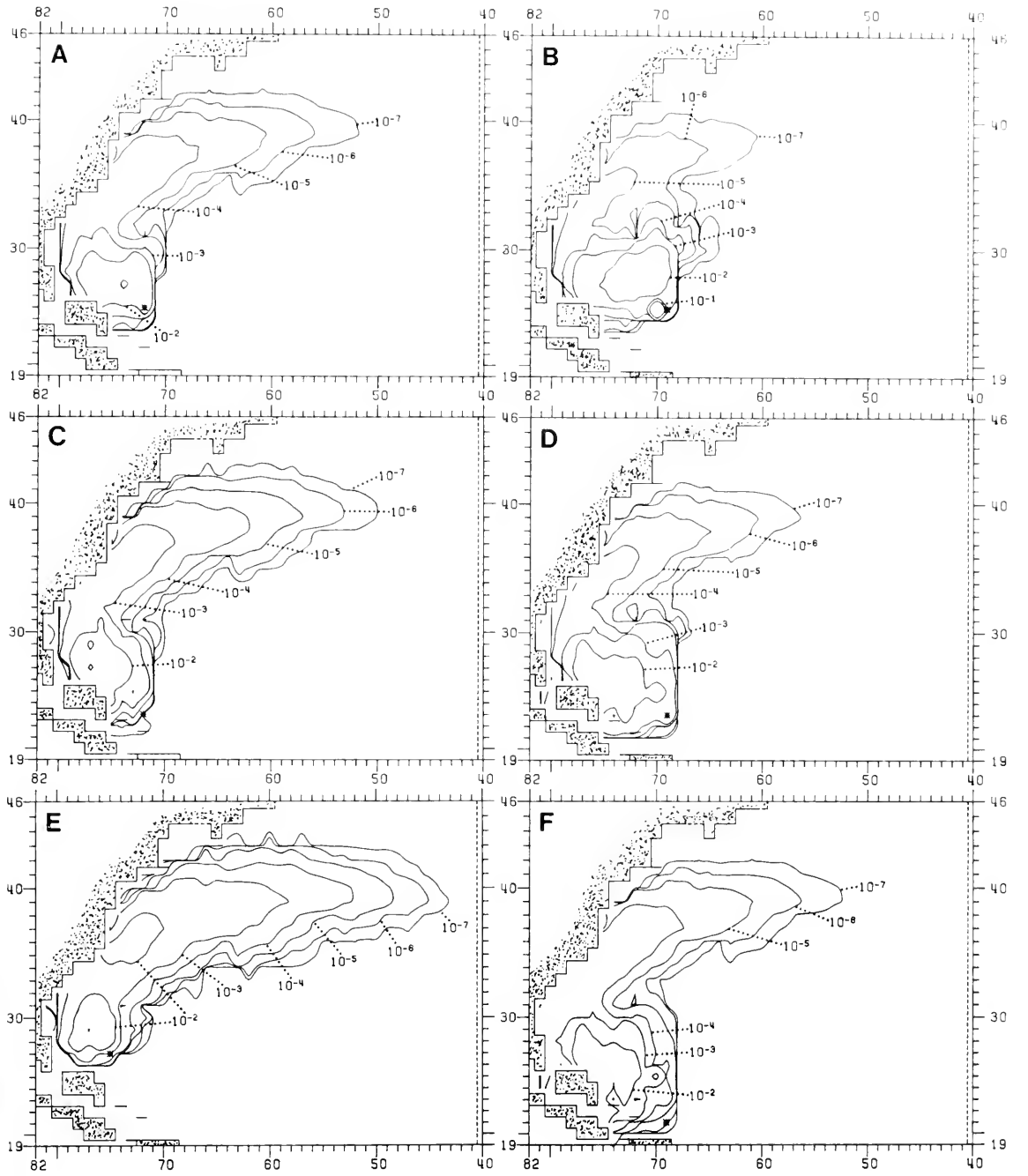

FIGURE 5.—Concentration contours of American eel leptocephali after 90 d of drift (30 May).

concentrations $>10^{-7}$ were now being advected past the long. 40°W border of the modeled area.

Run B's pattern at 5 mo was similar to those just discussed, but the main concentration of leptocephali was farther offshore of Florida and more broadly distributed (Fig. 6B) because the larvae were started in a region of weaker currents. There was a greater degree of northward transport from the main concentration, so that leptocephali joined the Gulf Stream at higher latitudes than in other runs.

The very large area enclosed by the 10^{-3} contour was the striking aspect of the pattern for run E at 5 mo (Fig. 6E). Cells in this area had a mean concentration of 0.002 and contained in total a concentration of 0.9. This region formed an exaggerated example of the results of prolonged leptocephalus entry into the Gulf Stream. In this case, the observed distribution is because larvae began close to the Gulf Stream, in the region where the main patch of concentration formed in other runs.

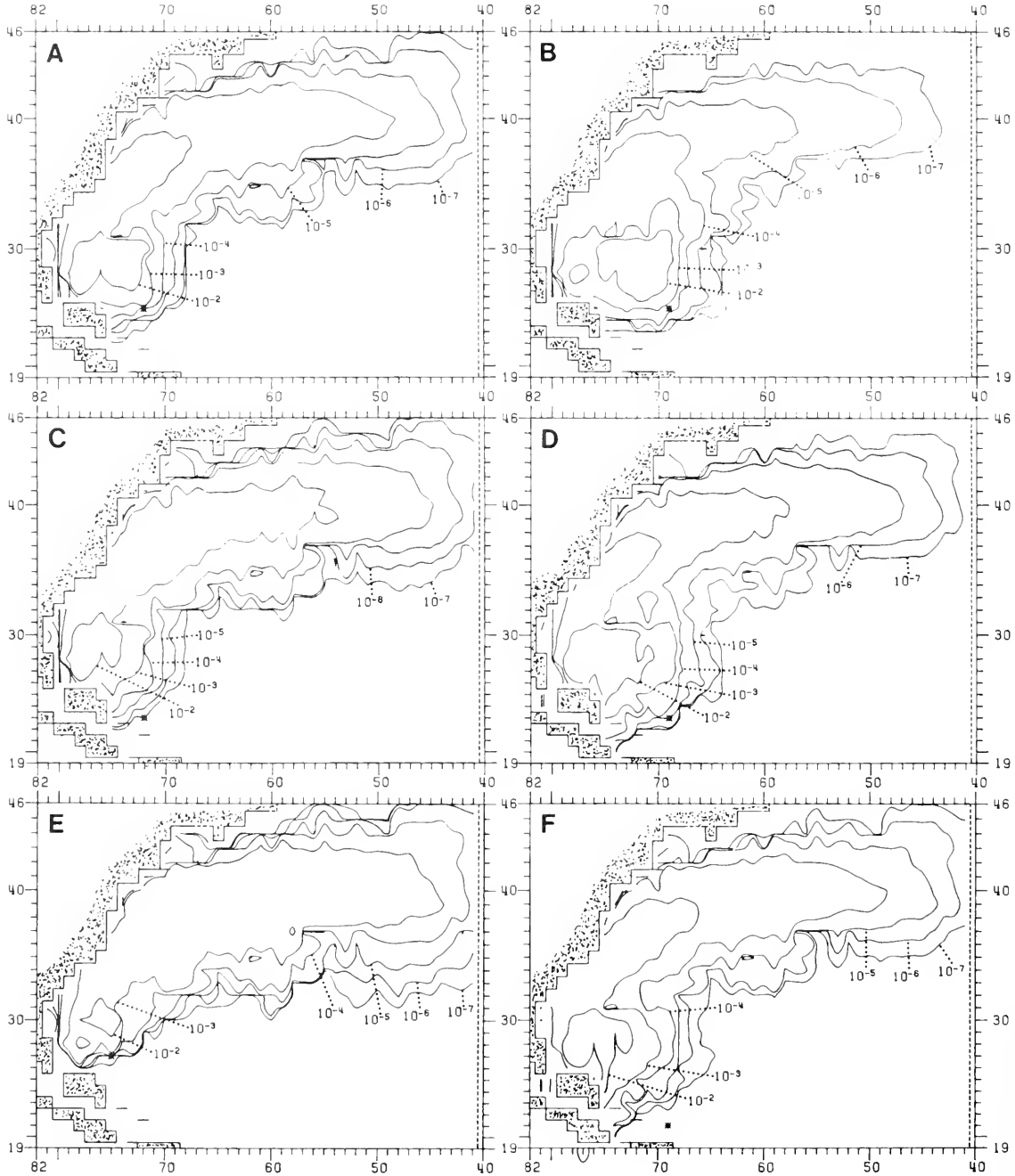

FIGURE 6.—Concentration contours of American eel leptocephali after 150 d of drift (29 July).

Distribution of Leptocephali After 210 Days of Drift

The patches of higher concentration persisted offshore of Florida and the Gulf Stream in all runs during the remainder of the summer (except E) and up to 7 mo after drift began, although they were beginning to dissipate (Fig. 7; 27 September). The cluster analyses still discriminated unequivocally between the patches and the lower concentrations to

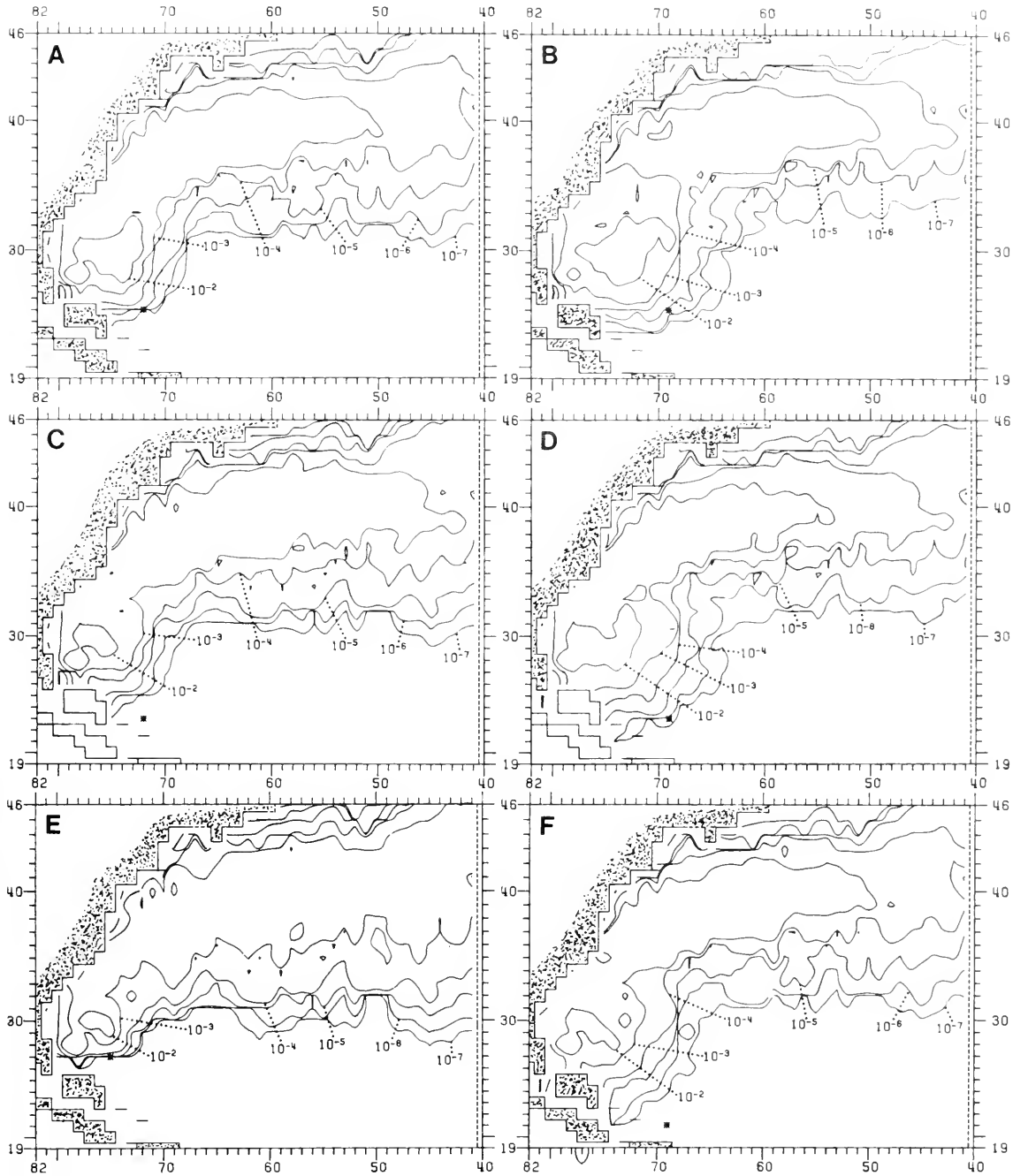

FIGURE 7.—Concentration contours of American eel leptocephali after 210 d of drift (27 September).

the immediate north in runs A and B and, to a lesser extent, in runs C, D, and F.

North of the patches the broad areas of uniform concentration were maintained and expanded by the continued entry of leptocephali into the Gulf Stream. This region extended along the North American coast to lat. 38°N, at which point it curved out into the Atlantic. It was best represented by the 10^{-3} contours in runs A, C, D, and F. The pattern was similar for run B, but the radial expansion of the main patch

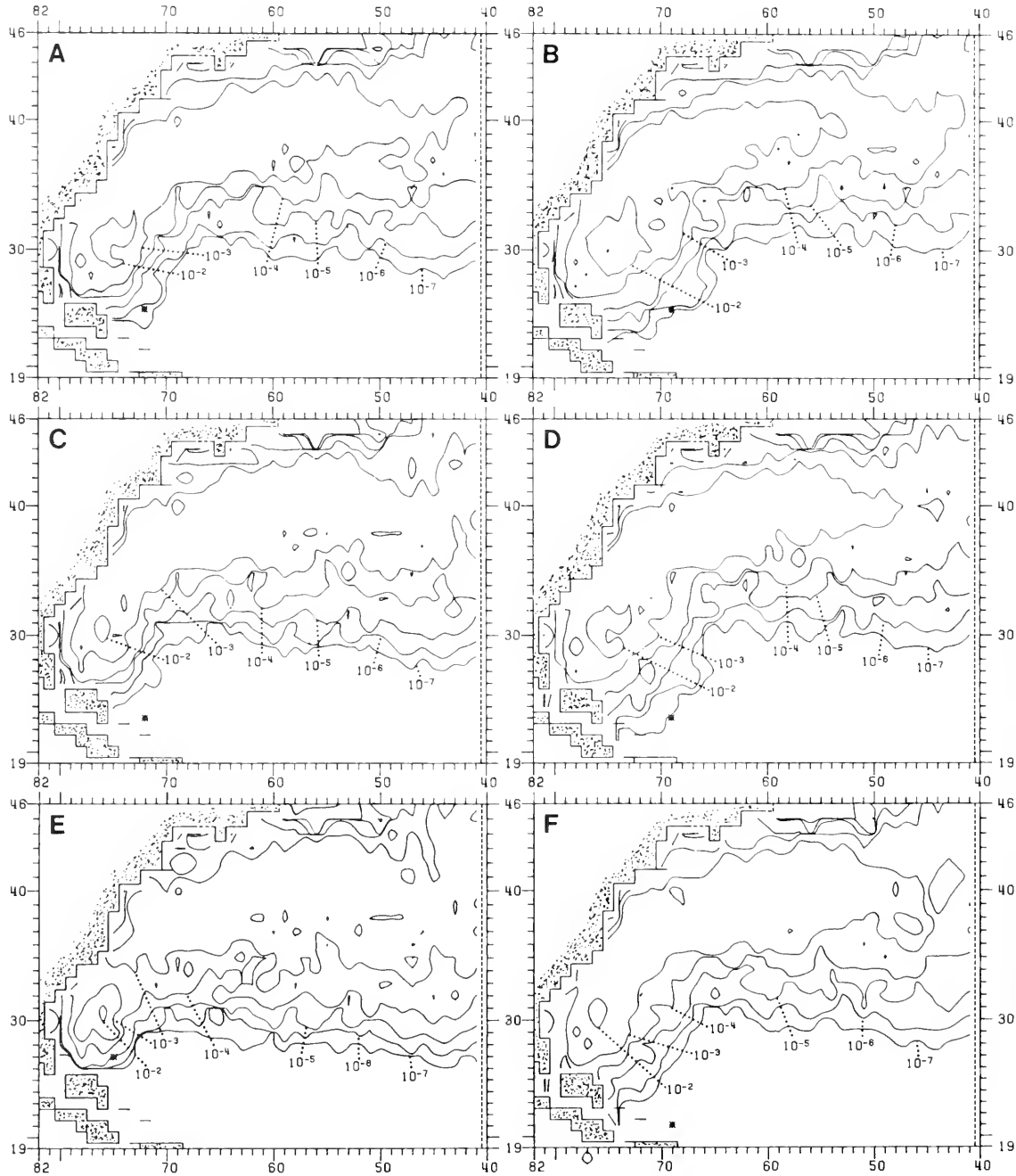

FIGURE 8.—Concentration contours of American eel leptocephali after 270 d of drift (26 November).

had continued. In most runs the plumes of leptocephali in the Gulf Stream had widened, so that concentrations $>10^{-7}$ were present across the modeled area between lat. 31° and 46°N. In run E the 10^{-3} concentrations extended completely from the patch area offshore of Florida to the right border of the modeled area.

Distribution of Leptocephali After 270 Days of Drift

Nine months after starting the leptocephali in runs A, C, D, and F had been distributed completely along the course of the Gulf Stream (Fig. 8; 26 November). There were very large areas with concentrations between 10^{-3} and 10^{-2} that spanned the modeled area from offshore of Florida to near the eastern border at long. 40°W. Run B still appeared to be in the process of developing the same distributional pattern as the others, because its pattern resembled those of the others 2 mo earlier. Leptocephali had progressed farthest in run E, in which the 10^{-3} concentrations were moving away from the mid-Atlantic coast.

At day 270 the simulations were halted, as some leptocephali would have begun metamorphosis to the glass eel phase by late November (Kleckner and McCleave 1980). It is unknown what behavioral components a glass eel or large leptocephalus may contribute during oceanic transport.

European Eel Drift Simulation

A simulation of European eel leptocephalus drift was done with the starting point at lat. 27°N and long. 57°W, and the starting date as 15 April. After 45 d of drift the larvae had spread to the northwest (Fig. 9A;

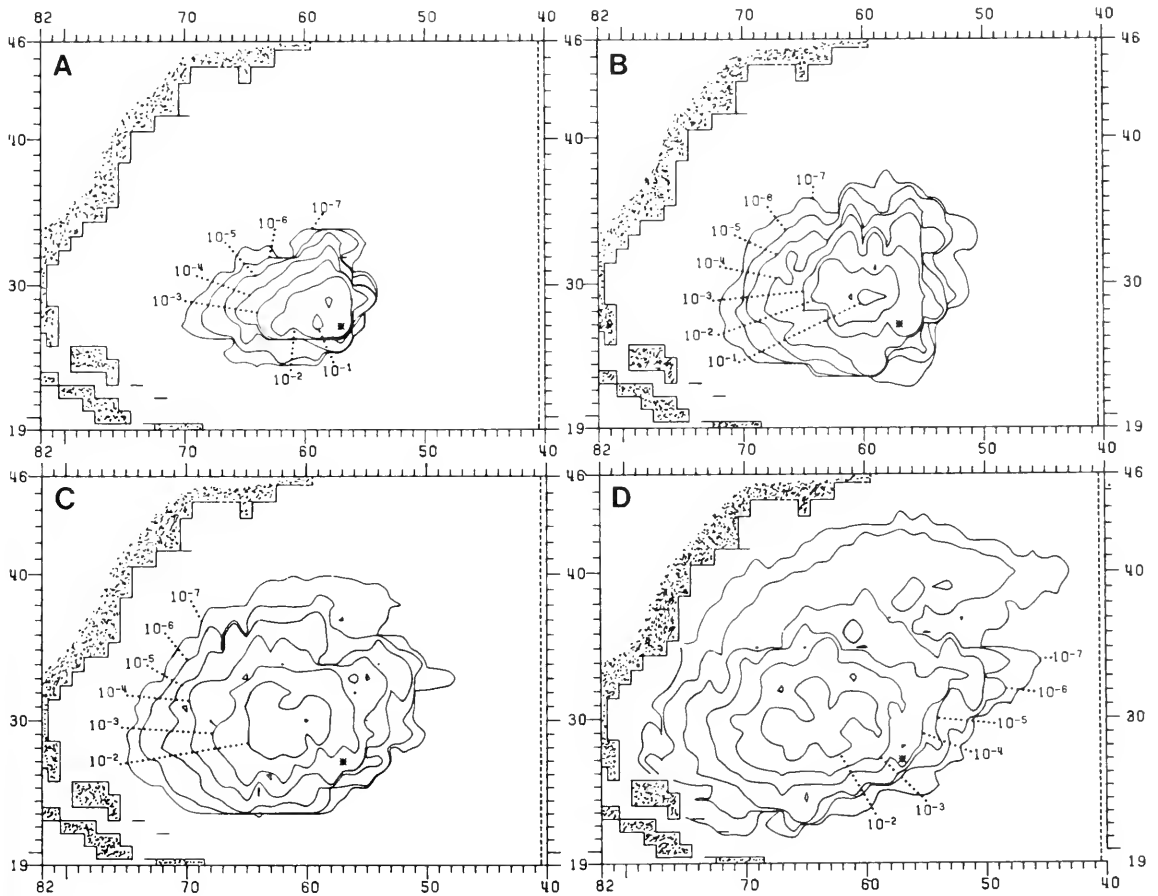

FIGURE 9.—Concentration contours of European eel leptocephali, expressed as a proportion of the starting concentration. Leptocephali were begun at the point marked with an × in Figure 1. A: contours for 30 May, 45 d after the 15 April start. B: contours for 29 July, 105 d after starting. C: contours for 27 September, 165 d after starting. D: contours for 26 November, 215 d after starting.

30 May). Two months later the 10^{-2} enclosed about the same area as before, but it had moved a few degrees to the northwest of the starting location (Fig. 9B; 29 July). The lower concentrations continued to spread, and dispersal occurred in most compass directions. By day 165, the lower concentrations had expanded still further, although concentrations $>10^{-2}$ maintained approximately the same position (Fig. 9C; 27 September). This same pattern of dispersal continued to day 215 of drift, at which point the concentrations $<10^{-5}$ at the northern limits of the distribution showed signs of being captured by the Gulf Stream (Fig. 9D; 26 November). The simulation was halted at day 215.

DISCUSSION

The simulations revealed several previously unsuspected features of the leptocephalus drift migration, such as the patch formation offshore of Florida and the Gulf Stream. This is in spite of the simplifications and assumptions that were made in a model encompassing such a large geographic area. The boundaries, currents, and eddy diffusivities all provided only an approximation to the physical system. Nonetheless, interpreting the simulation output using the available information on leptocephalus distribution and the eel's life history indicates that the model has realistically reproduced the large-scale features of the drift migration.

The simulated drift of American eel leptocephali can be divided into four phases, the first being initial northwest transport following spawning. This transport was largely on the Antilles Current, which flows northwesterly on a course parallel to the northeastern border of the Bahama Islands chain (Fig. 2). The extent of the initial larval transport depended on the starting location's position with respect to this current. Larvae started farther northeast in the Sargasso Sea (point B and other simulations not shown here) showed less unidirectional movement than those started in or nearer the Antilles Current. This current clearly appeared in ships' drift data for May (Fig. 2) and other late winter and spring months, so its effects in the simulations were no surprise. However, there are questions concerning the existence of the Antilles Current (Ingham 1975; Gunn and Watts 1982). Gunn and Watts (1982) showed that the Antilles Current was present in January-February 1973, but that the region was dominated by eddies in July-August 1972. They speculated that the Antilles Current may only exist seasonally. Its presence in January-February 1973 must have dominated the drift of newly hatched leptocephali from early spawning in that year. If the Antilles Current is seasonal, the question important to eel biology is how long does it persist through the spring and summer? The Antilles Current was important in the simulations from the time of spawning up to May-June. After that its influence on the distribution of 0-group leptocephali diminished, and by July-August, when Gunn and Watts (1982) did not find the current, most of the larvae were north of lat. 25°N. A study like that of Gunn and Watts is clearly needed for the months between February and July, and particularly for April and May.

There was little eastward transport from the starting locations in all American eel simulations, including those in which larvae were started along long. 66°W (not pictured in this paper). Schoth and Tesch (1981) collected American eel leptocephali east of long. 69°W (the longitude of the easternmost starting points in the simulations presented here), although the numbers of larvae they caught declined rapidly east of long. 65°W. Transport to the south was also minimal in the simulations, and few leptocephali entered the Caribbean. The simulations do not adequately explain the presence of leptocephali that have been collected in the Caribbean and Gulf of Mexico, and in particular the presence of young leptocephali near the Yucatan peninsula (Kleckner and McCleave 1980) was not reproduced. American eel spawning in the Caribbean remains a viable explanation for these collections.

The simulated drift of leptocephali south and west of the Bahamas must be interpreted cautiously, because this region's complicated bathymetry and currents were not well represented in the model. However, there were some striking correspondences between the simulations and the actual collection data for this region. Smith (1968) reported 10 May as the earliest collection date for 0-group leptocephali in the Straits of Florida between the Bahamas and Florida; Figure 3F shows larval concentrations of 10^{-6} (proportion of the starting concentration) had arrived in the Straits of Florida around 30 March, and by 30 April the concentration had increased to 10^{-4} (Fig. 4F). Kleckner and McCleave (1980) reported the collection of 0-group leptocephali in the Bahama Island chain in April to June, and the first collections of larvae in the Straits of Florida in May. Smith (1968) gave 28 August as the latest collection date of 0-group larvae in the Straits of Florida, and by that date most of the leptocephali in the simulations had departed the area as well.

The formation and maintenance of a patch of leptocephali north of the Bahamas and east of Florida and the Florida Current-Gulf Stream system were the

second phase in the simulated drift migrations. Regardless of starting location, most larvae converged upon the area and became part of this patch, except those that entered the Florida Current by the route south of the Bahamas. Gunn and Watts (1982) found evidence in the January-February 1973 data of a large anticyclonic eddy in the region of this patch formation (cf their figure 3D). If this eddy is a permanent or seasonal feature, it has substantial implications for American eel leptocephalus drift. It could be reasonably assumed that leptocephali collect in the eddy each year and that this patch phase is an integral part in the transport of most American eel leptocephali.

Transport of larvae from the patch and into the Gulf Stream seems to have been a result of turbulent diffusion, rather than advection, since currents east of the Florida Current are weak (Fig. 2). In the model, entry into the Gulf Stream was an example of large-scale shear induced diffusion, where large differences in adjoining northward current velocities resulted in concentration gradients down which a diffusive flux occurred. Whether this is the phenomenon that facilitates actual entrainment of leptocephali into the Gulf Stream is problematic. Alternatively, Gulf Stream cold-core rings occur in this area (The Ring Group 1981), and it may be that Gulf Stream eddies and meanders act to capture larvae.

The leptocephalus collection data are still inadequate to confirm the presence of a leptocephalus patch offshore of Florida and the Gulf Stream. However, there is empirical evidence that this is indeed the region where most leptocephali enter the Gulf Stream system. Kleckner and McCleave (1982) studied near synoptic collections of leptocephali taken on four transects of the Florida Current and Gulf Stream between 26 July and 16 August 1978. There were substantially higher concentrations of leptocephali in the waters sampled on the northern transects than there were in the southern ones (Fig. 10), indicating a significant input of leptocephali from the western Sargasso Sea. Combined with the present work, the studies of Kleckner and McCleave (1982) and Gunn and Watts (1982) indicate that processes important to the leptocephalus drift migration occur east of Florida and that further research should concentrate on this region.

The prolonged existence of the leptocephalus patch offshore of Florida and the Gulf Stream and the continuous capture of larvae by the Gulf Stream resulted in the broad and surprisingly uniform distribution of leptocephali along the North American coast. This transport along the North American coast formed the third phase of the drift migration. The patch can be viewed as a mechanism causing a more uniform distribution of leptocephali than would otherwise occur. Before developing the simulation model it had been

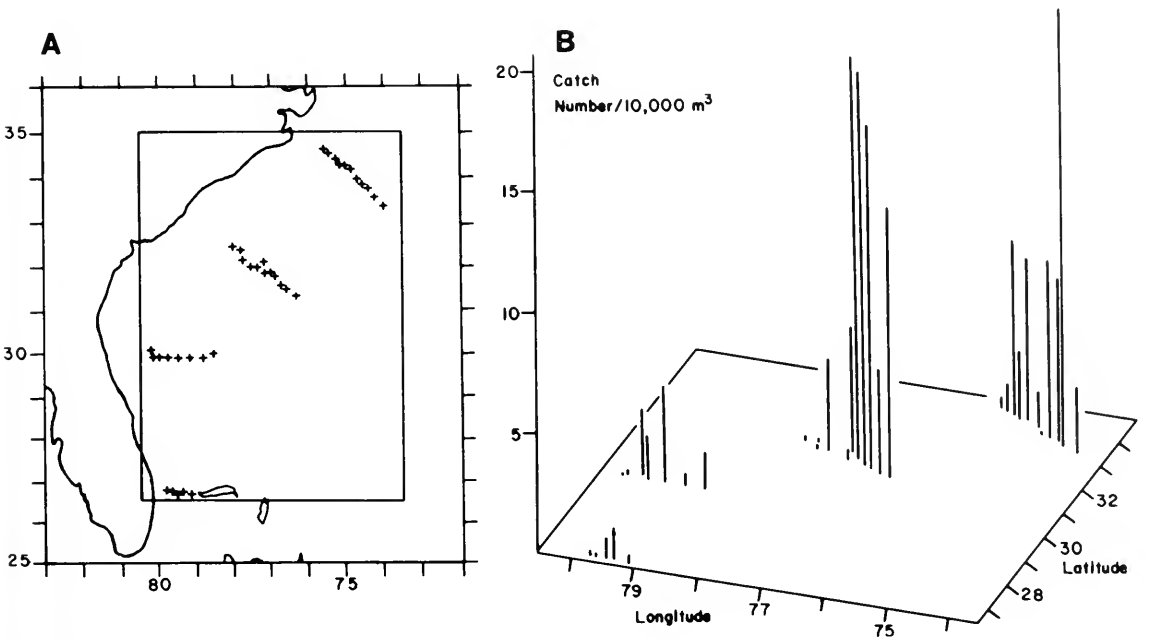

FIGURE 10.—A: Station positions on transects where American eel leptocephali were taken in the Gulf Stream system. B: Catches of leptocephali on the transects. Data from Kleckner and McCleave (1982).

assumed that leptocephali were quickly captured by the Gulf Stream and carried north and east, and it had been unclear how significant numbers of larvae remained in the southern portion of the eel's range. It is remarkable that a majority of the larvae remained so far south for such a prolonged period of time in the simulations.

Leptocephalus collections have not been made as systematically north of lat. 30°N as they have to the south, so it is difficult to compare the simulation results with the collection data north of this latitude. Kleckner and McCleave (1980, 1982[6]) stated that American eel leptocephali are abundant in the Gulf Stream from July through September, and the distributions of leptocephali they presented for these months correspond well with the simulation distributions (Fig. 11).

Up to about lat. 38°N the simulated concentrations formed wide bands along the coast; however, the simulations did not indicate how leptocephali in the eastern edges of the bands would move west towards the coast. The possibility of a behaviorally based, directed movement cannot be dismissed as unnecessary. Alternatively, it could be that these larvae are transported to Europe, or simply perish. McCleave and Kleckner (1982) demonstrated that in the tidal portion of an estuary American glass eels achieved upstream transport by selectively rising in-

[6]Kleckner, R. C., and J. D. McCleave. 1982. Spatial and temporal distribution of American eel larvae in relation to North Atlantic Ocean current system. Unpubl. manuscr., 46 p. Department of Zoology, Murray Hall, University of Maine at Orono, Orono, ME 04469.

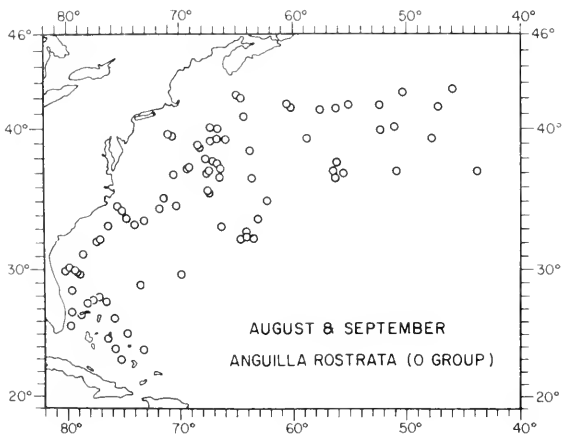

FIGURE 11.—Locations in the North Atlantic Ocean where one or more *Anguilla* leptocephali have been collected during August and September. Compare with Figures 6 and 7. From Kleckner and McCleave (text footnote 6).

to the water column during flood tides. This has also been demonstrated for European eels (Creutzberg 1961), and it is certainly possible that larval and juvenile eels could utilize this mechanism in offshore tidal areas such as Georges Bank (Magnell et al. 1980).

There are abundant examples in the literature of stochastic events whereby leptocephali could also be transported inshore. Recent examples include Gulf Stream intrusions off St. Augustine, Fla. (Atkinson et al. 1978) and in Onslow Bay (Blanton 1971), Gulf Stream frontal eddies off Jacksonville, Fla. (Yoder et al. 1981), and Gulf Stream intrusions along the New York Bight (Judkins et al. 1980). Cox and Wiebe (1979) discussed the mechanisms by which oceanic plankton are transported into the Mid-Atlantic Bight, such as Gulf Stream warm-core rings and meanders. These meso- and finer scale features all surely transport leptocephali, but they were not directly incorporated into the model, except as their effects were represented with other turbulent motions by the eddy diffusivity terms. It seems maladaptive for leptocephali to rely upon such unpredictable features to facilitate a migration that occurs with annual regularity.

Eastward transport into the North Atlantic on the Gulf Stream was the fourth and final phase evident in the simulations. These last simulation phases may not have accurately represented the eel's migration, because leptocephali begin metamorphosis to the glass eel stage as early as October (Kleckner and McCleave 1980), and it becomes questionable as to whether the eels were still drifting passively. Unless the loss of eels due to transport out into the Atlantic is substantial, it seems that by this point the eels must modify their drift in some way if they are to avoid transport to Europe. A small number of American eel are in fact found in European waters (Boëtius 1980). In the passive drift simulations, only a small portion of the larvae entered the Gulf of Maine, although this region also has complicated currents not accurately represented in the model. Meanders of the Gulf Stream will carry some larvae near the northeastern North American coast, as it has for other species (Colton et al. 1962; Markle et al. 1980). The transport of leptocephali out into the Atlantic was centered on lat. 40°N, and this agrees well with the results of Richardson (1981), who tracked buoys drifting on the Gulf Stream.

The European eel spawns in a region of weak and indeterminate currents, and in the simulation this resulted in a slow spreading of the leptocephali throughout the Sargasso Sea. It is clear that if the simulation presented in Figure 9 were continued, the

leptocephali would simply have continued to spread, with those moving west and north gradually entering the Gulf Stream. This simulation result agreed with the "moderate to rich" catches of 1-group European eel leptocephali reported by Tesch et al. (1979) as being present north of lat. 26°N and between Bermuda and Europe. Such gradual dispersal also makes it not surprising that the European eel spends 3 yr as a leptocephalus before reaching Europe.

In summary, the simulations have reproduced the important features of the leptocephalus drift migration. Some of the features, such as the patch formation offshore of Florida, were previously unsuspected, but seem highly plausible when considered in combination with the hydrographic data and the leptocephalus collection data for that region. This patch, and the remainder of the predicted leptocephalus distribution, remains to be verified by intensive and systematic sampling.

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WALRUS, *ODOBENUS ROSMARUS*, FEEDING IN THE BERING SEA: A BENTHIC PERSPECTIVE

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ABSTRACT

Walrus, *Odobenus rosmarus*, feed primarily on benthic bivalves and create a distinct record of their feeding activities on the sea floor. The record consists of furrows, pits, and discarded bivalve shells which were observed and sampled with scuba. Documentation of this benthic feeding record suggested that walrus commonly search for visually conspicuous prey by sight; that, in addition to "rooting" with the snout and vibrissae, walrus excavate bivalve prey by hydraulic jetting; that tusks are not used to excavate prey; and that all prey are excavated before consumption, which generally occurs close to the site of excavation. The mechanism of consumption appears to involve suction from between the shells. Continuous pit-furrow systems indicate the number of prey consumed in single dives, and suggest that a walrus can locate, excavate, and consume more then six clams per minute. The abundance of small infauna that are not walrus prey (e.g., polychaete worms, small bivalves, and crustaceans) was lower inside all excavations, indicating that the structure of bottom communities is highly modified by the extraction of a few large prey.

Marine mammals are observed primarily at the sea surface. Yet many important activities, especially feeding, occur underwater beyond the view of surface observers. While informative glimpses of feeding activities are sometimes obtained at the water surface (e.g., Watkins and Schevill 1976, 1979; Würsig and Würsig 1980), and the types of foods consumed are indicated by contents of gastrointestinal tracts (e.g., Lowry et al. 1980; Lowry and Frost 1981), knowledge of foraging behavior and the community role of marine mammals is generally poor. Electronic tags, depth recorders, and other instrumentation are improving this limited view (e.g., Watkins et al. 1981; Kooyman 1981). However, the greatest opportunities for studying the feeding ecology of marine mammals may involve species that prey on benthic organisms.

Bottom-feeding marine mammals often feed in shallow water, where general feeding grounds usually are known and local feeding areas can be relocated. Because benthic habitats and bottom prey are relatively immobile, prey communities can be sampled with considerable accuracy and precision, and can be experimentally manipulated as well. Largely for these reasons, we understand more about the community role of the sea otter, *Enhydra lutris*, a bottom feeder, than any other marine mammal (Estes and Palmisano 1974; Dayton 1975; Estes et al. 1978, 1982; Simenstad et al. 1978; Duggins 1980). In contrast to the very few species of bottom feeders, most marine mammals feed on mobile prey in the water column where foraging activities are difficult to observe, and no record is made. Nektonic prey are extremely difficult to sample quantitatively. Even if a feeding event were observed, the dynamic nature of prey patches and the pelagic habitat preclude direct measurement of the effect of mammal predation on prey communities.

Some bottom-feeding marine mammals leave a record of their feeding activities in soft-sediment environments. The record primarily consists of pits and furrows made in the sea floor. For example, the gray whale, *Eschrichtius robustus*, produces large, bowl-shaped pits while feeding on benthic infauna, especially amphipod crustaceans (Oliver et al. 1983). Gray whales capture and consume invertebrate prey by suction, but also kill, injure, and displace nonprey, modify local habitats, and attract scavenging animals to these excavated bottoms. Walrus; bearded seals, *Erignathus barbatus*; sea otters; dugongs, *Dugong dugon*; and manatees, *Trichechus* spp., also feed in soft-sediment habitats, but only the walrus and gray whale depend primarily on infaunal prey (Anonymous 1978).

Walrus are a common and conspicuous element of the marine mammal fauna inhabiting arctic and subarctic waters of the Northern Hemisphere. They are particularly abundant in the Bering and Chukchi Seas, where they forage among the bivalve communities found on the broad Beringian platform. The contents of numerous gastrointestinal tracts indicate

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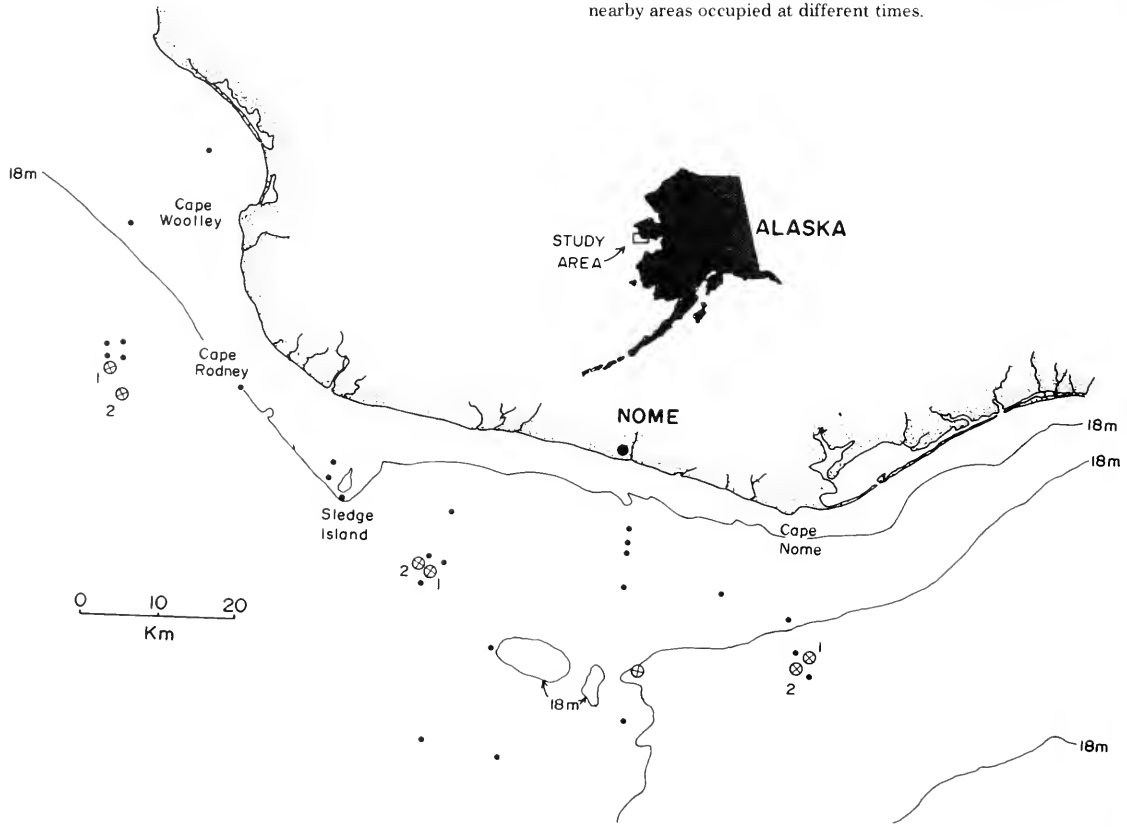
that bivalve mollusks are the primary prey (Fay 1982). However, because gastrointestinal samples are extremely difficult to relate to a particular feeding habitat and walrus feeding has not been observed in the field, present knowledge of foraging behavior largely depends on morphological arguments and observations of captive animals (Fay 1982). We cannot evaluate walrus disturbance of bottom communities from gastrointestinal samples. The diet and feeding method of walrus provide an opportunity to explore their feeding ecology by examining records of foraging activity on the sea bottom.

There are three principal objectives of this paper: 1) To describe the benthic feeding record of the walrus; 2) to demonstrate that the record provides important insights into patterns of searching, capturing, and consuming prey; and 3) to suggest the roles walrus play in structuring soft-bottom communities.

STUDY AREA

All of our observations and sampling were done near Nome, Alaska, in the northern Bering Sea (Fig. 1). The bottom is gently sloping, with extensive flat regions of fine and muddy sand (Sharma 1974). Bottom waters are cold (1°-8°C), and temperatures fluctuate seasonally (Muench et al. 1981). Water clarity is poor, usually allowing 0.5 to 1.5 m of visibility, but is occasionally 2 to 8 m. Sea ice forms during the fall and persists until late spring or early summer. Fast ice is relatively persistent nearshore, but offshore ice patterns are highly variable, particularly the occurrence and movement of the pack ice (McNutt 1981; Stringer 1981; Ray and Dupré 1981). No ice gouging of bottom sediments or gas cratering occurs in the study area (Larsen et al. 1979). Walrus are strongly associated with sea ice, where they haul out to care for young and to rest, often between foraging activities (Fay 1982). Large numbers of walrus pass through the study area, particularly during the spring northward migration (May-June). Small numbers may be present there during other months as well (Fay 1982; pers. obs.). Bearded seals are also abun-

FIGURE 1.—The major diving stations (large open circles with × in center) and other sites (small closed circles) surveyed by divers in May-June 1981 near Nome, Alaska. Numbered stations refer to nearby areas occupied at different times.



dant in the area during the spring (Lowry et al. 1980), but gray whales are seen infrequently (pers. obs.). The biomass of benthic animals is dominated by bivalve molluscs and echinoderms with large numbers of a few sedentary polychaete worms (Stoker 1978). The number and biomass of crustaceans are much lower in the study area compared with the central and western parts of the northern Bering Sea (Stoker 1978).

Field work was done from 22 May to 7 June 1981. Remnants of shore-fast ice moved away from Nome several days before our arrival. Well-developed pack-ice and large groups of walrus were observed in the general study area during the preceding month. These animals probably fed in the region for at least a month before our arrival. Therefore, the benthic feeding record was likely to be quite recent. No walrus were seen in the study area after the sea ice moved offshore around 15 May 1981.

METHODS

Thirty-three dives were made south and west of Nome (Fig. 1). At each site, divers using scuba thoroughly searched the bottom for traces of walrus feeding activity. The benthic feeding record was quantified at only several sites where feeding traces were found. Here, discarded bivalve shells were collected, and the distance to the nearest pits and furrows was recorded. Pit and furrow dimensions were measured, as well as the number of pits in a patch, and the area of bottom containing each distinct patch of pits. A patch of pits was considered distinct when no additional pits were found within 5 m of the group. Water clarity of <1 m limited the patch size observations in all areas except Cape Nome. Shell lengths and breaking strengths (using a hinged plate that was calibrated to pounds of pressure) were measured at the laboratory.

Small benthic infauna that are not walrus prey were sampled directly in feeding excavations, and in adjacent undisturbed bottoms with hand-held corers (area = 0.0075 m^2; depth = 12-15 cm). Samples were washed over a 0.5 mm screen, and preserved in a solution of 4% formaldehyde. Animals were identified to the lowest possible taxon and counted. Although juvenile bivalves and small species were adequately sampled by the corers, larger individuals were not, particularly the major walrus prey, *Macoma* spp., *Mya truncata*, and *Serripes groenlandicus*. However, the siphons and siphon burrows of the deep-burrowing clam, *M. truncata*, were counted in 1 m^2 areas to estimate the abundance of these large individuals. Sediment consolidation was measured with a simple penetrometer, which was a weighted rod (0.5 kg) dropped through a cylinder resting on the bottom. Penetration was estimated as distance of rod penetration into the surface sediments (e.g., Ronan 1975).

RESULTS

Benthic Feeding Record

We observed two basic types of excavations, furrows and pits. In both cases, shells of the excavated clams were discarded close to excavations. Therefore, different pits and furrows were easily linked to the species of excavated bivalve prey. There were three principal bivalve prey, *Mya truncata*, *Serripes groenlandicus*, *and Macoma* spp. (mostly *M. calcarea*). These groups are recognized as major prey by Vibe (1950) and Fay (1982). Feeding records generally contained one or two types of excavations: Furrows, *Mya* pits, or a mixture of *Mya* and *Serripes* pits. The relative abundance of discarded shells corresponded to the primary type of excavation in each area. For example, 92 to 100% of the shells were *Mya truncata* at stations that primarily had *Mya* pits; 76 to 83% of the shells were *Macoma* spp. at stations that primarily had *Macoma* furrows; and *Mya truncata* and *S. groenlandicus* shells were both abundant at stations that had mixed pits (Table 1). Bivalve prey thus were identified by discarded shells and by ex-

TABLE 1.—Excavation type and percentages of discarded shells from the three major prey found at the main feeding sites near Nome, Alaska. Percentages are based on the number of reconstructed whole clams.

Location	Depth (m)	Primary[1] excavation type	Percent of discarded shells			No. of bivalves
			Mya truncata	*Serripes groenlandicus*	*Macoma* spp.[2]	
Cape Rodney-1	24	*Mya* pit	100	0	0	17
Cape Rodney-2	24	furrow	18	6	76	17
Sledge Island	24	furrow	10	10	83	41
Nome	24	mixed pit	41	54	5	35
Cape Nome-1	17	*Mya* pit	92	4	4	26
Cape Nome-2	17	mixed pit	21	79	0	164

[1]Areas contained either mostly *Mya* pits, mixed pits of *Mya* and *Serripes*, or mostly furrows with *Macoma*
[2]Primarily *Macoma calcarea*.

cavation morphology. Each excavation was linked to a particular species of clam, and a larger region (dive station) was characterized both by the primary type of excavation and by the most abundant shells. Because each of two divers traveled at least 50 m and often over 100 m per dive, the primary type of excavation was easily assessed, albeit qualitatively, despite the poor water clarity. Benthic feeding records were located on 18 of 33 dive sites, but were only well quantified at 6 of the 18 sites (Table 1).

Furrows

The most extensive and distinct furrows were found near Sledge Island (Table 1). Water clarity in this area was relatively poor (about 1 m), but was adequate to see furrow widths and to trace lengths. By swimming rapidly over a long distance (>50 m), we estimated qualitatively that at least 40% of the bottom was furrowed at one Sledge Island dive site. Furrows generally formed a complex maze of excavations, but discarded shells always were abundant (as many as 5-10/10 m^2) within and along the furrow edges and were rare (<1/10 m^2) on undisturbed bottoms between furrows. The average furrow width was 45 cm and depth was 17 cm (Table 2). *Macoma* spp. were primarily excavated from furrowed bottoms (Table 1).

TABLE 2.—Morphological differences between the three major types of excavations of the walrus. Means and 95% confidence limits (sample size).

	Diameter or width (cm)	Depth (cm)
Mya truncata pit	30±1 (30)	32±3 (10)
Serripes groenlandicus pit	14±2 (9)	11±3 (14)
Macoma spp. furrow	45±3 (7)	17±2 (7)

Pits

Three distinct types of pits were made in excavating *Mya truncata*, *Macoma* spp., and *Serripes groenlandicus*. The pits differed in diameter or depth (Fig. 2, Table 2), reflecting a species position in the sediment.

Mya pits had a deep central shaft (Fig. 2). Divers readily identified these pits by thrusting a fist into a shaft. *Mya truncata* has a long, tough siphon and lives deep in the sediment (about 30 cm). Eighty-nine percent ($n = 190$) of the *Mya* pits contained only a *Mya* shell within 1 m of the pit.

Macoma pits were similar in diameter to *Mya* pits, but lacked the central shaft. They were relatively rare, as furrows were the primary excavations associated with *Macoma* shells (Table 1). *Macoma* spp. generally lives <20 cm into the sediment, and has a shorter siphon than *Mya truncata*.

The largest *Serripes* pits were much smaller than the *Mya* and *Macoma* pits (Fig. 2). Small *Serripes* pits were impossible to distinguish from sea star pits and surface irregularities. Some large *Serripes*-type pits may be made by larger sea stars (*Lethasterias* and *Asterias*). This bivalve has a short siphon, is a shallow burrower, and commonly occurs at the sediment surface. *Serripes* shells were conspicuous on the sediment surface. Therefore, although either the shells or pits of *Mya truncata* and *Macoma* spp. could be counted to estimate prey consumption, only the shells provided an adequate estimate of the number of *S. groenlandicus* eaten by walrus.

Pit-Furrows

Pit-furrow systems consisted of a series of pits connected by a shallow, continuous, and distinct furrow (Fig. 3). These systems were less common than the isolated pits or deeper furrows, and were found only at Cape Nome. Species excavated in the pit-furrow systems were primarily *Mya truncata* and *S. groenlandicus*.

Shells

The shells of primarily three groups of bivalves, *Mya truncata*, *Serripes groenlandicus*, and *Macoma* spp., were observed on the sea floor (Fig. 4). *Macoma* and *Serripes* shells were commonly attached at the umbus. About 6 to 8% of the shells from these groups were broken, while 78% of the *Mya* shells were broken (Table 3). Greater breakage of *Mya* shells appeared to be related to shell hardness (Table 3), and not necessarily to a different feeding method. The outer lining of the siphon (the periostracum) was attached to 83% of the *Mya* shells ($n = 65$), and the distal end of the siphon commonly was intact.

TABLE 3.—Percentage of broken shells found in major prey species (based on number of reconstructed whole shells), and an index of shell hardness.

	No. of bivalves	Percent broken	Shell hardness[1]
Mya truncata	96	78	4.9±1.7
Macoma spp.	32	6	7.2±2.3
Serripes groenlandicus	154	8	7.2±1.2

[1] Pounds of pressure required to break a single valve. Means and 95% confidence limits in 10 trials.

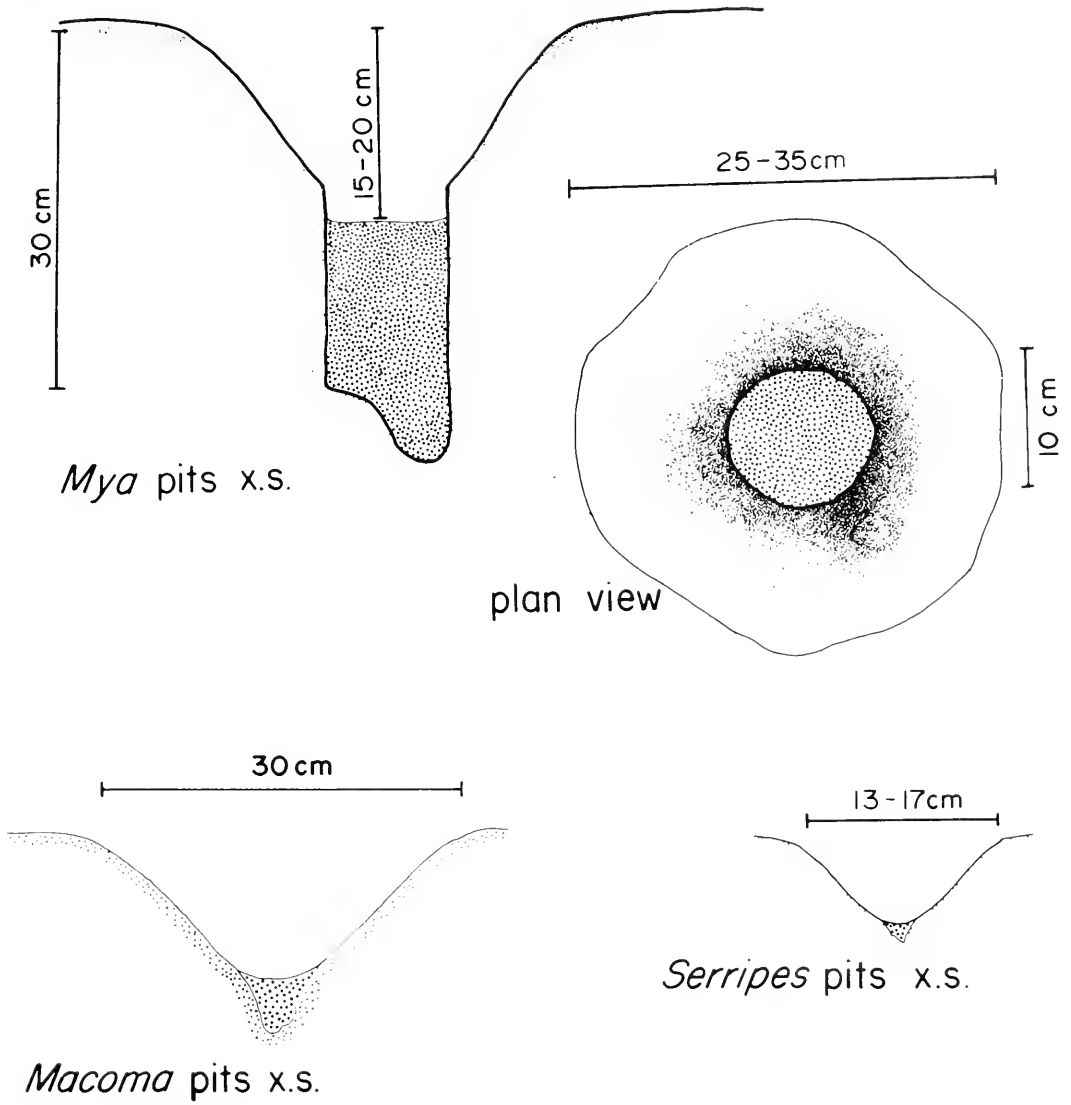


FIGURE 2.—Illustrations of the large *Mya truncata* and *Macoma* spp. pits, and the smaller pits created by excavating *Serripes groenlandicus*.

Evidence for Single Diving Events

Mya pits generally were found in distinct groups with a distance of at least 5 m between patches of pits. There was no significant difference between the number of pits per patch or the area covered by a group of pits when two similar dive sites were compared from Cape Nome (Table 4). Patches included from 1 to 20 pits, which may represent the activities of a walrus during a single dive.

We found one excellent record of the number of clams taken in a single feeding event in a pit-furrow system located off Cape Nome (Fig. 3). The pits or shells of 19 *M. truncata* and 15 *S. groenlandicus* were located in this continuous pit-furrow. Unfortunately, we could not survey the entire system because of a

TABLE 4.—Number of *Mya* pits found per group and area of the patches in two similar locations near Cape Nome. Means and 95% confidence limits in N samples.

	N	Cape Nome-2	N	Cape Nome-1	Prob.[1]
Pits per patch	15	6.1±2.6	12	5.6±3.2	$P>0.3$
Patch area (m^2)	15	10.6±7.6	12	18.0±9.8	$P>0.2$

[1]Probability of difference in t-test.

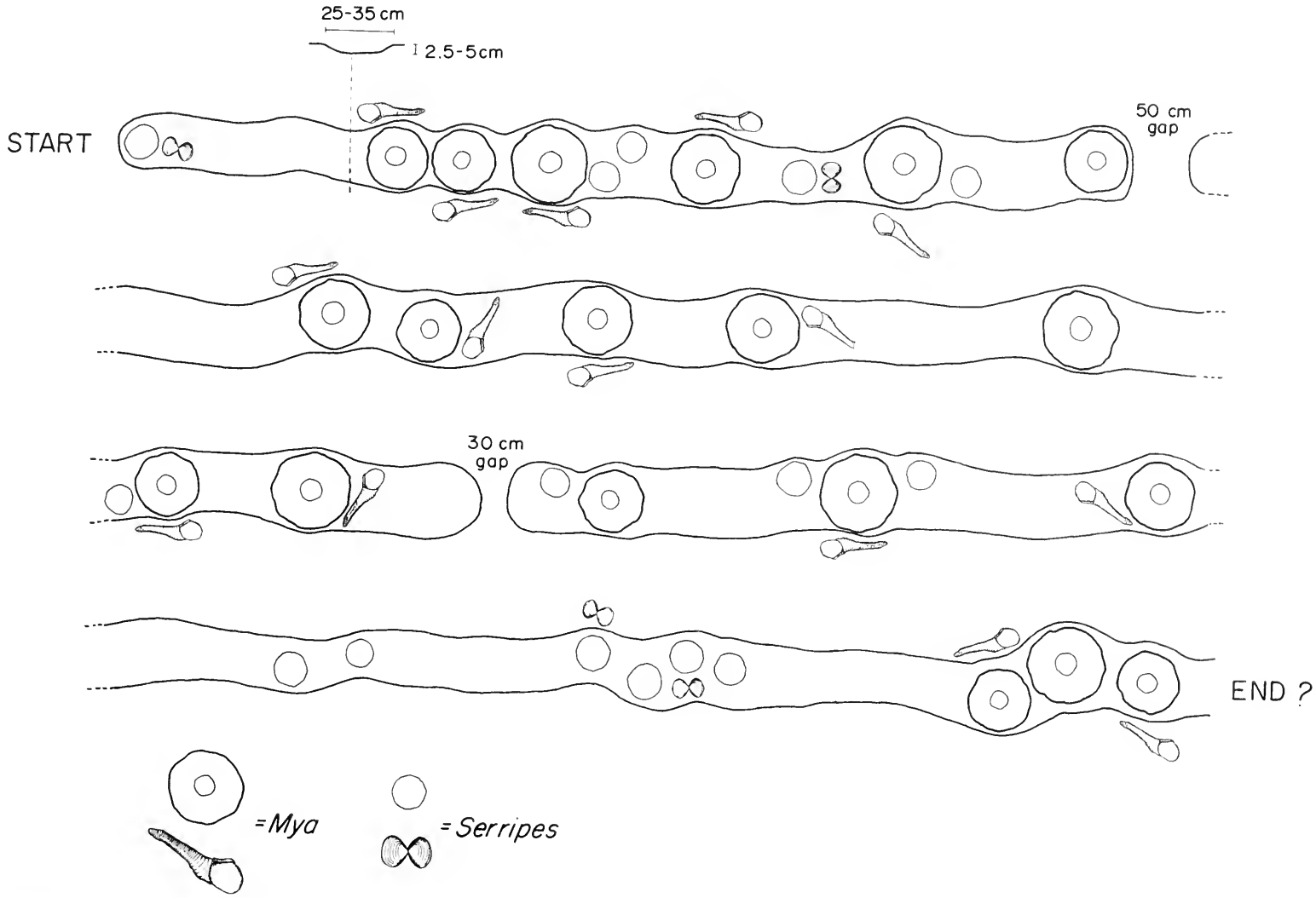


FIGURE 3.—A continuous pit-furrow system made by a feeding walrus showing pits found with and without bivalve shells. Divers did not reach the end of the system.

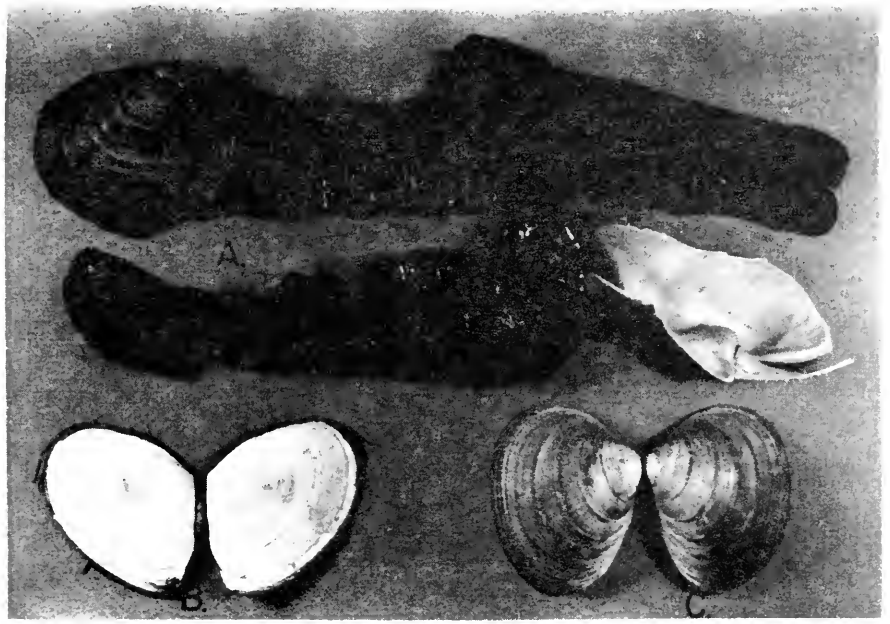


FIGURE 4.—Shells of *Mya truncata* (A), *Macoma calcarea* (B), and *Serripes groenlandicus* (C) discarded by feeding walrus.

low air supply. Nevertheless, this incomplete record is the most accurate estimate of the number of clams it is possible for a walrus to excavate during a single dive.

Effects on Benthic Communities

Walrus undoubtedly have a significant effect on abundance and size distribution of bivalve prey. Because we did not obtain adequate samples of the large individuals in living bivalve populations, we could not compare availability of various sizes of prey with the sizes of prey consumed. Nevertheless, discarded shells indicated that walrus consumed relatively large individuals from the three principal groups of bivalves (Fig. 5).

It is important to determine whether walrus disrupt different nonprey populations while feeding in different local habitats. Core samples were taken to document the species composition and relative abundance of the smaller infauna, which could be displaced, injured, or killed during excavation of the large bivalve prey. These samples indicate that benthic infaunal communities were strikingly different at the major feeding sites near Nome (Table 5). The western areas were near Cape Rodney and were numerically dominated by tube-building polychaete worms, *Myriochele oculata*, and *Polydora flava flava*.

TABLE 5.—Abundant infauna found at the three major feeding sites of walrus. Mean numbers per 0.0075 m^2 with standard deviations in parentheses. P = polychaete; C = crustacean; O = ophiuroid; T = tunicate; Pr = protozoan.

	Cape Rodney-1 (24 m)	Sledge Island-2 (24 m)	Cape Nome-2 (17 m)
Myriochele oculata (P)	133 (55)	45.7 (10.6)	448 (116)
Polydora cf. *flava flava* (P)	302 (171)	0	0
Exogone sp. (P)	9.7 (3.5)	0	0
Sabellidae (P)	8.3 (5.1)	0	1.3 (1.0)
Syllis sp. (P)	7.7 (1.8)	0	0
Amphiodia craterodmeta (O)	1.7 (1.2)	205 (48)	5.7 (2.3)
Leucon nasica (C)	0	18.3 (0.4)	0
Oligochaeta	0	14.0 (11.0)	0
Rhizomogula sp. (T)	0	0	201 (71)
Protomedeia fasciata (C)	1.7 (1.2)	4.7 (2.7)	51.3 (47.5)
Gromia sp. (Pr)	4.7 (1.8)	0	34.2 (8.7)
Podocopids (C)	3.3 (2.0)	2.0 (1.0)	14.0 (4.2)

We located an excellent record of *Mya* pits and shells there (Table 1), and observed the siphons and siphon-burrows of large, living *M. truncata*. At Sledge

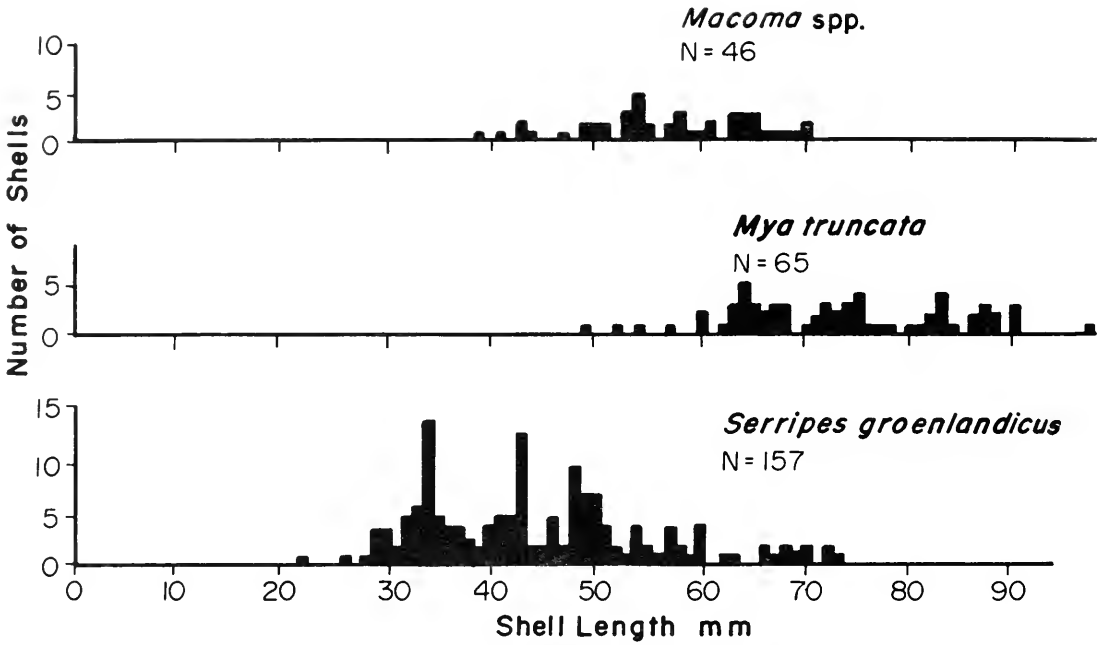


FIGURE 5.—Shell size of three groups of clams consumed around Nome, Alaska. Shells are from the benthic feeding record.

Island, the small ophiuroid, *Amphiodia craterodmeta* (disc diameter = 1-4 cm) was the most abundant species, and there was a record of furrowed sediment and *Macoma* shells (Table 1). Qualitative observations indicated few large, living bivalves, mostly *Macoma* spp. and fewer *Mya truncata*. Instead of a visually conspicuous tube mat of polychaetes, the bottom was covered with a dense carpet of interwoven ophiuroid arms. At Cape Nome, *Myriochele oculata*; the tube-building amphipod crustacean, *Protomedeia fasciata*; and the infaunal tunicate, *Rhizomogula* sp., were relatively abundant. *Mya truncata* was the major walrus prey taken at Cape Nome (Table 1) and was the only abundant large bivalve living here ($>5/m^2$). The number of sea stars, primarily *Asterias amurensis*, increased from Cape Rodney to Cape Nome. They were the predominant large epifaunal animals.

The feeding activities of walrus produced similar changes in the structure of these different benthic communities. The feeding excavations we discovered probably were <1 mo old (see section on Study Area), and occurred in highly mixed gravel and sand, in sand, and in sandy mud. Sediments were significantly less consolidated ($t = 10.2, P<0.0001$) in *Mya* pits (penetration = 11.9 cm; $n = 15$) than in undisturbed sediments (penetration = 4.4 cm; $n = 15$). The biogenic structure of surface sediments in excavations was poorly developed compared with the adjacent bottom.

Despite differences in the structure of nonprey communities, most infauna were less abundant inside the recent walrus excavations from all feeding sites. With few exceptions, the abundances of major groups (Fig. 6) and numerically dominant species (Fig. 7) were lower inside pits (Cape Rodney, Nome, Cape Nome) and furrows (Sledge Island). One exception was the polychaete worm *Myriochele oculata* at one Sledge Island site (Figs. 6, 7). These individuals were not recently settled, but were large adults in well-developed tubes. Because this species was relatively immobile, tubes probably were concentrated passively in the furrow bottom during walrus feeding. The small (diameter <1 cm) infaunal tunicate *Rhizomogula* sp. was very abundant in the Cape Nome region, and apparently rolled into *Mya* pits during and after excavation. Its abundance was significantly higher ($t = 5.1, P<0.01$) in the bottoms of pits ($\bar{X} =$ 576 per core inside, 251 outside; $n = 6$). One or two larger epifaunal anemones also occurred in many excavations. We observed several of these individuals rolling across the sediment surface in strong currents. Scavenging lysianassid amphipods were abundant in only two cores from recent excavations at Cape Nome (61 and 43/core; $1/133\ m^2$). These amphipods were rare in most core samples (<1/core;

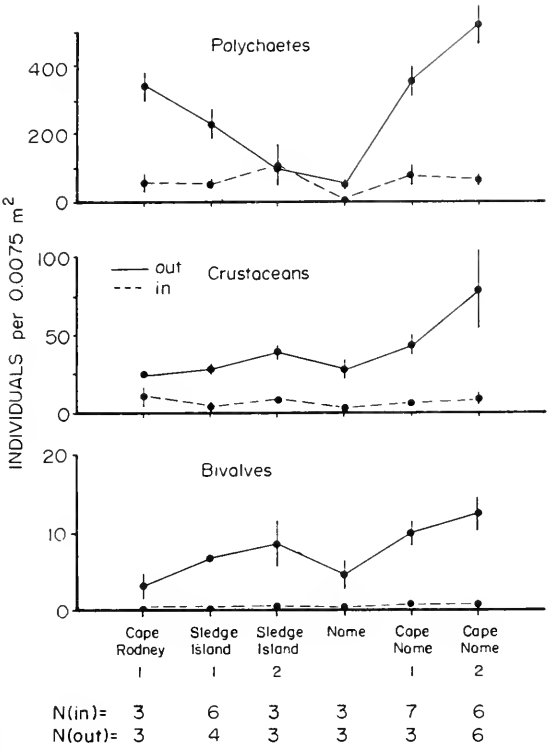


FIGURE 6.—Abundances of major infaunal groups inside and outside the furrows dug for *Macoma* spp. (Sledge Island), and the pits excavated for *Mya truncata* (all other areas). Means and standard errors in N cores.

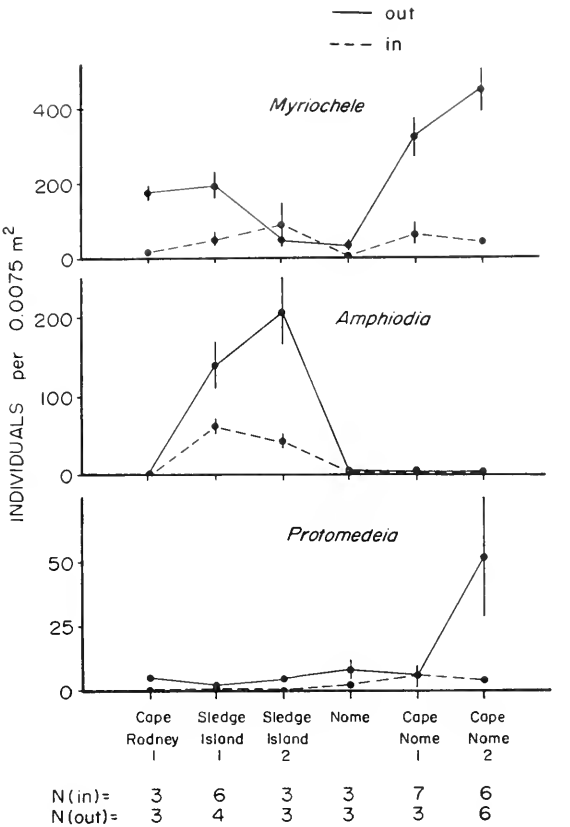


FIGURE 7.—Abundances of three numerically dominant infaunal species inside and outside walrus excavations. The polychaete worm *Myriochele oculata*, the ophiuroid *Amphiodia craterodmeta*, and the crustacean *Protomedeia fasciata*. See Figure 6 legend.

$n = 26$ cores). Lysianassids respond to various disturbances and are voracious scavengers (pers. obs.) that probably were attracted to the tissue on a discarded bivalve shell.

DISCUSSION

Walrus Feeding Behavior

Walrus are highly specialized for feeding on benthic infauna, especially bivalve molluscs (Fay 1982). Of other marine mammals, only the diet of bearded seals overlaps with the bivalve prey of walrus near Nome, but bearded seals have a much broader diet than do walrus (Lowry et al. 1980). Because bearded seals eat certain shallow-burrowing clams (e.g., *Serripes groenlandicus*) and rarely eat deep burrowers (e.g., *Mya truncata*), they cannot account for the diverse feeding records observed near Nome. No other biological or physical process can account for the record of excavations and discarded shells. While some large sea stars can make pits as large as the larger *Serripes* pits, none of the *Mya* and *Macoma* pits or the furrowed bottoms are produced by sea stars.

The low water clarity in the Bering and Chukchi Seas and the poorly developed eyes of walrus suggest that prey are not located by sight (Fay 1982). However, the benthic feeding records suggest that walrus often search for certain bivalves by sight. The most important evidence was the presence of many distinct, isolated pits with no indication of bottom disturbance between pits. These pits were made in excavating *Mya truncata*, the same species that divers routinely located by sight because of the large, conspicuous siphons. Apparently, walrus used the snout and vibrissae to search for prey without conspicuous siphons or shells (Fay 1982), as extensive furrowing only occurred in excavating *Macoma* spp., clams with small and cryptic siphons. These "rooting" activities clearly disturbed surface sediments and infaunal communities. Even the move-

ments of hermit crabs, gastropods, and sea stars produced distinct traces in surface sediments. Because the bottom was undisturbed around the isolated pits made in extracting the visually conspicuous prey, the snout and vibrissae were probably unimportant in locating these species.

The feeding excavations of walrus clearly indicate that clams are not excavated with the tusks. Fay (1982) gave a convincing argument based on anatomy and tusk abrasion patterns that the tusks are not used to excavate prey. Their main function apparently involves aggressive interactions, especially among the males (Miller 1975). None of the furrows or pits we discovered could be produced by plowing or digging with the tusks. As suggested by Vibe (1950) and Fay (1982), most excavations probably involve "rooting" with the snout and vibrissae. According to Fay[3], snout widths of subadult and adult walrus range from 29 to 41 cm for males and 23 to 35 cm for females. These sizes correspond exactly to the diameter of the upper portion of *Mya* pits and the width of furrows if the snout is swung in a narrow arc during excavation (Table 2).

We hypothesize that in addition to "rooting," a pulsing jet of water also was used to excavate prey. The walrus' mouth and tongue are well adapted for sucking and expelling water (Fay 1982) (a well-known fact to visitors who are sprayed regularly at Sea World Park in San Diego). Hydraulic jetting is the only feasible mechanism for producing the deep (30 cm) central shafts of *Mya* pits. These hydraulic pulses also may be used to produce furrows and other pits, probably in conjunction with snout and vibrissae movements. This idea was tested by constructing a suction-jet similar to the clam guns used to extract bait from intertidal mudflats. By manipulating the nozzle diameter and the volume of water exchanged per stroke, divers have produced excavations similar to the pits and furrows made by walrus.[4] A similar jetting process was observed in bat rays by Gregory et al. (1979), who suggested that it was used to excavate infaunal prey.

All clams were excavated prior to consumption. Shells were found on the surface of the sediment in a nonliving orientation. There was no evidence that biting (Vibe 1950) or suction was used to remove the soft parts of the clam while the shell was held in the sediment. Soft parts were clearly consumed near the sea floor, because discarded shells were closely associated with pits and furrows. The soft parts of clams probably were sucked from between the two shells (Vibe 1950; Fay 1982).

Perhaps the most exciting potential of the benthic feeding record is to quantify the activities of a single dive. The continuous pit-furrow system we discovered showed the location, excavation, and consumption of 34 clams along >60 m of the bottom. Over half of these clams (19) lived 30 cm deep in the sediment. At this water depth average dive times are about 5 min (Fay 1982), which suggests that one walrus ate more than six clams per minute. Divers can locate a number of long, continuous pit-furrow and furrow systems where the species, size, and number of prey can be measured. These may be the most accurate records of the diving and foraging activities of any marine mammal.

Effects of Bottom Disturbance

Walrus have an obvious impact on their large bivalve prey, but they also displace many of the small and abundant infauna that are not walrus prey. All the furrows and pits we observed were probably <1 or 2 mo, and probably <1 mo old (see section on Study Area). While there were dramatic differences between the structures of nonprey communities at the major feeding sites, the abundances of most small infauna were significantly lower inside all of the recent excavations (Figs. 6,7). The few exceptions were either immobile species that were passively concentrated in the excavations (e.g., *Myriochele oculata* and *Rhizomogula* sp.), or more motile species that may be attracted to the excavations or to scavenging events inside excavations (e.g., lysianassid amphipods). Walrus disturbance clearly produces new habitats, opens considerable space, and modifies resources that influence subsequent patterns of colonization. The tissue that remains attached to discarded shells may be an important source of food for several benthic scavengers, including asteroids, ophuiroids, and crustaceans.

Interactions Among Marine Mammals

Walrus may interact trophically with a number of other bottom-feeding marine mammals (Lowry et al. 1980; Lowry and Frost 1981). Gray whales and bearded seals share the walrus' feeding grounds in the Bering and Chukchi Seas, while the sea otter and walrus overlap in the southeastern Bering Sea. Because these other large predators produce a benthic feeding record that is distinct from the walrus, potential interactions can be examined by comparing

[3]F. H. Fay, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. May 1982.

[4]Oliver, J. S., and E. F. O'Connor. Hydraulic excavation of bivalve prey by walrus. Unpubl. manuscr. Moss Landing Marine Laboratories, Moss Landing, CA 95039.

benthic feeding records in areas where the species do and do not overlap.

Walrus and sea otters may compete for food in the southeastern Bering Sea, where sea otters forage extensively in soft-sediment habitats. In contrast to the situation in rocky shores (e.g., Estes et al. 1982), the feeding ecology of sea otters in soft sediments is poorly understood. Along the California coast, sea otters feed on several species of bivalves, including Pismo clams, *Tivela stultorum*; Washington clams, *Saxidomus nuttallii*; and gaper clams, *Tresus nuttallii* (Stephenson 1977; Hines and Loughlin 1980), on tellinid clams *Tellina* sp. in Prince William Sound (G. A. VanBlaricom[5]), and on razor, *Siliqua alta*, and surf, *Spisula polynma*, clams along the Alaska Peninsula (pers. obs.). They excavate pits with the forelimbs and commonly produce sediment piles next to the excavation. Unlike the sea otter, walrus pits do not have piles of extracted sediment. Because otters break shells to extract soft parts, the discarded shells of walrus and sea otters are easily separated as well. Walrus feed along the northeastern portion of the Alaska Peninsula,[6] while sea otters occur more to the southwest. However, their ranges do overlap in the central area. Therefore, feeding records can be quantified in areas of overlap and non-overlap for both species.

Walrus and bearded seals may compete for bivalves in the northern Bering and Chukchi Seas (Lowry et al. 1980). Although we have not observed the benthic feeding record of bearded seals, we predict that it is distinct from the walrus record, and thus amenable to the same sampling scheme outlined for the sea otter-walrus feeding grounds in the southern Bering Sea.

Gray whales do not consume large bivalves, but they may have a negative effect on the walrus food resource by reducing the recruitment or survival of walrus prey. One possible hypothesis is that gray whale feeding kills clams by direct burial, or by clogging feeding structures. We predict that this hypothesis is incorrect. A more likely hypothesis is that gray whale disturbance has a positive influence on several species of amphipod crustaceans, and that these crustaceans decrease the recruitment of young bivalves by predation, trampling, or some less direct interference. This idea can be tested by excluding whales from a bottom area with a large (perhaps 20 × 20 m) canopy made of net on a pipe frame. Walrus feeding probably has little or no effect on gray whales.

This discussion speculates broadly about the usefulness of the benthic feeding record. But much of the speculation can be formulated into hypotheses that are subject to critical tests. Comparable ideas about most other marine mammals, especially the non-bottom-feeding species, are extremely difficult to test, either by manipulative experiments or by sampling natural contrasts. For this reason, the benthic feeding record will undoubtedly make important contributions to our understanding of foraging behavior, community roles, and interactions among marine mammals.

[5]G. R. VanBlaricom, U.S. Fish and Wildlife Service, Piedras Blancas Field Station, P.O. Box 67, San Simeon, CA 93452, pers. commun. December 1981.

[6]Fay, F. H., and F. L. Lowry. 1981. Seasonal use and feeding habits of walruses in the proposed Bristol Bay clam fishery area. North Pac. Fish. Manage. Counc., Doc. 18, 60 p.

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A COMPARISON OF GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*, FEEDING IN THE BERING SEA AND BAJA CALIFORNIA

JOHN S. OLIVER, PETER N. SLATTERY, MARK A. SILBERSTEIN, AND EDMUND F. O'CONNOR[1]

ABSTRACT

Our observations indicate that gray whale feeding on benthic invertebrates is rare in the calving lagoons of Baja California and along the open coast near the Scammon's Lagoon complex. The biomass of benthic invertebrate prey is 20 times greater in the northern feeding grounds of the Bering Sea (482 vs. 24 g/m^2). Although the abundance of infaunal invertebrates is only 1.5 times greater in the Bering Sea, most infauna in the calving lagoons are very small polychaetes, bivalves, and crustaceans inhabiting dynamic, coarse sands. The low infaunal abundance and biomass are not caused by gray whale activities in the calving lagoons, as adjacent southern lagoons which are rarely utilized by gray whales have the same infaunal patterns. San Quintin has a unique bottom community which is strikingly different from the more southerly lagoons in Baja California, as well as the northern lagoons in California. Surprisingly, San Quintin shares a number of faunal similarities with gray whale feeding areas in the Bering Sea. No fecal material or bottom excavations made by feeding whales were found in the lagoons of Baja California, including San Quintin. However, the possible expansion of the gray whale population may lead to dramatic changes in the rich bottom communities of San Quintin, and perhaps in shallow water benthic assemblages along the migration route, and in the Gulf of California, which also may harbor potential infaunal prey of gray whales.

Gray whales, *Eschrichtius robustus*, are the only baleen whales that feed primarily on benthic invertebrates (Pike 1962; Rice and Wolman 1971). They consume large numbers of benthic infauna, especially amphipod crustaceans (Zimushko and Ivashin 1980), apparently by ingesting sediment and filtering the infauna on the baleen while expelling sediment and other particles that pass through the baleen fringes (Ray and Schevill 1974). The major feeding grounds are the northern Bering Sea, particularly the central and western regions, and the Chukchi Sea (Bogoslovskaya et al. 1981). Here, the water depths are generally 30 to 40 m and the extensive and shallow continental shelf, the Beringian Platform, supports the largest numbers of bottom-feeding marine mammals in the world. In addition to gray whales, walruses, bearded seals, and sea otters feed primarily on benthic invertebrates in the Bering and Chukchi Seas (Lowry and Frost 1981; Frost and Lowry 1981).

Most gray whales leave the northern feeding grounds in the fall and migrate over 10,000 km to Baja California, where calving occurs in several large, shallow, protected lagoons (Scammon 1874). The whales return to the Bering Sea as the sea ice degenerates in the late spring (Rice and Wolman 1971). Very little feeding is believed to occur outside the northern feeding grounds, as gray whale stomachs are generally empty along the migration route (Scammon 1874; Andrews 1914; Pike 1962; Rice and Wolman 1971), and in the southern lagoons (Scammon 1874). However, feeding has been suggested (Gilmore 1961; Pike 1962; Sund 1974) or documented (Howell and Huey 1930; Mizue 1951; Rice and Wolman 1971) outside the northern feeding grounds on several occasions.

There is additional evidence that gray whale feeding may be relatively common in and near the calving lagoons (Norris et al. in press). In the Bering Sea, many naturalists have observed distinct sediment plumes behind whales that apparently were filtering benthic invertebrates from ingested bottom sediments (Wilke and Fiscus 1961; Pike 1962; Harrison 1979; pers. obs. by authors). Similar sediment plumes or trails have been observed in the calving lagoons (Walker 1975; Norris et al. 1977; Sprague et al. 1978; Norris et al. in press), as well as sediment-laden water passing through the baleen (Norris et al. in press). This behavior suggests benthic feeding similar to that observed in the Bering Sea.

The bottom fauna has not been sampled from any of the lagoons of Baja California, except San Quintin (Barnard 1970). If bottom communities in the calving lagoons are similar to San Quintin, gray whale feeding should be common in Baja California. Laguna San Quintin is located 300 km north of the first calving lagoon, Guerrero Negro, and contains large numbers

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of amphipod crustaceans and polychaete worms (Barnard 1970). In fact, the most abundant crustacean, *Ampelisca agassizi* (*A. compressa* in Barnard 1970), is closely related to *A. macrocephala*, a major prey of gray whales in the Bering Sea (Rice and Wolman 1971). The total abundance of infaunal invertebrates in Laguna San Quintin is as high as 66,700 individuals/m^2 of bottom (Barnard 1970). Although there are no benthic biomass data from San Quintin, the species composition and abundance patterns suggest a significant quantity of potential gray whale prey. San Quintin may have been an important gray whale habitat in the past, and in the last several years has been visited by a few gray whales each season (Sprague et al. 1978).

The recent behavioral observations in the breeding lagoons and the quantity of potential prey in Laguna San Quintin suggest that gray whale feeding on benthic invertebrates may be relatively common in Baja California. If this hypothesis is accurate, perhaps gray whales migrate to the southern lagoons because of the availability of benthic prey, as well as for the warm temperature and protection for calves. Many whales occur at the entrances and outside the calving lagoons where apparent feeding behavior also has been observed (Norris et al. in press). Although we were primarily concerned with bottom communities within the lagoons, lagoon entrances and offshore habitats were explored as well.

Because stomach contents of gray whales are unavailable from recent years, we were unable to examine diets directly. Instead, we compared populations of benthic prey in the Bering Sea with the abundance and biomass of potential benthic prey in San Quintin and five other lagoons of Baja California (three calving and two noncalving lagoons). In addition, we searched the calving and noncalving lagoons for two important signs of gray whale feeding: Benthic feeding excavations and fecal material.

METHODS

Benthic invertebrate communities were surveyed in six coastal lagoons of Baja California during January 1981 (Fig. 1). Laguna San Quintin is the most northerly lagoon and is visited only infrequently by gray whales. There is little or no gray whale activity in Laguna Manuela and Estero Coyote, which are small southern lagoons with shallow entrances and channels. Laguna Guerrero Negro, Ojo de Liebre (Scammon's Lagoon), and San Ignacio are large lagoons and major calving areas for gray whales. The other important calving area, the complex of lagoons around Bahia Magdalena, was not surveyed in the present study (Fig. 1).

The six lagoons were surveyed by divers with and without scuba. Because even the deeper lagoon channels are relatively shallow (often <10 m), bottom communities were surveyed by skin divers without scuba. Scuba was used to collect quantitative samples and to make more detailed observations of areas of special interest. About 40% of the dive areas shown in Figure 1 involved scuba. Each lagoon was surveyed by two sets of divers from two small boats.

Quantitative bottom samples were taken with diver-held corers (0.018 or 0.0075 m^2), washed over a 0.5 mm screen, and preserved in a solution of 4% formaldehyde. Samples were taken in three major habitats: The central channel, eelgrass beds on the channel edges, and unvegetated sandflats above the eelgrass. Most benthic invertebrates were identified to the lowest possible taxon, and wet weight of the total fauna from each core sample was recorded. The

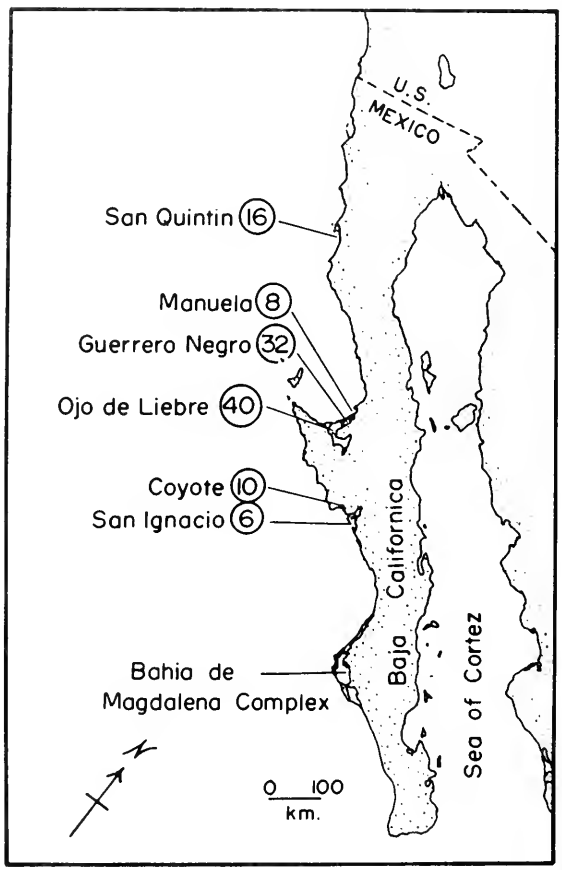

FIGURE 1.—Study sites along the Pacific coast of Baja California. Number of survey dives indicated for each site.

total length of several abundant crustaceans and polychaete worms was measured under a compound microscope with an ocular micrometer. Divers also made numerous visual observations in the relatively clear waters (visibility = 1 to 6 m) and collected qualitative samples of plants and animals.

Benthic invertebrate communities also were surveyed in the central portion of the northern Bering Sea and near St. Lawrence Island from 29 June to 10 July 1980 (Nerini in press) and the northeastern Bering Sea from May to June 1981 (Fig. 2). Water depths varied from 9 to 40 m and bottom-water visibility was generally low, ranging from 0.5 to 3 m. Bottom samples were taken by divers using scuba. The same techniques used to procure and process infaunal and sediment samples in Baja California were employed in the Bering Sea.

RESULTS

Fecal Material

Several fecal slicks were observed floating on the surface waters during the two Bering Sea visits. One large slick was sampled on 10 July 1980 on the southeastern side of St. Lawrence Island (Fig. 2). This region is a feeding ground for gray whales, and earlier bottom sampling documented extensive crustacean communities dominated by the amphipod, *Ampelisca macrocephala* (Stoker 1978, 1981). Although *A. macrocephala* was abundant in the fecal sample (Table 1) and in our bottom samples (see section on Infaunal Prey), a group of large prey, including 10 species of gammaroid and talitroid amphipods (Table 1), did not occur in any of the bottom cores taken in 1980 or 1981 (core number = 156). Gam-

TABLE 1.—Prey items in a gray whale fecal slick collected from the sea surface near St. Lawrence Island, Bering Sea. From triplicate 1,000 ml subsamples.

	Size (mm)	No./1,000 ml
Amphipods		
Gammaroids (6 species)	15-20	176
Ampelisca macrocephala	15-20	154
Talitroids (2 species)	15-20	4
Talitroids (2 species)	5-10	140
Calliopius sp.	5	219
Ischyrocerus sp.	4-8	4,305
Isopods		
Idotheids	10-50	72

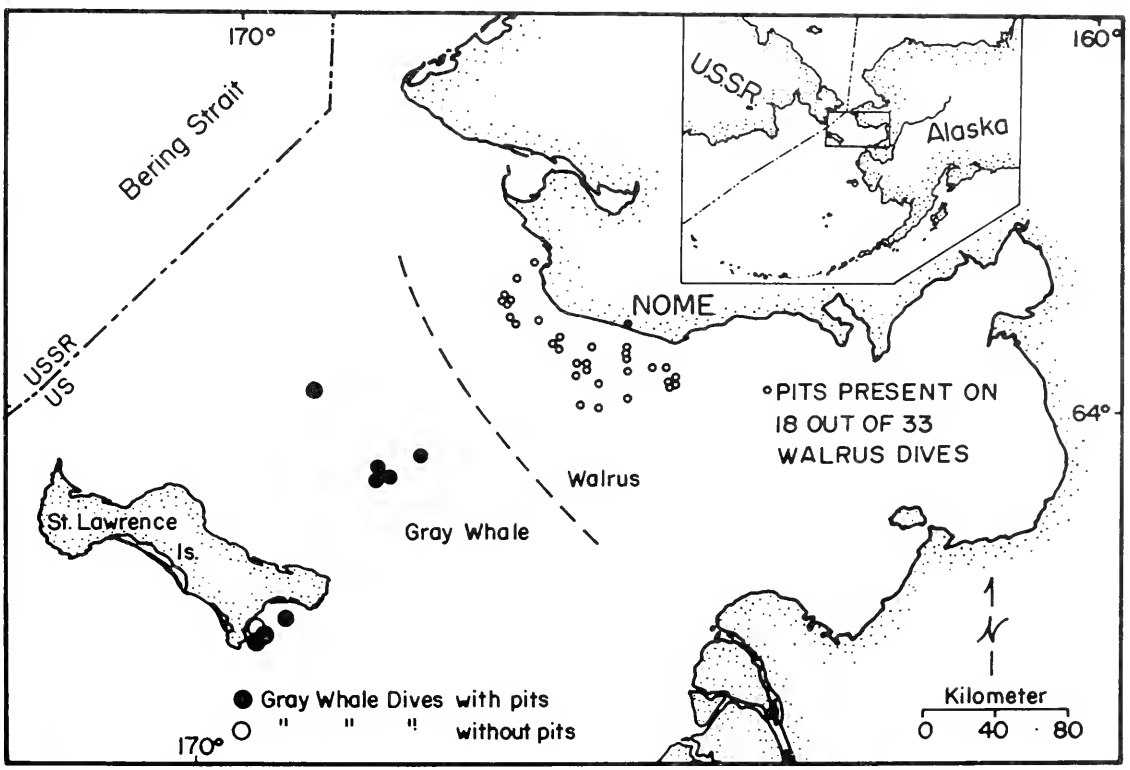

FIGURE 2.—Diving survey stations in the northern Bering Sea. No walrus excavations occurred outside the walrus feeding ground and no gray whale excavations occurred within this area.

maroids and talitroids commonly occur in intertidal, estuarine, and freshwater habitats (Bousfield 1973), and may be nestled among macroalgae in shallow, rocky areas around St. Lawrence Island. These large species (>10 mm) were conspicuous and easily counted without a microscope. Inspection of subsamples of the fecal slick under a dissecting microscope revealed a large number of smaller crustaceans (<5 mm), which were undetected by even the keen observer with the naked eye. The most abundant smaller forms were calliopiid and ischyrocerid amphipods (Table 1), nestlers and tube builders, respectively (Barnard 1969).

We were unable to locate the fecal slicks in the southern lagoons or to find anyone who has seen prey remains in fecal material.

Feeding Excavations

A remarkable record of the feeding activities of gray whales was found in the bottom sediments of the Bering Sea (Fig. 2) (Nerini in press). Divers located many large pits (more than 50) covering as much as 70% of a local bottom area near St. Lawrence Island. Figure 3 is a scale drawing of a less disturbed pitted site observed during another dive. Although we did not observe a whale making an excavation (bottom visibility was about 2 m), a feeding whale is included in Figure 3 for scale. Gray whales and the fecal slick described earlier (Table 1) occurred within 1 km of the site depicted in Figure 3. These large excavations were 1 × 2 m and 0.5 m deep. Most pits had a distinct, oblong, bowl shape. The bottom of many pits contained a deposit of broken bivalve shells (nonliving) that were concentrated from the large volume of ingested sediment. The undisturbed level bottom at the highly pitted site was present only on the ridges between the large excavations. However, a well-developed, dense tube mat of *A. macrocephala* was located on a second dive within 50 m of this highly excavated bottom. Large and small gray whale excavations were encountered on several dives in deeper water (Fig. 2). No gray whale excavations were located on many dives along the eastern shore,

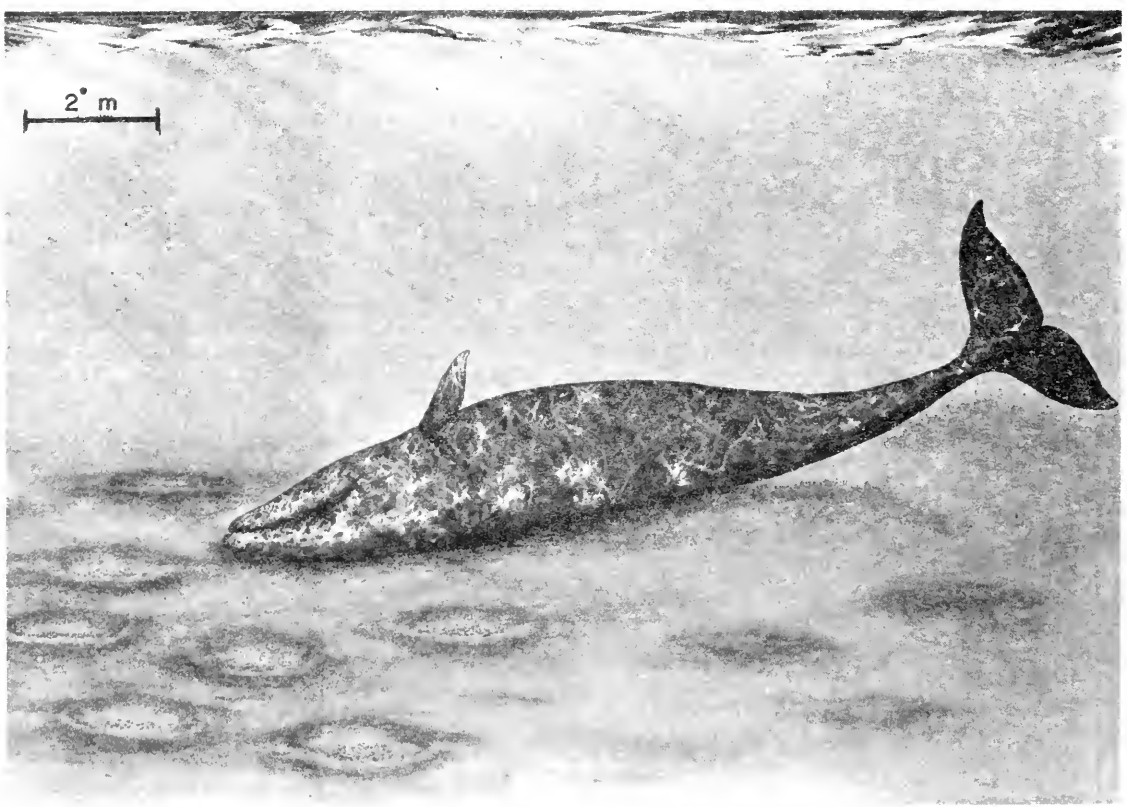

FIGURE 3.—A scale drawing of a heavily excavated bottom area observed by divers near St. Lawrence Island (21 m). No feeding whale was seen here, but a whale is included in the drawing for scale. (Drawn by Sandy Strause.)

where walrus feeding excavations were common (Fig. 2) (Oliver et al. 1983).

No gray whale feeding excavations were observed in Baja California, despite a large number of survey dives (Fig. 1) and better water clarity than the Bering Sea. Although the currents were relatively strong in many of the lagoons, other excavations and sediment structures were maintained in the surface sediments. For example, a large number of excavations produced by feeding rays was observed. These pits persisted in a number of lagoon habitats, but were usually found in the intertidal and shallow subtidal areas where gray whales did not occur. Rays were observed creating pits on several occasions. Qualitative bottom samples commonly revealed large bivalves, especially *Chione* spp., in areas where ray pits occurred. Dense infauna and other patches of potential gray whale prey did not occur in the ray feeding areas.

Infaunal Prey

The abundance of infaunal invertebrates in the gray whale feeding grounds of the Bering Sea was only 1.5 times greater than the total abundance of animals in the calving lagoons, which included Guerrero Negro, Ojo de Liebre, and San Ignacio (Fig. 4). However, ampeliscid amphipods were never abundant in the calving lagoons, while *A. macrocephala* dominated the Bering Sea fauna (also see Neiman 1963 and Stoker 1978). The abundance of infaunal crustaceans and *A. macrocephala* in the gray whale feeding grounds (Fig. 2) was as high as 67,746/m² and 21,448/m², respectively. Infaunal abundance was highest in San Quintin, the most northerly lagoon surveyed in Baja California (Fig. 4). Here we sampled from dense beds of *A. agassizi*, which accounted for 95% of the total individuals and occurred in abundances as high as 135,912/m².

In contrast to abundance, the biomass of the infauna was 20 times greater in the Bering Sea than in the calving lagoons (Fig. 5). Over 70% of the biomass in San Quintin was *A. agassizi*, and the total biomass was more than half of the Bering Sea value (Fig. 5). However, the Bering Sea data were averaged over a large group of stations sampled by Stoker (1978). The value shown for San Quintin was the densest *Ampelisca* bed we observed.

Most of the benthic invertebrates living in the southern lagoons were quite small. This was clearly reflected in the biomass data (Fig. 5). In addition to the rarity of large species and individuals, deposit feeders also were relatively rare among the polychaete worms, especially in the unvegetated sedimentary habitats. For example, a suspension-feeding sabellid worm (probably *Fabricia)* was the only species that occasionally occurred in relatively high abundance (maximum of 250 in a 0.0075 m² core). This species was usually <5 to 6 mm long, and

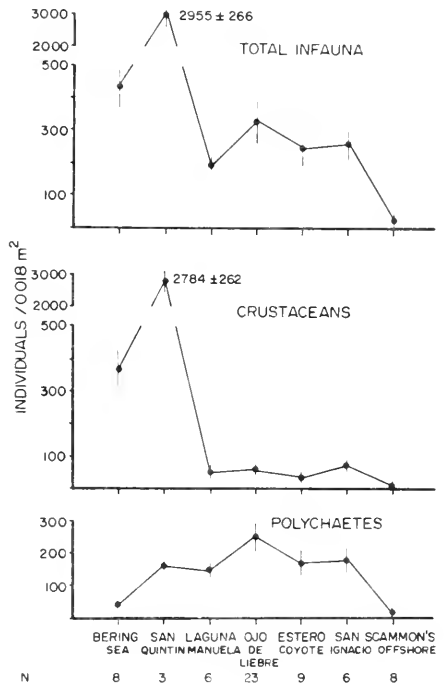

FIGURE 4.—Abundances of total infaunal invertebrates, crustaceans, and polychaete worms in the gray whale feeding grounds of the Bering Sea and in Baja California. Means and standard errors.

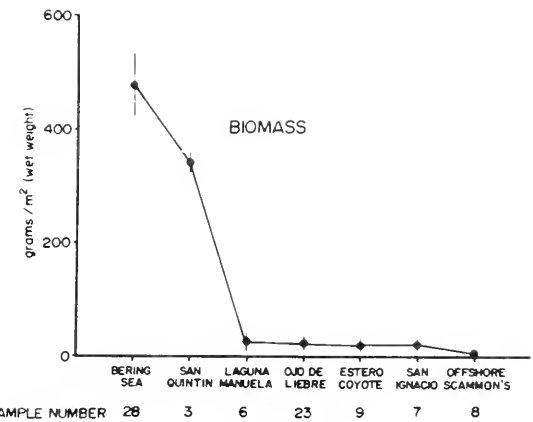

FIGURE 5.—Wet weight biomass of the total infauna from the gray whale feeding grounds in the Bering Sea (from Stoker 1978) and in Baja California. Means and standard errors.

accounted for the relatively high abundance of polychaetes in Ojo de Liebre (Fig. 4). The few infaunal crustaceans (Fig. 4) also were small species and individuals <6 mm in length vs. 20 mm for typical Bering Sea individuals). Although *A. agassizi* was a relatively large benthic crustacean for the lagoons of Baja California, this species was much smaller than *A. macrocephala* from the Bering Sea (Fig. 6).

Samples from the channel and eelgrass habitats in each lagoon were lumped for Figures 4 and 5, but infaunal abundance and biomass were highest in the eelgrass beds. When Laguna Manuela and Estero Coyote were considered together with the three calving lagoons (Fig. 1), the overall infaunal biomass was 24.3 ± 0.9 g/m^2 ($\pm$ SD; $n = 45$). Infaunal biomass in eelgrass habitats was 35.9 ± 2.7 g/m^2 ($n = 21$) and was only 13.2 ± 1.6 g/m^2 ($n = 24$) in the channels. This difference was highly significant ($P < 0.001$; Mann Whitney U test).

All the lagoon entrances were surveyed in the present study except San Ignacio. Qualitative sampling of the infaunal and epifaunal invertebrates revealed very low numbers and biomass. Quantitative core samples taken at the entrance of Laguna Ojo de Liebre substantiated these observations (only 14 g/m^2).

The biomass of potential benthic prey was extremely low outside the lagoon entrances as well. Benthic invertebrate communities were surveyed outside the Scammon's Lagoon complex between Laguna Manuela and Guerrero Negro (Fig. 1). The infauna were sampled at two water depths (9 and 17 m) and in areas that were likely to harbor well-developed infaunal populations. The substrate was a coarse, mobile sand at each depth. When the depths were combined, the infaunal biomass was 2.7 ± 3.3 g/m^2 (SD; $n = 8$). This was considerably lower than the low biomass recorded from the lagoon channels ($P < 0.0001$; Mann Whitney U test). A dense concentration (100-200/m^2) of the heart urchin, *Lovenia cordiformis*, was not included in the biomass figures because this species is not a potential prey for gray whales. Our experiences along other wave-exposed coasts (Oliver et al. 1980) indicate that unobserved patches of dense infaunal prey probably do not occur in offshore habitats.

No large zooplankton, including euphausiids and galatheid crabs, were seen by divers in the offshore habitats, in the lagoons, or in the lagoon mouths (Norris et al. in press).

In addition to the plankton, conspicuous mobile epifauna were not abundant at the lagoon entrances or anywhere in the lagoons, either on reefs or over the soft sediments. Several groups of the mysid crustacean, *Mysidopsis californica*, were observed near eelgrass beds, but these patches were rare, covered a relatively small area (10 to 20 m^2), and did not contain a large number of individuals. Small groups of shrimp were even rarer.

The calving and adjacent noncalving lagoons in the southern part of Baja California had highly dynamic sedimentary environments. We observed tidal currents of 2 to 3 kn in several lagoons. Sediments were primarily coarse sand and gravel (see Phleger and Ewing 1962), and surface structures indicated highly mobile substrates. These structures included broken shell debris and ripple marks as large as 1 m in height. Surprisingly, these structures were not restricted to the lagoon mouth. For example, large lunate ripples (length about 10 m, height 30 cm) occurred in the channel of Estero Norte, an arm of the extreme back lagoon in Ojo de Liebre. These ripple marks were more than 10 m wide, were highly mobile, and changed direction with the tide. Unlike the more southerly lagoons, we encountered relatively fine sands and silts in San Quintin. Similar differences between the sedimentary habitats in San Quintin

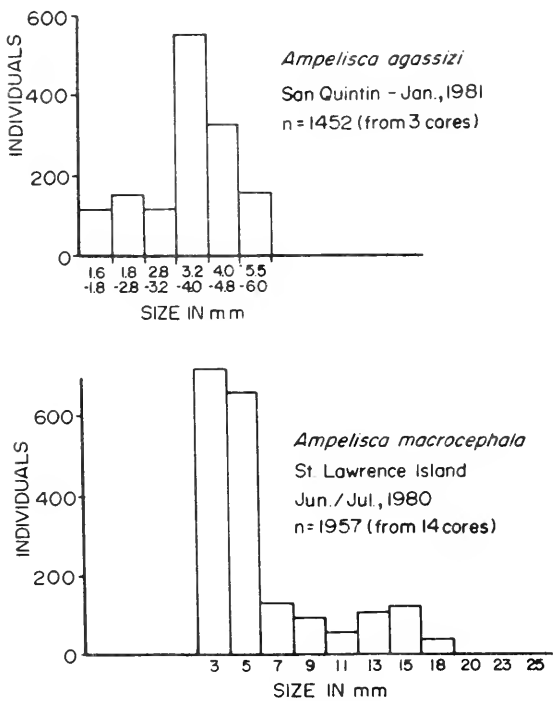

FIGURE 6.—Length-frequency histograms of *A. macrocephala* collected from a variety of stations in the Bering Sea and of *A. agassizi* from San Quintin. *Ampelisca macrocephala* populations were dominated by recently released young in summer samples (molt stages I and II). Most *A. agassizi* were preadult individuals from a midwinter population.

(Gorsline and Stewart 1962) and Ojo de Liebre (Phleger and Ewing 1962) were observed in earlier studies. The Bering Sea areas, like San Quintin, contained less mobile fine sands (Nelson 1982) harboring many relatively large infauna in tubes and burrows (Stoker 1978).

DISCUSSION

The absence of fecal material, benthic feeding excavations, and significant quantities of potential gray whale prey suggest that gray whale feeding on benthic invertebrates is not common in Baja California. No evidence of benthic feeding was encountered within the calving and noncalving lagoons, at lagoon entrances, and along the offshore sand bottoms. Gray whale stomachs collected in the southern lagoons also contained no benthic prey (Scammon 1874; Rice and Wolman 1971).

In contrast to Baja California, there is considerable evidence of gray whale feeding in the northern Bering Sea. Stomach contents are dominated by benthic infauna, especially a few species of large amphipod crustaceans (Table 2). Crustacean communities are well developed in the central and western portion of the area (Neiman 1963; Stoker 1978), the major gray whale feeding grounds. The Russian literature reports a benthic biomass of almost 1,000 g/m^2 in the feeding grounds (Neiman 1963; Alton 1974), and Stoker (1978) found a range from 149 to 991 g/m^2. Over 90% of the biomass was crustaceans, especially *A. macrocephala* in the central basin. Although we only located a few fecal slicks in the Bering Sea, benthic feeding excavations were common.

All the large benthic excavations observed in this study were undoubtedly created by feeding gray whales. Other likely explanations for their origin can be excluded. There are few bottom-feeding fish such as rays or skates in the northern Bering Sea (Shmidt 1950; Wilimovsky 1974). These fish produce large pits in other habitats (Howard et al. 1977; Gregory et al. 1979; VanBlaricom 1982). The abundant bottom fish are in the cottid family (Wilimovsky 1974) and are relatively nondestructive bottom feeders (pers. obs.). One other bottom-feeding marine mammal, the walrus, occurs in the gray whale feeding grounds, but walrus produce entirely different bottom excavations than gray whales (Oliver et al.[2]). We know of no other likely biological explanation for the large pits.

Two physical processes produce large excavations on the sea floor, ice gouging and biogenic gas cratering. Although ice gouging produces deep excavations in the sea floor (Reimnitz et al. 1977), this scour does not produce regular, bowl-shaped depressions and usually causes much more extensive bottom disturbance (Reimnitz et al. 1977; Larsen et al. 1981; Thor and Nelson 1981; pers. obs. by authors). Release of biogenic gas from the sediment apparently produces large craters in Norton Sound, and several other areas with gas-producing strata, but not in the gray whale feeding grounds (Nelson et al. 1979).

Gray whale feeding excavations can be easily distinguished from the benthic feeding record of walrus (Oliver et al. 1983). Walrus excavations were common along the eastern shore, and gray whale excavations only occurred in the central study area (Fig. 2). Here, the gray whale prey (Stoker 1978) and feeding gray whales (Moore and Ljungblad in press) are much more abundant. Gray whales are infrequently encountered along the eastern shore, where bivalve

[2]Oliver, J. S., P. N. Slattery, M. A. Silbertstein, and E. F. O'Connor, 1983. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. Unpubl. manuscr. Moss Landing Marine Laboratories, Moss Landing, CA 95039.

TABLE 2.—Dominant prey species contained in gray whale stomachs. All are benthic and all but *Synidotea* sp. are amphipods. Stomachs usually contain one prey species which comprises 80 to 100% of total contents (Zimushko and Lenskaya 1970; Bogoslovskaya, et al. 1981).

Prey species	Number stomachs dominated by prey species					
Ampelisca macrocephala	12	11	1	1	[1]	[1]
Pontoporeia femorata	23	10				
Atylus spp.	7	1			[1]	
Anonyx nugax	10					
Byblis gaimardi		4				
Ampelisca eschrichti	1					
Synidotea sp.	1					
Source	Zimushko and Ivashkin 1980	Bogoslovskaya et al 1981	Coyle unpubl. manuscr.[2]	Pike 1962	Zenkovich 1934	Tomlin 1957

[1]Dominant species where number of stomachs examined were unreported.
[2]Coyle, K. O. 1981. The oceanographic results of the cooperative Soviet-American cruise to the Chukchi and East Siberian Seas aboard the Soviet whale hunting ship Razyashchii, Sept.-Oct. 1980. Unpubl. manuscr. University of Alaska, Institute of Marine Science, Fairbanks, AK 99701.

molluscs dominate the benthic biomass. The separation of the feeding grounds of gray whales and walrus can be documented by side-scan sonar, which clearly relates general changes in surface sedimentary structures to the large-scale feeding activities of gray whales and walrus.[3] When properly calibrated with in situ observations, individual feeding excavations and multiple excavation patterns (footnote 2) may be accurately interpreted on side-scan sonographs (pers. obs. by authors).

Gray whales also produce benthic feeding excavations along Vancouver Island in British Columbia (footnotes 3, 4). Fecal material has been collected along this coast as well.[5] We recently discovered dense beds of ampeliscid amphipods and an extensive benthic feeding record of gray whales near the Bamfield Marine Station (see footnote 2). Many whales apparently feed along Vancouver Island during the northward migration, and some individuals spend the entire summer here (Darling 1977).

In summary, despite considerable evidence of benthic feeding in northern habitats, there is no compelling evidence for benthic feeding in or near the lagoons of Baja California. The southern lagoons contain highly dynamic, coarse sediment harboring very small infauna and little prey biomass for gray whales. Most infauna are much smaller than the spaces between the gray whale baleen. The structure of benthic communities within the calving lagoons is not influenced by gray whale activities, because bottom communities in adjacent noncalving lagoons are similar to those in the calving lagoons.

Earlier studies of the gray whale diet imply highly selective feeding on large crustaceans (e.g., Pike 1962). While two species of large amphipods, *Pontoporeia femorata* and *A. macrocephala*, generally account for much of the prey biomass (Table 2), careful examination of the prey remains in a fecal slick revealed a surprisingly large number of smaller prey. Gray whales probably are relatively nonselective filter feeders, consuming most of the large and small infaunal forms. Despite the importance of benthic prey, gray whales are clearly opportunistic feeders, consuming both large and small benthic invertebrates, epifaunal invertebrates in kelp forests (Wellington and Andersen 1978) and along rocky shores (see footnote 2), zooplankton (Rice and Wolman 1971; Norris et al. in press), and fish (Gilmore 1961; Sund 1975).

Although some observations of apparent feeding behavior in the breeding lagoons undoubtedly involve planktonic feeding (Norris et al. in press), and opportunistic consumption of some benthic animals, much of this behavior probably results in little or no food. A number of other explanations are likely. For example, a local fisherman and naturalist, Mario Rueda, directed us to a specific habitat near Piedras Island in Ojo de Liebre, where apparent feeding behavior was consistently observed. This area contained no concentrations of potential infaunal or epifaunal prey. However, the bottom relief was spectacular. Rocky outcrops formed a series of parallel ridges much like giant and stable ripple marks on the bottom. The vertical relief was 2 to 3 m. Between the rocky crests, there were deep basins where water currents were very low. The distance between crests was 5 to 10 m. The tidal currents above these ridges were extremely strong. Perhaps gray whales are attracted to this current regime where individuals can rapidly swim in and out of mild and strong currents over an undulating bottom.

Laguna San Quintin contains a unique bottom community, which is strikingly different from the lagoons of California and the five lagoons that were surveyed in central and southern Baja California. San Quintin harbors a large number of potential gray whale prey in a relatively small area. Future expansions of the gray whale population may bring more whales to San Quintin. If the whales arrive and do not avoid the lagoon because of human activities, we predict a dramatic change in the bottom communities of San Quintin. A small group of whales might spend much of the winter and spring feeding in San Quintin. Like the relatively small feeding areas along the coast of British Columbia, San Quintin could become a regular stopping place for certain individuals. There may be equally suitable areas for feeding around the Gulf of California, where gray whales were known to breed in the past (Gilmore et al. 1967). While these local patches of prey may be unimportant to the entire population, they may become important to certain individuals. Relatively few feeding gray whales could have considerable effects on local benthic habitats, and could produce long-term patterns of bottom population and community change.

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[3]Hans Nelson and Kirk Johnson, U.S. Geological Survey, Menlo Park, CA 94025, pers. commun. August 1982.

[4]J. Hudnall showed underwater slides and a movie of feeding excavations and behavior at the 4th Biennial Conference on the Biology of Marine Mammals, San Francisco, Calif., December 14-18, 1981.

[5]J. Darling reported, at the 4th Biennial Conference on the Biology of Marine Mammals in San Francisco, Calif., December 14-18, 1981, that K. Norris and students collected this sample near the Bamfield Marine Station, British Columbia.

ka Department of Fish and Game). Luis Fleisher and his collegues kindly helped provide access to the calving lagoons (Permiso No. 2 de Investigacion Cientifica, 1981). The field work in Baja California depended on our coworkers, James Oakden and Linda Martin. Paul Dayton, Glenn VanBlaricom, and Lloyd Lowry introduced us to the feeding ecology of gray whales and stimulated many ideas. Sheila and Alan Baldridge generously contributed to almost all aspects of our studies. Sandy Strause and Lynn McMasters drew the figures and Rosie Stelow typed the manuscript. The American Cetacean Society, World Wildlife Fund, and National Science Foundation (DPP 8121722) provided essential funds and encouragement. Collection of the 1980 Bering Sea data was funded by the Outer Continental Shelf Environmental Assessment Program, Juneau Project Office (principal investigators Mary Nerini, Howard Braham, and Linda Jones, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle, Wash). The manuscript was improved by comments from Glenn VanBlaricom, Bernd Wursig, and Kathy Frost.

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ANALYZING THE WIDTH OF DAILY OTOLITH INCREMENTS TO AGE THE HAWAIIAN SNAPPER, *PRISTIPOMOIDES FILAMENTOSUS*

STEPHEN RALSTON[1] AND GARRET T. MIYAMOTO[2]

ABSTRACT

Studies of otolith microstructure in Hawaiian snapper, *Pristipomoides filamentosus*, indicate that growth increments are deposited daily in immature fish (<40 cm FL and <3 yr of age). Laboratory experiments with tetracycline-injected fish and analysis of modal progression in size-frequency distributions of field-sampled fish validate this conclusion. Given a 1:1 correspondence between increments and days, one can determine otolith growth rate by measuring increment width. Based on the relationship between otolith growth rate and otolith length, we conclude that increment deposition in mature *P. filamentosus* is episodic, i.e., interrupted.

Using regression analysis, a model is developed relating otolith growth rate to otolith length. It is shown that integration of the regression equation provides estimates of the age of individual fish. Assumptions involved in the model are discussed, and it is concluded that this method of aging adequately represents the growth of *P. filamentosus* when time is measured on a scale of years. Age estimates derived here are entirely consistent with those of related forms (Lutjanidae) reported in the literature.

Studies of fish otoliths have now revealed that these calcified structures often grow by daily accretion of increments, in a manner analogous to the annual rings of trees. Pannella (1971, 1974) was the first to demonstrate this, and now many other researchers have substantiated and extended his findings to a wide variety of temperate and tropical species in both marine and freshwater environments (Brothers et al. 1976; Struhsaker and Uchiyama 1976; Le Guen 1976; Ralston 1976; Timola 1977; Taubert and Coble 1977; Barkman 1978; Brothers 1978; Methot and Kramer 1979; Dunkelberger et al. 1980; Pannella 1980; Schmidt and Fabrizio 1980; Steffensen 1980; Wild and Foreman 1980; Wilson and Larkin 1980; Worthmann 1980; Brothers and McFarland 1981; Mugiya et al. 1981; Uchiyama and Struhsaker 1981; Tanaka et al. 1981; Ralston and Miyamoto 1981; Campana and Neilson 1982; Watabe et al. 1982; Radtke and Dean 1982; Radtke[3]). Daily growth structures from a wide variety of plant and animal tissues were known for some time prior to Pannella's discovery (Choe 1963; Neville 1967). In fact, several publications which predate his work presented photographs of otoliths in which typical daily increments are evident (Hickling 1931; Morris and Kittleman 1967; Degens et al. 1969), yet their temporal significance was unappreciated at the time.

We are now developing a more sophisticated understanding of the processes which control the incremental growth of otoliths, with multiple factors influencing accretion, including photoperiod, food, and temperature (Hickling 1931; Irie 1960; Degens et al. 1969; Mugiya 1974, 1977; Taubert and Coble 1977; Brothers 1978; Dunkelberger et al. 1980; Pannella 1980; Mugiya et al. 1981; Tanaka et al. 1981; Watabe et al. 1982; but see Campana and Neilson 1982). Furthermore, some studies have revealed the existence of subdaily increments (Taubert and Coble 1977; Brothers 1978; Pannella 1980; Wilson and Larkin 1980; Campana and Neilson 1982) which complicates considerably the temporal interpretation of increment periodicities.

A powerful application of daily increment research has been the use of increment width as a measure of otolith and somatic growth rate. Pannella (1974) first presented this view when he stated, "Increment thickness is the spatial expression of time" and "... is the faithful expression of the conditions and rate of growth." In substantiating this claim, Struhsaker and Uchiyama (1976), Taubert and Coble (1977), and Barkman (1978) showed that otolith ring counts depend purely on specimen age and not otolith size. Slow-growing fish had small otoliths, while in comparably aged fast-growing fish the otoliths were larger but contained no more increments. Moreover, Wild and Foreman (1980) used the change in otolith dimension subsequent to mark-

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[3]Radtke, R. L. Scanning electron microscope observations of daily increments and structure in otoliths of the adult tropical fish *Pristipomoides filamentosus*. Manuscr. in prep. Pacific Gamefish Foundation, P.O. Box 25115, Honolulu, HI 96825.

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ing to estimate change in fish length and, ultimately, somatic growth rate. Similarly, Brothers et al. (1976) and Methot and Kramer (1979) numerically integrated increment thickness data to estimate age. Although of some significance, no formal or detailed treatment of the subject was presented. More recently Methot (1981) has measured the widths of the outer three daily increments in the otoliths of larval fishes, using them as explicit measures of recent daily growth rate. Brothers (1981) discussed this kind of application and cautions against short-term uncouplings of otolith growth with changes in fish length.

In this paper, we intend to analytically formalize the concept that increment width can be used as a measure of otolith growth rate. This eliminates the constraint of having to count all increments in an otolith, providing a framework for studying age and growth in large, slow-growing species of fish in which increment microstructure frequently becomes ambiguous with age (Brothers 1979; Pannella 1980). Rather than attempting a numerical solution to this problem, we have analytically integrated increment growth-rate data obtained from the otoliths of Hawaiian snapper, or opakapaka, *Pristipomoides filamentosus* (Lutjanidae). This is a commercially important species of bottomfish harvested in the Hawaiian deep-sea handline fishery (Ralston 1981; Ralston and Polovina 1982). While admittedly sacrificing some of the extreme precision theoretically possible with daily increments, the intent here is to provide reasonably reliable age estimates, economically obtained, when age is measured on a scale of years. Preliminary results of this research have been reported elsewhere (Ralston and Miyamoto 1981).

METHODS

Marking Experiment

A marking experiment was done to validate the existence of daily growth increments in opakapaka. Otoliths are composed primarily of the aragonitic crystalline form of calcium carbonate in association with small amounts of otolin protein (Hickling 1931; Irie 1960; Degens et al. 1969). The presence of calcium carbonate allows otoliths to be successfully marked in vivo with the antibiotic tetracycline (Blacker 1974; Wild and Foreman 1980; Campana and Neilson 1982). A dated, visible time-mark in otoliths provides direct validation of the periodicity of presumed daily increments.

Six juvenile opakapaka (30-34 cm FL (fork length)), captured by hook and line, were acclimated to a 1,135 l flowthrough aquarium. The fish were exposed to a natural photoperiod through an overhead skylight and were fed to satiation twice daily (midmorning and late afternoon). All six fish were initially in good condition, and after 12 d they appeared well adjusted to the tank, having resumed what seemed to be normal feeding behavior.

Three 1 kg specimens were injected intraperitoneally with 30 mg of oxytetracycline (dosage from A. Wild[4]). Following injection, all six fish were exposed for 18 h to 125 ppm acetazolamide in seawater (dosage from J. Dean[5]). This compound has been shown to affect otolith calcification by inhibition of carbonic anhydrase (Mugiya 1977), providing a simple means of creating a checkmark on otoliths. The fish resumed feeding 2 d after treatment. One fish jumped out of the tank 27 d later, and the experiment ended prematurely when the remaining five specimens died unaccountably 38-39 d after treatment.

Preparation of Otoliths

All otoliths in this study were prepared for viewing as outlined in Ralston and Miyamoto (1981). Thin sections (0.5 mm) were made through the focus along a frontal plane to the most distal portion of the postrostrum (Figs. 1, 2). Preliminary observations showed that increment counts made in a transverse plane were less than those made from frontal sections, presumably due to pinching and coalescing of rings along the shorter transverse axis (Pannella 1974; Taubert and Coble 1977; Dunkelberger et al. 1980). Tetracycline marks were obliterated by the clearing agent (Euparal[6]) and were located prior to etching by viewing with an ultraviolet fluorescence microscope. In addition, several otoliths were prepared for scanning electron microscope (SEM) examination.

Otolith Growth Rate and Specimen Age

After otoliths had cleared, they were read with a compound binocular microscope using transmitted light at a magnification of 400×. The distance in microns (μm) between the focus and the postrostral margin, representing the total length (L) of the otolith along the postrostral radius, was measured with a

[4]A. Wild, Inter-American Tropical Tuna Commission, La Jolla, CA 92037, pers. commun. May 1980.
[5]J. Dean, Professor, Belle Baruch Institute, University of South Carolina, Columbia, SC 29208, pers. commun. May 1980.
[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

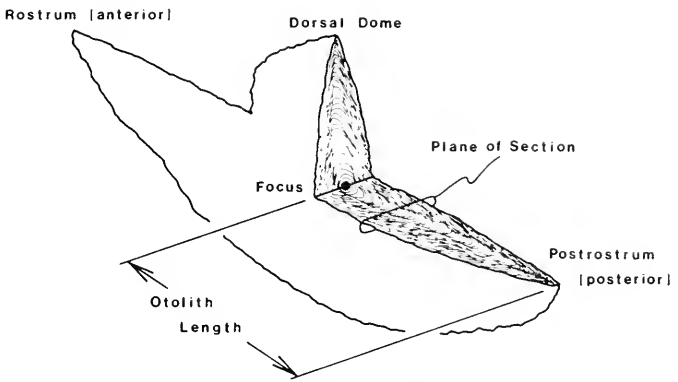

FIGURE 1.—Schematic of an otolith from *Pristipomoides filamentosus* with specific points of reference discussed in the text.

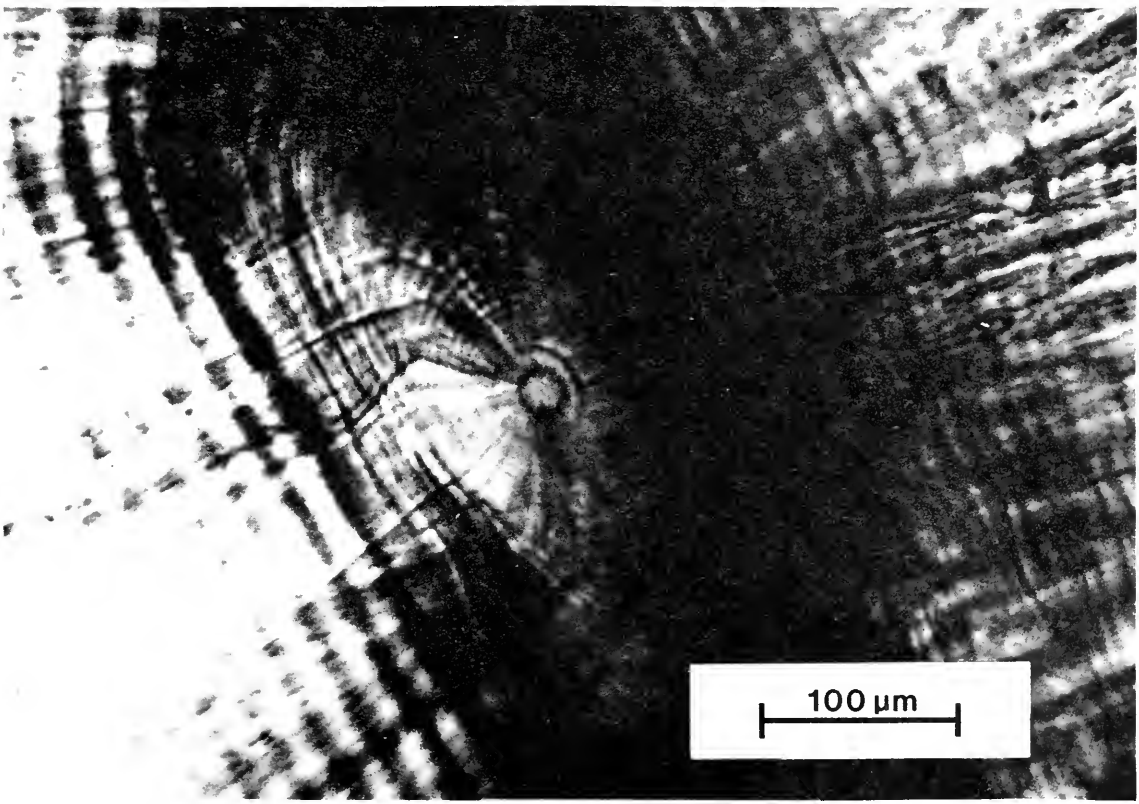

FIGURE 2.—Photomicrograph through the nuclear core region of an otolith from *Pristipomoides filamentosus*. Note increments become compressed in this area.

calibrated ocular micrometer (Fig. 1). Readings were then made at selected points along the postrostral growth axis, wherever increment microstructure was clearly viewed. At such locations the average width of increments was determined by counting the number of increments visible ($\bar{x} = 15.95$, SD = 11.24) and by measuring the radial length of the short segment in which the increments were observed. In addition, the distance between the midpoint of the sample region and the otolith focus (ℓ) was measured along the

same postrostral growth axis. As many readings as possible were made from each preparation ($\bar{x} = 31.9$), subject to the constraint that counts be made only in regions where increments were clear.

Data were summarized for each specimen by computing the ratios of segment length in μm to the number of increments included at each specific segment examined in the preparation. These figures represent the average increment width at given points in the otolith. Under the assumption that one increment forms each day, it is possible to approximate the otolith growth rate on a size-specific basis as follows:

$$\frac{\Delta \ell}{\Delta \text{ increments}} = \frac{\Delta \ell}{\Delta t} \simeq \frac{d\ell}{dt}$$

where $\Delta \ell$ is the change in length (μm) of the otolith over a given subregion, and Δt is the change in time (days). The finite approximation to the differential was always computed on a sufficiently small scale of time and length.

Given the series of ordered pairs, $\frac{d\ell}{dt}$ at otolith length ℓ, it is possible to evaluate the functional relationship between these quantities, $\frac{d\ell}{dt} = f(\ell)$, and to estimate the parameters of the function using regression analysis. The regression equation can then be solved by separation of variables and treated as a definite integral, bounded by the focus and the total length (L) of the otolith at death, providing an explicit estimate of age in days (T). That is:

$$\int_{t=0}^{T} dt = \int_{\ell=0}^{L} [f(\ell)]^{-1} d\ell. \qquad (1)$$

Size at Maturity

Samples of opakapaka gonads were obtained from throughout the Hawaiian Archipelago. Sampling was haphazard with respect to both time and location. Gonads were preserved in 10% Formalin until examined, when they were weighed to the nearest gram after excess moisture had been removed by blotting with a paper towel. Sex was determined by microscopic examination of smeared gonadal tissues, and ovaries were staged according to the following classification:

Stage I. Inactive ovary
- a) egg diameters 75-100 μm
- b) transparent primary oocytes in ovary
- c) nucleii faintly visible
- d) eggs ovoid

Stage II. Developing ovary
- a) egg diameters 100-325 μm
- b) some opaque eggs in ovary
- c) nucleii clearly visible
- d) eggs wedge-shaped

Stage III. Gravid/spawning ovary
- a) egg diameters 325-850 μm
- b) presence of oil globules
- c) evidence of yolk granules
- d) eggs ovoid

RESULTS

Typical looking increments are found in the sagittae of opakapaka (Fig. 3). In this SEM photograph the distinct incremental growth of the otolith is readily apparent, with a structure similar to that described in previous descriptions of daily increments. Discernible under high magnification is a more deeply etched, discontinuous zone which transects the radial growth of aragonite crystals found in the incremental zone (Hickling 1931; Pannella 1971, 1974, 1980; Blacker 1975; Brothers et al. 1976; Timola 1977; Dunkelberger et al. 1980; Mugiya et al. 1981; Tanaka et al. 1981; Watabe et al. 1982; Radtke footnote 3).

Tetracycline Validation

Photomicrographs of a sagittal section through the otolith of one of the three experimental fish injected with oxytetracycline are presented in Figure 4. In the upper photograph the specimen was illuminated with ultraviolet light, clearly showing the fluorescing tetracycline checkmark. The lower photograph shows the same specimen illuminated with visible light. A discontinuity coincident with the tetracycline label is evident. We interpret this latter checkmark to be due to exposure to acetazolamide and handling trauma. The close coincidence of the two marks allowed us to positively identify the experimentally induced checkmark in all six specimens.

The results of marginal increment counts from these fish are summarized in Table 1. Several sections were taken from each otolith, although not all preparations were readable. Furthermore, because the quality of all sections was poor, multiple counts of each section were made. The figures under the heading "Number of marginal increments" represent the range of counts.

It is evident from these data that the number of increments deposited on the otoliths after marking was quite similar to the number of days elapsed after the fish were marked. Since these fish were stressed dur-

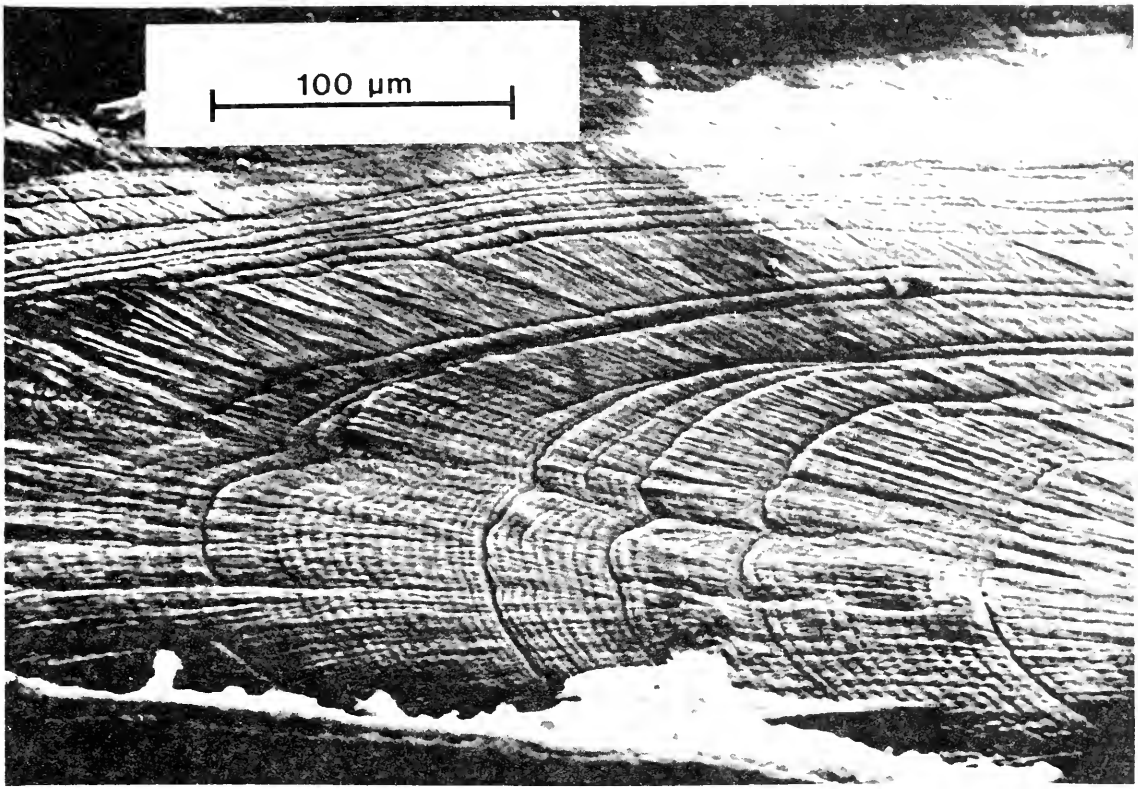

FIGURE 3.—A scanning electron microscope (SEM) photograph of a sagitta from *Pristipomoides filamentosus*, showing radial development of aragonite crystals transected by incremental and discontinuous zones.

ing captivity and did not feed for 2 d after treatment, we interpret these as confirming results. During the course of the experiment a 1:1 correspondence was maintained between increments and days, demonstrating the presence of daily marks rather than features entrained to other periodicities (e.g., subdaily marks).

Otolith Growth

Due to the likelihood of allometric relationships, it is important to distinguish between the growth of the otolith and the growth of the whole fish. Figure 5 shows that the slope of the log-linear power function regression of otolith length on fork length, based on measurements from 66 individuals, is significantly <1 ($\beta = 0.6286, t = -14.12, \mathrm{df} = 64$). This is typical of many fish species (Hickling 1933; Templeman and Squires 1956; Blacker 1974; but see Taubert and Coble 1977) and implies that the growth rate of opakapaka otoliths $\left(\frac{d\ell}{dt}\right)$ is not related in a simple linear fashion to somatic growth rate.

TABLE 1.—The results of marginal increment counts on tetracycline- and acetazolamide-marked otoliths of *Pristipomoides filamentosus*.

Specimen no.	Days marked	Number of marginal increments
E-1, Section D	27	24-27
E-2, Section B	38	33-39
Section C		35-38
E-3, Section F	38	30-31
E-4, Section A	38	30-32
Section B		30-38
E-5, Section A	38	37-39
Section C		30
E-6, Section C	39	27-30
Section D		35-39

A total of 81 sagittae from 68 individuals were examined with light microscopy for presence of daily increments. In 13 cases both left and right otoliths from the same individual were viewed. These 81 samples provided 2,957 separate estimates of otolith growth rate along the postrostral growth axis. Initially the data were pooled to elucidate the functional relationship between otolith growth rate and otolith length. The results are presented in Figure 6.

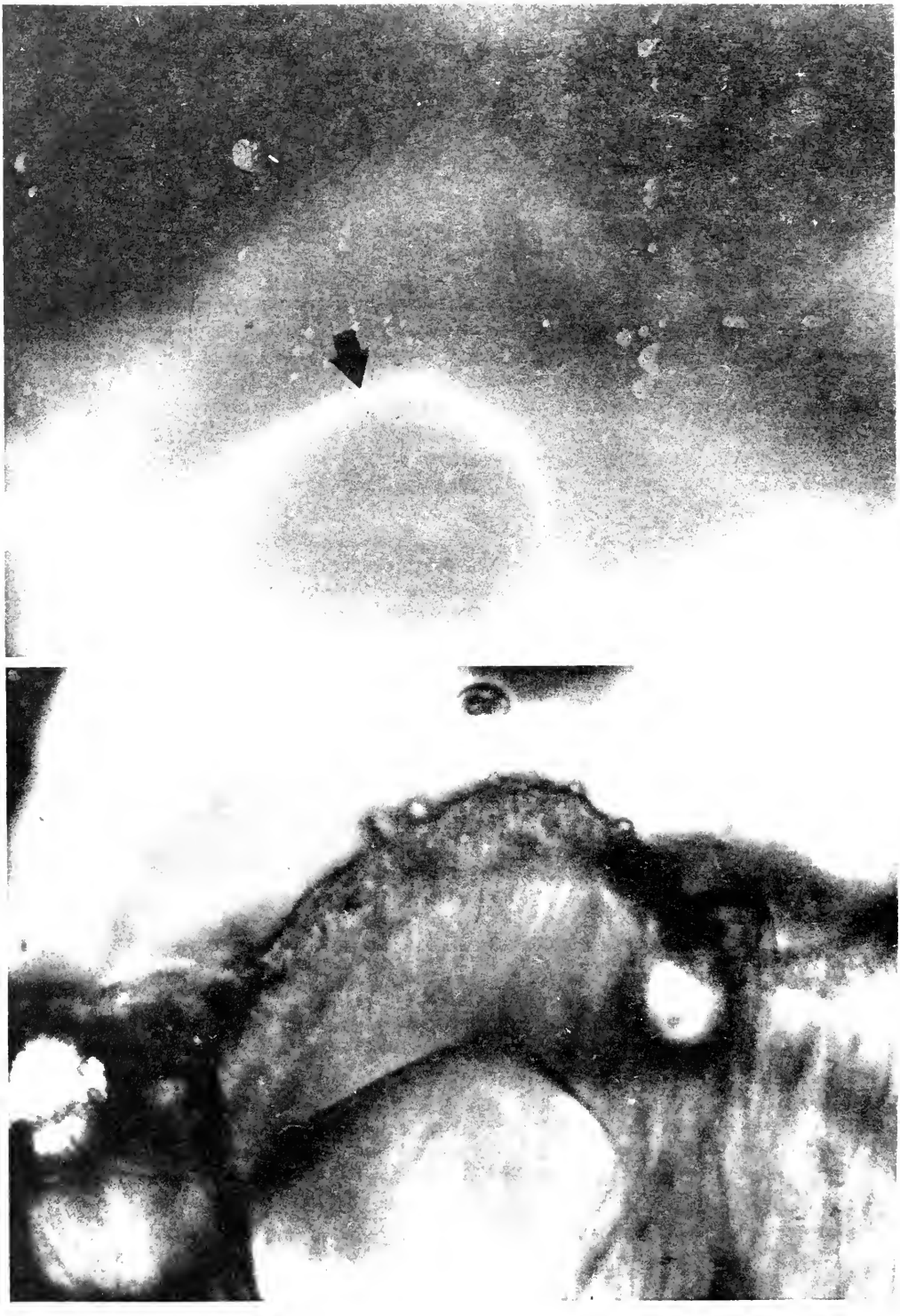

FIGURE 4.—(top) Photomicrograph of a tetracycline-marked otolith of *Pristipomoides filamentosus*, illuminated by ultraviolet light. Note checkmark at arrow. (bottom) Photomicrograph of the same sample illuminated under visible light. 300× magnification.

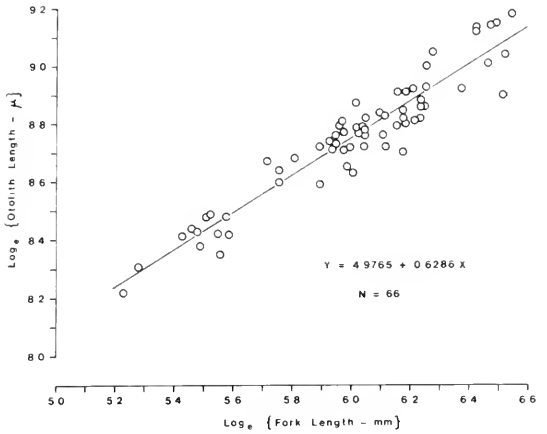

FIGURE 5.—Relationship between otolith length and fork length in *Pristipomoides filamentosus*.

There is pronounced curvilinearity in the data, as well as heteroscedastic variance. The von Bertalanffy growth model (Ricker 1979) asserts that somatic growth rate in length is a linear decreasing function of length, with the X-intercept defining the asymptotic upper bound on growth (L_∞). The observation that the growth-rate curve of opakapaka otoliths is a concave (upwards), monotonic decreasing function of otolith length (Fig. 6) is consistent with this notion, given the previously deduced allometric relationship between fork length and otolith length.

Growth-rate data were logarithmically transformed to linearize the trend line and stabilize the variance (Fig. 7). It is evident that once the otolith reaches about 6,000 μm in length, an alteration occurs in the rate (slope) at which log-transformed growth rate declines, maintaining a higher rate than would be expected otherwise. This noticeable change in slope is apparently due to attainment of reproductive maturity.

Of those female opakapaka collected during the summer spawning season (Kikkawa 1980; Ralston 1981), the incidence of gravid/spawning ovaries is strongly dependent upon fish size (Fig. 8). These data indicate that female opakapaka reach reproductive maturity at about 40 cm FL. Fish this length have otoliths about 6,250 μm long (Fig. 5). Thus the distinct change in trend of otolith growth rate coincides closely with maturation. Males show a similar pattern of gonad maturation (Ralston 1981).

Based on these observations, it is likely that periods of episodic growth commence in opakapaka otoliths with the onset of maturity. That growth dynamics should improve at this time, as suggested by a moderation in the decline of log-transformed otolith

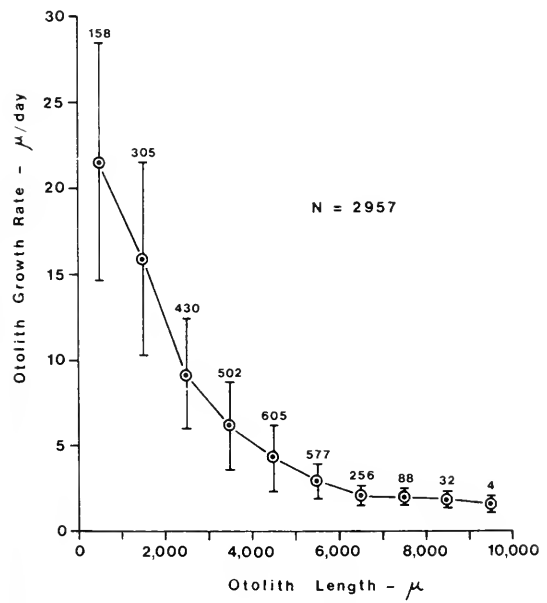

FIGURE 6.—Relationship between otolith growth rate (increment width) and otolith size in *Pristipomoides filamentosus*. Points represent means bracketed by standard deviations. Sample sizes are given above each length class.

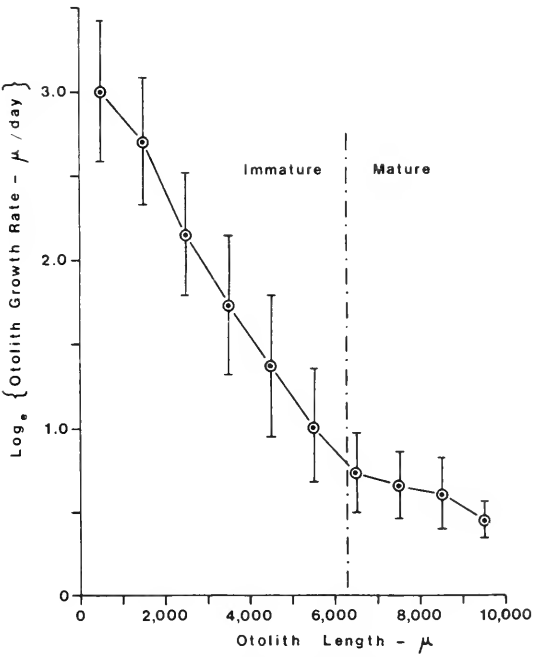

FIGURE 7.—Linearization of otolith growth rate data by logarithmic transformation for *Pristipomoides filamentosus*. Points represent means bracketed by standard deviations.

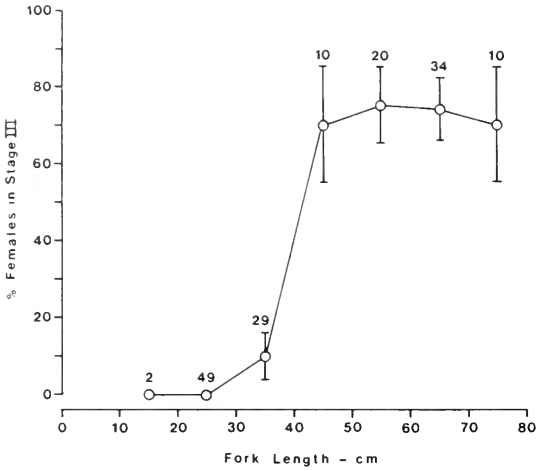

FIGURE 8.—Maturation in *Pristipomoides filamentosus* female. Stage III represents gravid/spawning individuals. Only samples collected during the spawning season are presented. Points represent means bracketed by standard deviations. Sample sizes are given above each length class.

growth rate, is completely counterintuitive to our understanding of the trade offs involved in optimizing growth and reproductive processes. Rather, it is more likely that episodic growth leaves an incomplete time record in the otolith (i.e., increments are not deposited) while concurrently, changes in otolith length are tightly coupled to changes in fork length (see Figure 5 where $r^2 = 0.899$). The resulting process would tend to underestimate Δt and thus to overestimate $\frac{d\ell}{dt}$. This hypothesis of interrupted otolith growth could explain the anomalous trend in otolith growth rates; consequently, we have regarded all data from otolith lengths >6,000 μm to be equivocal. We excluded these points from the remaining analyses, reducing the data set by 13% (2,957 ordered pairs to 2,577).

It is evident from Figure 7 that for otoliths ≤6,000 μm the logarithmic transformation was effective in linearizing the trend line and in stabilizing the variance, allowing the formulation of an analytical model describing the functional relationship between $\frac{d\ell}{dt}$ and ℓ. We write

$$\log_e \left(\frac{d\ell}{dt}\right) = \alpha - \beta\ell + \varepsilon \qquad (2)$$

where ℓ is otolith length in μm, t is time in days, α and β are model parameters, and ε is a normal random variable with mean zero and finite variance. When this model is cast in the form of Equation (1) and integrated, the solution is

$$\hat{T} = (e^{\alpha}\beta)^{-1}\,(e^{\beta L} - 1) \qquad (3)$$

where T is the estimate of age in days, and L is the total length of the otolith along the postrostral radial axis. Thus, to estimate the age of a sample specimen, one need only acquire estimates of α, β, and L.

Von Bertalanffy Growth Curve

A regression of log-transformed otolith growth rate against otolith length (Equation (2)) was performed for each of the 81 otolith samples. The age of each specimen was then estimated by Equation (3).

The fork length of the sample specimens is plotted against the point estimate of age in Figure 9. Because 13 of the 81 determinations were duplicates based on left and right otoliths from the same fish, and 4 of the remaining preparations had excessive coefficients of variation (≥20%), only 64 points are presented. These data were fitted to the von Bertalanffy growth model (Ricker 1979) using a nonlinear regression routine (NLIN Procedure) (Statistical Analysis System 1979). In this three-parameter formulation, L_∞ signifies the asymptotic upper bound on growth in length, K is an instantaneous growth-rate constant, and t_0 is a scaling factor equal to the X-intercept. When the model was freely fitted to the data, an unrealistically low estimate of L_∞ resulted (Table 2, solid line in Figure 9). As part of a related study in

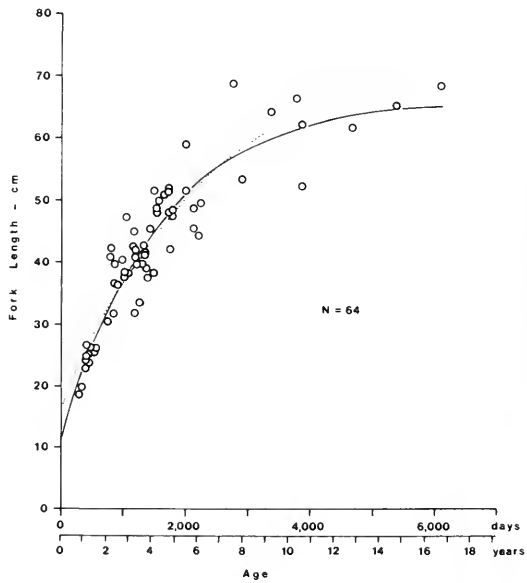

FIGURE 9.—Estimated growth curve for *Pristipomoides filamentosus*. Solid line represents a freely fitted von Bertalanffy curve whereas the L_∞ parameter was constrained to 78.0 cm in the fit of the dotted line.

TABLE 2.—Parameter estimates from the von Bertalanffy model fitted to 64 integrated age estimates of *Pristipomoides filamentosus*.

Parameter	Estimate	Standard error	Units
Freely fitted			
K	0.235	0.034	yr^{-1}
t_0	−0.807	0.298	yr
L_∞	66.4	28.15	cm
Constrained (L_∞ = 78.0 cm)			
K	0.146	0.010	yr^{-1}
t_0	−1.67	0.327	yr

which more than 2,500 opakapaka were measured, many fish exceeded 70 cm FL. Consequently, the 64 data points were refitted to the model with L_∞ constrained to a value of 78 cm FL, the largest specimen we have observed (Table 2, dotted line in Figure 9).

Analysis of Size-Frequency Distributions

The data presented in Figure 10 represent three length-frequency distributions of opakapaka sampled at French Frigate Shoals in the Hawaiian Islands. All three samples were taken on different dates but at the same position on the west side of the atoll (lat. 23°47'N, long. 166°22'W). In each distribution a large mode of small fish is plainly visible. If one accepts the premise that these small fish represent a single cohort of juveniles, these data afford the opportunity to estimate their size-specific growth rate by examining the progression of modes in time (Ricker 1975; McNew and Summerfelt 1978).

The simplified calculations presented in Table 3 show that these fish grew, on the average, at the rates of 0.020 cm/d during the winter growth period (October-May), 0.022 cm/d during the summer growth phase (May-November), and an average 0.021 cm/d over the entire year (October 1979-November 1980). If we compute the expected size-specific (31 cm FL) growth rate of these fish, based upon the fit of the integrated otolith age data to the von Bertalanffy model (Table 2, Fig. 9), we predict growth rates of 0.023 and 0.019 cm/d for the freely fitted and the constrained versions of the model, respectively. These results compare favorably with the modal growth rates, further substantiating our age estimates.

TABLE 3.—Growth rate calculations for *Pristipomoides filamentosus* based on size-frequency distributions. Samples from French Frigate Shoals, Hawaiian Islands.

	Sample no.		
	I	II	III
Date:	16 Oct 1979	27 May 1980	3 Nov. 1980
Modal size (FL cm):	27.0	31.5	35.0
Samples compared	I-II	II-III	I-III
Elapsed time (d)	223	160	383
Change in length (cm)	4.5	3.5	8.0
Growth rate (cm/d)	0.020	0.022	0.021

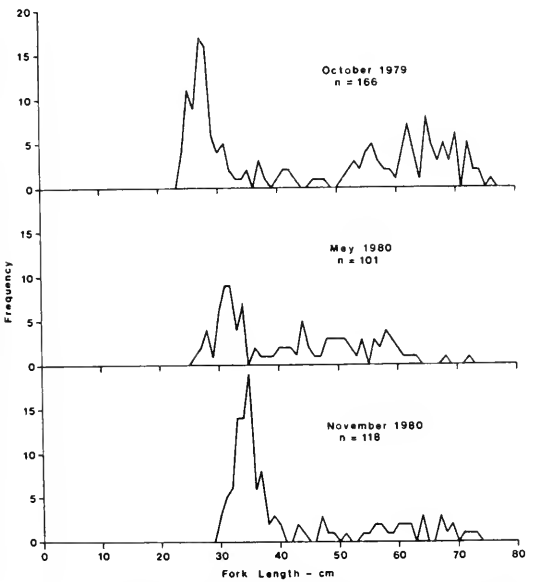

FIGURE 10.—Length-frequency distributions of *Pristipomoides filamentosus* sampled at French Frigate Shoals, Hawaiian Islands (lat. 23°47'N, long. 166°22'W).

DISCUSSION

Elsewhere we have shown that the increment thickness model presented here provides reasonably precise age estimates from a purely statistical standpoint (Ralston and Miyamoto 1981). The frequency distribution of coefficients of variation of T is centered on 6%, with 67 of the 81 values ≤10%. Thus, a typical preparation provides an age estimate for which the 95% confidence interval is about ±12% of the estimate. Furthermore, the regression technique is an effective means of accounting for variation in otolith growth rates. The frequency distribution of r^2 values for the 81 regressions had a median value of 78% (Ralston and Miyamoto 1981).

Several explicit and implicit assumptions, however, underlie the aging method presented here. It is important to address these at this time and to review to what extent they may or may not be justified. One important assumption is that it is appropriate to use the interpolative power of the regression Equation (2) to predict otolith growth rates in intermediate regions where increment microstructure is unclear. This

assumption implies that similar processes occur in regions of the otolith that appear somewhat different superficially. We feel it is not an unreasonable assumption, however, because one can usually enhance the quality of a preparation by increasing the amount of time and care devoted to it, bringing out distinct increments in regions which otherwise would remain uninterpretable. For example, Radtke (footnote 3) has shown that the core area of opakapaka otoliths requires substantially more etching time than does the marginal zone. He improved the quality of his samples by employing differential etching times, a tedious but effective technique. Wild and Foreman (1980) used similar methods in their study. Presumably, the visual quality of a preparation is largely limited by the ability of the investigator to unveil its contents.

A second and more important assumption is that it is reasonable to extrapolate the growth of a sexually mature fish based on its individual pattern of growth prior to gonad maturation. Because all data gathered at otolith lengths >6,000 μm were deleted, age estimates obtained from Equation (3) are bound by this constraint. We have argued that otolith increments become equivocal chronometers past maturity, due to interrupted growth. Both Pannella (1971) and Wild and Foreman (1980) reached similar conclusions in their studies of red hake, *Urophycis chuss*, and skipjack tuna, *Katsuwonus pelamis*, respectively. Significantly, in the latter study growth interruptions were not evident in yellowfin tuna, *Thunnus albacares*, and almost all specimens were of immature size (Schaefer et al. 1963). Not only has maturation been implicated in interrupting otolith growth, but also reduced food (Irie 1960; Methot and Kramer 1979; Uchiyama and Struhsaker 1981) and low temperature (Irie 1960; Taubert and Coble 1977). It is apparent from these studies that any factor which arrests the growth of the whole fish, temporarily or otherwise, can lead to errors in the time chronicle of daily increments (Pannella 1980). Clearly, if the additional energy burden incurred at sexual maturity is substantial (sensu Gadgil and Bossert 1970), extrapolation beyond 6,000 μm may be an unrealistic exercise and growth rates of large fish may in fact be overestimated. However, it is pertinent to note that the proportions in opakapaka of both ovarian and testicular tissues relative to total body weight are not great, ranging from 1 to 4% among Stage III females and slightly less among males (Ralston 1981). Furthermore, most models of fish growth currently in use (e.g., von Bertalanffy and Gompertz models) do not treat maturity as a growth singularity, i.e., a time when the pattern of growth changes. In spite of their relative simplicity, these models have adequately described fish growth dynamics in a surprisingly large number of situations (Ricker 1979). Undoubtedly this is because fine scale departures from model growth (e.g., seasonal trends) are averaged out when treating a lifespan measured in years. Finally, the procedure we have used involves extrapolating, at most, 68% beyond the range of the data (6,000-10,000 μm). In most cases, the amount we extrapolated was far less. Nonetheless, this particular assumption is critical and yet remains unresolved. Additional research on this topic is essential.

At the other extreme, by applying a linear model to the data (Equation (2)), we have assumed that otolith growth rate is greatest as otolith length approaches zero. This is unrealistic (see, for example, Pannella 1974; Brothers and McFarland 1981). The average width of increments actually decreases very near the focus (Fig. 2). We evaluated the extent of bias introduced by this computational simplification, however, by comparing age estimates derived from both analytical (Equation (3)) and complete numerical integration of all the otolith growth-rate data, broken down by 100 μm size classes. The largest absolute difference between the two types of age estimates was 18 d. This was for the youngest of fish, as might be expected, and indicates that the analytical method provides a poor approximation for fish <1 mo old. However, because our results are intended to describe growth over the entire size range of opakapaka, measured on a time scale of years, and because the difference between the two estimates becomes progressively smaller among the larger fish, we consider this a negligible error.

A final assumption is that one increment forms each day in preproductive individuals. We have presented evidence that validates this assumption, at least for fish 30-34 cm FL, in the form of in vivo marking of otoliths with tetracycline. Furthermore, evidence from the field (Fig. 10) also strongly supports this conclusion, again for immatures (27-35 cm FL). A final assessment of this assumption can be made by comparing the growth of opakapaka, as developed here, with studies available in the literature on lutjanid growth.

Researchers have long recognized the interdependence of growth parameters. Beverton and Holt (1959) presented values of K and L_∞ computed from the von Bertalanffy growth model and noted an inverse relationship between these parameters. Similarly, Cushing (1968) presented graphs relating growth parameters for several large taxonomic categories (e.g., Clupeoidei, Gadiformes, Salmonoidei, etc.). Pauly (1979) has attempted to quantify the relation-

ship between asymptotic weight (W_∞ or the weight of an individual at length L_∞) and K by developing the concept of the auximetric grid. He has argued that the logarithm of the product of K and W_∞ is relatively uniform for families of fishes. That is

$$P = \log_{10}(KW_\infty)$$

where P can be considered characteristic of taxa.

A review of the lutjanid growth literature allowed us to estimate P for lutjanids by computing the arithmetic average of the eight P values presented in Table 4 ($\bar{P} = 3.03$). An estimate of the asymptotic weight of opakapaka is 7,670 g (Ralston 1981). Using these two figures, we calculate an estimate of K for opakapaka to be 0.140 yr^{-1}. This figure compares very favorably with the estimate of K obtained from the constrained fit of the von Bertalanffy model to otolith data from immature fish presented earlier (0.146 yr^{-1}). The results of our marking experiments, length-frequency data, and literature comparisons all support the conclusion that increments are formed daily in subadult opakapaka (up to 3 yr old).

After considering all of the assumptions that underlie our analysis, we conclude that the results presented in Figure 9 accurately reflect the growth of opakapaka. Other investigators (Moffitt 1980; Radtke footnote 3) have presented growth curves for opakapaka, also based on otolith microstructure, but which show somewhat faster growth, especially for large, mature fish. Both studies were based upon complete counts of growth increments. We attribute the differences between our estimates and theirs to growth interruptions confounding the otolith time record in adults. These earlier studies neglected to entertain this possibility, an oversight which could lead to serious underestimates of age.

TABLE 4.—Growth relationships among the Lutjanidae with application of the auximetric grid (Pauly 1979).

Species	K (yr^{-1})	W_∞ (g)	P[1]	Source
Lutjanus apodus	0.180	3.774	2.83	Munro 1974
L. bohar	[2]0.106	9.100	2.99	Talbot 1960
L. campechanus	0.162	13.480	3.34	Nelson and Manooch 1982
L. johnii	[2]0.135	—	—	Druzhinin 1970
L. malabaricus	[2]0.064	13.600	2.94	Druzhinin 1970
L. purpureus	0.090	—	—	Menezes and Gesteira 1974
L. sanguineus	0.142	10.597	3.18	Lai and Liu 1974
	0.148	12.469	3.27	Lai and Liu 1974
L. synagris	[2]0.101	—	—	Druzhinin 1970
Ocyurus chrysurus	0.250	3.600	2.95	Munro 1974
Rhomboplites aurorubens	0.198	2.800	2.74	Grimes 1978

[1] $P = \log_{10}(KW_\infty)$
[2] Estimated from Walford plots of size-at-age data

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SPECIES ASSOCIATIONS AND DAY-NIGHT VARIABILITY OF TRAWL-CAUGHT FISHES FROM THE INSHORE SPONGE-CORAL HABITAT, SOUTH ATLANTIC BIGHT[1]

CHARLES A. WENNER[2]

ABSTRACT

Biomass, species composition, diversity, and community structure of demersal fishes were studied during the spring of 1978 in the sponge-coral habitat of the South Atlantic Bight. These results were compared with sampling at an open-shelf site. Otter trawl catch rates were an order of magnitude higher in the sponge-coral habitat than at the open-shelf site. Density and biomass estimates in the sponge-coral habitat averaged 384 individuals/ha and 31.0 kg/ha, respectively, whereas at the open-shelf site they averaged 57 individuals/ha and 3.2 kg/ha. In sponge-coral habitat samples, 101 species of demersal teleosts were taken. The Sparidae accounted for the greatest number of species (9), as well as 59% of the total number and 48% of the weight of demersal teleosts. Species diversity was highest in night-trawl tows in the sponge-coral habitat. Species associations, described by numerical classification, showed major differences in faunal assemblages between reef and open-shelf sites and between day and night samples.

Struhsaker (1969) presented a generalized habitat classification based on substrate type and species composition in a summary of demersal fish resources off the southeastern United States (Fig. 1). The open-shelf habitat extends offshore from 18 m (10 fm (fathoms)) to about 55 m (30 fm) and is characterized by a sandy bottom and relatively stable hydrographic conditions due to the moderating influence of the Gulf Stream (Struhsaker 1969; Mathews and Pashuk 1977). The ichthyofauna of the open shelf are relatively diverse but have a low biomass (Wenner et al. 1979a, b, c). Abundant teleostean families are the Sparidae, Synodontidae, Serranidae, Bothidae, and Triglidae (Wenner et al. 1979a).

The sponge-coral habitat (= Struhsaker's [1969] "live bottom") is composed of isolated areas within the open-shelf habitat. These locales have a hard substrate composed of a carbonate, shell, and quartz sand conglomerate which is either exposed or covered with a thin veneer of sand to a depth of 8 cm or less (Powles and Barans 1980). This substrate provides suitable sites for the growth of dense stands of attached invertebrates (sponges, corals, echinoderms, tunicates, hydroids, and bryozoans) and algae. A recent classification divides the sponge-coral habitat into estuarine and nearshore sites (<18 m [<10 fm]), intermediate sites (18-55 m [10-30 fm]), and offshore sites (55-183 m [30-100 fm]) (Miller and Richards 1979).

The most productive areas in the South Atlantic Bight, in terms of fish diversity and biomass, are the hard-bottom areas (Struhsaker 1969; Huntsman and Manooch 1978; Miller and Richards 1979; Powles and Barans 1980). The purposes of this report are to present distribution, relative abundance, and species composition of trawl-caught fishes from inshore and intermediate reefs sampled during the late spring of 1978 and to comment on the suitability of otter trawl gear for stock assessment of commercial finfish in this habitat.

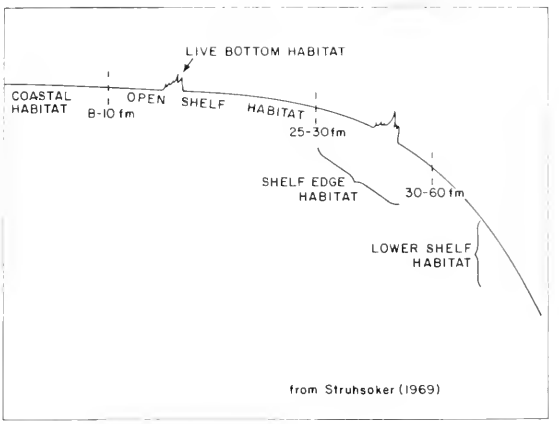

FIGURE 1.—South Atlantic Bight habitat types as defined by Struhsaker (1969).

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MATERIALS AND METHODS

Sampling was conducted at seven sites (Fig. 2) from 18 June to 16 July 1978 from the 32.6 m RV *Dolphin*. White line recorder tracings and bottom observations made with a Hydro Products TC-125 SDA[3] low light level underwater television system in conjunction with loran-C positions were used to produce maps of each site. The camera was suspended from the hydrographic wire (Fig. 3) and towed at low speed (~0.5 m/s; 1.0 kn) across each potential study area. The sponge-coral habitat was defined by the presence of attached invertebrate growth. In addition to the six sponge-coral habitat sites, an open-shelf (non-reef) area was studied to compare the species composition and biomass of both communities. Following habitat delineation, fishes were sampled by 10-min day and night trawl tows with a ¾ scale version of a Yankee No. 36 trawl (Wilk and Silverman 1976) at a speed of 6.5 km/h. The 16.5 m long footrope and the 11.9 m headrope of the net are attached to a 19 mm diameter ground cable by 12.7 mm diameter 11.6 m long leg lines. Each 17.7 m long ground cable attaches to a 226 kg wooden door. The footrope has about 1,000 rubber discs (114 mm diameter) attached to it which enable the net to bounce over small bottom irregularities. Day tows were made from 1 h after sunrise to 1 h before sunset, whereas night tows were made from 1 h after sunset to 1 h before sunrise.

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

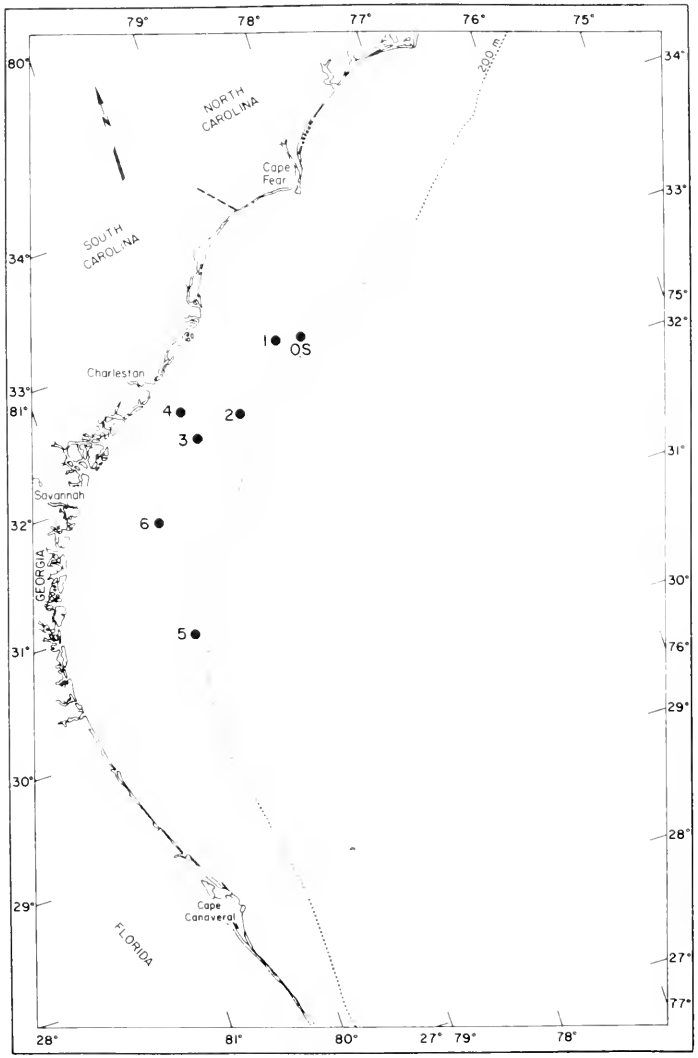

FIGURE 2.—Reef sampling sites for the 1978 survey. OS = open-shelf study area.

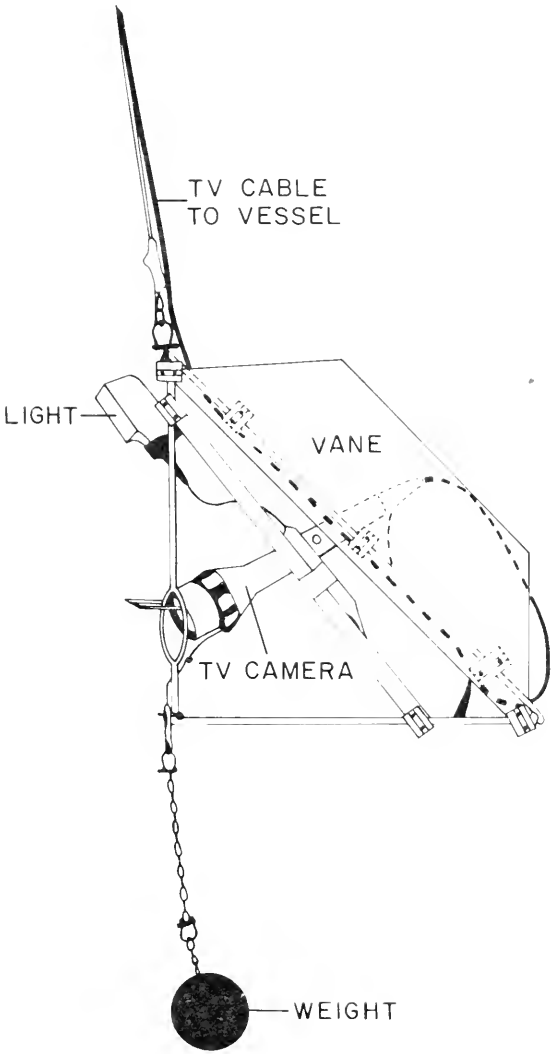

FIGURE 3.—System for deployment of underwater television equipment used in habitat documentation.

Fishes caught in nets that were not damaged during trawling operations were identified, measured, and weighed.

Initial calculations showed that the variance of the number of individuals per tow and the weight per tow far exceeded the mean and approximated a negative binomial distribution. Therefore, data were transformed ($\ln [x + 1]$) before analysis to standardize the variance and approximate the normal distribution (Taylor 1953; Elliott 1977). The number of species per tow was normally distributed and thus was not transformed. The Bliss (1967) approximation was used in retransforming the data from logarithmic to original units.

Since occasional catches of large elasmobranchs and large catches of pelagic fishes contributed significantly to the variance, biomass estimates were made only for demersal teleosts. Density estimates were calculated by the swept area method (Rohr and Gutherz 1977), with the sweep of the net being 8.748 m (Azarovitz[4]) and 1.080 km distances covered during a 10-min tow. These density estimates should be viewed as minimum, since the effectiveness of the ¾ Yankee trawl in sampling reef fish populations is unknown.

Species diversity (H') and its components, evenness (J') and richness, were calculated for elasmobranchs and demersal teleosts in each trawl tow using the following formulae:

$$H' = -\sum_{i=1}^{S} (p_i)(\log_2 p_i) \qquad \text{(Pielou 1969)}$$

where H' = index of species diversity expressed in bits/individual
S = number of species
p_i = proportion of total sample belonging to ith species;

$$J' = H'/H'_{\max} \qquad \text{(Pielou 1969)}$$

where J' = equitability or evenness
H' = observed species diversity
$H'_{\max}$ = $\log_2 S$;

$$\text{Species richness} = S - 1/\ln N \qquad \text{(Margalef 1968)}$$

where S = number of species
N = number of individuals.

Normal and inverse cluster analysis (Clifford and Stephenson 1975) were used to analyze trawl data. Prior to the analysis, data were edited to eliminate species occurring in only one trawl tow. These species have no discernible distribution pattern and, therefore, contribute no information to the analysis (Boesch 1977). Species abundance scores were then $\log_{10}$ transformed, thus reducing the dominance of species having high abundance. The Bray-Curtis similarity coefficient (Clifford and Stephenson 1975) (= the Czekanowski Quantitative Index of Bloom 1981) was used on the modified data set and is expressed by

[4]T. Azarovitz, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun., 1977.

$$S_{jk} = 2 \frac{\Sigma_i \min(X_{ij}, X_{ik})}{\Sigma_i (X_{ij} + X_{ik})}$$

where S_{jk} = similarity between entities j and k
X_{ij} = value of the ith attribute for entity j
X_{ik} = value of the ith attribute for entity k.

The Bray-Curtis similarity measure was chosen, since it most accurately reflects similarity in these types of analyses (Bloom 1981).

Normal analysis compared similarities among sites as indicated by the assemblages of fishes collected in trawl tows (entities are sites; attributes are the transformed species abundance scores). Inverse analysis compared similarities among the distribution patterns of species [entities are species, and attributes are the sites where they occur (Boesch 1977; Clifford and Stephenson 1975)]. The sorting strategy was flexible with $\beta = -0.25$ (see Clifford and Stephenson 1975 and Boesch 1977 for explanation).

Nodal analysis was used to examine the cooccurrence of species and site groups based on patterns of constancy and fidelity. Constancy, a measure of how consistently the members of a particular species group occur among the stations of a given site group, was calculated by the expression:

$$C_{ij} = a_{ij}/(n_i n_j) \qquad \text{(Boesch 1977)}$$

where C_{ij} = constancy of species group i in site group j
a_{ij} = actual number of individuals of species group i in site group j
$n_i n_j$ = number of entities in groups i and j, respectively.

Fidelity, the degree to which a given species group is restricted to a particular site group was determined by

$$F_{ij} = (a_{ij} \Sigma_j n_j / n_j \Sigma_j a_{ij}) \qquad \text{(Boesch 1977)}$$

where F_{ij} = fidelity of species group i in site group j
a_{ij} = actual number of individuals of species group i in collection group j
n_j = number of entities in group j.

RESULTS

Biomass

Otter trawl catches from the sponge-coral habitat were highly variable, ranging from 6 to 2,976 individuals (1.6-244.8 kg) in a standard tow (Table 1). The means of the natural log-transformed values of the number of individuals per haul from all reef sites were not significantly different between day and night ($t = 1.135$, df = 55), whereas mean weight of fishes was significantly greater in day tows ($t = 2.145$, df = 55). Mean values and density estimates for all trawl tows within the sponge-coral and open-shelf habitats were

	Mean values/tow		*Mean density estimates[1]/ha*	
Habitat	*No. individuals*	*Weight (kg)*	*No. individuals*	*Weight (kg)*
Sponge-coral	363 [2](268; 491)	29.3 [2](24; 35.8)	384 [2](284; 520)	31.0 [2](25.4; 37.9)
Open shelf	54 [2](24; 121)	3.0 [2](2.2; 4.0)	57 [2](25; 128)	3.2 [2](2.3; 4.2)

[1]Using 0.95 ha as the swept area of a standard tow.
[2]Upper and lower 90% confidence limits.

TABLE 1.—Mean catch/tow of demersal teleosts, 90% lower and upper confidence limits (LCL and UCL), and ranges for ¾ Yankee trawl tows by site for the spring 1978 sponge-coral survey, South Atlantic Bight.

Site	Depth (m)	Time	No. of tows	No. of individuals LCL	$\bar{x}$	UCL	Range	Weight (kg) LCL	$\bar{x}$	UCL	Range
Open shelf	46	Day	5	3	6	10	2-10	0.3	1.4	2.3	0.0-3.6
Open shelf	46	Night	6	55	75	101	42-101	3.1	4.4	6.2	1.9-6.2
Reef 1	37	Day	6	86	257	766	39-1,376	17.0	34.7	70.0	12.3-116.7
Reef 1	37	Night	5	105	172	280	64-248	12.9	16.7	21.7	11.2-24.0
Reef 2	44	Day	4	48	361	2,670	6-247	9.3	40.9	169.7	2.5-42.3
Reef 2	44	Night	4	103	164	260	87-214	13.7	19.1	26.5	11.7-25.6
Reef 3	29	Day	6	678	3,518	18,233	32-2,976	54.0	206.1	778.8	2.9-244.8
Reef 3	29	Night	6	125	188	284	66-307	14.1	19.8	27.6	8.1-27.8
Reef 4	18	Day	6	344	1,325	5,094	47-2,853	16.1	44.2	125.4	1.6-132.6
Reef 4	18	Night	7	148	220	328	64-413	8.5	13.8	23.0	2.6-27.6
Reef 5	42	Day	4	198	599	1,812	108-847	14.7	23.9	35.7	14.6-37.3
Reef 5	42	Night	1	—	45	—	—	—	12.0	—	—
Reef 6	27	Day	2	—	100	—	79-118	—	13.9	—	13.0-14.7
Reef 6	27	Night	6	110	150	205	86-202	13.1	18.1	24.9	10.9-32.3

Species Composition and Relative Abundance

Eleven trawl tows in the open-shelf habitat collected 470 individuals distributed among 26 species (16 families) with a total weight of 31.4 kg. Day catches (11 species, 8 families) accounted for only 6% of the number and 18% of the total weight of demersal teleosts taken at this site, and were not dominated by a single species. Night tows (22 species, 13 families) were dominated by planehead filefish, *Stephanolepis hispidus*, which accounted for 68% of the number and 46% of the weight of demersal teleosts at the open-shelf site (Table 2).

Trawl tows in the sponge-coral habitat ($n = 57$) collected 22,046 demersal teleosts belonging to 102 species (37 families) and having a total weight of 1,832 kg (Table 3). The Sparidae dominated the catches with the greatest number of species (9) and accounted for 59% of the total number and 48% of the total weight of demersal teleosts. The five most numerically abundant families comprised 92% and 77% of the total catch by numbers and weight. The 10 most numerically abundant species accounted for 54% of the total abundance in all 57 trawl tows. Catches of the southern porgy, *Stenotomus aculeatus*, were an order of magnitude higher than those of other species (Table 4), contributing 57.3% of the total. This species also ranked first by weight, comprising 42.1% of the trawl-caught fish weight (Table 5).

Community Structure

One's perception of fish community structure in the South Atlantic Bight depends upon the habitat and time of sampling. Numerical classification indicated that four major divisions were present, consisting of 12 site groups (Fig. 4). The first major division contained, with one exception, otter trawl collections made during the day (site group 1) and night (site group 2) in the open-shelf area. A second division within the classificatory scheme included all trawl tows from reef 5 (site group 3). The two remaining broad divisions were composed of day tows (site groups 4 through 7) and night tows (site groups 8 through 12) from the five remaining reef sites. In general, major faunal distinctions were made, not only between collections from different habitats (open shelf vs. reef), but also between day and night samples taken at the same site.

The groundfish communities of the open-shelf and sponge-coral habitat formed 9 species groups containing from 5 to 11 species (Fig. 5). Each group was associated with specific spatial and temporal conditions. The five species of demersal fishes in group A showed a high frequency of occurrence and abundance at all reef sites, as reflected in the moderate to very high nodal constancy values (Fig. 6). The low and moderate constancy values for this species group in site groups 1 (5 open-shelf day tows, 1 day tow at reef 2) and 2 (6 open-shelf night tows) are a result of

TABLE 2.—Demersal teleosts taken in ¾ Yankee trawl tows at the open-shelf study site, South Atlantic Bight, spring 1978. n = number of occurrences in 5 day or 6 night otter trawl tows.

		Day			Night		
Family	Species	No.	weight (kg)	n	No.	weight (kg)	n
Muraenidae	*Gymnothorax saxicola*	—	—	—	4	0.37	3
Synodontidae	*Synodus foetens*	3	0.57	2	—	—	—
	Synodus intermedius	2	0.14	2	3	0.40	1
	Trachinocephalus myops	—	—	—	1	0.08	1
Ogcocephalidae	*Ogcocephalus parvus*	2	0.04	1	1	0.01	1
Ophidiidae	*Ophidion beani*	—	—	—	4	0.23	3
	Ophidion holbrooki	—	—	—	4	0.34	2
Serranidae	*Centropristis ocyurus*	3	0.09	1	17	1.02	6
	Diplectrum formosum	3	0.23	2	9	1.13	3
Priacanthidae	*Pristigenys alta*	—	—	—	1	0.03	1
Lutjanidae	*Rhomboplites aurorubens*	—	—	—	2	0.10	2
Haemulidae	*Haemulon aurolineatum*	—	—	—	69	6.20	3
Sciaenidae	*Equetus lanceolatus*	—	—	—	2	0.09	1
Mullidae	*Mullus auratus*	—	—	—	1	0.07	1
Labridae	*Hemipteronotus novacula*	2	0.13	1	—	—	—
Scorpaenidae	*Scorpaena brasiliensis*	—	—	—	1	0.19	1
Dactylopteridae	*Dactylopterus volitans*	2	2.3	1	—	—	—
Bothidae	*Bothus ocellatus*	—	—	—	1	0.02	1
	Cyclopsetta fimbriata	—	—	—	1	0.09	1
	Gastropsetta frontalis	—	—	—	2	0.11	2
	Paralichthys dentatus	—	—	—	1	0.40	1
	Syacium papillosum	1	0.30	1	2	0.37	2
Balistidae	*Aluterus heudeloti*	2	1.60	1	1	0.05	1
	Monacanthus ciliatus	—	—	—	1	0.03	1
	Stephanolepis hispidus	4	0.14	3	315	14.30	6
Tetraodontidae	*Sphoeroides dorsalis*	3	0.19	3	—	—	—

TABLE 3.—Families and species of demersal fishes taken in 57 ¾ Yankee trawl tows in the sponge-coral habitat, South Atlantic Bight, during the spring of 1978. * = <0.1 kg.

Family	Species	No.	Weight (kg)	Family	Species	No.	Weight (kg)
Carcharhinidae	*Rhizoprionodon terraenovae*	1	1.3	Sciaenidae	*Equetus lanceolatus*	72	8.1
Rajidae	*Raja eglanteria*	11	6.6		*Pareques acuminatus*	1	*
Dasyatidae	*Dasyatis americana*	2	3.0		*Pareques umbrosus*	178	12.6
	Dasyatis centroura	1	90.7	Mullidae	*Mullus auratus*	12	0.6
	Dasyatis sayi	1	0.1	Chaetodontidae	*Chaetodon aya*	4	0.3
Muraenidae	*Anarchias yoshiae*	3	*		*Chaetodon ocellatus*	33	7.5
	Gymnothorax moringa	1	0.1		*Chaetodon sedentarius*	21	1.2
	Gymnothorax saxicola	6	0.9		*Chaetodon striatus*	1	0.1
	Muraena retifera	1	0.1	Pomacanthidae	*Holacanthus isabelita*	263	167.9
Congridae	*Ariosoma balearicum*	1	*		*Holacanthus ciliaris*	2	1.0
	Conger oceanicus	4	0.2		*Pomacanthus paru*	2	0.2
Synodontidae	*Saurida brasiliensis*	1	*	Pomacentridae	*Chromis enchrysurus*	1,801	40.0
	Synodus foetens	19	2.5	Labridae	*Halichoeres bathyphilus*	1	0.1
	Synodus intermedius	17	1.5		*Halichoeres bivittatus*	8	0.4
	Synodus poeyi	24	0.1		*Halichoeres caudalis*	10	0.4
	Trachinocephalus myops	2	0.2		*Hemipteronotus novacula*	2	0.2
Batrachoididae	*Opsanus* c.f. *pardus*	7	0.1	Labridae unidentified		1	*
	Porichthys plectrodon	44	0.9	Scaridae	*Nicholsina usta*	1	*
Gobiesocidae	*Gobiesox strumosus*	1	*	Uranoscopidae	*Kathetostoma albigutta*	11	0.5
Antennariidae	*Antennarius ocellatus*	1	0.5	Clinidae	*Starksia ocellata*	8	*
Ogcocephalidae	*Halieutichthys aculeatus*	1	*	Blenniidae	*Hypleurochilus geminatus*	4	*
	Ogcocephalus corniger	2	0.2		*Parablennius marmoreus*	32	*
Gadidae	*Urophycis earlli*	19	3.0	Callionymidae	*Callionymus pauciradiatus*	1	*
	Urophycis regia	5	0.3	Gobiidae	*Evermanichthys spongicola*	1	*
Ophidiidae	*Ophidion beani*	11	0.7		*Ioglossus calliurus*	1	*
	Ophidion holbrooki	51	4.0	Scorpaenidae	*Scorpaena brasiliensis*	17	2.7
	Ophidion selenops	6	*		*Scorpaena calcarata*	16	0.7
	Otophidium osmostigmum	4	*		*Scorpaena dispar*	2	0.2
Carapidae	*Carapus bermudensis*	22	0.1		*Scorpaenodes tredecimspinosus*	1	*
Holocentridae	*Holocentrus ascensionis*	2	0.6	Triglidae	*Prionotus carolinus*	120	7.5
Syngnathidae	*Hippocampus erectus*	3	0.1		*Prionotus ophryas*	9	0.7
Serranidae	*Centropristis ocyurus*	158	6.9		*Prionotus roseus*	5	0.3
	Centropristis striata	435	61.6		*Prionotus salmonicolor*	1	0.2
	Diplectrum formosum	84	5.0		*Prionotus scitulus*	7	0.3
	Mycteroperca microlepis	5	24.2	Bothidae	*Ancylopsetta quadrocellata*	18	6.2
	Mycteroperca venenosa	1	0.1		*Bothus ocellatus*	11	0.4
	Serranus phoebe	37	5.0		*Bothus robinsi*	7	0.2
Priacanthidae	*Priacanthus arenatus*	5	1.9		*Cyclopsetta fimbriata*	5	0.5
	Pristigenys alta	31	4.7		*Etropus microstomus*	3	*
Apogonidae	*Apogon pseudomaculatus*	174	0.4		*Paralichthys albigutta*	2	1.0
Lutjanidae	*Lutjanus campechanus*	3	0.4		*Paralichthys dentatus*	19	5.4
	Rhomboplites aurorubens	384	33.7		*Paralichthys lethostigma*	1	0.6
Haemulidae	*Haemulon aurolineatum*	3,153	239.5		*Syacium papillosum*	24	2.7
	Haemulon plumieri	16	13.6	Balistidae	*Aluterus heudeloti*	7	3.3
	Orthopristis chrysoptera	1	0.2		*Aluterus schoepfi*	28	19.8
Sparidae	*Archosargus probatocephalus*	11	11.7		*Balistes capriscus*	20	25.7
	Calamus bajonado	2	9.3		*Monacanthus ciliatus*	3	0.1
	Calamus leucosteus	319	135.4		*Stephanolepis hispidus*	1,392	93.8
	Calamus nodosus	25	26.6	Ostraciidae	*Acanthostracion polygonius*	2	1.4
	Diplodus holbrooki	3	0.2		*Acanthostracion quadricornis*	53	21.5
	Lagodon rhomboides	2	0.2	Tetraodontidae	*Spoeroides spengleri*	6	0.4
	Pagrus pagrus	46	23.5	Diodontidae	*Chilomycterus schoepfi*	8	2.9
	Stenotomus aculeatus	12,630	771.2		*Diodon holacanthus*	4	1.0
	Stenotomus caprinus	1	*				

the infrequent occurrence of *Stephanolepis hispidus* and *Haemulon aurolineatum* in some of these tows. The widespread distribution pattern of this species group is apparent in the low nodal fidelity values (Fig. 7).

Species group B consisted of an assemblage of fishes that were widely distributed in night reef samples. Species showed very low to low constancy and negative fidelity to site groups 1 through 7. Group B species displayed moderate to high constancy in the remaining site groups which consisted entirely of night trawl tows. This wide distributional pattern among night samples was reflected in the low fidelity values for all site groups.

Fishes of group C, although not very abundant, occurred almost exclusively in night trawl tows. Species in this group had low and high constancy, moderate and high fidelity to site groups 8 and 9, respectively, which were composed of night trawl tows from reefs 1 (38 m) and 2 (44 m). *Synodus intermedius* was the only species of this group that had a wide distribution in other site groups regardless of time of collection. *Bothus robinsi* and *Prionotus roseus* were found only in site groups 8 and 9, whereas the remaining species (*Kathetostoma albigutta*, *Cyclopsetta fimbriata*, *Ophidion selenops*, *Otophidium omostigmum*) occurred only in night tows of these and other site groups.

TABLE 4.—Ten most numerically abundant demersal teleosts taken spring 1978 in 57 sponge-coral habitat trawl tows, South Atlantic Bight.

Species	No. of individuals	% of total catch	Cumulative %	No. of occurrences
Stenotomus aculeatus	12,630	57.3		40
Haemulon aurolineatum	3,153	14.3	71.6	49
Chromis enchrysurus	1,801	8.2	79.8	9
Stephanolepis hispidus	1,392	6.3	86.1	52
Centropristis striata	435	2.0	88.1	37
Rhomboplites aurorubens	384	1.7	89.8	20
Calamus leucosteus	319	1.4	91.2	44
Holacanthus isabelita	263	1.2	92.4	28
Pareques umbrosus	178	0.8	93.2	24
Apogon pseudomaculatus	174	0.8	94.0	16

TABLE 5.—Ten most important demersal teleosts by weight in 57 sponge-coral habitat trawl tows taken spring 1978, South Atlantic Bight.

Species	Weight (kg)	% of catch	Cumulative %	No. of occurrences
Stenotomus aculeatus	771.2	42.1		40
Haemulon aurolineatum	239.5	13.1	55.2	49
Holacanthus isabelita	167.9	9.2	64.4	28
Calamus leucosteus	135.4	7.4	71.8	44
Stephanolepis hispidus	93.8	5.1	76.9	52
Centropristis striata	61.6	3.4	80.3	37
Chromis enchrysurus	40.0	2.2	82.5	9
Rhomboplites aurorubens	33.7	1.8	84.3	20
Calamus nodosus	26.6	1.4	85.7	11
Balistes capriscus	25.7	1.4	87.1	7

The five species of group D were rare in the trawl collections but had their greatest frequency of occurrence in night trawl tows from reef sites in depths >30 m. Members of group E were more abundant than group D and were collected primarily in night samples. They were not, however, restricted to reef sites, since five species (*Synodus foetens*, *Aluterus heudeloti*, *Scorpaena brasiliensis*, *Syacium papillosum*, and *Ophidion beani*) cooccurred in site group 2 (night open-shelf collections). Generally, this group was rarely found in day trawl tows but was widely distributed and abundant in night samples from all sites.

Species group F occurred almost exclusively at night and was most frequently encountered and abundant at site group 10 (6 night tows at reef 3; 1 night tow at reef 4). Low constancy values were observed for species at site groups 2, 7, 8, 9, and 12, whereas they exhibited high constancy and fidelity values for site group 10.

Group G had seven species that were relatively rare but most frequently found in daytime tows with maximum abundances in site group 7 (11 day samples from 4 reef areas). Group H also contained fishes that were widely distributed among site groups but not very abundant. Highest constancy and fidelity values were in site group 3 where species in group H had maximum abundance and frequency of occurrence.

Although members of species group I were found in several site groups, this assemblage was considered to be a regular component of the deeper reef sites where their greatest frequencies of occurrence and abundance were observed in day tows. Their affinity for deeper reefs is supported by high constancy and fidelity values in site groups 4 (3 day tows at reef 2, depth = 44 m), and moderate constancy and fidelity values in site groups 3 (4 day and 1 night tow at reef 5, depth = 42 m) and 5 (5 day tows at reef 1, depth = 37 m).

Diversity

More species were collected in night trawl tows in both open-shelf and reef habitats than in day tows. Comparisons of the mean number of species per tow in day and night samples at the open-shelf site showed night tows ($\bar{x} = 7.3$) had significantly more species than day tows ($\bar{x} = 3.6$) at the 95% probability level ($t = 2.905$, df = 9). The same trend was observed for samples from the sponge-coral habitat, pooled by time of collection. The 28 day tows had significantly fewer species ($\bar{x} = 10.8$) than night tows ($\bar{x} = 19.6$) at the 99% level ($t = 7.777$, df = 55).

Comparisons of the number of species per tow for each time period in the two habitat types showed that mean values for the open-shelf habitat were one-third to one-half the mean values for various reef sites. Night tows in the reef habitat had higher species diversity values than day tows. This was attributed to increased evenness and species richness (Table 6).

DISCUSSION

Standard otter trawl collections in the sponge-coral habitat (inshore and intermediate reefs of Miller and Richards 1979) yielded demersal teleost biomass estimates that were an order of magnitude higher than those of the open shelf (Table 7). Although these

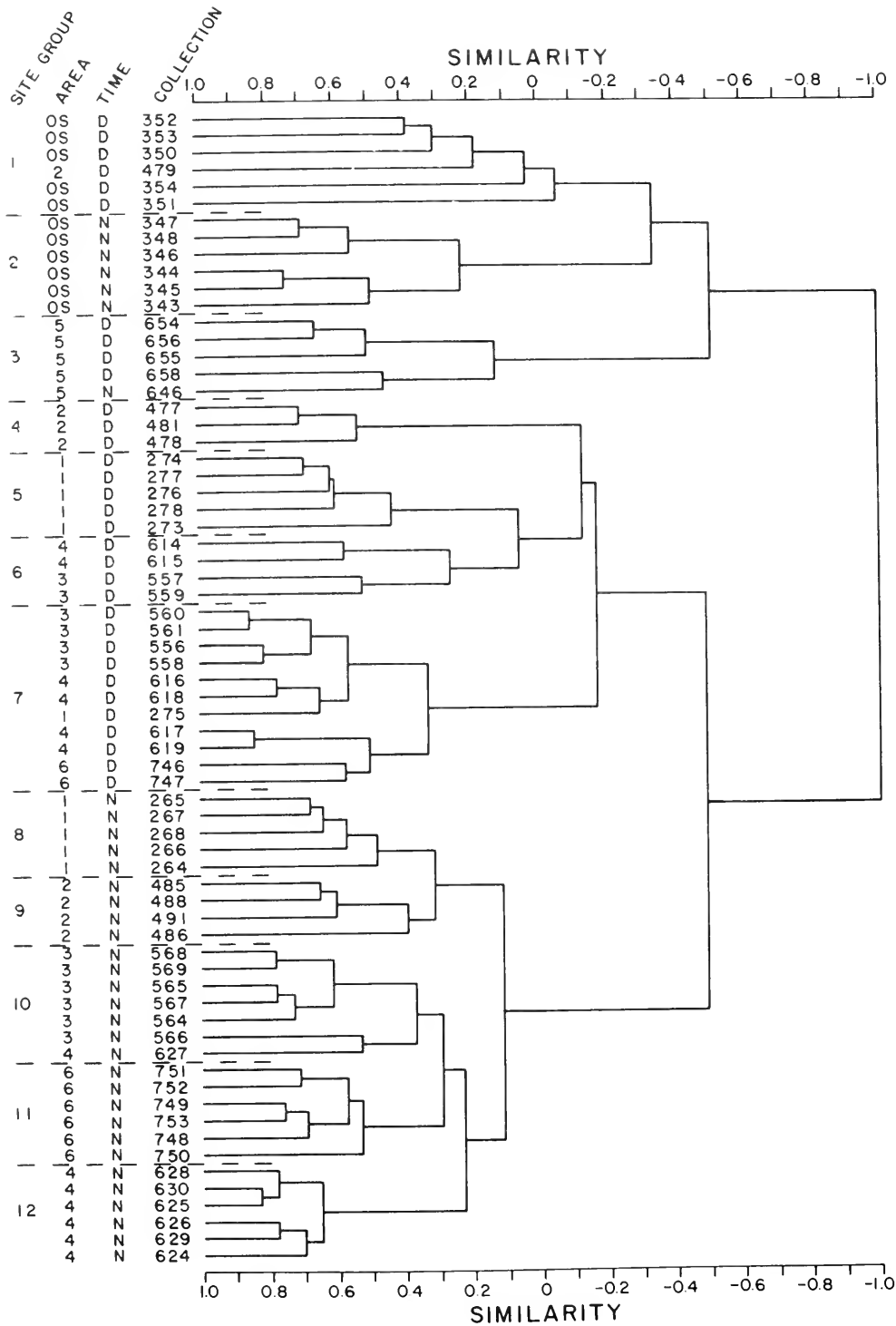

FIGURE 4.—Normal analysis (station cluster) of 1978 late spring sponge-coral habitat survey. OS = open shelf; D = day; N = night. Area refers to collection location; see Figure 2.

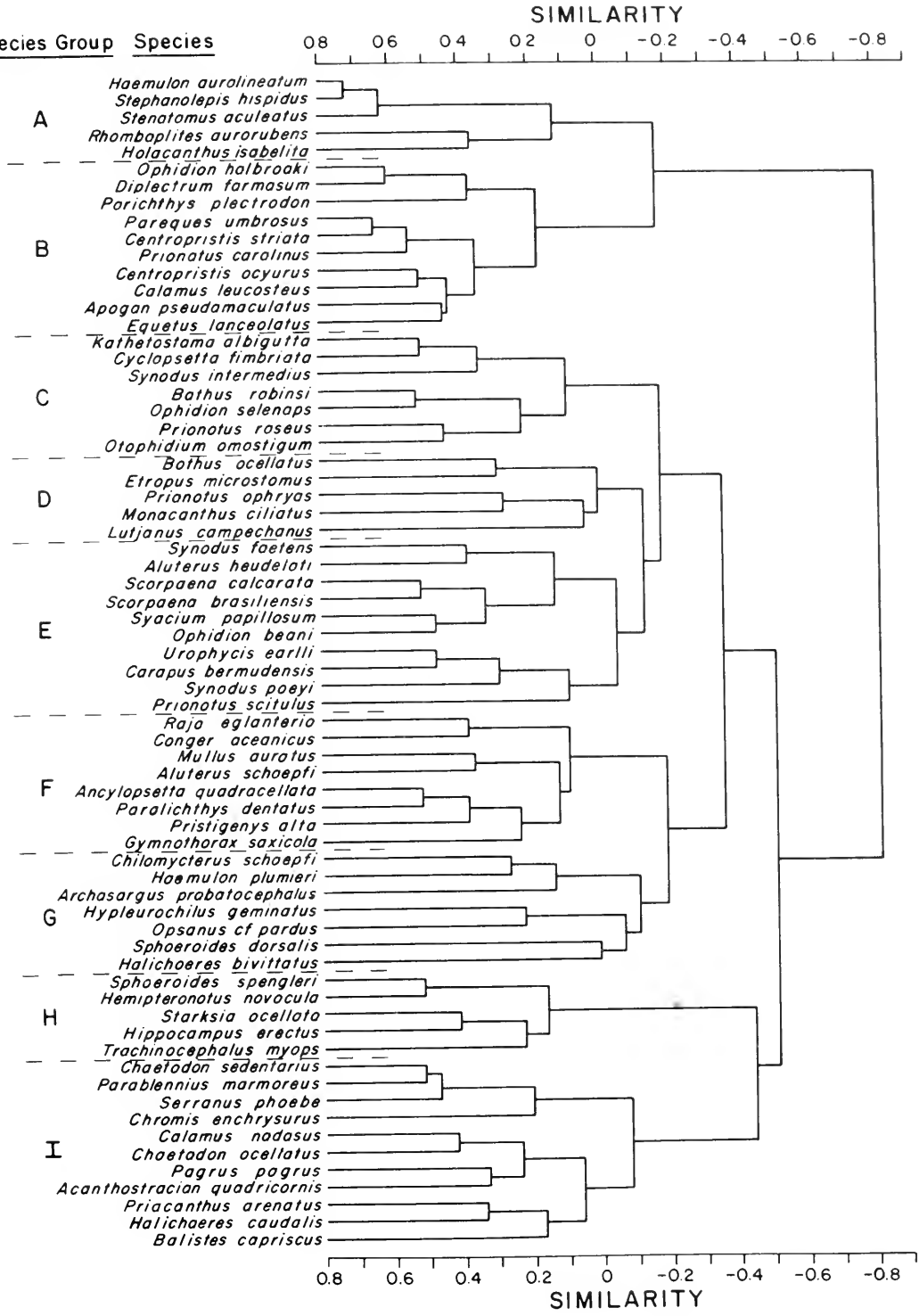

FIGURE 5.—Inverse analysis (species cluster) of 1978 late spring sponge-coral habitat survey.

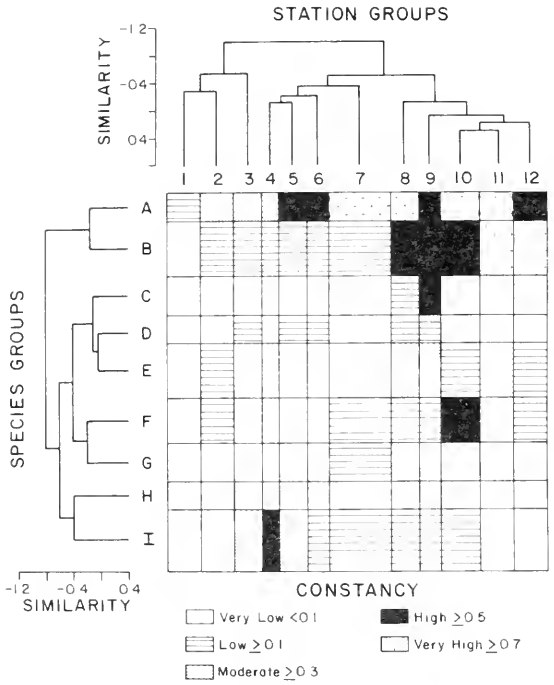

FIGURE 6.—Nodal constancy for station and species groups as defined by cluster analysis for the 1978 late spring sponge-coral habitat survey.

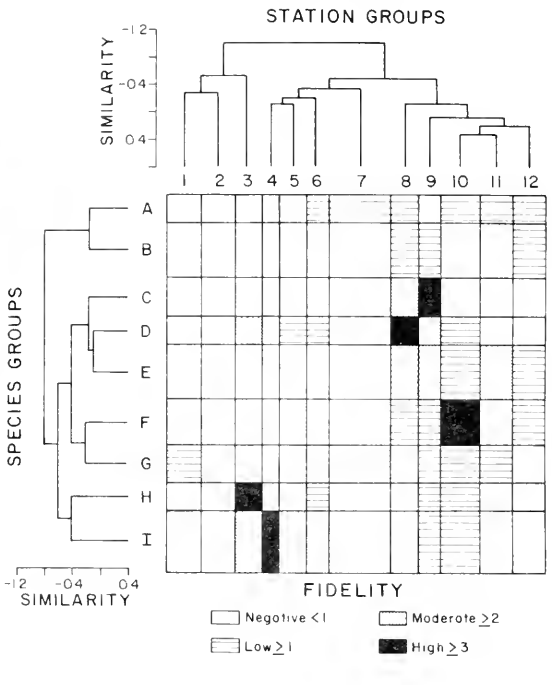

FIGURE 7.—Nodal fidelity for station and species groups as defined by cluster analysis for the 1978 late spring sponge-coral habitat survey.

TABLE 6.—Number of species/tow, diversity, evenness and species richness values for demersal fishes taken spring 1978 in ¾ Yankee trawl tows in the open shelf and sponge-coral habitat, South Atlantic Bight, LCL and UCL = lower and upper 90% confidence limits.

Site	Time	No. of species LCL	$\bar{x}$	UCL	Range	Diversity (bits/individuals) range	Evenness range	Species richness range
Open shelf	Day	1 9	3 6	5 3	2-7	0 918-2 646	0.918-1 000	0-1.242
Open shelf	Night	5 5	7 3	9 1	4-10	0.443-1 947	0.221-0 586	0 779-2 140
Reef 1	Day	9 0	13 3	17 6	6-22	1 697-3 185	0.380-0 920	1.364-3 143
Reef 1	Night	17 2	20 0	22 8	16-24	2 102-3 667	0.525-0 863	2 867-4 312
Reef 2	Day	3 8	9 2	14 7	5-15	0 383-2 251	0 148-0.394	0 911-2 541
Reef 2	Night	17 4	23.8	30 2	16-28	3 108-3 408	0 677-0 819	3.350-5 175
Reef 3	Day	7.0	9 2	11 4	6-13	0 311-2 119	0 093-0 706	0 894-1 849
Reef 3	Night	18 1	21 8	25.7	16-27	1 494-3 727	0.373-0 817	2 619-4 990
Reef 4	Day	9 1	10 0	10 9	9-12	0 621-2 621	0.196-0 789	1 131-2 324
Reef 4	Night	12 5	15 4	18 3	9-21	2 227-3 171	0 559-0.746	1 923-3.336
Reef 5	Day	6 9	12 5	18 1	8-18	0 131-1.037	0.041-0 345	1 212
Reef 5	Night	—	18 0	—	—	3 758	0 901	4 465
Reef 6	Day	—	10 5	—	8-13	1 654-2 515	0 551-0.697	1.467-2 746
Reef 6	Night	16.9	19 5	22 1	15-22	3 063-3.575	0.714-0 827	3.065-4.265

compared closely with values for a reef at a depth of 37 m off the South Carolina coast (Powles and Barans 1980), they were one to two orders of magnitude lower than tropical reef systems (Table 7), with the exception of an estimate of 40.4 kg/ha based on five visual transects at Rabbit Island in Hawaii (Brock 1954). This latter value, however, was indicative of marginal reef habitat, since the estimate was derived from counts taken largely over sandy bottom with an occasional rocky ledge or coral head.

Edwards (1968) provided a rationale for obtaining biomass estimates from otter trawl catches for resource surveys in the western North Atlantic. Catches are adjusted on a species-by-species basis using a correction factor which is derived from the individual species' availability and vulnerability to the survey gear. In addition, areal and seasonal changes in the species' distribution pattern are figured into the adjustment. Correction factors are determined from long-term distribution and relative

TABLE 7.—Summary of biomass estimates from South Atlantic Bight sponge-coral and open-shelf habitats and selected tropical reefs.

Area	kg/ha	Citation	Comments
South Atlantic Bight sponge-coral	27.3	Powles and Barans 1980	
South Atlantic Bight sponge-coral	31.0	Present study	
South Atlantic Bight open-shelf	5.6	Wenner et al. 1979a	fall, 1973
South Atlantic Bight open-shelf	5.0	Wenner et al. 1979b	spring, 1974
South Atlantic Bight open-shelf	2.9	Wenner et al. 1979c	summer, 1974
South Atlantic Bight open-shelf	3.2	Wenner et al. 1979d	winter-early spring, 1975
South Atlantic Bight open-shelf	3.2	Present study	
Keahole Point, Hawaii	1,856	Brock 1954	rock, boulders and coral
Waiane, Hawaii	417	Brock 1954	rock, coral and small sand patches
Hilo, Hawaii	214	Brock 1954	rock and coral
Waikiki, Hawaii	195	Brock 1954	some rock and coral, mostly thin sand over rock
Kealekekua Bay, Hawaii	145	Brock 1954	rock and coral with sand
Kumakahi Puna, Hawaii	144	Brock 1954	rock and sand, little coral
Hanauma Bay, Hawaii	154	Brock 1954	sand, rock and coral
Rabbit Island, Hawaii	40	Brock 1954	largely sand; occasional rocky ledge or coral head
Bermuda	490	Bardach 1959	
Virgin Islands	1,600	Randall 1963	

abundance data, observations from submersibles, underwater television observations of fish and their reactions to trawls, and comparative gear observations. Since we lack the necessary data to compile these values for South Atlantic Bight reef species and, hence, to judge trawl efficiency in sampling this habitat, the estimates of the present study should be considered minimum values. However, some qualitative gear efficiency observations can be made.

Since the ¾ Yankee otter trawl net has an average vertical mouth opening of only 1.25 m at a towing speed of 6.5 km/h, it is inefficient in sampling many of the commercially important lutjanids and sparids. Although *Pagrus pagrus*, the most commercially important sparid in the South Atlantic Bight (Ulrich et al. 1976), is a generalized benthic feeder (Manooch 1977), it frequently forms aggregations 2 m off the bottom on intermediate depth reefs. Vermilion, *Rhomboplites aurorubens*, and red snapper, *Lutjanus campechanus*, often show the same behavior. Although these species are represented in trap collections from various reef sites and are taken with hook-and-line gear, their low relative abundance (with the exception of small *R. aurorubens* in day trawl tows) can be explained by their unavailability to the net due to their position in the water column.

Comparisons of the dominant species from sponge-coral and open-shelf habitat studies in the South Atlantic Bight show that, with one exception, the sparid *Stenotomus aculeatus* is the most numerous trawl-caught demersal teleost. Powles and Barans (1980) cited tomtate, *Haemulon aurolineatum*, as the most abundant fish taken with the ¾ Yankee trawl at a sponge-coral site at a depth of 37 m. *Stenotomus aculeatus* taken in stratified-random otter trawl sampling in the open-shelf habitat were most abundant in depths <28 m (Wenner et al. 1979a, b, c, d). The means of the natural logarithmic values of the number of *S. aculeatus* per tow for each of the sponge-coral habitat sites are negatively correlated with the depth of the site ($r = -0.89$, $n = 7$). The numerical dominance of tomtate in the previous trawl study (Powles and Barans 1980) is a reflection of the greater site depth.

The most apparent feature of the species diversity and community analysis is the marked difference between day and night tows. The increased species diversity for night collections is attributed to a greater number of species and a more even distribution of individuals among species. Hoese et al. (1968) reported more species taken in night than day trawl tows in Texas coastal waters and attributed the differences to changes in species availability (movement from the sampling area; vertical movement above the headrope; burrowing into the substrate) or vulnerability (increased daytime net avoidance due to trawl visibility).

Most reef studies using visual census techniques have shown the diversity of fish species to be higher during the day than at night (Collette and Talbot 1972; Goldman and Talbot 1976; Helfman 1978). The results of the present study indicate the opposite to be true. Day trawl tows in the sponge-coral habitat had a lower diversity because these areas lack many of the diurnal species of labrids, scarids, pomacentrids, and acanthurids found in tropical systems. In addition, where night trawl samples contained fish that may be diurnal, the lack of hiding places associated with the luxuriant coral growth in the tropics increased the vulnerability of these fish to night trawl tows, despite the fact they were not actively moving about and feeding.

In the present study, certain families were collected more frequently in, or were restricted to, night trawl tows (Table 8). Ophidiids (4 species), sciaenids (3 species), and gadids (2 species) occurred only in night tows. Seven of the 15 most abundant species were taken significantly more frequently in night collections (Table 9). The explanation for these patterns varies according to the species.

The significantly greater frequency of occurrence in night catches of black sea bass, *Centropristis striata*, was caused by this species' increased vulnerability to night trawl tows. Trap and handline collections, as well as underwater television observations, have shown *C. striata* to be much more abundant than was indicated by our otter trawl tows. This supports the findings of Powles and Barans (1980).

Ophidioid fishes of the sponge-coral habitat are nocturnal species that were unavailable to day trawl tows. Starck and Davis (1966) indicated that although cusk eels were abundant in rotenone collections, they were never visually observed moving about reef systems during the day. These investigators found, however, that *Ophidion holbrooki* was active over the sandy portion of a Florida reef at night. When this species was disturbed with lights, it burrowed tail-first into the sand. Another species (*O. selenops*) was seen by Starck and Davis (1966) swimming near bottom in night dives at deeper water reef sites. The four species (*O. holbrooki*, *O. beani*, *O. selenops*, *Otophidium omostigmum*) collected during the present study were taken only in night trawl tows indicating that because of their daytime burrowing behavior, cusk eels are unavailable to day collections.

Atlantic midshipman, *Porichthys plectrodon*, is another nocturnal species that burrows into the sediment during daylight thus making itself unavailable to day trawl tows (Lane 1967). In laboratory tests (Lane 1967), *P. plectrodon* emerged from the substrate 45 min after sunset and burrowed about 45 min to 1 h before sunrise. Nocturnal feeding on near-bottom crustacean plankton was shown (Lane 1967).

Sciaenids (*Pareques umbrosus*, *Equetus lanceolatus*, *P. acuminatus*) were absent from all day samples but occurred in 27 of 29 night tows. Their absence from day collections can more likely be attributed to their unavailability rather than their decreased vulnerability to day trawl tows. Unlike the burrowing ophidioids and *Porichthys plectrodon*, these secretive sciaenids (Parker et al. 1979) seem to hide around or under available structures. Starck and Davis (1966) reported that *Pareques acuminatus* hides under rocks on the reef during the day and ventures out to feed at night. Hobson (1965) indicated that the closely related *P. viola* is a nocturnal foraging fish that hides under ledges and rocks during the day.

The daytime residence of *Apogon pseudomaculatus* in caves and crevices on the reef (Starck and Davis 1966) effectively excluded this species from the sampling capability of the trawl. The emergence of *A. pseudomaculatus* and other apogonids at night to forage on midwater plankton over the reef (Collette and Talbot 1972) explains the occurrence of this species only in night tows.

Triglids (*Prionotus carolinus*, *P. ophryas*, *P. scitulus*, *P. roseus*, *P. salmonicolor*) were found in only a single day tow but were in 23 of 29 night tows. The dominant northern searobin, *P. carolinus*, is a nocturnal species, however, which would seem to suggest that its greater frequency of occurrence in night trawl tows cannot readily be explained by a concomitant increase in its vulnerability to the gear. *Prionotus carolinus* is a common member of the South Atlantic Bight open-shelf ichthyofauna in depths from 9 to 55 m (Wenner et al. 1979a). Analysis of stratified, random ¾ Yankee trawl collections from summer 1974 and 1975 and fall 1973 showed that although this

TABLE 8.—Families of fishes taken primarily in night otter trawl tows in the sponge-coral habitat of the South Atlantic Bight.

	Day		Night	
Family	Present	Absent	Present	Absent
Ophidiidae	0	28	24	5
Scorpaenidae	2	26	16	13
Triglidae	1	27	23	6
Synodontidae	4	24	17	12
Bothidae	5	23	26	3
Sciaenidae	0	28	27	2
Gadidae	0	28	13	16
Batrachoididae	1	27	12	17

TABLE 9.—Comparison of frequency of occurrence of the 15 most numerically abundant species in day and night trawl tows in the sponge-coral habitat, South Atlantic Bight. * = significant at the 95% probability level.

	Day tows		Night tows		
Species	Present	Absent	Present	Absent	χ^2
Stenotomus aculeatus	17	11	23	6	1.54
Haemulon aurolineatum	20	8	28	1	5.00*
Chromis enchrysurus	7	21	2	27	0.07
Stephanolepis hispidus	23	5	28	1	1.79
Centropristis striata	13	15	24	5	6.73*
Rhomboplites aurorubens	12	16	6	23	2.29
Calamus leucosteus	22	6	22	7	0.01
Holacanthus isabelita	17	11	11	18	1.38
Pareques umbrosus	0	28	11	18	10.83*
Apogon pseudomaculatus	0	28	16	13	18.83*
Prionotus carolinus	0	28	17	12	20.67*
Acanthostracion quadricornis	13	15	13	16	0.00
Ophidion holbrooki	0	28	22	7	31.46*
Porichthys plectrodon	0	28	11	18	10.83*
Chaetodon ocellatus	8	20	6	23	0.07

species was encountered in more night (53%) than day tows (12%), the frequency of occurrence was not significantly different ($x^2 = 0.18$, df = 108). Based on the percent of fish with stomach contents, Ross (1977) found that peak feeding activity for eight species of searobins (*P. carolinus* not included) was in the morning. He indicated, however, that these triglids had some food items in the stomach at all times. Bigelow and Schroeder (1953) noted that *P. carolinus* burrows with only the eyes and head showing, and Bardach and Case (1965) confirmed that this species buries itself in the substrate. The available evidence, then, indicates that *P. carolinus* is a nocturnally active species that either buries itself in the sandy portions of the sponge-coral habitat during the day or makes nocturnal feeding forays into this habitat from the surrounding sandy areas where it resides during the day. Conclusive evidence can only be obtained from analysis of its food habits as determined from specimens collected in the sponge-coral habitat.

Haemulon aurolineatum were taken in significantly more night tows because dense day-resting schools dissociate at night when this species disperses to feed. It is well documented that grunts form resting schools on various reefs during the day (Starck and Davis 1966; Collette and Talbot 1972; Hobson 1973; Ebeling and Bray 1976; Ogden and Ehrlich 1977). At dusk, members of the school become active and undertake feeding migrations into areas near the reef which may have sandy bottom or algal cover. The dispersal of *H. aurolineatum* from dense daytime schools is reflected in the present study by changes in Morisita's index of dispersion (Elliott 1977) for day and night trawl tows. The index equals 1 for a random distribution, >1 for a contagious distribution, and <1 for a regular distribution (Elliott 1977). Day trawl tows had an index of dispersion of 5.51 which indicates a highly significant contagious distribution of *H. aurolineatum*. Night collections also had a significant contagious distribution, but the value of the index was much lower (1.44). By comparing both Morisita's index and the frequency of occurrence of *H. aurolineatum* in day and night tows, it can be inferred that tomtate disperse over the habitat during the night hours. In addition, the occurrence of tomtate in three of six night tows in the open-shelf study area provided evidence that the species leaves the sponge-coral habitat at night.

Although *Stenotomus aculeatus* occurred more frequently in night tows (79%) than in day tows (39%), the results were not significantly different. Southern porgy are daytime feeders (Harris 1979) which, as indicated by trawl results, form relatively large schools. The index of dispersion showed significant contagion in both day ($I_\delta = 4.14$) and night tows ($I_\delta = 2.43$); however, the lower night values indicate that the cohesiveness of the schools decreases at night. As a result of the greater nocturnal dispersal of this species throughout the sponge-coral habitat, the frequency of its occurrence in trawl tows increases. This accounts for the more consistent but lower catch rate at night, in comparison with day catches.

Stephanolepis hispidus showed the same pattern as *Stenotomus aculeatus* in its distribution and abundance in sponge-coral habitat tows. Planehead filefish were more aggregated during the day ($I_\delta = 3.99$) than at night ($I_\delta = 1.96$) and had a slightly higher frequency of occurrence in night trawl tows (97%) than in day collections, although the difference was statistically insignificant.

In addition to the species discussed above, several other less abundant fishes showed increased availability to night trawl tows in the sponge-coral habitat. The gadid *Urophycis earlli* was found only in night collections. Parker et al. (1979) reported *U. earlli* to be a secretive species that hid in and under artificial reef structures off the South Carolina coast. Daytime observations in winter revealed hundreds of Carolina hake under reef material (see Parker et al. 1979, fig. 10). Data from historical surveys indicate that *U. earlli* is a nocturnal species since almost all specimens collected by traps, handlines, and trawls were taken at night in the sponge-coral habitat or the rugged areas of the shelf-break (Wenner, unpubl. data). During the day, *U. earlli* probably hides under small ledges where it is unavailable to the trawl gear.

Carapus bermudensis is a nocturnal species that was unavailable to day otter trawl tows. This species spends its day residing in the respiratory tree of several species of holothurians and emerges at night to feed on near-bottom plankton (Starck and Davis 1966; Smith et al. 1981). Most bothids were encountered in night tows, probably due to these species' increased vulnerability at night.

In summary, day otter trawl catches were more variable in numerical abundance but frequently weighed more than night catches. This was due to the dense schools formed during daylight by species such as *Haemulon aurolineatum* and *Stenotomus aculeatus*. Night tows had more species because of the nocturnal availability of such species as *Apogon pseudomaculatus*, *Carapus bermudensis*, the ophidioids, etc., as well as the increased vulnerability of diurnal species such as *Holacanthus isabilita* and *Chromis enchrysurus*.

Comments on Use of Otter Trawl Nets in Sponge-Coral Habitat Surveys

Demersal trawl surveys are conducted in the northeast region of the United States to determine the species composition, distribution, and relative abundance of finfish, squids, and decapod crustaceans (Grosslein 1969). This survey has been designed so that the investigators can use some aspect of the catch per unit effort from research vessels to obtain an index of relative abundance for some groundfish stocks. This index, with appropriate adjustments, can be used (see Clark and Brown 1977) to derive regional stock-size estimates independent of the commercial catch. These, in turn, can be utilized for management decisions. In addition, some indication of the abundance of prerecruits can be obtained from the juveniles retained in the small mesh cod end liner of most research survey nets.

Although trawl gear can determine the size and relative abundance of many species that are available and vulnerable to the gear, its use to assess commercially harvested species of the sponge-coral habitat is suspect for the following reasons. First, as previously indicated, most commercially important lutjanids, sparids, and serranids are adept at avoiding the survey gear. High rise nets (otter trawls with greater vertical mouth openings) are more efficient in obtaining representative samples of these fishes, but swept-area estimates of the density of these species are unreliable. Most sponge-coral habitats have sections of small rock outcroppings and ledges where epinepheline serranids, lutjanids, and sparids aggregate. Because of possible gear destruction due to the high relief, these areas are untrawlable and catches in the remainder of the habitat show these species to be either absent or of minor importance. Trap and handline collections in untrawlable areas of this habitat document the localized abundance of these animals and indicate the importance of these species to the fish community.

Second, even with cod end liners, the ¾ Yankee and high-rise roller trawl nets fail to give indications of the abundance of prerecruits (Wenner unpubl. data). Available data indicate that the juveniles of epinepheline serranids are either spatially separated from the adults (*Mycteroperca microplepis*) or are cryptic forms which hide in cracks and crevices in this habitat (Johnson[5]). Juvenile *Rhomboplites aurorubens* are available and vulnerable to the gear during late summer months on 30-40 m sampling sites. This is the only species of the commercially important complex that is taken with any regularity.

Thus, otter trawl gear is neither effective in predicting recruitment of most commercially important species, nor reliable in providing accurate abundance estimates of these species. In addition, the physical habitat may sustain considerable damage caused by the bottom trawl net.

The ¾ Yankee trawl net effectively covers a much wider area of the bottom than the measured sweep (8.7 m) due to the configuration of the otter doors, ground cables, and bottom leg lines. Although this arrangement cannot increase the actual spread of the net beyond the headrope length, the passage of these cables over the substrate creates a disturbance that serves to herd fish in the path of the net (Baranov 1969). This net does, however, damage the sponge-coral habitat by shearing off sponges, soft corals, bryozoans, and other attached invertebrates. The 56 trawl tows made in the sponge-coral habitat for this study collected 2,351 kg of attached invertebrates (including sponges, soft corals, tunicates, bryozoans, and hydroids) yielding an average 42 kg/tow. This is only the amount of bottom material actually removed from the habitat. An estimate of the total amount of bottom destroyed by the doors, ground cables, and leg lines cannot be ascertained from the current study.

Personal observations and interviews with commercial fishermen attest to the productivity of the sponge-coral habitat. Most studies indicate the importance of habitat availability and space in determining the abundance and diversity of reef fishes (Emery 1978). With this in mind, and given the knowledge that 1) the use of the ¾ Yankee trawl net reduces the amount of attached invertebrate growth (the amount damaged by doors and ground cables is presently not quantifiable); 2) the places where the invertebrates had been attached may be sanded over and rendered unsuitable for recolonization; and 3) the removal of these attached invertebrates reduces refugees for decapods, polychaetes, etc., that are food items for *Centropristis striata* and other benthic feeders, one must conclude that the continued use of this trawl net reduces the amount of productive fish habitat. For these reasons, in addition to the ineffectiveness of the gear in sampling commercially important species, alternate nondestructive methods, such as direct observations or the use of mark-recapture techniques with trap catches, should be employed in assessment surveys of the commercially important species of this habitat.

[5]G. David Johnson, South Carolina Wildlife and Marine Resources Dept., P.O. Box 12559, Charleston, SC 29412, pers. commun., 1981.

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REPRODUCTIVE BIOLOGY OF THE BLUELINE TILEFISH, *CAULOLATILUS MICROPS*, OFF NORTH CAROLINA AND SOUTH CAROLINA[1]

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ABSTRACT

Blueline tilefish, *Caulolatilus microps*, were obtained by hook and line fishing and port sampling operations off North Carolina and South Carolina from 1972 to 1977. *Caulolatilus microps* spawn off the Carolinas from April through October, with peak activity off North Carolina in May-June and September-October. Multiple spawnings by individual females were indicated by multimodel size distributions of ova; this is complemented by the continuous production of spermatozoa in testes, which is facilitated by dynamic spermatogenic tubules. Fecundity is best predicted by fish weight: ln Fecundity = 0.016 + 1.832 ln Weight. Fecundity estimates ranged from 0.2 million ova for a 412 mm TL (0.82 kg) fish to 4.1 million ova for a 736 mm TL (4.85 kg) fish. Females attained sexual maturity between 425 and 450 mm TL (age IV-V). Males showed pronounced testicular development after age V (500 mm TL). Females were more abundant from 300 to 500 mm TL; the sex ratio was 1:1 between 500 and 600 mm TL; males predominated in size classes greater than 600 mm TL. Protogynous sex reversal in three juvenile specimens (156-202 mm TL) was indicated by transitional gonads or testes with residual oocytes. Previtellogenic oocytes in 8 of 42 mature males (436-700 mm TL) further suggest protogyny, although no adult fish with transitional gonads were observed. Whether blueline tilefish are strictly juvenile or functional hermaphrodites has yet to be determined.

The blueline tilefish, *Caulolatilus microps* Goode and Bean, is a semitropical demersal branchiostegid that constitutes a significant component of the deepwater grouper-snapper fishery off North Carolina and South Carolina (Huntsman 1976). It inhabits the outer continental shelf, shelf edge, and upper slope (70-235 m) from Cape Charles, Va., to Key West, Fla., and in the Gulf of Mexico from Pensacola, Fla., to Campeche, Mexico (Dooley 1978).

In 1972 scientists at the Southeast Fisheries Center of the National Marine Fisheries Service (NMFS) began studying the biology, community relationships, and population dynamics of the offshore demersal (reef) fishes off the southeastern United States, ultimately to provide effective management of this fishery (Huntsman 1976). The reproductive biology of blueline tilefish was investigated as part of that program, and is herein described with respect to 1) spawning seasonality, 2) descriptive gonadogenesis, 3) fecundity, 4) age/size of sexual maturity, 5) sex ratio with size, and 6) sexual transition.

The reproductive biology of *C. microps* is previously undescribed. Dooley (1978) reported the capture of ripe females in January and May through September off North Carolina. Brief notes on reproduction for other branchiostegids suggest protracted spawning seasons for *C. princeps* (Fitch and Lavenberg 1971), *C. affinis* (Dooley 1978), *Lopholatilus chameleonticeps* (Freeman and Turner 1977; Grimes[4]), and *Branchiostegus japonicus japonicus* (Hayashi 1977). Dooley and Paxton (1975) related the presence of several size classes of ova in maturing *B. wardi* and *B. serratus* to multiple spawning and found anomalous sex ratios within size classes. Pelagic eggs and larvae of *Caulolatilus* sp. and *L. chameleonticeps* have been collected off the Carolinas and in the northwest Atlantic (Freeman and Turner 1977; M. Fahay[5]).

MATERIALS AND METHODS

Blueline tilefish were captured over rugged precipitous bottoms as well as gently sloping sections of the shelf edge (Fig. 1). Specimens were obtained by hook and line fishing with electric reels and rods from

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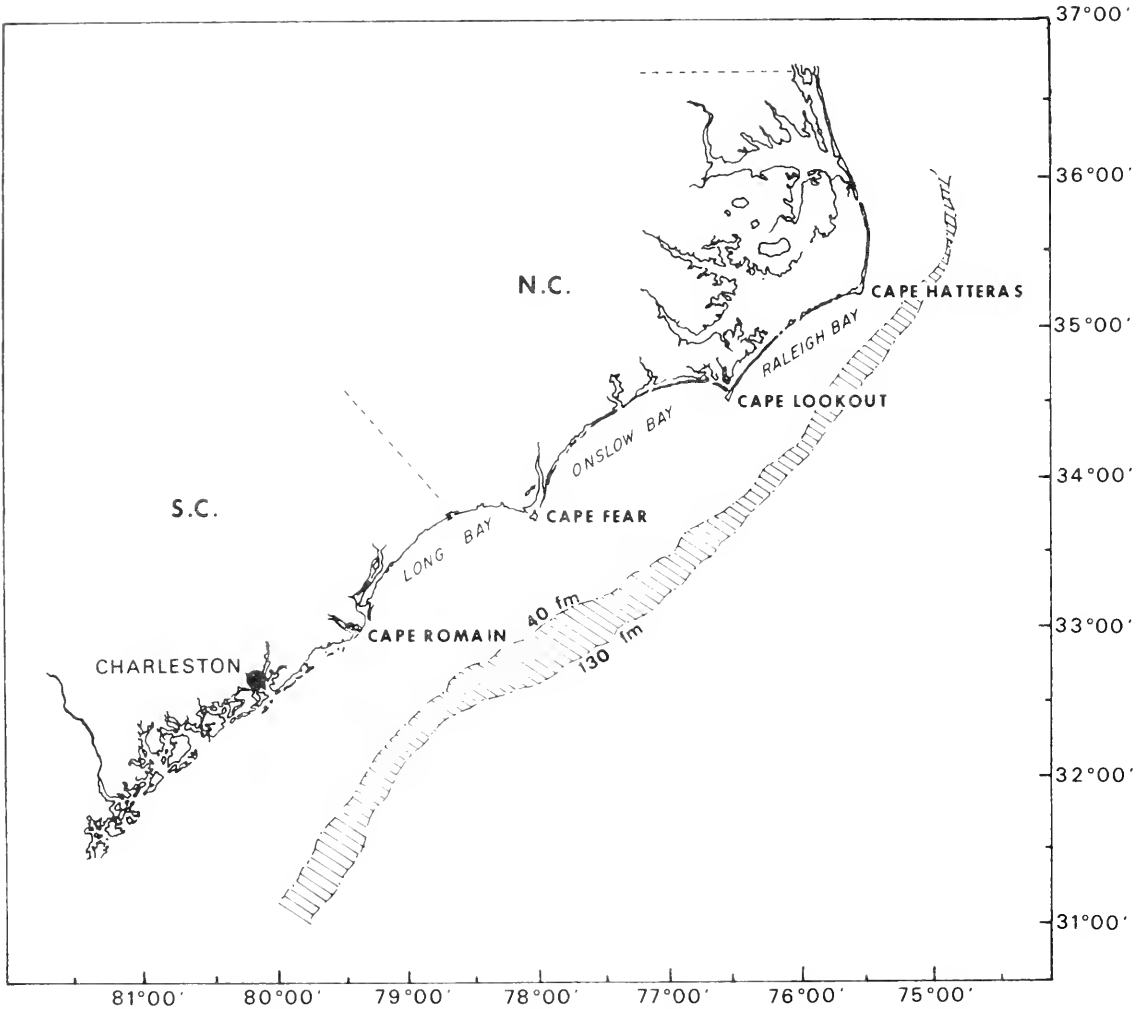

FIGURE 1.— Distribution of *Caulolatilus microps* off North Carolina and South Carolina (noted by hatch marked area).

1972 to 1977 in the northern and central portions of Onslow Bay aboard the RV *Onslow Bay* (NMFS). Fishing was most successful when baits were maintained as close to the bottom as possible. Total length (TL, mm) and total weight (W, g) were recorded for each fish, gonads excised and stored in 10% Formalin[6] and otoliths removed and stored in glycerine. Sampling of headboats fishing out of North Carolina and South Carolina ports provided ancillary records of total length and total weight, and samples of gonads and otoliths.

A gonosomatic index (GSI) was calculated according to the formula

$$GSI = \frac{GW}{W} \times 100$$

where GW = preserved gonad weight (0.1 g) and W = total body weight (g). GSI was used to determine spawning seasonality and sexual maturity.

Sex was determined by gonad examination since blueline tilefish apparently exhibit no sexually dimorphic characteristics. Ovaries and testes were staged macroscopically and histologically after preservation in 10% Formalin (Tables 1, 2). Ova stages corresponded to those described by Moe (1969) for red grouper, *Epinephelus morio*: oogonia, 2-8 μ; stage I, early oocytes, 20-50 μ; stage II, previtellogenic oocytes, 40-170 μ; stage III, early vitellogenic oocytes, 110-260 μ; stage IV, active vitellogenic oocytes, 215-650μ; stage V, mature ova, 735-910 μ

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

with 140-196 μ oil globule. Spermatogenic stages were analogous to those described by Moe (1969) for red grouper and Hyder (1969) for *Tilapia*. Routine histological methods were used for slide preparations from Formalin-fixed gonads.

Frequency distributions of ova diameters were plotted by gonad stage to determine individual spawning patterns. Representative females were selected for each ovarian stage. The diameter of 50 ova from each occurring stage (previtellogenic, early vitellogenic, active vitellogenic, and mature oocytes) were measured from each sample using a gridded petri dish and a magnification of 70×. A ratio of the four stages was then determined by reducing the magnification to 20× and counting two or more entire grids until about 500 ova were counted. This ratio was reduced to a base of 200 and combined with ova diameter frequencies per stage data using the ratio

$$\frac{\text{frequency of ova stage}}{200} \times \frac{\text{ova diameter frequency}}{50}$$

to determine the relative frequency of each size group.

Well-Developed and Ripe ovaries from fish captured from April through September were used for fecundity estimates. One ovary randomly selected from each pair was weighed to the nearest 0.1 g. The ova were teased free of the ovarian tunic. Two subsamples were removed and all vitellogenic ova (stages III-V; determined by relative size and opacity of cytoplasm) were counted. The sample and subsamples were oven dried and weighed to the nearest 0.001 g. The formula

$$Y = \frac{(W)\ (w_t)}{(W_t)\ (w)}\ y$$

was used to estimate fecundity, with Y = total number of eggs in both ovaries, W = wet weight of both ovaries, W_t = wet weight of selected ovary, w_t = total dry weight, w = total dry weight of subsamples, and y = number of ova in subsamples (Manooch 1976).

TABLE 1.—Developmental stages of *Caulolatilus microps* ovaries.

Maturity stage	External appearance	Ova composition
Immature (stage 1) (>250 mm TL)	Small, maroon, sausage to teardrop shaped hollow organs	Ovigerous lamellae composed of dense aggregations of undifferentiated oogonia and primary oocytes
Resting (stage 2)	Flaccid triangular sacs with translucent tunic and dark reddish internal mass	Primarily early and previtellogenic oocytes with <1% early vitellogenic oocytes.
Developing (stage 3)	Ovary becomes increasingly rotund while maintaining a basic triangular shape; yellowish orange appearance due to granular ovigerous mass tunic becomes more transparent, and ova are discernable	Previtellogenic oocytes numerically dominant with some early and active vitellogenic oocytes Well-developed ovaries contain an increasing number of vitellogenic oocytes evenly distributed over a large size range (215-650 μ).
Well-Developed (stage 4)	Ovarian tunic becomes nearly transparent yellowish ova densely packed and discernable	Vitellogenic oocytes predominant and evenly distributed over a large size range (215-650 μ).
Ripe (stage 5)	May-August. Greatly distended, bulbous and occupying more than 1/3 of the peritoneal cavity, very light orange to white in color, 2-4% body weight. Ova clearly visible through delicate, nearly transparent tunic.	Broad size distribution of vitellogenic oocytes, with a mode of very large (420-640 μ) vitellogenic oocytes together with stage III and small (215-400 μ) stage IV oocytes. Mature oocytes (785-910 μ) characteristically contained in lumen, free of ovigerous lamellae.
	September-October Ovaries comparatively smaller, firm, more triangular though rotund, 1-2.4% body weight.	A mode of large stage IV oocytes with stage V oocytes present and relatively few small (215-400 μ) stage IV oocytes.
Recently Spent-Redeveloping. (stage 6-3)	Resemble deflated early developing ovaries; distinguished by inflamed ventral, posterior portion, otherwise cream colored.	Stage III and small stage IV oocytes occur together with some very large stage IV and stage V oocytes, the latter often in an atretic state.
Spent (stage 6)	Flaccid, reduced in size; muscular tunic contracting and becoming firm, inflamed.	No evidence of vitellogenesis, stage IV and V oocytes are atretic; a few stage III oocytes occur.

TABLE 2.—Developmental stages of *Caulolatilus microps* testes.

Maturity stage	External appearance	Spermatogenic activity
Immature/Resting	Basically threadlike maroon organs with slight laterally compressed expansion posteriorly above sperm duct.	Spermatogenic tubules generally inactive, though spermatozoa may occur in lumen of spermatogenic tubules and collecting tubules.
Developing	Maroon, thin, elongate, laterally compressed, with widest portion directly above sperm ducts, tapering rapidly to filamentous anterior projection.	Spermatogenic tubules contain crypts at all developmental stages with spermatozoa collecting in the lumen and collecting tubules.
Well-Developed	More robust, triangular to nearly cornucopia shaped, tapering anteriorly. Maroon to creamy off-white color.	Extensive collections of spermatozoa in expanded lumens of actively developing spermatogenic tubules, with channeling of spermatozoa into medial collecting tubules.
Ripe	No running ripe testes observed	

Juvenile specimens were obtained for gonadal analysis from the Field Museum of Natural History, Chicago, Ill., and the Institute of Marine Science, University of North Carolina, Morehead City, N.C.

RESULTS

Gonadal Development

The paired ovaries of *C. microps* are suspended below the swim bladder by mesovarium in the most posterior portion of the body cavity. The mesovarium extends the length of the ovary and contains the ovarian arteries. Oogenesis and vitellogenesis occur within the ovigerous lamellae which are distributed evenly and project laterally and medially from the tunica albuginea. The absence of lamellae from a narrow band in the ventral portion of the ovary forms an ovocoel. This facilitates ovarian expansion and collection of ripe ova released from the lamellae prior to extrusion through the common oviduct (Moe 1969).

Testes of blueline tilefish are solid, smooth textured, compressed laterally, and relatively more elongate than ovaries. They are suspended from the swim bladder by the mesorchium, which has a wide base of attachment along the medial surface. Each testis enters the urinary papilla by a separate sperm duct.

The structure and developmental pattern of the testes are similar to that described by Smith (1965) as tubular. The primary spermatogenic units are radial spermatogenic tubules and spermatogenic crypts. In cross section, the spermatogenic tubules are essentially a ring, one spermatogonium or one spermatogenic crypt thick (Fig. 2). An elastic connective tissue, the Sertoli cells, encapsulates and maintains the integrity of the tubules and the individual developing crypts. It presumably serves as the site of steroidogenesis (Lofts 1968; Hoar 1969). Development proceeds at varying rates within each spermatogenic tubule, analogous to that in the ovigerous lamellae, so that active spermatogenic tubules usually contain crypts at all stages of development (Fig. 3). Spermatids were the most advanced stage observed within a crypt. Spermiogenesis, the morphogenesis of spermatid to spermatozoa, occurred around the time of passage from crypt to the lumen of the spermatogenic tubule.

Whereas in many fishes the interstitial tissue separating the developing tubules breaks down at later stages of development resulting in extensively

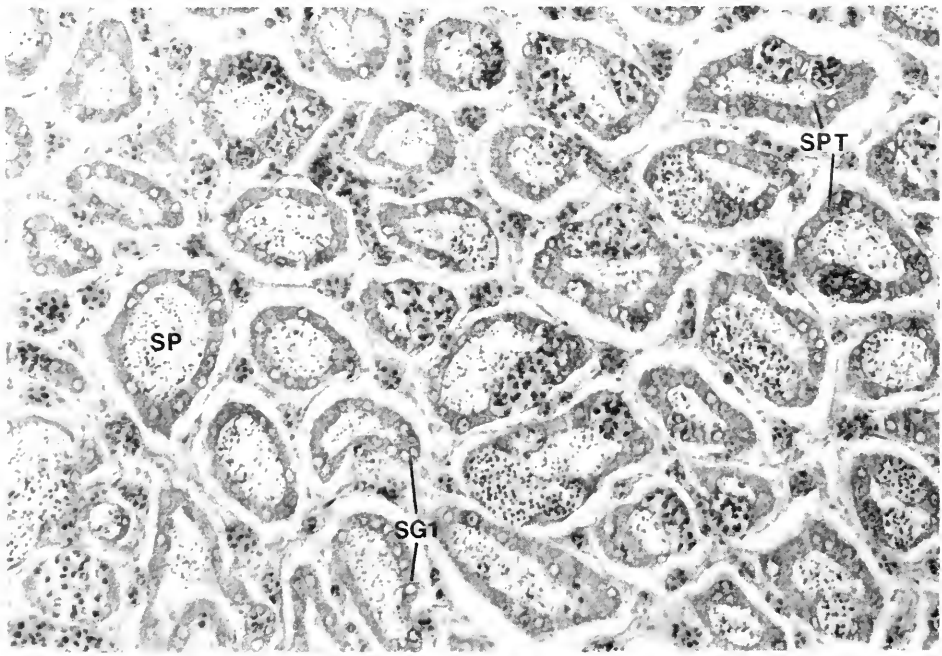

FIGURE 2.—Cross section of Early-Developing testes from a 530 mm TL *Caulolatilus microps* collected 15 March 1977. Note radial spermatogenic tubules (SPT) composed principally of primary spermatogenia (SG1) with few developing crypts, and the presence of spermatozoa (SP) in the lumen of the spermatogenic tubules (Haematoxylin × 200).

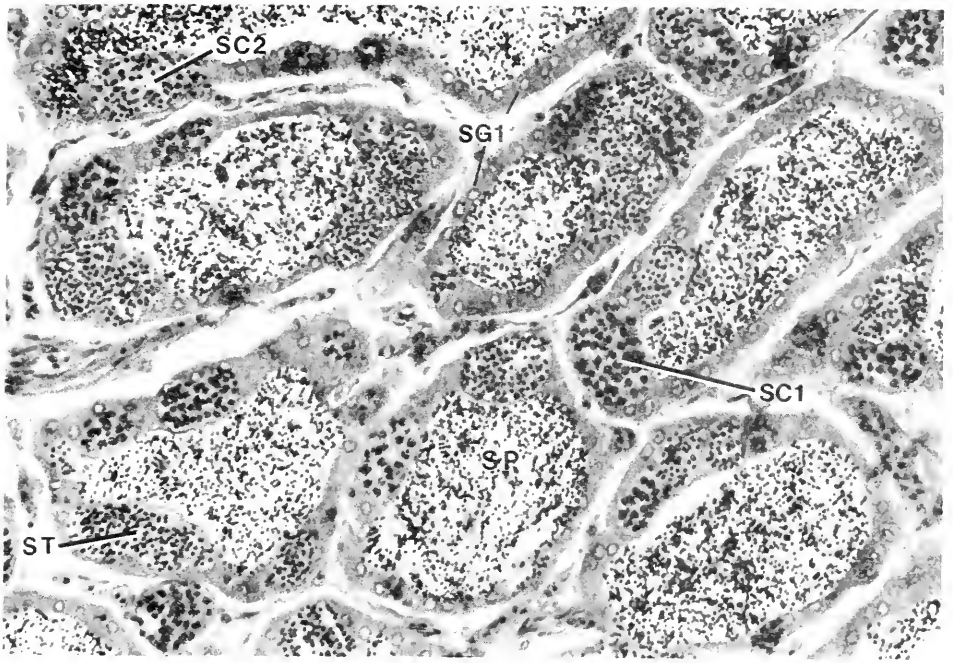

FIGURE 3.—Cross section of Developing testes from a 664 mm TL *Caulolatilus microps* captured 9 September 1974. Note spermatogenic tubules composed of the spectrum of developing crypt stages, with primary (SG1) spermatogonia; primary (SC1) and secondary (SC2) spermatocytes; spermatids (ST); and collections of spermatozoa (SP) in the lumen (Haematoxylin and eosin × 200).

packed sinuses of spermatozoa, the spermatogenic tubules of *C. microps* maintain their integrity. Drainage of spermatozoa from the testes results from the dynamic nature of the tubules. In the course of their development, they migrate medially from the lateral epithelium. Several observations support this hypothesis. In an early-developing male captured in May (Fig. 4), the lateral spermatogenic tubules are undeveloped and inactive with small amounts of spermatozoa in the lumen. Those adjacent to the dorsomedial portions of the testes are also generally inactive but contain larger collections of spermatozoa. This suggests that longevity of spermatogenic tubules exceeds one season and that spermatogenic tubules generate from the peripheral interstitium (Lofts 1968). The spermatogenic tubules adjacent to the dorsomedial connective tissue in developing testes are generally the most well developed, and can be seen merging with the medial collecting tubules (Fig. 5). The collecting tubules have boundary cells that are essentially connective tissue, and contain only spermatozoa. The spermatogenic tubules can be distinguished, since they are bordered by active spermatogenic crypts. Testicular drainage is thus accomplished by a dorsomedial migration of spermatogenic tubules and their merging with and releasing of spermatozoa into the collecting tubules. The collecting tubules channel the spermatozoa posteriorly and ventrally into the separate sperm ducts.

Spawning Seasonality

Caulolatilus microps spawn off North Carolina and South Carolina between April-May and September-October. Monthly mean GSI values for 138 females and 101 males captured off North Carolina exhibited peaks in May and September (Fig. 6). Early-Developing ovaries were predominant from February through April. High GSI values in May corresponded to the greatest incidence of Well-Developed and Ripe females (Fig. 7). The lower mean GSI values observed in June, July, and August corresponded with a diversity of gonad stages including Early-Developing, Well-Developed, Ripe, and Recently Spent-Redeveloping ovaries. Ovaries were again synchronously Well-Developed or Ripe in September though considerably smaller than gonads observed in May and June. Low GSI values from November through March reflect a period of gonad

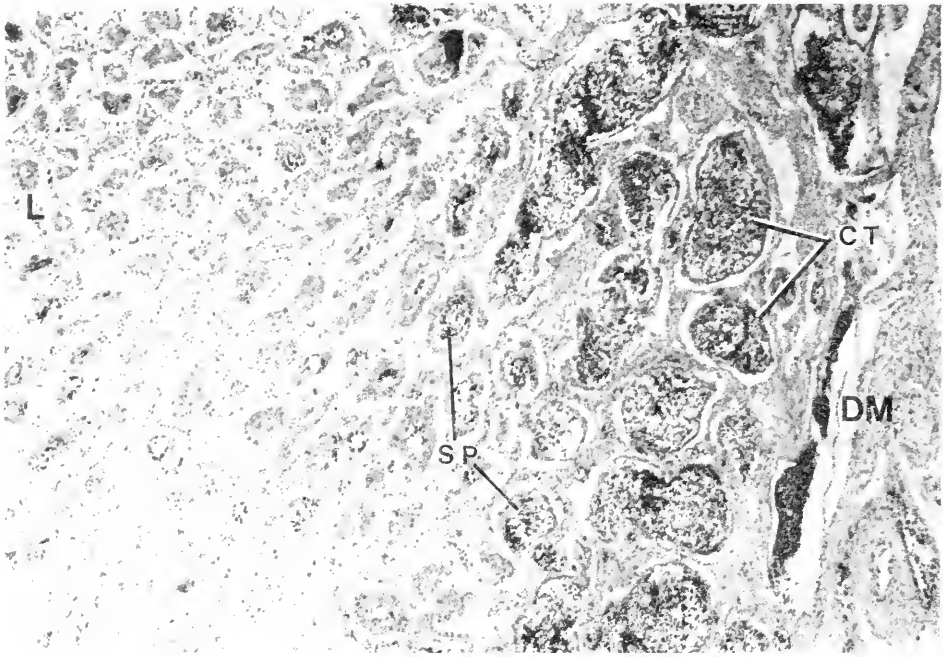

FIGURE 4.—Cross section of Resting testes from a 410 mm TL *Caulolatilus microps* collected 15 March 1977. Note undeveloped state of lateral (L) spermatogenic tubules and increased collections of spermatozoa (SP) in spermatogenic tubules and collecting tubules (CT) located along dorsomedial (DM) region (Haematoxylin and eosin × 78).

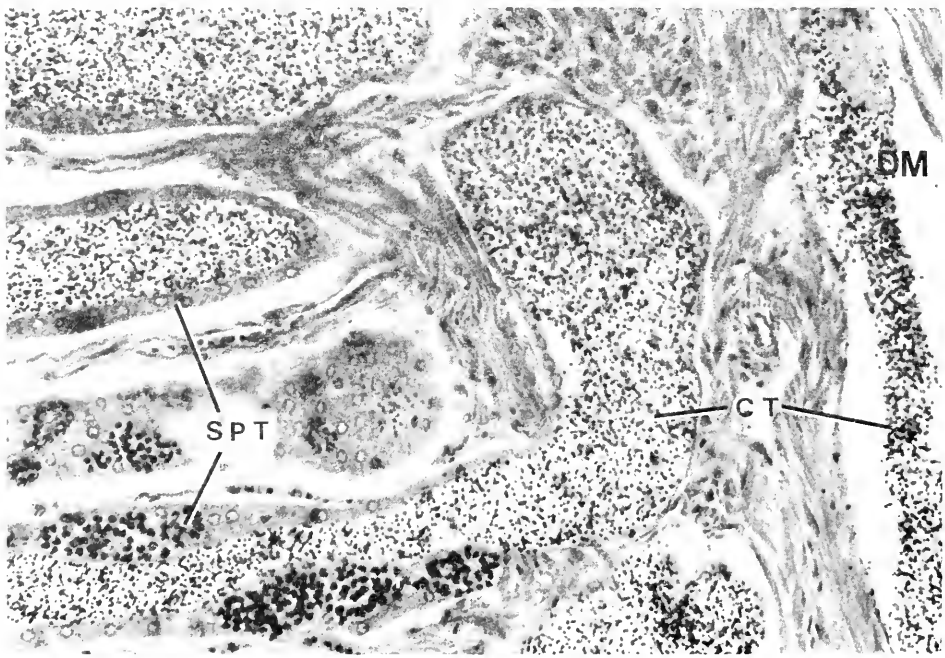

FIGURE 5.—Cross section of Developing testes from a 664 mm TL *Caulolatilus microps* collected 9 September 1974. Note spermatogenic tubules (SPT) composed of active crypts merging with and channeling spermatozoa into collecting tubules (CT) which occur along the dorsomedial (DM) tunica albuginea (Haematoxylin and eosin × 256).

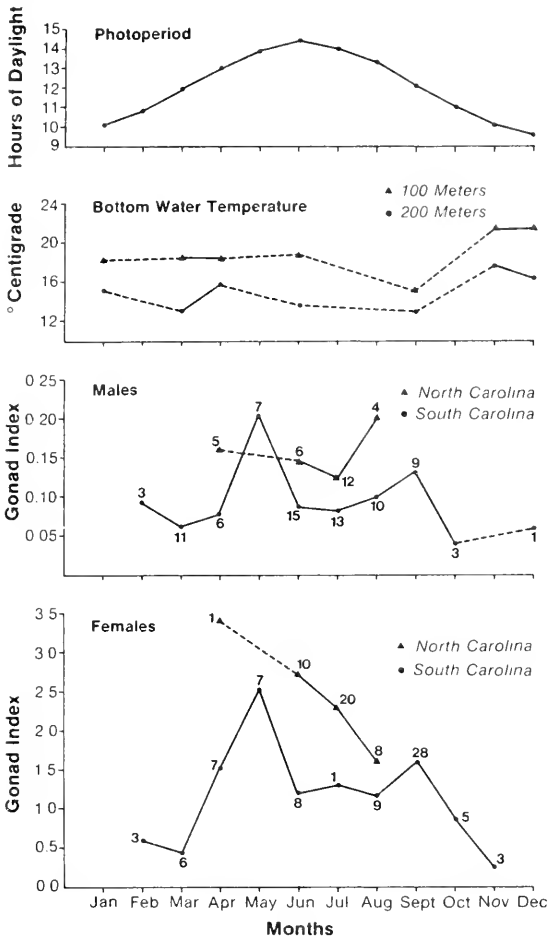

FIGURE 6.—Monthly mean gonad index values for male and female *Caulolatilus microps* from North Carolina and South Carolina, mean bottom temperatures off Beaufort, N.C. (Stefansson and Atkinson 1967), and photoperiod.

regression and early development. Ripe females were captured off South Carolina during April and July, which could indicate a more continuous or three-peaked spawning season. Monthly mean GSI as well as mean standard length were greater for females off South Carolina, but data are too limited to draw any further conclusions.

Analysis of ova development within individual ovaries suggested that blueline tilefish are multiple spawners (Fig. 8). Ovaries considered Resting characteristically contained primary oocytes and previtellogenic oocytes. Early-Developing ovaries showed a progression of early vitellogenic oocytes developing from the residual stock. Well-Developed ovaries in late April contained a mode of late vitellogenic oocytes cooccurring with previtellogenic

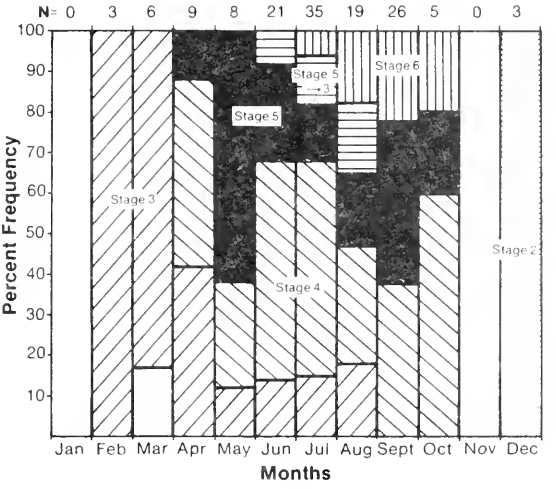

FIGURE 7.—Percent frequency histogram of gonad developmental stages observed each month for female *Caulolatilus microps* from North Carolina and South Carolina.

and early vitellogenic oocytes (Fig. 9). Ripe females from May and June exhibited modes of previtellogenic oocytes, early vitellogenic oocytes, late vitellogenic oocytes, and mature eggs. This indicated continuous development from the residual stock of oocytes occurred when spawning was imminent. Early vitellogenic ova are predominant in Spent-Redeveloping ovaries and cooccur with residual mature, atretic mature, and late vitellogenic oocytes. Late vitellogenic oocytes were again the predominant oocytes in Well-Developed ovaries during September. There was also a decreased proportion of early vitellogenic oocytes in comparison with Well-Developed gonads from May.

Males accommodate the protracted season of oogenesis by maintaining a constant state of development during the spawning season. The two peaks in GSI of testes coincided with those observed for ovaries (Fig. 6). Testes contained some spermatozoa in all months sampled and observed histologically, while those from April through September generally contained large quantities of spermatozoa in the collecting tubules. However, we never captured any males with free-running milt.

Fecundity

We estimated the fecundity of blueline tilefish from three periods during their spawning season. Fecundity ranged from 210,000 ova (412 mm TL) to 3,220,000 ova (637 mm TL) for 18 fish captured from April to early June (Fig. 10). Fecundity was significantly correlated with both length and weight:

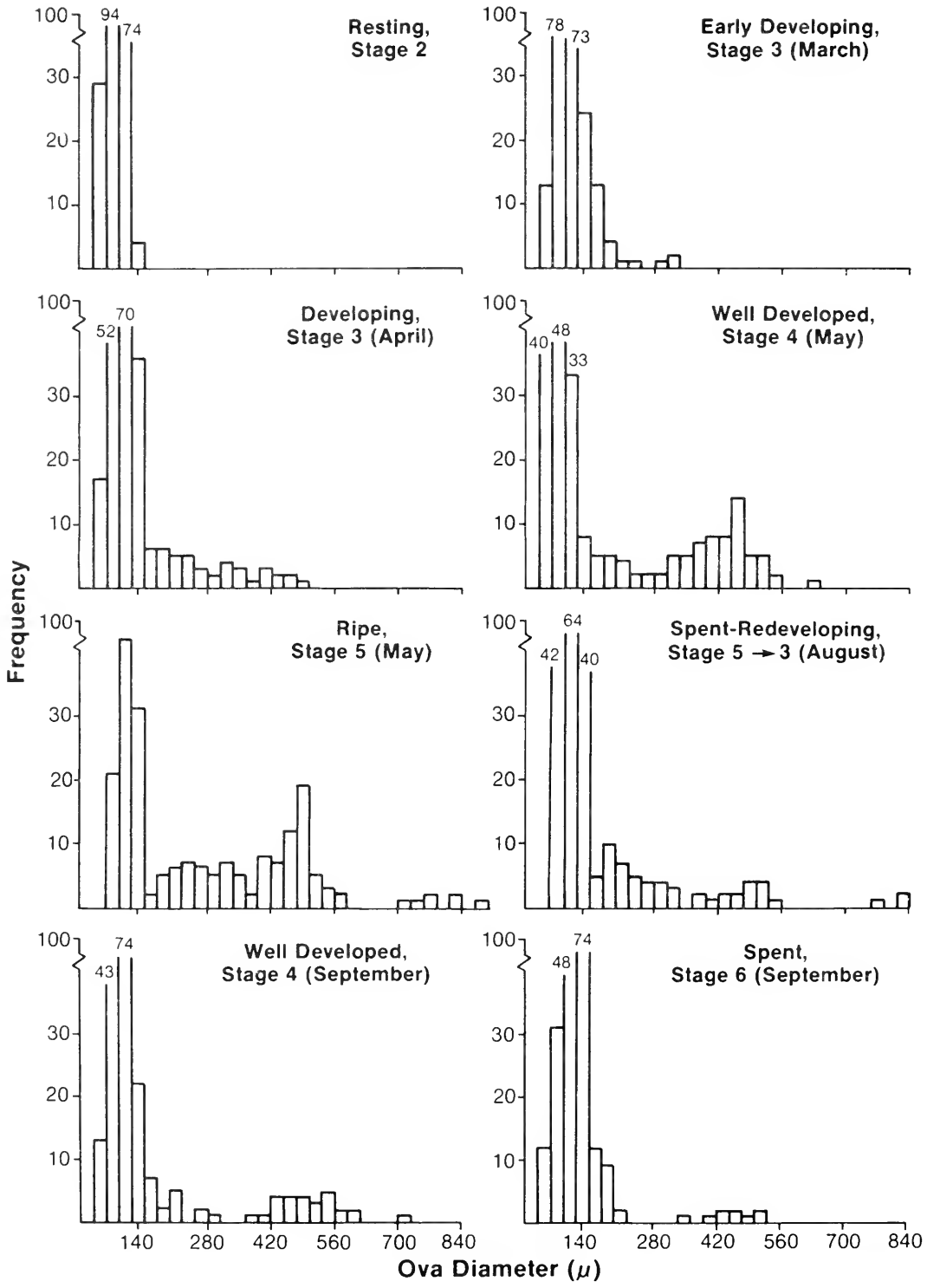

FIGURE 8.—Ova diameter frequency distributions for designated ovarian developmental stages for female *Caulolatilus microps* from North Carolina.

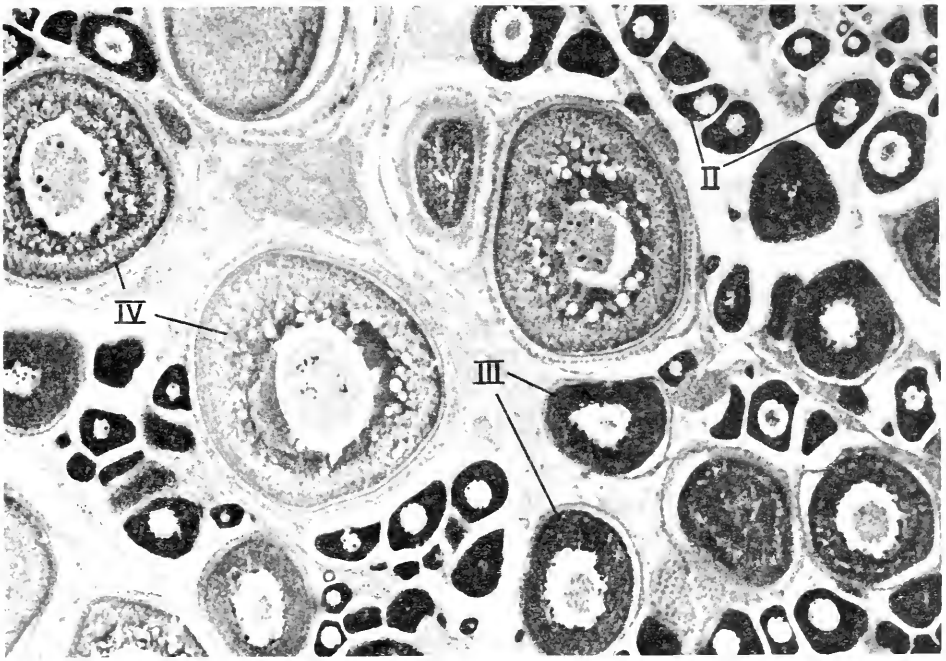

FIGURE 9.—Cross section of Well-Developed ovary from a 515 mm TL female *Caulolatilus microps* (21 April 1977) with lamellae composed of residual stock previtellogenic oocytes (II), early vitellogenic oocytes (III), and late vitellogenic oocytes (IV) (Haematoxylin and eosin × 63).

$$\ln \text{Fecundity} = 8.830 + 0.00986 \text{ Total length}$$
$$r^2 = 0.74, \text{ and}$$
$$\ln \text{Fecundity} = 0.016 + 1.832 \ln \text{Weight}$$
$$r^2 = 0.78.$$

Fecundity for 14 Ripe females captured in July basically agreed with the above fecundity relationship; the estimates ranged from 196,000 (436 mm TL) to 4,107,035 ova (736 mm TL). The estimated fecundity of 12 Well-Developed and Ripe females from September decreased approximately one-third to one-half. The production of vitellogenic ova appears greater during the late spring-early summer spawning peak than the early fall peak. However, insufficient data on the frequency of spawnings by individuals within age/size groups and the number of eggs released preclude further refinement of individual annual fecundity estimates.

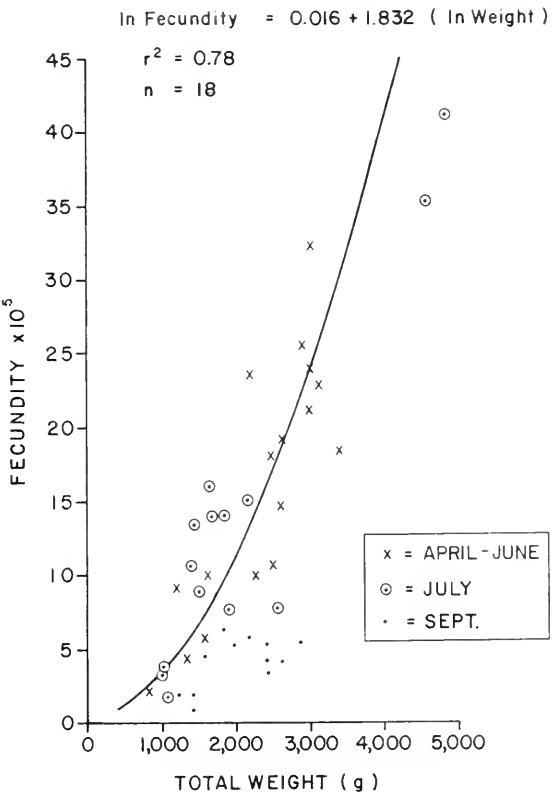

FIGURE 10.—Fecundity-weight relationship for *Caulolatilus microps* collected in April to June. Fecundity estimates are plotted for fish captured in July (South Carolina) and September (North Carolina).

Sexual Maturity

Maturity of females, defined as the size at which >50% of the individuals were gonadogenically active, occurred between 425 and 450 mm TL (Table 3) which is typically a 4- or 5-yr-old fish (Ross and Huntsman 1982). One of three age III females (387-421 mm TL), 50% of the age IV ($n = 8$; 427-506 mm TL), 73% of the age V ($n = 15$; 430-546 mm TL), and 100% of the age VI+ females were mature. The pattern of ovarian development corroborated the macroscopic maturity analysis. Relative gonad weight increased with total length after initial steep increases in relative gonad size between 400 and 500 mm TL. Mean GSI and maximum relative gonad weights were consistently greater for females captured off South Carolina than those captured off North Carolina, although the biological reason for this is unknown.

TABLE 3.—Percentage of sexually mature female and male *Caulolatilus microps* from North Carolina and South Carolina.

Total length	Females		Males	
	N	Percent mature	*N*	Percent mature
250-300	3	0		
301-325				
326-350	1	0		
351-375	2	0		
376-400	5	20.0	1	0
401-425	11	45.5	1	0
426-450	8	75.0	4	0
451-475	11	81.8	3	0
476-500	11	90.9	5	20.0
501-525	24	100.0	8	50.0
526-550	24	100.0	9	77.8
551-575	18	100.0	9	77.8
576-600	8	100.0	8	87.5
601-625	13	100.0	7	100.0
626-650	11	100.0	13	100.0
650+	4	100.0	41	100.0

Male *C. microps* show little gross testicular development under 500 mm TL (Table 3). Macroscopically, 50% were considered immature between 500 and 525 mm TL and 100% attained maturity above 600 mm TL. No age IV ($n = 4$; 436-453 mm TL) and only 12.5% of the age V males ($n = 8$; 485-574 mm TL) were considered mature, and a majority (62.5%) had not matured until age VI ($n = 8$; 520-556 mm TL). The initial and most pronounced increase in relative testis size occurred in males >500 mm off North Carolina and males >600 mm off South Carolina. Histological examination of testes from males 390-500 mm TL ($n = 11$) revealed spermatogenesis and collections of spermatozoa in fish macroscopically considered immature. These testes were very small (<0.08% body weight) and maroon in color. We could not determine whether this represented precocious development or functional maturity.

Sex Ratio and Sexual Transition

Males outnumbered females in the combined North Carolina and South Carolina collections (195 to 176), but this was not significantly different from a 1:1 ratio ($\chi^2 = 0.97$). However, sex ratios become skewed when size (Table 4) or age (Table 5) are considered. Females were more numerous between 300 and 500 mm TL, and in several cases there were significant deviations from 1:1. Between 500 and 600 mm TL

TABLE 4.—Frequency of male and female *Caulolatilus microps* from North and South Carolina within 25 and 100 mm TL intervals, with Chi-square values assuming a 1:1 sex ratio.

Length	Male	Female	Percent female/25 mm	χ^2	Percent female/100 mm	χ^2
101-200	3	1			25	1.0
201-300		1			100	
301-325						
326-350		1	100		88	5.4*
351-375		1	100			
376-400	1	6	86	3.57		
401-425	1	6	86	3.57		
426-450	7	12	63	1.32	67	9.89*
451-475	6	20	77	7.54*		
476-500	14	19	58	0.75		
501-525	20	23	53	0.21		
526-550	15	18	55	0.27	52	0.32
551-575	19	22	54	0.22		
576-600	18	16	47	0.12		
601-625	19	16	46	0.26		
626-650	16	8	33	2.67	30	16.9*
651-675	20	3	13	12.57*		
676-700	15	2	12	9.94*		
701-725	11	0	0			
726-750	5	1	17		9	15.6*
751-775	3	1	25			
776-800	2	0	0			

*$P \leq 0.05$.

TABLE 5.—Frequency of male and female *Caulolatilus microps* from North and South Carolina within age groups with Chi-square values assuming 1:1 sex ratio.

Age	Females	Males	χ^2
II	1		1.8
III	3	1	
IV	16	4	7.2*
V	26	15	2.95
VI	16	9	1.96
VII	11	7	0.89
VIII	11	16	0.93
IX	7	4	0.82
X	4	12	4.00*
XI	1	3	1.0
XII	0	6	6.0*
XIII	0	2	
XIV	0	2	3.57
XV	1	2	

*$P \leq 0.05$

the sex ratio was essentially 1:1. In fish >600 mm TL, males became increasingly and significantly more abundant. Similarly, females outnumbered males in ages III through VII while males became predominant for ages X through XV.

Histological evidence from four juvenile blueline tilefish indicated prematurational sex reversal. The gonad from a 186 mm TL specimen was ovarian and composed of basophilic oogonia with some primary oocytes (Fig. 11). The remaining three specimens had gonads which exhibited progressive stages of sex reversal. The earliest stage (202 mm TL) was predominantly ovarian with an acidophilic germinal testicular mesothelium proliferating through the ovigerous lamellae from the dorsomedial connective tissue (Fig. 12). The proliferating mesothelium contained primary spermatogonia and would be the site of steroidogenesis, inducing atresia and the recycling of ovarian elements (Hoar 1969). Gonads of two specimens (178 and 184 mm TL) in advanced stages of sex reversal had differentiated into the basic testicular components with spermatogenic tubules present and spermatogenesis proceding (Figs. 13, 14). Both specimens revealed evidence of a previous ovarian stage in the form of atretic structures, residual oocytes, or proliferating testicular mesothelium along the peripheral epithelium. These specimens were all captured in March and were within the size range predicted for *C. microps* after one year of growth (Ross and Huntsman 1982). Residual oocytes were also observed in 8 of 41 developing testes from adult males (Fig. 15). These fish were 430-700 mm TL and had solid testes which exhibited no other remnant ovarian structures.

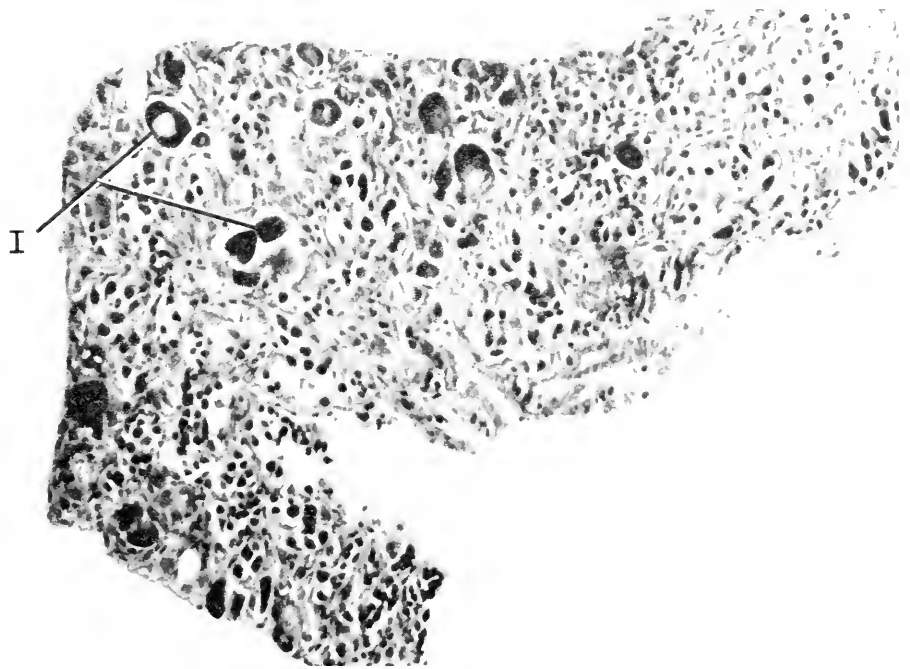

FIGURE 11.—Cross section of ovary from a juvenile 186 mm TL *Caulolatilus microps* collected 13 March 1961 with oogonia and primary oocytes (I) (Haematoxylin and eosin × 200).

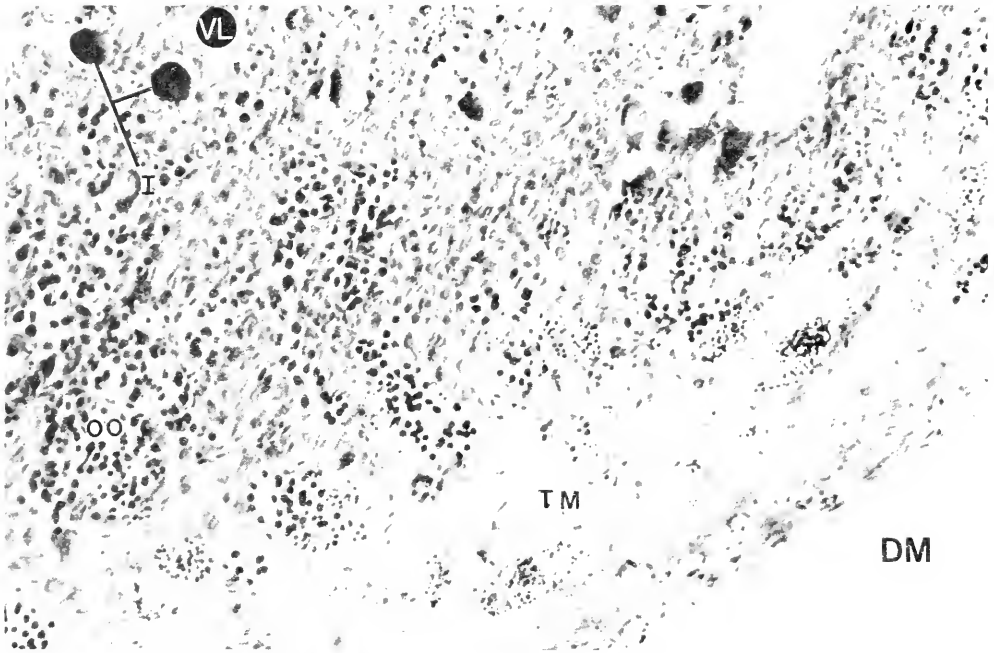

FIGURE 12.—Cross section of gonad from a juvenile 202 mm TL *Caulolatilus microps* collected 13 March 1961. Note occurrence of oogonia (OO) and primary oocytes (I) along ventrolateral region (VL) with proliferating testicular mesothelium (TM) originating from dorsomedial areas (DM) (Haematoxylin and eosin × 200).

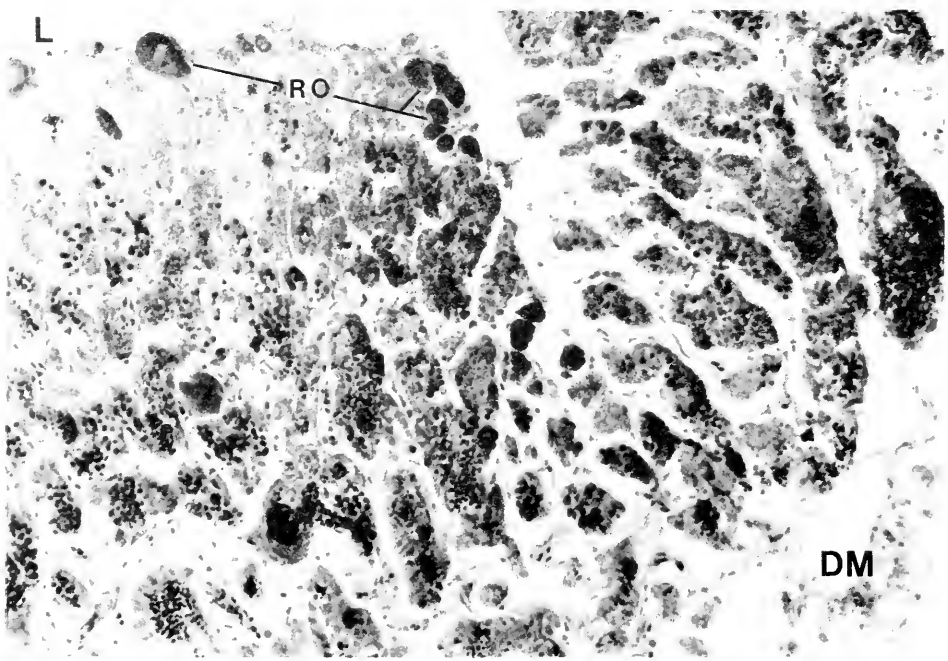

FIGURE 13.—Cross section of gonad from a juvenile 184 mm TL *Caulolatilus microps* collected 13 March 1961. Note spermatogenic tubules composing dorsomedial region (DM) and residual oocytes along lateral (L) gonadal margin (Haematoxylin and eosin × 200).

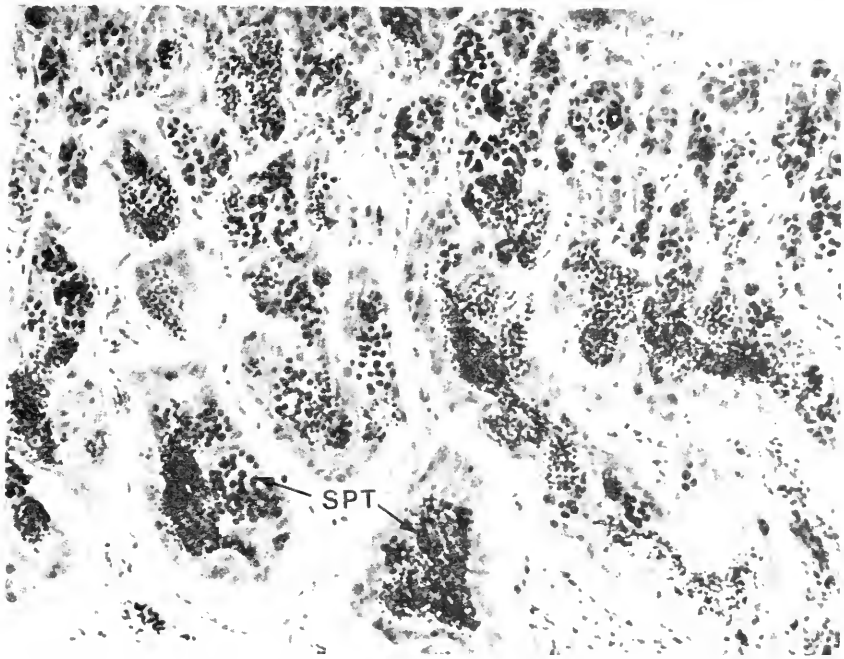

FIGURE 14.—Cross section of gonad from a juvenile 184 mm TL *Caulolatilus microps* collected 13 March 1961. Note in this closeup of previous gonad the well-defined spermatogenic tubules (SPT) (Haematoxylin and eosin × 400).

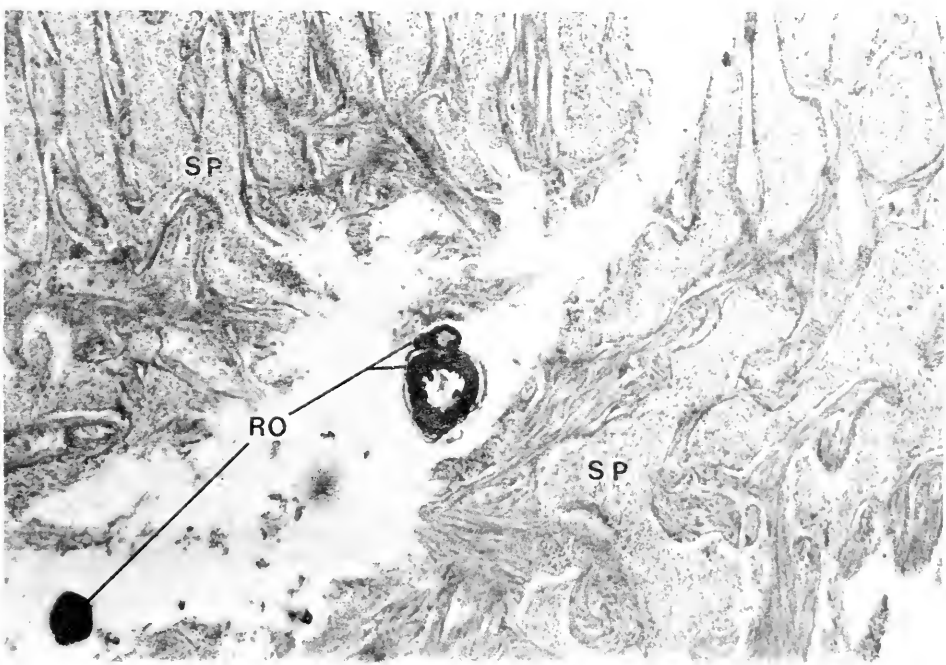

FIGURE 15.—Cross section of Well-Developed testes from a 562 mm TL *Caulolatilus microps* captured 22 April 1977. Note extensive collection of spermatozoa (SP) and occurrence of residual previtellogenic oocytes (RO) (Haematoxylin and eosin × 78).

DISCUSSION

The initiation of gonadogenesis in blueline tilefish during March and April and the termination in September-October coincide with the periods of rapidly increasing and decreasing photoperiods (Fig. 6). This is a more conservative environmental cue than temperature when considering the shelf edge habitat. Temperature fluctuations are not necessarily seasonal, but also subject to cold-water intrusions from outer continental shelf bottom waters and meanderings of the axis of the Gulf Stream (Stefansson and Atkinson 1967). The initiation of gonadal development has also been correlated with photoperiod for the cooccurring red porgy, *Pagrus pagrus*, (Manooch 1976). The protracted spawning of vermilion snapper, *Rhomboplites aurorubens*, was correlated with both photoperiod and water temperature (Grimes and Huntsman 1980); however, its occurrence over the continental shelf increases its susceptibility to seasonal temperature variation.

Blueline tilefish ovaries seasonally undergo a progressive maturation of residual stock oocytes to vitellogenic state with several modes generated and no sharp distinctions between residual and maturing eggs. The multimodal size distribution of oocytes observed is characteristic of fishes that spawn several times during a protracted spawning season (Clark 1934; Warner 1975a; Grimes and Huntsman 1980). Off North Carolina it appears that most *C. microps* spawn during May-June and September-October. The capture of large females (>600 mm TL) that were Ripe in July and August might indicate more frequent spawning by larger fish. The generally larger females captured off South Carolina might spawn earlier and more frequently than those off North Carolina, although data supporting this conclusion are incomplete. The continuous developmental pattern of male testes would certainly accommodate protracted spawning by females.

If local spawning is directed toward the maintenance of regional populations (Marshall 1966), the production of several batches of eggs during a protracted spawning season should improve chances of concurrence with favorable environmental conditions. Of particular relevance to *C. microps* spawning are the influence and extent of transport of eggs and larvae by the Florida Current (Gulf Stream). The ridge and trough bottom irregularity off South Carolina known as the Charleston Bump causes a seasonal deflection of the Gulf Stream and resulting inshore southwest setting eddy currents occurring as far north as Cape Hatteras (Brooks and Bane 1978). These are effective around the 50-100 fathom curves and could be an important means of regional retention of eggs and larvae produced by *C. microps* and other shelf edge inhabitants.

Whether *C. microps* are strictly prematurationally or also functionally protogynous cannot as yet be confirmed. Winter (between spawning periods) collections are needed to determine whether transitional adults occur. The skewed sex ratios with size and age could indicate that sex reversal occurs over an extended range of ages rather than just prematurationally. However, skewed sex ratios with size could be attributable to differential growth rates, which have been noted for *C. microps* (Ross and Huntsman 1982) as well as *L. chameleonticeps* (Turner et al.[7]) and other tilefishes (Dooley 1978). Skewed sex ratios with age could result simply by <50% of the juvenile females changing sex to males. Furthermore, functional protogyny is questionable since 1) all males possessed solid testes, whereas secondary males generally retained remnants of the hollow ovarian lumen (Smith and Young 1966; Warner 1975a) and 2) the existence of 400-500 mm males would have entailed their sex reversal prior to functioning as reproductive females.

Prematurational sex reversal, evidenced by histological examination of juvenile gonads, accounts for the presence of oocytes in developing testes. The development of remnant ovarian gonocytes to previtellogenic oocytes in a testis could result from the activation of estrogens, the presence of which is implicit had there been a juvenile female stage (Bruslé 1969; Bruslé and Bruslé 1975). The males with residual oocytes were captured in the spring, the period of maximum hormonal induction for initiating gonadogenic activity (Hoar 1969). The residual oocytes were previtellogenic oocytes which 1) are reported to be the most resistant oocytes to resorption and atresia (Bruslé and Bruslé 1975) and 2) were observed in medial connective tissue or in collecting tubules and not interspersed within active spermatogenic tissue.

The occurrence of prematurational sex reversal in *C. microps* should indicate protogyny elsewhere in its genus or family. This is possible though not yet confirmed for several related species. Atlantic goldface tilefish, *C. chrysops*, captured off North Carolina and in the Gulf of Mexico ($n = 20$) include 7 females 385-

[7]Turner, S. C., C. B. Grimes, and K. W. Able. In prep. Age, growth mortality and age/size structure of the fisheries for tilefish, *Lopholatilus chameleonticeps*, in mid-Atlantic and southern New England waters. Department of Environmental Resources, Rutgers University, P.O. Box 231, New Brunswick, NJ 08903.

503 mm TL and 13 males 503-562 mm TL (Ross unpubl. data). The sex ratio for anchor tilefish, *C. intermedius*, off Texas is 66 females:5 males between 100 and 270 mm TL, and 0 females:8 males >270 mm TL (Ross, Pavela, and Chittenden unpubl. data). Dooley (1978) reported anomalous sex ratios for *L. chameleonticeps*, *B. wardi*, and *B. serratus*. Clark and Ben-Tuvia (1973) reported pairs of *Malacanthus hoedtii* outside burrows including a large male and a smaller female. Prematurational sex reversal is also suspected of the tilefish, *L. chameleonticeps*, based on juvenile gonadal histology and adult sex ratio data (Grimes footnote 4).

Prematurational sex reversal in *C. microps* is likely a regression from monandric protogyny to functional gonochorism. The size-advantage model, which attributes protogyny to cases where an individual reproduces most efficiently as a female when young and a male when it gets older (Ghiselin 1969) is generally applicable when such things as inexperience, male dominance, mate selection, or territoriality lead to a differential in male reproductive success at older ages (Warner 1975b). Caulolatilids presumably evolved in the Caribbean and are often associated with reef-type habitat (Dooley 1978) where protogyny is widespread (Choat and Robertson 1975; Smith 1975; Warner 1975a, b). A radiation of *C. microps* (or ancestor) in the evolutionary past from a reef-type environment to more extensive outer continental shelf and upper slope habitats may have reduced the selection pressure favoring protogyny. The increase in utilizable habitat and more continuous distribution would allow more frequent opportunities for smaller males to engage in spawning, hence favoring sex reversal at an earlier age and ultimately tending toward secondary gonochorism.

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TEMPORAL AND SPATIAL PATTERNS OF NEARSHORE DISTRIBUTION AND ABUNDANCE OF THE PELAGIC FISHES OFF SAN ONOFRE-OCEANSIDE, CALIFORNIA

LARRY G. ALLEN[1] AND EDWARD E. DEMARTINI[2]

ABSTRACT

The pelagic fishes off San Onofre-Oceanside, California, were sampled nearshore (within 0.5-3.0 km of shore) during September 1979 to March 1981, using standardized lampara net gear. Sixty-two taxa were collected in 643 net-hauls systematically partitioned among three depth strata during day and night periods. *Engraulis mordax* dominated the catch and accounted for about 81% of all fishes. *Seriphus politus*, *Genyonemus lineatus*, *Peprilus simillimus*, and one species complex (atherinid spp.), together with *E. mordax*, made up >98% of the total numerical catch. Total catch per unit effort (CPUE) was greatest during the summer months (June-September), due mainly to the increased abundance of *Engraulis mordax*. The CPUE of other common species fluctuated little throughout the year except for a general decline during October-December because of the decreases in catches of *Seriphus politus* and *Genyonemus lineatus*. Four species groups were defined by quantitative clustering. Species Group I contained the above five most abundant and ubiquitous species. Groups II and III consisted of periodic species that occurred nearshore primarily during warmer and cooler water months, respectively. Group IV was composed of nine species of relatively rare bottom-oriented fishes.

The most conspicuous pattern exhibited by the common species in the assemblage involved a marked shift in depth over a diel period. *Engraulis mordax*, *Seriphus politus*, *Genyonemus lineatus*, and, to a lesser extent, *Peprilus simillimus* schooled in shallow water (5-11 m depths) during the day and dispersed offshore of these depths at night. Analysis of gut fullness during day and night suggested that *Seriphus politus*, and possibly *Genyonemus lineatus* and *Engraulis mordax*, disperse at night in part to feed on nocturnally active prey.

The marked depth and diel patterns of abundance that were observed could only be attributed in small part to depth-specific differences in water clarity and diel differences in catch efficiency.

Knowledge of pelagic fish assemblages that inhabit the waters off California is limited to general accounts from commercial catch records, larval fish studies and surveys (reviewed in Lasker 1982), and hydroacoustic surveys of adults (Mais 1974). These sources have provided general information on composition, distribution, and behavior of the offshore component of the pelagic ichthyofauna. This fauna is heavily dominated in numbers and biomass by the schooling clupeiform—northern anchovy, *Engraulis mordax*—especially within 37 km of the coast between Santa Barbara and San Diego (Mais 1974). Jack mackerel, *Trachurus symmetricus*; Pacific mackerel, *Scomber japonicus*; Pacific sardine, *Sardinops sagax*; Pacific saury, *Cololabis saira*; and Pacific hake, *Merluccius productus*, are also important components of this fauna, although their relative abundances are poorly known (Mais 1974). Information on the relative abundances of pelagic fish stocks of nearshore (<3.0 km from shore) waters was limited to a few unpublished reports prior to the initiation of the present study.

Little is known about the diel and seasonal movements of fishes within the Southern California Bight, although the diel activity patterns of some fishes associated with kelp beds in the Bight have been documented (Ebeling and Bray 1976; Hobson and Chess 1976; Hobson et al. 1981). Several of these species (queenfish, *Seriphus politus*; salema, *Xenistius californiensis*; walleye surfperch, *Hyperprosopon argenteum*) are known to make diel migrations between kelp beds and nearshore pelagic and other coastal (e.g., sandy surf zone) habitats (Hobson and Chess 1976).

This study is the first direct, systematic assessment of the pelagic fish assemblage inhabiting nearshore (<3 km) waters off southern California. The specific purposes of this paper are to characterize this assemblage by 1) species composition, 2) major spatial and temporal patterns of abundance and distribution, 3) species associations, and 4) important environmental factors.

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METHODS

Field Sampling

Two longshore locations were sampled in the nearshore waters (0.5-3.0 km offshore) between San Onofre and Oceanside in southern California (Fig. 1). Fish abundances at these locations were monitored as part of an environmental impact assessment of the San Onofre Nuclear Generating Station (SONGS), located about 5 km downcoast of San Clemente, performed for the Marine Review Committee of the California Coastal Commission. The upcoast location is situated several kilometers downcoast of SONGS and the downcoast location ~18 km downcoast (Fig. 1). The sand and sand-cobble bottom in the area slopes gradually from shore with an increase in depth of about 5 m/km. The upcoast location is ~0.5-1.5 km downcoast of the San Onofre kelp bed (designated by stippling, Fig. 1).

Samples (net-hauls) were taken at randomly chosen positions within each of three depth blocks (shallow: 5-11 m; mid: 12-16 m; and deep: 18-27 m) at both locations during day (1-6 h after dawn) and night (1-6 h after sunset) periods from September 1979 to March 1981, inclusive. (Samples could not be taken in January-February 1980, when our sampling vessel was drydocked for repairs.) The three depth blocks used were chosen as most appropriate for partitioning onshore/offshore variation in catches, based on the results of prior (May 1978-August 1979) lampara sampling at various depths in the general area. The number of cruises ($N = 1$-4) and net-hauls ($N = 4$-8) per month differed between diel periods and depth blocks, with most samples allocated to the daytime period and shallow depth block wherein catches were most variable. Because we suspected a significant date (cruise) effect on our catches, a paired sampling design was established in which the same depth blocks were sampled during the same diel period at both longshore locations on each cruise.

Two sizes of lampara net (semipursing round haul, Scofield 1951) were used: 1) A small net with each of two wings 118 m long of 15 cm stretch mesh, tapering to a bag of 1.25 cm mesh, was used to sample surface-to-bottom within the 5-11 m and 12-16 m depth blocks. The small net sampled about 4,600 m^2 of sea surface area. 2) A large net with wings each 136 m long of mesh identical to the small net was used to sample the 18-27 m depth block, wherein it also fished surface-to-bottom. The large net sampled about 6,200 m^2 of sea surface area. Catch was standardized to the area of the small lampara net. Both nets took about 10 min to set and retrieve, using a commercial fishing vessel. The same vessel and procedures of net deployment were used for the duration of the study.

Fishes collected in net-hauls were transferred by dip net to a holding tank on the vessel and were then identified and counted. Subsamples of major species were taken for life history analysis, and other fishes were returned to the sea as soon as possible. Large catches were subsampled with standard bait brailers.

In order to evaluate the potential effects of variable net catch efficiencies under varying water clarity conditions during the day, an index of water clarity (visibility to shipboard observer of 30 cm Secchi disk) was measured immediately following most net-hauls. Potential diel differences in catch efficiency were evaluated on the basis of the percentage recapture of marked *Seriphus politus* in net-hauls made during a pilot (June-September 1978) study. A constant number (50) of fin-clipped adult *S. politus*, captured on the previous net-haul, were released within the center of the area being encircled as the net was deployed. Test releases were made in all depth blocks, both at the surface and near bottom (via a messenger-tripped holding cage), and during both day and night. Secchi disk indices of water clarity were measured at night between test net-hauls, using a standard shipboard light source.

Data Analysis

Analyses were carried out using the Statistical Analysis System (SAS) installed at the Marine Review Committee's Computer Center in Solana Beach, Calif.

Preliminary tests (t-test for paired comparisons, $P > 0.05$) failed to detect significant differences between locations in all but a few of the common species using log-transformed catch data. Log transformation ($\log_{10} X + 1$) of catch data was necessary to satisfy the parametric assumptions of normality and equality of variances within depth blocks and diel periods. The general lack of longshore differences allowed us to pool the data at both locations for subsequent analyses.

Catch per unit effort (CPUE) was calculated by month based on log-transformed catch data for individual depth blocks and diel periods. Combined CPUE of all three depth blocks was expressed as the grand mean and associated standard error of depth means.

Comparisons of untransformed catch data between depths, diel periods, and dates were made by using Wilson's nonparametric analysis of variance (Wilson

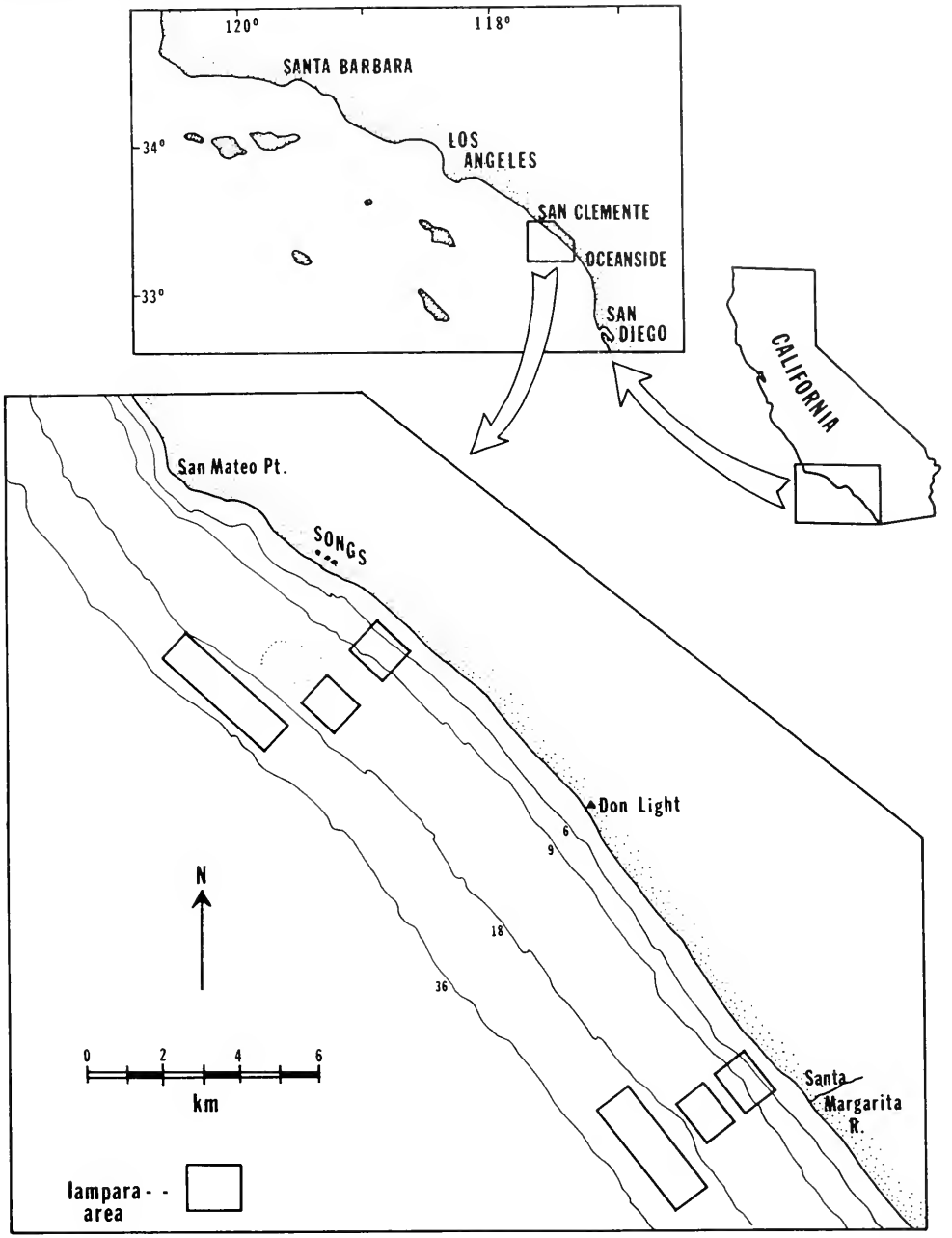

FIGURE 1.—Map of the study area, San Onofre-Oceanside, Calif. Rectangles represent the various depth blocks sampled at the two longshore locations; note that all depth blocks are 1 km distance in onshore-offshore extent. Stippled area represents the location of the San Onofre kelp bed.

1956), available in the IMSL Library's[3] statistical package. Variances of catches were heteroscedastic among depth blocks and between diel periods, which precluded use of parametric analysis of variance. Wilson's three-way ANOVA's (either with unequal replication or without replication) were used, depending on the category (e.g., total individuals or species counts) or species being considered.

Quantitative clustering of species was carried out using the Ecological Analysis Package (EAP)[4]. Mean abundance of species by cruise date, depth, and diel period was transformed by its square-root in order to counter the tendency of the Bray-Curtis Index (Clifford and Stephenson 1975) to overemphasize abundant species. Flexible sorting was used to maximize the separation between groups. Only species with a minimum total occurrence of 20 were considered in this analysis.

Spearman's rank correlations (r_s) were calculated to examine the relationships between diel period, water depth, and surface water temperature and CPUE for 1) total individuals, 2) total individuals minus *E. mordax*, 3) certain major species, and 4) species counts. CPUE data for taxonomic categories 1-3 were related to water clarity by using Spearman's rank test within each depth block; in addition, a parametric analysis of covariance (ANCOVA), with water clarity as covariate of CPUE and depth block as the treatment effect, was performed to estimate the general magnitude of the potential influence of depth-specific differences in water clarity on daytime catches. Diel catch efficiency data for *Seriphus politus* were related to water clarity by parametric or Spearman rank correlation, as appropriate.

Day-Night Comparison of Foregut Fullness

Preliminary examination of the variance: mean ratios of CPUE data indicated that fishes were dispersed more at night than during the day. In order to investigate the possible role of feeding behavior in this nocturnal dispersal pattern, we examined archived stomachs from paired day (1000-1300 h) and night (2100-0100 h) samples of fishes of comparable sizes for the five most abundant taxa (*E. mordax*; *Seriphus politus*; white croaker, *Genyonemus lineatus*; Pacific butterfish, *Peprilus simillimus*; and atherinid spp., the latter represented by jacksmelt, *Atherinopsis californiensis*). Contents of the foregut were removed, either dried at 40° C (for *E. mordax*, *S. politus*, and *G. lineatus*) or blotted dry (*P. simillimus* and *A. californiensis*), and weighed. A contents index (CI) was then calculated for each specimen as follows:

$$CI = (\text{weight contents}/\text{weight of fish}) \times 10^5.$$

Diel overlap in gut evacuation did not create a major problem except that it tended to make the analysis more conservative (i.e., more difficult to detect day-night differences).

The CI's for day-caught versus night-caught fishes were compared by either Wilcoxon signed-ranks test for paired comparisons or Wilcoxon two sample test, depending on the number and temporal distribution of samples.

RESULTS

Species Composition

Sixty-two taxa representing 33 families of teleost and elasmobranch fishes were collected in 643 net-hauls partitioned among the three depth blocks and two diel periods made during the 19-mo period, September 1979-March 1981 (Table 1). The catch was overwhelmingly dominated by *E. mordax*. *Seriphus politus*, *G. lineatus*, *P. simillimus*, and a species complex of silversides (atherinid spp.) were also abundant in the catch. These top five taxa accounted for >98% of the numbers of total individuals sampled (Table 1). The atherinid species complex was a composite of three species (*Atherinopsis californiensis*; topsmelt, *Atherinops affinis*; California grunion, *Leuresthes tenuis*) that were not readily identifiable in the field. Subsamples of "atherinid spp." field catches were about 48% *Atherinopsis californiensis*, 42% *L. tenuis*, and 10% *Atherinops affinis*.

Location Comparison

Location differences were insignificant ($P > 0.05$) for most categories and species within depth blocks and diel periods based on *t*-tests for paired comparisons. Differences were detected in the following cases: 1) Atherinids were more abundant at night in the upcoast area ($P < 0.01$); 2) Pacific barracuda, *Sphyraena argentea*, occurred in greater numbers at night upcoast ($P < 0.01$); 3) *T. symmetricus* was more abundant both day and night upcoast ($P < 0.01$); and 4) *Scomber japonicus* was also caught in greater numbers upcoast ($P < 0.05$), but only at night during the

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period November 1980-March 1981. *Xenistius californiensis* was consistently more common upcoast ($N = 170$ sample fish) than downcoast ($N = 13$) at night, although its low frequency of overall occurrence precluded a statistical test for longshore differences.

TABLE 1.—Number of individuals and frequency of occurrence of 62 species/taxa in 643 lampara net samples on 129 cruises from September 1979 to March 1981, inclusive. Species/taxa are ranked according to total number of individuals.

Species/taxa	Number	Percent number	Frequency	Percent frequency
Engraulis mordax	819,872	80 79	440	68.4
Seriphus politus	80,513	7.93	413	64 2
Genyonemus lineatus	53,994	5.32	335	52.1
Peprilus simillimus	26,003	2.56	238	37.0
Atherinid spp	15,811	1.56	326	50.7
Scomber japonicus	7,386	0.73	194	30 2
Trachurus symmetricus	2,750	0.27	92	14 3
Anchoa compressa	1,915	0 19	85	13 2
Sarda chiliensis	1,394	0 14	115	17 9
Sphyraena argentea	1,066	0.11	99	15.4
Hyperprosopon argenteum	936	0.09	106	16 5
Phanerodon furcatus	665	0.07	101	15.7
Myliobatis californica	455	0.04	212	33 0
Menticirrhus undulatus	412	0 04	117	18.2
Umbrina roncador	269	0.03	38	5.9
Amphistichus argenteus	211	0.02	51	7.9
Xenistius californiensis	182	0.02	25	3 9
Paralichthys californicus	139	0 01	79	12.3
Sardinops sagax	130	0.01	15	2.3
Paralabrax nebulifer	108	0.01	56	8.7
Cymatogaster aggregata	86	0.01	34	5.3
Squalus acanthias	66	0.01	23	3.6
Scorpaena guttata	57	0.01	28	4.3
Urolophus halleri	34	<0 01	19	2.9
Citharichthys stigmaeus	28	<0.01	16	2.5
Otophidium scrippsi	27	<0.01	19	2.9
Rhinobatos productus	22	<0.01	12	1.9
Platyrhinoidis triseriata	21	<0.01	18	2.8
Anisotremus davidsoni	19	<0.01	8	1.2
Medialuna californiensis	19	<0.01	5	0.8
Torpedo californica	18	<0.01	15	2.3
Cynoscion nobilis	17	<0.01	12	1.9
Pleuronichthys verticalis	12	<0.01	13	2.0
Raja inornata	12	<0.01	8	1.2
Rhacochilus toxotes	11	<0.01	4	0.6
Porichthys myriaster	9	<0.01	5	0.8
Porichthys notatus	8	<0.01	4	0.6
Alopias vulpinus	8	<0.01	5	0.8
Pleuronichthys ritteri	8	<0.01	5	0.8
Embiotoca jacksoni	8	<0.01	6	0.9
Sebastes auriculatus	7	<0.01	1	0.1
Roncador stearnsi	6	<0.01	2	0.3
Hypsopsetta guttulata	6	<0.01	5	0.8
Dorosoma petenense	4	<0.01	4	0.6
Paralabrax clathratus	4	<0.01	4	0.6
Damalichthys vacca	4	<0.01	1	0.1
Leptocottus armatus	4	<0.01	3	0.5
Syngnathus spp.	4	<0.01	4	0.6
Citharichthys xanthostigma	3	<0.01	3	0.5
Triakis semifasciata	3	<0.01	3	0.5
Raja binoculata	2	<0.01	1	0.1
Xystreurys liolepis	2	<0.01	2	0.3
Heterostichus rostratus	2	<0.01	2	0.3
Cypselurus californicus	2	<0.01	2	0.3
Heterodontus francisci	1	<0.01	1	0.1
Sebastes rastrelliger	1	<0.01	1	0.1
Balistes polylepis	1	<0.01	1	0.1
Synodus lucioceps	1	<0.01	1	0.1
Symphurus atricauda	1	<0.01	1	0.1
Mugil cephalus	1	<0.01	1	0.1
Icichthys lockingtoni	1	<0.01	1	0 1
Mustelus californicus	1	<0.01	1	0.1
Grand total	1,014,762		643	

Monthly and Longer Temporal Patterns

CPUE for total individuals, number of *E. mordax*, and total individuals minus *E. mordax*, when plotted on a monthly basis, revealed general temporal patterns of abundance (Fig. 2). Catches were generally higher at night for all three categories (see below). Day catches were generally much more variable than night catches, as the standard errors indicate (Fig. 2). The longer term (i.e., "seasonal") temporal changes in the catch of total individuals largely reflect the increase in primarily juvenile-sized (<10 cm standard length, Hunter and Leong 1981) *E. mordax* during the summer months. When the abundances of all species other than *E. mordax* are combined, the catch remained relatively constant throughout the study period except for a general decline in numbers during October-December of both 1979 and 1980.

The abundances of *Seriphus politus* and *G. lineatus* also remained relatively constant except for the October-December declines. These two species (Fig. 3) were primarily responsible for the pattern observed for total individuals minus *E. mordax*. Night catches were higher than day catches for *G. lineatus* and (especially) *S. politus*. The abundances of *P. simillimus* and atherinids in general showed patterns which were similar in terms of seasonality. Both were usually more abundant during cooler water months (December-April). Three species of higher level (mainly piscivorous) carnivores showed dissimilar patterns of nearshore abundance (Fig. 3). *Scomber japonicus* was more abundant in warmer water months from about June to October. Pacific bonito, *Sarda chiliensis*, occurred in greatest numbers from March to August, but only during the day. *Sphyraena argentea* was more abundant during the cooler water months of October through March.

Diel and Depth Patterns

Day and night catches of total individuals varied among depth blocks throughout the study (Fig. 4). Day catches were consistently highest at 5-11 m depths, but the variability in catches was high. Night catches did not differ ($P > 0.05$, Wilcoxon's signed rank test) from day catches in the shallow depth block. However, night catches were higher and less variable than day catches in both the 12-16 m and 18-27 m depth blocks (Fig. 4).

All categories and species common enough to test showed significant diel, depth, and date (cruise) main effects, as well as diel × depth interactions, based on Wilson's three-way ANOVA with unequal replication

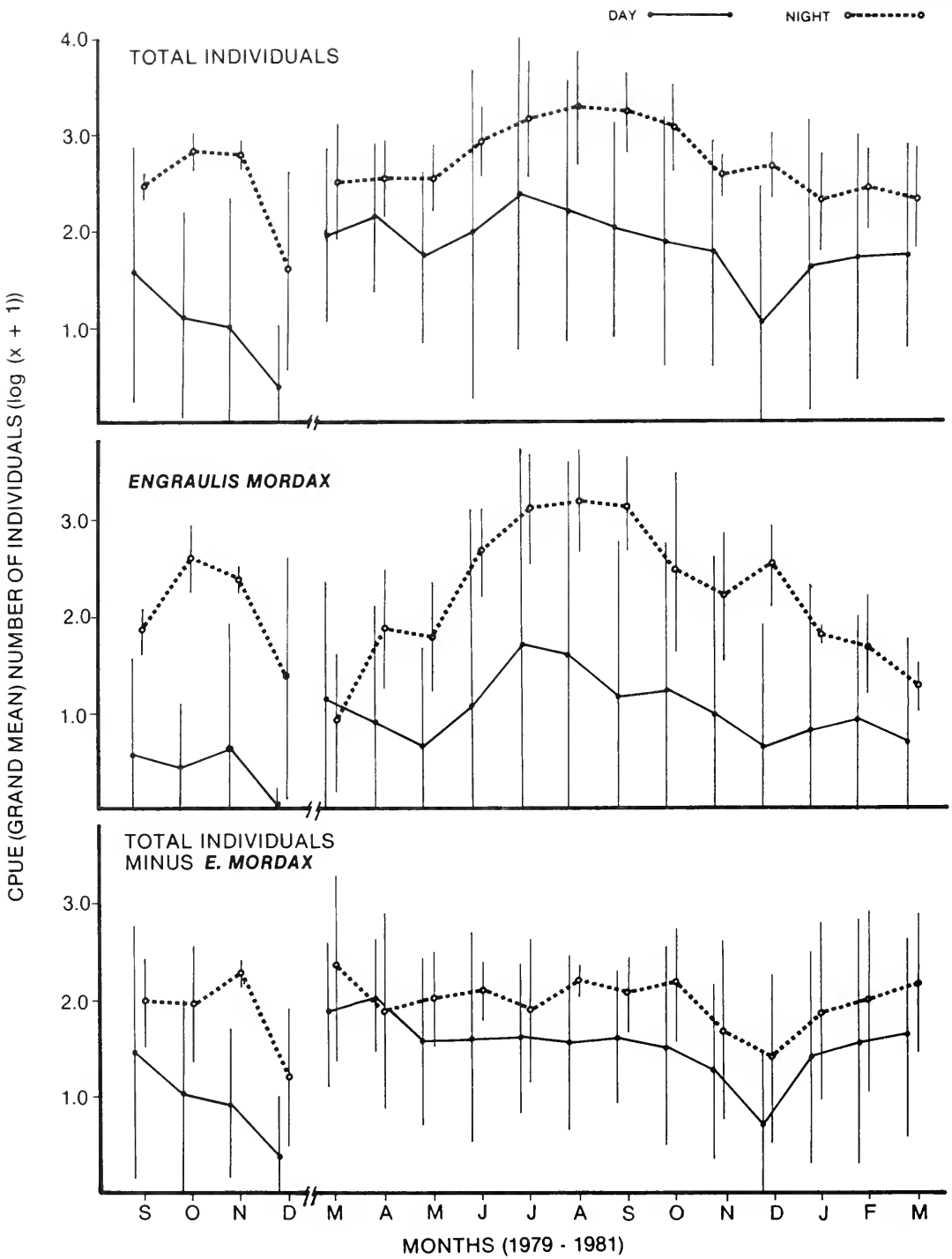

FIGURE 2.—Monthly variation in the abundance (CPUE) of total individual fishes, *Engraulis mordax*, and total individuals minus *E. mordax* over the study period. Each value represents the grand mean of $\log_{10}(X + 1)$ transformed catches from day and night net-hauls. Vertical bars depict ±2 standard errors of the respective grand mean.

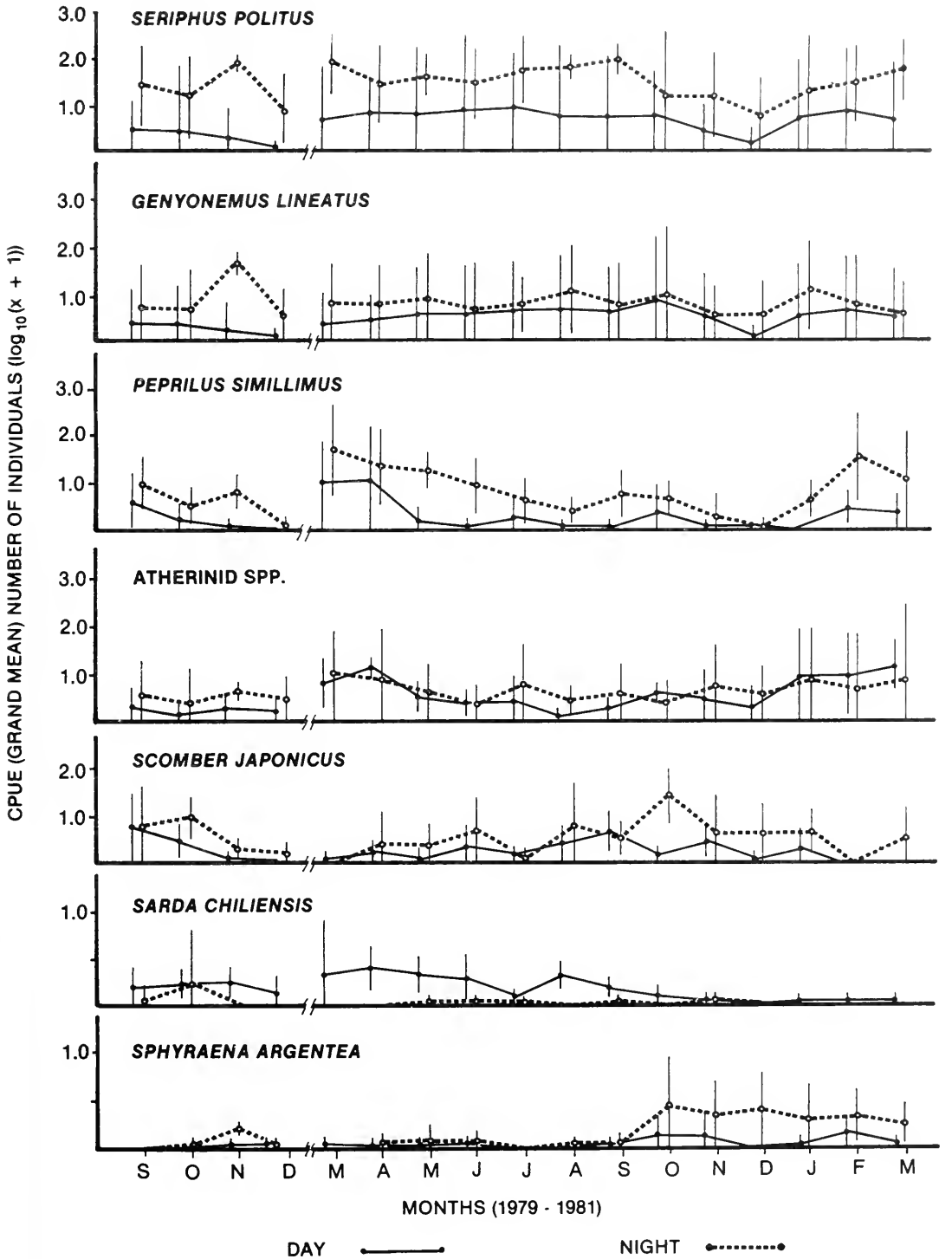

FIGURE 3.—Monthly variation in day and night catches of seven common species and one taxon of fishes over the study period. Each value represents the grand mean of $\log_{10}(X + 1)$ transformed catches from day and night net-hauls. Vertical bars depict ±2 standard errors of the respective grand mean.

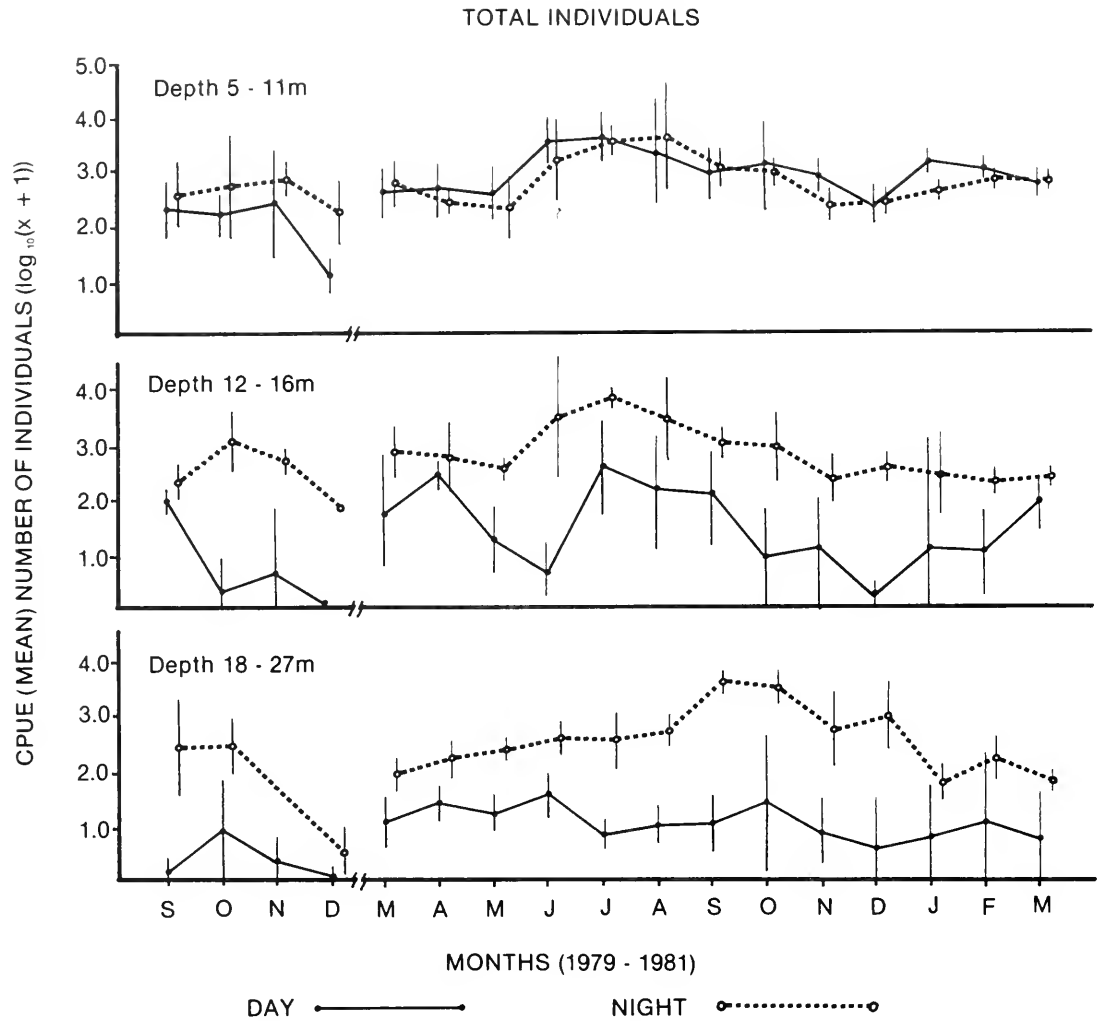

FIGURE 4.—Monthly variation in the total number of individual fishes captured during the day and night in each of three depth blocks over the study period. Each value represents the grand mean of $\log_{10}(X + 1)$ transformed catches from day and night net-hauls. Vertical bars depict ±2 standard errors of the respective grand mean.

(Table 2). The probability for a date effect on *E. mordax* was marginal at $P = 0.09$.

Diel, depth, and date effects were variously important for four other common taxa or categories (Table 3). Interactions between main effects could not be evaluated for these species because we were forced to use Wilson's ANOVA without replication in order to minimize the number of zeros in the catch data. *Peprilus simillimus* was more abundant at night (diel effect) and on certain cruises during the study period (date effect). Catches of *G. lineatus* were higher at night and at the shallow depth. *Scomber japonicus* was more abundant offshore and at certain times of year.

Species Associations

Quantitative clustering of species by sample abundance among depth blocks and diel periods produced four distinct groups within 21 species (Fig. 5). The largest dichotomy (~160% distance) occurred between members of Groups I-II and Groups III-IV. Separation within both Groups I-II and Groups III-IV occurred at ~65% distance.

In Group I *E. mordax* was most dissimilar, fusing with other group members at ~55% distance. *Seriphus politus* and *G. lineatus* formed a very close association, being linked at ~12% distance. *Peprilus*

TABLE 2.—Summary of significant chi-square values from Wilson's three-way ANOVA with unequal replication for three categories and two species of fishes present in lampara net samples, September 1979-March 1981, inclusive (*=$P<0.001$). Dashes indicate insignificant ($P<0.05$) results.

Category or species	Diel	Depth	Date	Diel × depth	Diel × date	Depth × date	D × D × D
Total individuals	42.7**	58.9**	22.6*	29.3**	—	—	—
Total individuals minus *Engraulis mordax*	8.1*	87.4**	24.9*	10.6*	—	—	—
Species counts	26.2**	90.9**	26.8*	22.4**	—	—	—
Engraulis mordax	82.4**	22.2**	—	37.7*	—	—	—
Seriphus politus	63.4**	79.4**	26.0*	32.6*	—	—	—
df	1	2	13	2	13	26	26

TABLE 3.—Results of Wilson's three-way ANOVA without replication for four species that were common in lampara net samples, September 1979-March 1981, inclusive. (* = $P \leq 0.05$; ** = $P \leq 0.001$.)

Factor	χ^2	df	P
Peprilus simillimus			
Diel	17.30	1	<0.001**
Depth	1.15	2	0.563
Date	24.36	13	0.028*
Genyonemus lineatus			
Diel	4.76	1	0.029*
Depth	48.29	2	<0.001**
Date	8.00	13	0.844
Atherinid spp.			
Diel	0.05	1	0.827
Depth	27.86	2	<0.001*
Date	13.64	13	0.400
Scomber japonicus			
Diel	2.34	1	0.126
Depth	8.90	2	0.012*
Date	25.70	13	0.019*

simillimus and atherinid spp. also formed a close association (~18% distance).

Sarda chiliensis was the most dissimilar member of Group II, and linked to *Scomber japonicus* and *T. symmetricus* at ~40% distance.

The four species in Group III formed a relatively tight group with a maximum dissimilarity of only 38% distance (yellowfin croaker, *Umbrina roncador*, to the other three species). *Sphyraena argentea* and *X. californiensis* were most closely associated (~20% distance), with deepbody anchovy, *Anchoa compressa*, occupying the intermediate position.

Group IV was composed of nine bottom-oriented species which were relatively rare in the samples.

Influences of Diel Period, Surface Water Temperature, and Depth

Sea surface temperature ranged from about 14.2° to 24.0°C during the study period. Highest water temperatures were encountered during the summer months (July-September) and lowest in winter (December-February) as would be expected in a temperate marine habitat. Sampling depths ranged from 5 to 25 m. Day collections were made between 0700 and 1300 h and night collections between 1900 and 0100 h.

Spearman rank correlations of 2 categories and 21 individual species (Table 4) with time of collection, depth of water column, and sea surface temperature yielded numerous significant relationships. Depth (20 significant values) and time of collection (14) were important factors for most categories or species. Temperature was significantly correlated with 10 categories or species. The total individuals category was significantly correlated with all three abiotic factors (negative with depth). Species counts correlated only with depth (negative) and time of collection. In general, both the numbers of individuals and numbers of species were greatest at

TABLE 4.—Summary of Spearman's rank correlation (r_s) values and significance levels for 2 categories and the 21 abundant species/taxon collected. Time = time of collection (military time); Depth = bottom depth (m); Temp = surface water temperature (°C). (df = 210; * = $P \leq 0.05$; ** = $P \leq 0.0001$.)

Category or species/taxon	Environmental variables			Species group
	Time	Depth	Temp.	
Total individuals	0.44**	−0.46**	0.22*	—
Species counts	0.43**	−0.62**	0.11	—
Engraulis mordax	0.48**	−0.33**	0.22*	I
Seriphus politus	0.46**	−0.56**	0.11	I
Genyonemus lineatus	0.31**	−0.71**	0.08	I
Peprilus simillimus	0.54**	−0.21*	0.04	I
Atherinid spp.	0.16*	−0.52**	−0.22*	I
Scomber japonicus	0.12	0.28**	0.40**	II
Trachurus symmetricus	0.15*	0.25**	0.08	II
Sarda chiliensis	−0.27**	0.05	0.27**	II
Anchoa compressa	−0.01	−0.52**	−0.14*	III
Sphyraena argentea	0.20*	−0.25**	−0.14*	III
Umbrina roncador	0.11	−0.32**	−0.14*	III
Xenistius californiensis	0.12	−0.14*	−0.06	III
Myliobatis californicus	0.04	−0.22**	0.26**	IV
Phanerodon furcatus	0.14*	−0.46**	−0.02	IV
Hyperprosopon argenteum	0.05	−0.54**	−0.01	IV
Menticirrhus undulatus	−0.09	−0.60**	0.06	IV
Amphistichus argenteus	−0.17*	−0.45**	0.01	IV
Cymatogaster aggregata	0.14*	−0.35**	0.07	IV
Paralichthys californicus	0.07	−0.48**	0.01	IV
Paralabrax nebulifer	−0.03	0.01	0.22**	IV
Scorpaena guttata	0.27**	−0.11	0.02	IV

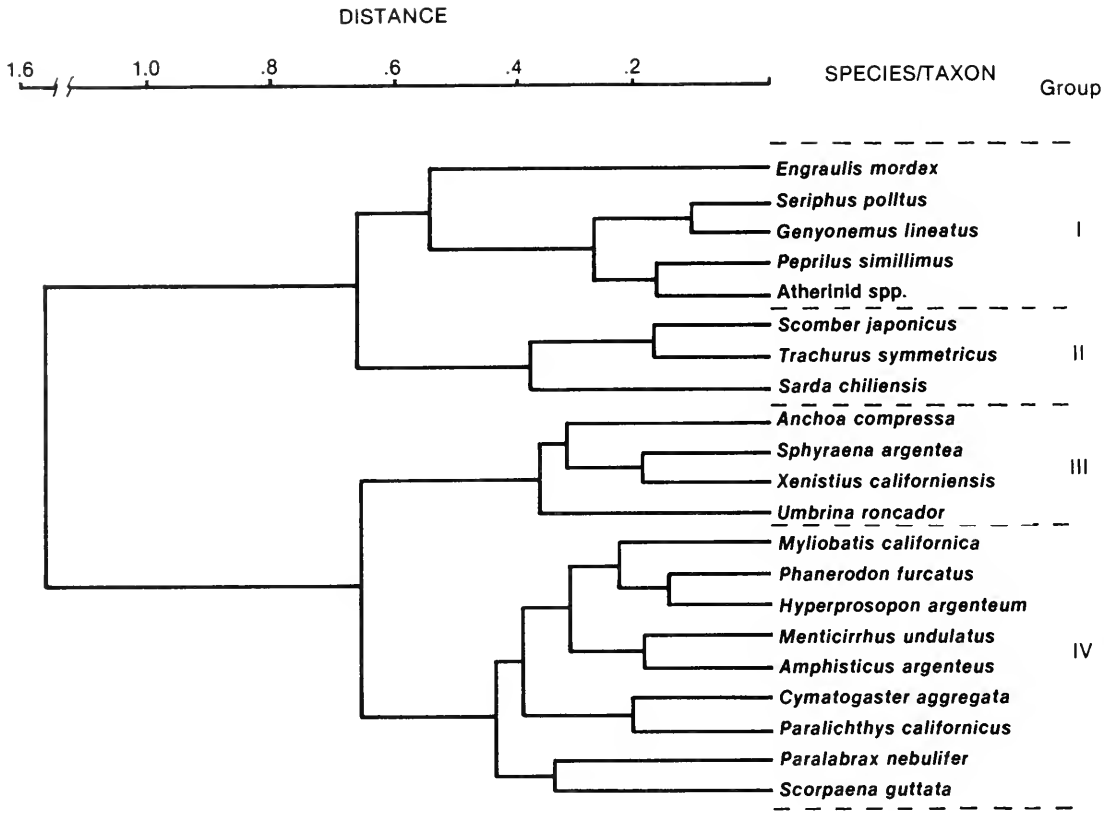

FIGURE 5.—Dendrogram depicting the clustering of 20 species and 1 taxon based on abundance within lampara samples. Four species groups (Roman numerals) are recognized according to the Bray-Curtis index of dissimilarity (ecological distance).

shallow depths during the night. More individuals were collected during the warmer months, although this relationship was highly dependent on the catches of *E. mordax*.

The catches of all the members of species Group I were correlated with time of collection and depth (negative) (Table 4). Only the abundances of *E. mordax* (positive) and atherinid spp. (negative) were correlated with temperature. *Scomber japonicus* and *T. symmetricus* of Group II were usually found farther offshore in the study area (positive with depth). The catches of *S. japonicus* and *Sarda chiliensis* were positively correlated with temperature. However, *T. symmetricus*, like many of the other species, was collected in greater numbers at night, while *S. chiliensis* was captured almost exclusively during the day. The catches of all members of species Group III were negatively correlated with depth and temperature, although the temperature correlation for *X. californiensis* was not significant. Six of the eight species in species Group IV were negatively correlated with depth, although no other consistent pattern was apparent.

The occurrence and distribution of the 21 abundant species are displayed graphically in relation to diel period and depth in Figures 6 and 7. Species are presented in the species groups derived for the dendrogram of species associations (Fig. 5). Only species with $>10\%$ occurrence during the particular diel period are included in the illustrations.

During daylight periods, species Groups I, III, and IV were distributed close to shore, mostly within the 5-11 m depth block (Fig. 6). The high variance of catches during the day indicated that the species are highly clumped in distribution and are probably schooling at this time (especially members of Groups I and III). Species of Group II were primarily found offshore within the 12-16 m and 18-27 m depth blocks and occurred mainly during the warmer months. Group III on the other hand occurred during the colder months.

At night the distribution of species was quite dif-

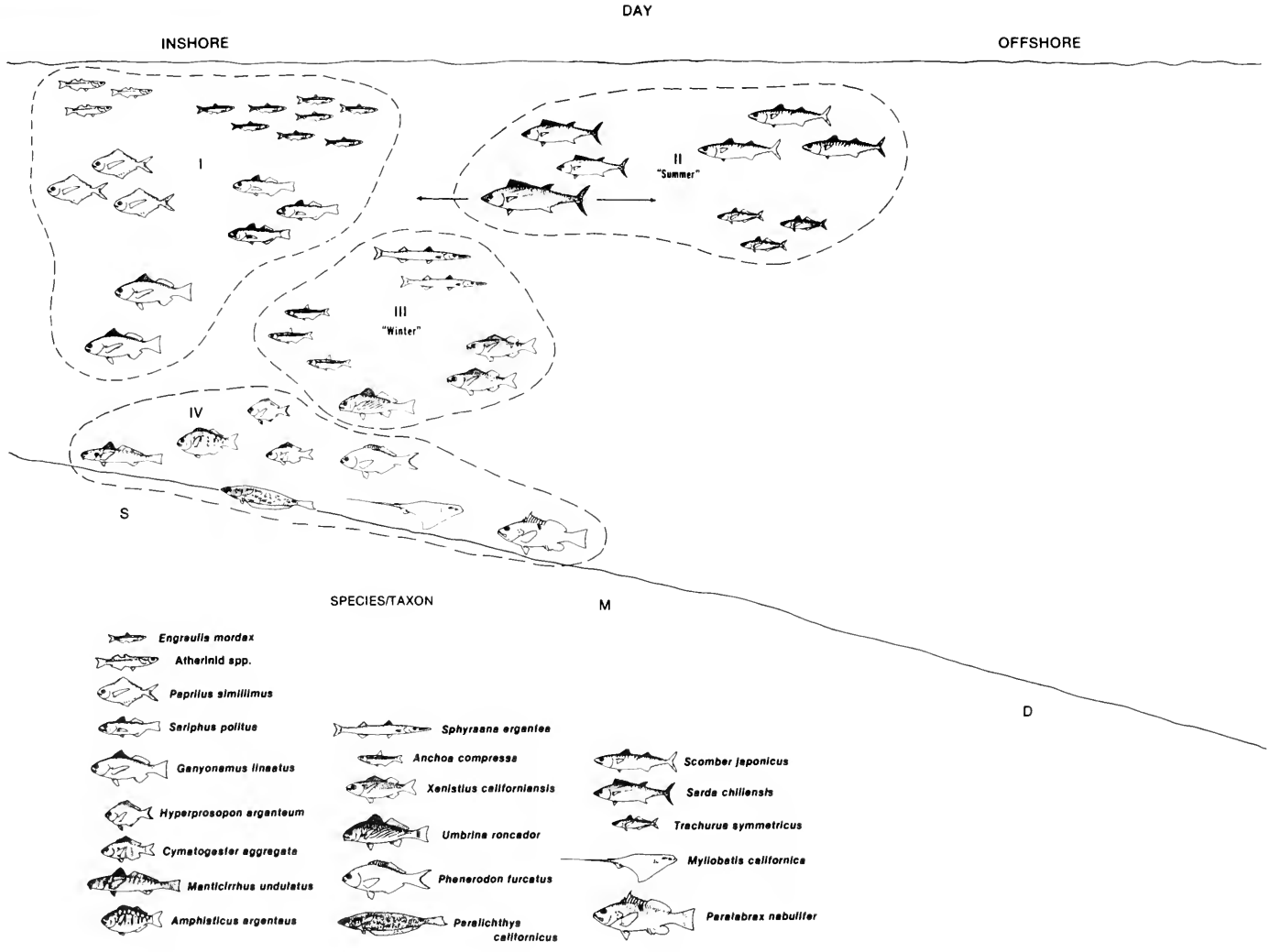

FIGURE 6.—Generalized illustration of the principal fish species (and taxon) present in the nearshore waters off San Onofre-Oceanside, Calif., during daylight hours. Dashed lines enclose species groups derived from the Figure 5 dendrogram. Inclusion of species is limited to those that were caught on >20 cruises. Arrows indicate onshore-offshore movement. Fishes are not drawn strictly to scale. S, M, and D represent shallow, middepth, and deep blocks, respectively.

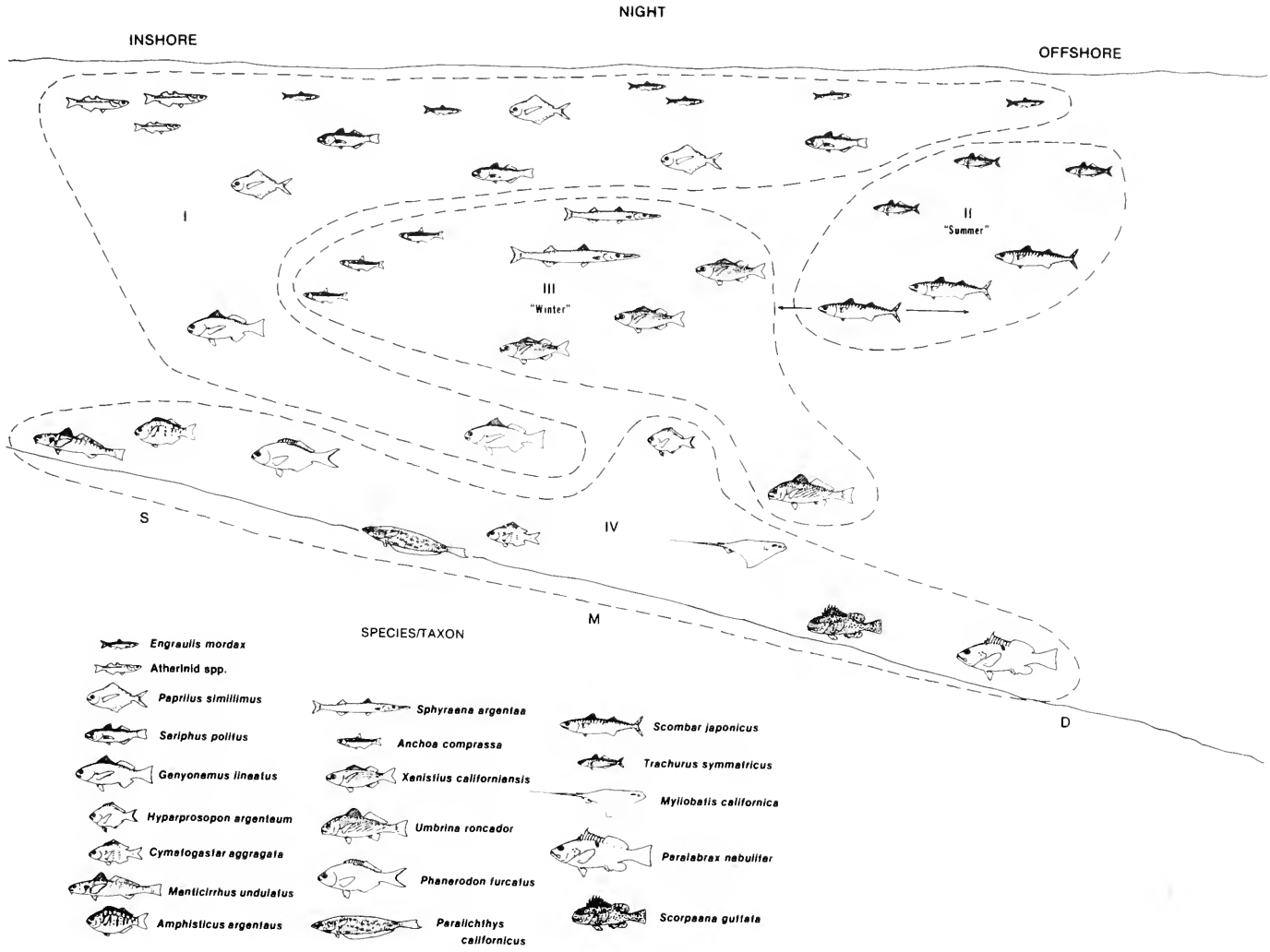

FIGURE 7.—Generalized illustration of the principal fish species (and taxon) present in the nearshore waters off San Onofre-Oceanside, Calif., at night. Other information as in Figure 6.

ferent (Fig. 7). Members of Group I (especially *E. mordax*, *Seriphus politus*, and *G. lineatus*) dispersed offshore, resulting in a much more even distribution of individuals among net-hauls. Certain species in Groups III and IV also moved offshore at night. Group II persisted over the deeper portions of the study area, with *Sarda chiliensis* absent at night.

Interrelations of Depth Block, Water Clarity, and CPUE

The relations between CPUE and water clarity were significantly negative for five of seven major taxa in one or more depth blocks during the day (Table 5). Water clarity differed significantly among depths (Shallow block: $\bar{x} = 4.4$ m; middepth block: 6.8 m; deep block: 9.6 m; Kruskall-Wallis $H = 33.8$, df $= 2$, $P < 0.001$). ANCOVA results, however, indicated that, although water clarity in addition to depth block were in general negatively related to daytime catches, there were no depth by water clarity interactions (all $P > 0.10$). On average, only an estimated 12-16% of the total variation in the CPUE of major taxa was attributable to variations in water clarity with any depth block (Table 5).

Diel Effects on Catch Efficiency

The percentage recapture of fin-clipped *Seriphus politus* on average was significantly ($P < 0.05$) greater ($\bar{x} \pm$ SE $= 13 \pm 3\%$, $N = 40$ net-hauls) during the day versus night ($25 \pm 3\%$, $N = 24$ hauls). Parametric estimators for the percentage recapture versus water clarity relation were not possible for daytime tests due to the nonnormality of these data; however, about 30% of the variation in the ranks of daytime recapture data was attributable to water clarity ($r_s = -0.54$, $P < 0.001$). Queenfish recaptures at night were insignificantly (Pearson's $r = -0.31$, $P = 0.14$) related to water clarity.

Day-Night Feeding Comparison

No significant differences in stomach fullness (CI) were found between day- and night-caught specimens of *E. mordax*, *G. lineatus*, and *P. simillimus* (Table 6). Specimens of *Seriphus politus*, however, had significantly greater foregut fullness at night, while those of *Atherinopsis californiensis* had significantly greater fullness during the day (Table 6).

TABLE 5.—Summary of Spearman's rank correlation (r_s) values and significance levels for comparisons of CPUE and water clarity within depth blocks for two categories and four major species plus one taxon (* $= P < 0.05$; ** $= P < 0.001$). Dashes indicate insignificant ($P > 0.05$) results. Also indicated is the estimated percentage of total variation (R^2) of daytime CPUE explained by variation in water clarity in each depth block. R^2 approximations reflect results of parametric regressions performed in an ANCOVA with water clarity as covariate and depth block as treatment.

Category or species/taxon	Rank correlation (Spearman's r_s)			Estimated % variance (= R^2)		
	5-11 m	12-16 m	18-27 m	5-11 m	12-16 m	18-27 m
Total individuals	−0.36*	−0.61**	—	20	37	24
Total individuals minus *Engraulis mordax*	—	−0.58**	−0.60*	13	32	33
Engraulis mordax	—	−0.34*	—	15	11	8
Seriphus politus	−0.31*	−0.34*	—	18	9	9
Genyonemus lineatus	—	—	—	8	2	—
Peprilus simillimus	—	—	—	6	7	6
Atherinid spp.	—	−0.45*	—	3	17	12

TABLE 6.—Summary of results of day versus night comparisons of the contents index (CI) of foregut samples of the five most abundant fishes present in lampara collections (* denotes statistical significance).

TEST—Wilcoxon signed-rank test of median CI for paired day-night samples

Species	N (day-night)	Paired N	Ts	P	
Engraulis mordax	40/36	8	14	0.29	NS
Seriphus politus	49/49	9	4	0.02	(night>day)*
Genyonemus lineatus	42/44	9	18	0.30	NS

TEST—Wilcoxon two-sample test

Species	N (day-night)	Z	P	
Peprilus simillimus	26/16	0.13	0.90	NS
Atherinopsis californiensis	29/33	5.42	<0.001	(day>night)*

DISCUSSION

The nearshore pelagic ichthyofauna between San Onofre and Oceanside, Calif., was dominated by silvery-sided, schooling fishes. *Engraulis mordax*, the dominant pelagic species offshore (Mais 1974), was also the most abundant species nearshore. *Seriphus politus* and *G. lineatus*, the two abundant sciaenids in this assemblage, are best characterized as bottom associated fishes which rise into the water column. Both of these species are well represented in bottom-trawls in the area.[5] *Genyonemus lineatus* is generally more abundant in trawls, indicating that it is more closely associated with the bottom than *S. politus*. The three species above, together with *P. simillimus* and atherinid spp., constituted species Group I. Members of this group were abundant and ubiquitous within the area and accounted for >98% of the total individuals collected. Species Groups II and III represented periodic components (Tyler 1971) within the assemblage. Group II comprised three species of higher carnivores that generally occurred in the offshore portion of the study area during the warmer months (spring-summer). Group III, on the other hand, contained four species that were more abundant at shallow depths during the colder water months (fall-winter). Two of these species, *Anchoa compressa* and the sciaenid *Umbrina roncador*, are known to occur in bay-estuarine habitats such as Newport Bay during the summer months (Horn and Allen 1981). Both *A. compressa* and *U. roncador* belong to primarily tropical families. The presence of these two species in the study area during fall-winter suggests that they may seasonally migrate out of embayments and into shallow coastal waters in response to cool-water temperatures. The bottom-associated species of Group IV were relatively rare in catches with the exception of the bat ray, *Myliobatis californica* (California bat ray). *Myliobatis californica* occurred in about one-third of all net-hauls and ranked sixth in number of total occurrences. Its relatively large size ($\bar{x} \simeq 2$ kg) and high frequency of occurrence make *M. californica* a more important component of this nearshore assemblage than numerical abundance alone would indicate.

Upcoast and downcoast locations were generally similar in terms of total individuals, species counts, and in the abundances of most common species. The few exceptions (atherinids, *Sphyraena argentea*, *Trachurus symmetricus*, *Xenistius californiensis*) that were more abundant at the upcoast location probably reflect the proximity of the San Onofre kelp bed. All of these species are known to associate with kelp beds or rocky reefs at some time during the year (Feder et al. 1974; Hobson and Chess 1976; Mais 1974).

Significant date effects found by Wilson's ANOVA's reflected a certain amount of temporal variation within this assemblage of fishes. Some of these date effects can be attributed to spatial patchiness and sampling error; other date effects undoubtedly reflect short-term, temporal changes in the environment. Upwelling is probably a major factor contributing to short-term variation in the abundance and distribution of these fishes. The waters within the Southern California Bight can be subjected to bouts of upwelling anytime during the year, although upwelling is most likely to occur during March-July (Parrish et al. 1981). Both short-term temperature variations due to upwelling and long-term seasonal warming and cooling of coastal waters probably influenced the 10 observed correlations between sea surface temperature and the abundance of individual taxa. The abundances of only two of the top five taxa however were significantly correlated to sea temperature (*Engraulis mordax*, positive; atherinids, negative). *Peprilus simillimus*, the fourth most abundant species, varied significantly between dates (ANOVA results), but showed no significant relationship to temperature. Extremely patchy distributions and high vagility might account for the observed short-term variations in the abundance of *P. simillimus*. Neither *Seriphus politus* nor *Genyonemus lineatus* varied greatly in seasonal abundance although *S. politus* did show a significant date effect (ANOVA) that was apparently unrelated to temperature. These two sciaenids were largely responsible for the uniformity of catch seen when *Engraulis mordax* was excluded from the catch totals. The only major change in catches of *S. politus* and *G. lineatus* occurred during the October-December periods of 1979 and 1980 when CPUE was depressed. During this time of year the adults of both species presumably migrated out of our sampling area into deeper water.

Temporal distributions differed for *Scomber japonicus*, *Sarda chiliensis*, and *Sphyraena argentea*, the major higher carnivores of the assemblage. The observed temporal differences probably reflect differences in general longshore migratory patterns and residence of juveniles within the study area (e.g., presence of juvenile *S. argentea* near San Onofre kelp bed during fall-winter, authors' pers. obs.). A pos-

[5]DeMartini, E. E., and L. G. Allen. Temporal and spatial patterns of distribution and abundance of benthic, soft-bottom fishes at shallow depths off San Onofre-Oceanside, California. Manuscr. in prep. Marine Science Institute, University of California, Santa Barbara, CA 93106.

sible explanation for the virtual absence of *Sarda chiliensis* from night collections is that they may migrate offshore of 30 m depth before or at dusk on a daily basis. Net avoidance can be effectively discounted, since this fast swimming scombrid can presumably see the net better during the day than at night.

Although location differences and temporal changes were evident for some species within this assemblage, the dominant pattern shown by the most abundant species was one of a general dispersal offshore at night from nearshore diurnal schools. Diel interactions with depth were found for total individuals, total individuals minus *Engraulis mordax*, species counts, numbers of *E. mordax*, and numbers of *Seriphus politus*. Various diel and/or depth effects were also found for other taxa, including *Peprilus simillimus*, *Genyonemus lineatus*, atherinid spp., and *Scomber japonicus*. These results plus the significant correlations between species abundances and time of collection and depth underscore the general importance of diel and depth factors to the abundance and distributions of fishes in this assemblage.

Greater net avoidance under conditions of increasing water clarities, such as occur at greater distances offshore, potentially confounds our evaluation of depth (onshore/offshore) patterns. Correlations between the CPUE of major taxa and water clarity indicate persistent, negative relationships (Table 5). Variations in water clarity, however, were never observed to explain $>16\%$ of the variance in catch; and among the major taxa analyzed in detail for CPUE-water clarity relations, mean CPUE differed by more than a factor of 10 to over four orders of magnitude between the 5-11 m and 18-27 m depth blocks during the day. For this reason, we strongly feel that the potentially greater net avoidance in clearer waters farther offshore is insufficient to explain the observed daytime onshore/offshore stratification of these fishes.

Net avoidance also is a possible complicating factor to our interpretation of day-night differences in catch (i.e., higher night catches). Our test results in fact indicate an approximately twofold greater average catch efficiency for *Seriphus politus* at night versus during the day. However, CPUE of *S. politus* differed by a factor of four and by over three orders of magnitude between diel periods at the 12-16 m and 18-27 m depths, respectively. As above for the potential confounding of daytime depth patterns, we feel that diel differences in catch efficiencies alone cannot explain the marked diel patterns that we have observed.

Dispersal of schooling (especially pelagic) fishes under low light conditions has been noted repeatedly in the literature (Shaw 1961; Loukashkin and Grant 1965; Woodhead 1966; Hobson 1968). Four possible hypotheses (or a combination thereof) can be proposed to explain the phenomenon of nocturnal dispersal.

1. Schools disperse because light levels are insufficient for fish to maintain visual contact. Vision is an important factor in the maintenance of a polarized state and parallel swimming in schooling fishes (Shaw 1978). Some fishes can maintain polarized schools in light intensities as low as 0.5-0.01 footcandle (Shaw 1961), but disperse in total darkness (Shaw 1961; Loukashkin and Grant 1959, 1965). Some species have the ability to form polarized schools by the light of the full moon alone (Shaw 1961, 1978). The acousticolateralis system may also play an important role in polarization and spacing within schools (Shaw 1978) and is not dependent on light levels. Highly sensitive visual and acoustic systems may allow nearshore pelagic fishes to school even under minimal light intensities. If the visual and acoustic systems of these fishes prove to be sufficiently sensitive, an explanation for the observed nocturnal dispersal probably lies elsewhere.

2. Schools disperse because predation pressure is less intense at night. Hobson (1978) has argued that the threat from predators is a major force behind aggregating (i.e., schooling) behavior in fishes. At low light intensities pressure from visual predators such as those found in this nearshore habitat should be less. However, for this hypothesis to be valid there must be some disadvantage to schooling at night. Theoretically (Eggers 1976) and empirically (Koslow 1981), schooling occurs at the expense of prey consumption. With the threat from predators diminished at night, dispersal of fishes within a school may allow greater food consumption by lessening visual-field overlap (Eggers 1976). Dispersal under these conditions, however, would only be advantageous if the species feeds at night (see hypothesis 4 below).

3. Schools disperse offshore at night to facilitate reproduction among members. DeMartini and Fountain (1981) presented evidence for dusk spawning in *Seriphus politus* during March-August along the same stretch of southern California coastline. Crepuscular spawning probably helps conceal adults and planktonic eggs from visual predators. Unbalanced, day-night sex ratios at shallow depths[6] and egg

[6]DeMartini, E. E., and L. G. Allen. Diel and seasonal shifts in the

hydration rates (DeMartini and Fountain 1981) indicate that most male *S. politus* migrate offshore to spawn each night while individual females on average move offshore only once every week.

Engraulis mordax spawns exclusively at night (Hunter and Macewicz 1980) during its peak (January-April) spawning period. Spawning activity may be partially responsible for nocturnal dispersal in this species during this period of year. However, since most *E. mordax* in our catches were juveniles, its offshore dispersal at night is probably unrelated to spawning.

We believe that at least part of the general nocturnal dispersal pattern may be explained by the reproductive behavior of *Seriphus politus*. However, not enough is known about the reproductive habits of the other abundant fishes of this assemblage to assess the overall importance of spawning behavior to nocturnal dispersal.

4. Schools disperse at night for individuals to feed on nocturnally active prey. Hobson (1968) stated that some authors have greatly underestimated the extent to which vision can be used at night by predatory fishes. Many species of California nearshore fishes possess scotopic visual pigments which have spectral sensitivities best suited for twilight and night vision (Hobson et al. 1981). Five species that were important in our study (*Hyperprosopon argenteum*; spotted scorpionfish, *Scorpaena guttata*; *Seriphus politus*; *Xenistius californiensis*; and *Umbrina roncador*) were included in Hobson et al.'s (1981) list of fishes that forage at night. Hobson and his colleagues were able to characterize the feeding behavior of these nocturnal species through extensive field observations. Midwater planktivores oriented in a tail-down attitude in the water column at night. This presumably allowed them to feed on organisms overhead which were silhouetted against back-lighted surface waters.

Our comparison of day versus night gut fullness has assumed that most planktonic prey are evacuated from foreguts in <12 h at 14°-24°C and that any remaining contents would be in a highly digested state and, therefore, weigh less during nonfeeding periods. These assumptions seem reasonable in light of a recent determination of gastric evacuation rates in *Engraulis mordax*. At 15°C, foregut excavation rates were <30 min for small *E. mordax* larvae and about 2 h for the egg yolks and embryos of *E. mordax* (Hunter and Kimbrell 1980). Our interpretations of day-night CI's are based on the further reasonable assumption that gut evacuation rates are not seriously confounded by different digestabilities of planktonic prey eaten during the day versus at night.

Engraulis mordax has been described as a diurnal planktivore by Loukashkin (1970). However, a great deal of indirect evidence including 1) the predicted inadequacy of diurnal ration (Leong and O'Connell 1969); 2) eye and retinal morphology (O'Connell 1972); 3) size selective biting and filtering behavior (Leong and O'Connell 1969; Koslow 1981); and 4) the ability to capture and consume large copepods and euphausids (Loukashkin 1970, cited in O'Connell 1972) suggest that *E. mordax* feeds at night as well as during the day. The results of our gut fullness analysis lend support to the hypothesis of nocturnal feeding in *E. mordax*. Day-collected fishes did not contain greater amounts of food in the foregut than night specimens, which would be expected if *E. mordax* was strictly a diurnal feeder. Thus, the observed nocturnal dispersal of this species is likely due in large part to feeding behavior. It is also possible that predation pressure interacts with feeding to influence the diel behavior of *E. mordax*.

Hobson and Chess (1976) determined that *Seriphus politus* was primarily a nocturnal feeder. Schools of *S. politus* migrated offshore at night from shallow water where they had formed resting schools during the day; and specimens collected at night in open water contained large, nocturnally active zooplankters (Hobson and Chess 1976). Our analysis of gut fullness corroborates these findings. Night-captured specimens of *S. politus* contained a greater amount of (primarily mysid) prey than those of day-captured specimens. Hence we conclude that dispersal at night facilitates feeding in *S. politus*. Differential offshore dispersal of juvenile, female, and male *Seriphus politus* at night is undoubtedly related to the aforementioned breeding as well as feeding behavior.

Genyonemus lineatus probably feeds day and night as evidenced by gut fullness during both diel periods. A trend toward more food in the foregut was evident in night-collected specimens, but the difference was not statistically significant. Gut contents of *G. lineatus* collected at dawn and dusk from Long Beach Harbor have also suggested a greater amount of food in dawn-captured specimens, but, as with our study, the difference was not statistically significant at the 0.05 level (Richard N. Bray[7]). *Genyonemus lineatus*

depth distributions of immature versus adult queenfish (*Seriphus politus*). Manuscr. in prep. Marine Science Institute, University of California, Santa Barbara, CA 93106.

[7]Richard N. Bray, California State University, Long Beach, CA 90840, pers. commun. April 1982.

can be characterized as an opportunistic feeder that forages both day and night (M. J. Allen[8]). Nighttime dispersal in this species as in *Seriphus politus* could be related to feeding activity.

Results of day-night comparisons of foregut fullness in *Peprilus simillimus* were inconclusive due to the limited time period over which samples were available (June and July 1980 only). Our data nonetheless indicate that, at least during this time period, *P. simillimus* fed both day and night.

Atherinopsis californiensis appears to be strictly diurnal in its feeding activities. The observed dispersal within the inshore section of the study area probably has some other cause(s) than feeding behavior.

In summary, feeding behavior is probably an important factor related to nocturnal dispersal in *Seriphus politus*, *Engraulis mordax*, and *Genyonemus lineatus* but not in *Atherinopsis californiensis*. Crepuscular spawning may also be important in determining diel movements in *S. politus* during March through August. The cause of school dispersal in atherinids (represented by *A. californiensis*) is unknown, but deprivation of visual schooling cues and relaxed predation pressures remain as two possibilities.

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REPRODUCTION, GROWTH, AND OTHER ASPECTS OF THE BIOLOGY OF THE GOLD SPOT HERRING, *HERKLOTSICHTHYS QUADRIMACULATUS* (CLUPEIDAE), A RECENT INTRODUCTION TO HAWAII[1]

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ABSTRACT

The gold spot herring, *Herklotsichthys quadrimaculatus*, was introduced to Hawaii by unknown means probably in the early 1970s and apparently spread and increased in abundance very rapidly. On the island of Oahu, it has been regularly present in inshore areas since 1976 and has been most abundant during late spring to early fall. Among adult fishes sampled, females slightly outnumbered males in seine collections by day in shallow water, but males predominated in nighttime collections from deeper water. Both sexes began to mature at 75-80 mm SL and females carried distinct size groups of nearly mature ova by 90 mm SL. Gonad to somatic weight ratios from both sexes indicated a spring-to-fall spawning season with a midsummer peak. Batch fecundity of females was 1,100-6,300. There was no direct evidence of multiple spawning, but secondary size groups of small ova were observed in some females which also carried a distinct batch of larger ova. Holding experiments showed that juveniles deposit daily growth increments on sagittae. Age estimates from increment counts of fish 17-121 mm long indicated that herring metamorphose at about 1 month, mature at 5-6 months, and probably live no more than 1 year. The reproductive life span of females appears long enough to ripen more than one batch of ova.

Only three species of marine clupeid fishes are known to occur in Hawaii. The round herring, *Etrumeus micropus*, and the sprat, *Spratelloides delicatulus*, are both native to the islands, while the Marquesan sardine, *Sardinella marquesensis*, was introduced in the late 1950s in hopes of increasing the supply of baitfish for the local skipjack tuna fishery. The introduction was successful in that *S. marquesensis* reproduced and spread throughout the islands soon afterwards, but the species never became abundant nor contributed significantly to local baitfish catches (Murphy 1960; Hida and Morris 1963).

In 1975, small clupeids began to appear regularly in Kaneohe Bay on the island of Oahu and by 1976 had become very abundant both in the bay and apparently at other areas of Oahu. Because these fishes closely resembled Marquesan sardines and no other similar species was expected to occur in Hawaii, we blithely assumed them to be *S. marquesensis*. Their sudden obvious presence and consistent occurrence in various collections for other purposes prompted us to undertake further sampling in order to investigate their biology in Hawaii.

After the study had been largely completed, careful examination of a few specimens by W. J. Baldwin of the Hawaii Institute of Marine Biology and subsequent rechecking of our material plus more recent collections showed that we were not dealing with the Marquesan sardine, but rather with the gold spot herring, *Herklotsichthys quadrimaculatus*. No attempts to introduce *H. quadrimaculatus* to Hawaii have been reported and, although its range is uncertain due to probable misidentification in many reports, there is no evidence that it occurs naturally anywhere within ca. 3,500 km of Hawaii. Thus our study became one of an apparently inadvertently introduced species, whose introduction was considerably more successful than the more carefully planned introduction of the Marquesan sardine.

This paper summarizes available data on the introduction and spread of *H. quadrimaculatus*, briefly considers several aspects of its general biology in Hawaii, and presents results of investigations of its reproduction and growth. In the course of the latter we demonstrate that growth increments on otoliths are valid estimates of age in days as has already been shown for several temperate and tropical species including the Hawaiian anchovy or nehu, *Stolephorus purpureus* (Struhsaker and Uchiyama 1976). Although there are few comparable data on other tropical clupeids, some comparisons and contrasts of *H. quadrimaculatus*' life history pattern with those of

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other species are possible. Unfortunately, we are only able to speculate about many aspects of the introduction and subsequent spread of this species in Hawaii.

METHODS

Herklotsichthys quadrimaculatus were taken at night with small purse seines in water 12-13 m deep in the southern end of Kaneohe Bay on the island of Oahu. All sets were "blind," i.e., the net was set more or less at random within the general area to be sampled, and no lights were used to attract fish prior to the set. Most herring were taken with a 61 m long by 12 m deep seine of ca. 0.3 mm square mesh. Up to several hundred juveniles and up to 12 adults were taken per set. Between September 1974 and December 1976, 99 sets were made with this net. This series was initially intended to sample the Hawaiian anchovy. Over most of this period, samples were taken at 2-3 wk intervals; the longest interval between sampling was slightly more than a month. Most adult herring were taken with a few exploratory purse seines of a larger (153 m long by 11 m deep), coarser mesh (ca. 25 mm stretch mesh netting); this purse seine was first tested in May 1975 and set at about monthly intervals between December 1975 and December 1976. Other sporadic samples were taken with both nets during 1977-79.

Herklotsichthys quadrimaculatus were found only in shallow water (≤3-4 m) during the day and were collected by a variety of methods from several locations on Oahu. Juveniles were readily captured by small beach seines or cast nets over reef flats in Kaneohe Bay; however, to obtain adults from all seasons of the year, particularly when they were absent from night purse seine collections, we used specimens from beach seining on exposed coasts on the northeast side of Oahu as well as on reef tops in Kaneohe Bay, from baited hook or three-pronged hook "snag" fishing in harbors at Haleiwa and in Kaneohe Bay, and from bait captured in Pearl Harbor by a skipjack tuna vessel.

In addition to our collections for biological analyses, we have also examined specimens caught by others from a wide variety of habitats and locations on Oahu in order to confirm that *H. quadrimaculatus* was present all around the island. We have very few data on the occurrence of *H. quadrimaculatus* elsewhere in the archipelago and thus cannot be certain that our observations apply to all Hawaiian Islands.

Inshore areas in southern Kaneohe Bay were surveyed visually by day, and the presence of gold spot herring schools, their approximate size composition, and approximate numbers noted. Surveys were made at nearly weekly intervals from June 1978 to September 1979; prior to this time they were made sporadically and unsystematically.

Most fish were immediately preserved and held in ca. 4% formaldehyde seawater solution. Those fish used for age determination were frozen until otoliths were removed. Standard length (SL) was measured to the nearest mm and wet weight (ww) to the nearest 0.01 g after blotting dry. Dry weight was measured to the nearest 0.01 mg after 24 h at 60°C. Stomach contents of the fish were removed before drying. Sex was determined for all adults and a sample of about 200 juveniles 50-80 mm SL. Rough estimates of stomach fullness and types of prey eaten were recorded from 390 fish. When desired, gonads were dried and weighed separately. The gonad/somatic weight ratio (G/S) was calculated from the dry weight of the gonads and dry weight of the fish excluding gonads (dw_s), rather than total dry weight of the fish including gonads (dw_t).

Portions of the ovaries of mature-sized females from each month's sample were examined, and diameters of several of the largest ova measured to the nearest 0.02 mm with an ocular micrometer. For 20 females with well-developed ova, a section of the ovary containing about 200 ova >0.20 mm was teased apart and all ova >0.20 mm were measured. Preliminary data indicated no differences in ova density or size composition within or between ovaries of the same fish. The examined sections and remaining portions of the ovaries were dried and weighed separately, and the total number of ova in the largest mode was calculated from the weights of the section and remaining ovary and the ova count from the section. For 26 other females with a clearly separated mode of large ova, all ova in that mode were counted from both ovaries.

The growth increments or rings on sagittae of fish less than ca. 50 mm SL faded within a few hours to days after dissection; consequently, counts were made as soon as possible after removal from a fresh or thawed specimen. The sagittae were mounted in glycerine and rings of each counted at least three times under 100-400× magnification. Generally otolith rings from fish of this size were easy to discriminate and the repeated counts rarely disagreed; however, if a consistent count could not be made, the data were discarded.

The denser otoliths from fish >50 mm SL were allowed to air dry and then mounted in Euparol[3]. The

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

rings became clearer with time; consequently, the otoliths were stored for 2 wk, counted, and then recounted 2 wk later to confirm the first counts. On each occasion, counts were made along the rostral, postrostral, and antirostral axes, when possible. Especially prominent rings were noted and were of great use in tracking and comparing counts of the numerous closely spaced rings of large fish.

To determine if growth increments on the otoliths were formed daily, small metamorphosing herring were captured in Kaneohe Bay and held alive in shaded tanks which received a continuous flow of seawater from the bay at near ambient temperature. A subsample of the collected herring was frozen immediately after capture, and subsamples were removed from the tanks at later dates but at the same time of day (± 1 h) as the original capture. The differences in numbers of rings between fish from the different subsamples were compared with the number of days elapsed. In the first two of these experiments, the fish were fed frozen zooplankton from Kaneohe Bay 3-4 times/wk on an irregular schedule, but in the last two experiments they were fed brine shrimp once or twice daily, 6 d/wk. The fish also probably ate some plankton from the seawater supply to the tanks.

RESULTS

Appearance and General Biology

Catches of the purse seine sets indicated that the gold spot herring first appeared in Kaneohe Bay in mid-1975, but did not begin spawning in the area until 1976. No herring were taken in a total of 25 sets with the small purse seine on 12 dates between September 1974 and July 1975. The first catch was an adult taken on 23 July 1975, and 11 others (66-117 mm SL) plus a 28 mm juvenile were taken in 27 sets on 11 dates between July and December 1975. In the first six months of 1976, 28 sets on 12 dates yielded 65 fully transformed herring 45-120 mm SL—most of them adults. Two of these sets (in March and April) also collected a total of 14 herring just beginning transformation from the larval stage. Catches increased markedly in the second half of the year. A single set taken in late June 1976 took 131 transforming or small juveniles (19-37 mm SL), and almost all subsequent sets with the small purse seine took herring of a wide size range. Two experimental sets with the large seine in May 1975 caught no herring. Adults (up to 120 per set) were taken in subsequent sets in April, May, and October 1976 and June 1977.

There was general agreement between collections made by others in the bay and our visual observations that gold spot herring were not present in the bay prior to mid-1975 and that recruitment of juveniles was not substantial until 1976. Adult or near-adult herring first appeared over reef flats during the day shortly after the first purse seine catches. Although our records do not unequivocally indicate whether or not juveniles were present in 1975, large schools (thousands of individuals) of transforming herring were definitely not observed until 1976. Subsequent to 1976, transforming or small juvenile herring were observed or caught in all months of the year, but were more abundant from June to November or December. In 1976-79, adults were present in catches or observations from March to December, and except for 1979 were present in abundance primarily from May to October. Their presence was, however, sporadic even during the latter months, and in 1979 few were seen or caught at any time.

Our observations in Kaneohe Bay appear to be representative of inshore areas all around the island of Oahu. Casual reports by other scientific personnel as well as by commercial and recreational fishermen indicated that "sardines" appeared and subsequently increased markedly in abundance elsewhere on Oahu at about the same times as in Kaneohe Bay and that subsequently they were most abundant from spring to fall. Unfortunately, we did not obtain any specimens of "sardines" from other areas of Oahu until late 1976, but it is extremely unlikely that the casual observations refer to the Marquesan sardine, the only species with which the gold spot herring might be confused. We have examined specimens taken in 1976-82 from a wide variety of locations on Oahu (from day collections in the surf zone to specimens taken under night lights several km offshore) and found all to be *H. quadrimaculatus*. We find no evidence that, prior to 1975, "sardines" of any sort were ever sufficiently abundant to attract attention, and the most recent specimens of *S. marquesensis* from Oahu were taken in 1968.

During the day, the gold spot herring of all sizes in Kaneohe Bay were mostly found over sand-rubble reef flats 1-2 m deep in fairly clear water or in somewhat deeper water around piers, floating docks, etc. They were absent from these areas at night. Although our nighttime purse seine sampling was inadequate to properly consider dispersion, the catches indicated that juveniles moved into deeper water at night, but tended to remain within a few hundred meters of the reef or shore. Adults were taken routinely up to 1 km away from the nearest shallow water. We have also examined adults taken under

night lights as far as 10 km offshore in water hundreds of meters deep.

Before the appearance of the gold spot herring, the dominant pelagic planktivorous fishes in Kaneohe Bay were the Hawaiian anchovy or nehu (which is the main source of bait for the local skipjack tuna fishery) and the iao, *Pranesus insularum* (Atherinidae). Although the nehu and gold spot herring cooccurred in almost all purse seine catches and adult herring occasionally eat larval or juvenile nehu (see below), there was no evidence that the herring's appearance substantially affected the nehu population. The nighttime areas of highest abundance for the two species appear to be slightly different within the bay, and nehu by day prefer more turbid, brackish areas than do the herring. The iao population, however, appears to have been affected markedly by the herring. Prior to the appearance of herring, iao were regularly present in large numbers over shallow reef flats during the day, but since have been nearly completely replaced by herring in the same situations and are much less frequently seen.

Qualitative examination of stomach contents of gold spot herring showed that they eat a wide variety of zooplankton and indicated that they feed primarily but not exclusively at night. Fish <30 mm SL (116 examined) had eaten small (<1.0mm) copepods almost exclusively. Those 30-80 mm SL (31 examined) also ate copepods but included larger zooplankton such as decapod zoeae, the pelagic shrimp *Lucifer chacei*, mysids, and small fish larvae. Adult herring (243 examined) ate copepods less frequently and larger zooplankton more frequently than did juveniles and also took considerably larger prey such as chaetognaths, polychaetes, shrimp, and fish (*Pranesus insularum* 23-25 mm SL and *Stolephorus purpureus* 6-31 mm SL). In one late afternoon sample of adults, the stomachs were mostly packed with what appeared to be planulae. Usually, however, both fullness and composition of prey in individual fish were variable even with the same sample; some fish contained several types of prey while others were mainly full of a single type. As with Marichamy's (1970) study of *Herklotsichthys punctatus*, we found no evidence that any sizes of *H. quadrimaculatus* eat phytoplankton. Overall, fresh prey was more frequent in fish caught at night and empty stomachs more so during the day, but fish in both conditions were found in almost every sample examined.

Gold spot herring apparently spawn mostly or entirely outside Kaneohe Bay. No eggs or larvae were found in any plankton tows taken in the bay while adult sardines were present; these tows included eight oblique tows taken during the peak spawning season in the same areas where adults had been collected. The smallest fish collected or observed were 17 mm SL and in the process of transforming from larvae to juveniles.

There were other movements of gold spot herring both within the bay and between the bay and exposed areas. Adult herring on several occasions vanished from all areas of the bay for varying periods and then reappeared with no obvious relation to any environmental factor. What appeared to be the same schools of juveniles were often observed in the same place for several days in a row, but before there was any observable change in size composition, the schools vanished—often to be replaced by another school of obviously different-sized fish. Similarly, the size composition of juveniles from purse seine catches showed no coherent seasonal trend.

Between 17 and ca. 30 mm SL, body depth of the transforming herring obviously increased relatively more rapidly than the standard length. Matsuura (1975) showed that in *Sardinella brasiliensis* the ossification of ventral scales is not completed until a similar size. For 50 gold spot herring 17-29 mm SL, the relationship between SL (mm) and dw_t (g), as determined by linear least squares regression on the logarithms, was

$$dw_t = 1.691 \times 10^{-9}\ SL^{5.200}\ (r^2 = 0.94).$$

The relationships calculated from data for 60 juveniles 31-79 mm SL and 157 adults 80-128 mm SL were, respectively:

$$dw_t = 8.335 \times 10^{-7}\ SL^{3.377}\ (r^2 = 0.98),$$

$$dw_t = 3.462 \times 10^{-6}\ SL^{3.044}\ (r^2 = 0.90).$$

These differed significantly (analysis of covariance, $P < 0.01$) and indicated progressively more nearly isometric growth with increasing size. The equations for somatic weight vs. standard length differed little from those for total dry weight. Somatic weights of adult females tended to be lower than those of similar-sized males, but the difference was not significant. Wet weights of 108 fish 42-121 mm SL were related to standard length by

$$ww = 9.168 \times 10^{-6}\ SL^{3.121}\ (r^2 = 0.99).$$

The relationship (based on linear least squares regression) between ww and dw_t for 123 fish 42-121 mm SL was

$$dw_t = 0.053 + 0.278\ ww\ (r^2 = 0.98).$$

Sex ratio of juveniles 50-80 mm SL did not deviate from 1:1, but there were deviations from 1:1 among larger fish depending upon time of collection. Of 348 adults from open-water night collections, the proportion of males in the total, 86.9% (95% limits: 82-91%), and in all size groups from 85 to 110 mm SL (Fig. 1) differed significantly from that expected for a 1:1 sex ratio. Males made up only 42.6% (95% limits: 37-49%) of the 392 adults from shallow-water day collections; females predominated in all size classes but one and significantly so in two (Fig. 1). The pattern in all large samples was consistent with the trend of the total collection, except for some day samples where the sex ratio was not different from 1:1. For example, a beach seine collection on a reef top in Kaneohe Bay at 1400 h in June 1977 yielded 56 males and 86 females, while a purse seine collection taken at 2000 h on the same date and 1 km away yielded 94 males and 25 females. For both the pooled collections and the above pair of samples alone, there were significant day-night differences in size composition of either sex considered separately or of the total fish collected, but there were no differences between males and females taken at the same time of day (Kolmogorov-Smirnov test, $P <$ or > 0.05, respectively). Among all the specimens examined, several females were larger (up to 128 mm) than the largest male (118 mm).

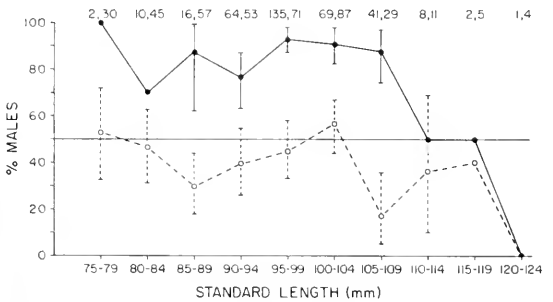

FIGURE 1.—Percentages of males among different size groups of *Herklotsichthys quadrimaculatus* for night (solid circles and lines) and day (open circles, dashed lines) collections, Kaneohe Bay, Oahu. Vertical lines indicate 95% confidence limits for observed proportions; for seven points represented by 10 or fewer fish, the limits, which included 50% (light horizontal line) were omitted for clarity. Pairs of numbers at the top represent numbers of fish of each size group examined; night collections on the left, day on the right.

Reproduction

The G/S ratios (Fig. 2) indicated that both sexes begin to mature at about 75-80 mm SL, and both the G/S and maximum ova diameters indicated that females continue to grow while ova are maturing. Although G/S values of 80-90 mm SL fish were higher than those of juveniles, values >2.5% in males and >7% in females were found only in fish >90 mm SL. With one exception, the largest ova from females <90 mm SL were <0.6 mm in diameter, while values for larger females ranged up to 0.9 mm. There was no trend in G/S or maximum ova diameter with female length for fish >90 mm SL; even during the spawning season (see below and Figure 3), the G/S ratios of some large females were almost as low as those of juveniles or presumably reproductively inactive females from winter. G/S of females was generally positively correlated with diameter of the largest ova (Fig. 2), but the relationship was highly variable. Fish carrying large numbers of small ova often had the same G/S as others carrying smaller numbers of larger ova.

Seasonal differences in G/S ratios of both males and females (Fig. 3) indicated that the principal spawning season is May-July and that at least some fish are fully mature or nearly so between March and October. Ova with yolk were not found in several of the females from August to October and in none of the 13 from November and December; yolked ova were present in all females examined from March through July. The few or no data from November to February do not preclude some spawning during the entire year, and, in fact, recently transformed juveniles about 1-mo-old (see below) were observed

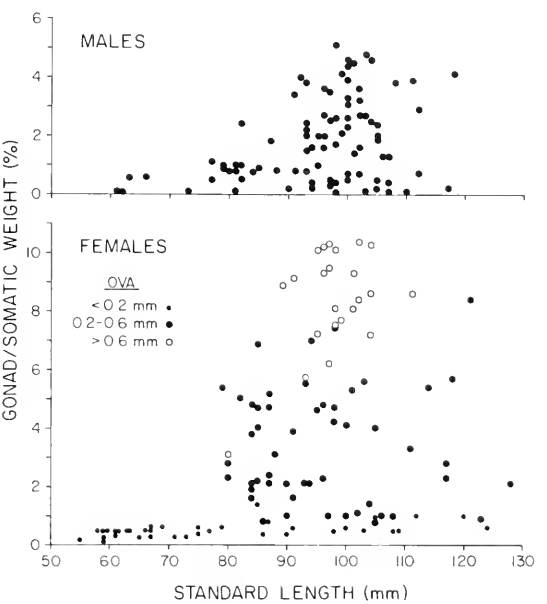

FIGURE 2.—Relationship between gonad/somatic weight and size of male and female *Herklotsichthys quadrimaculatus* collected in Kaneohe Bay, Oahu.

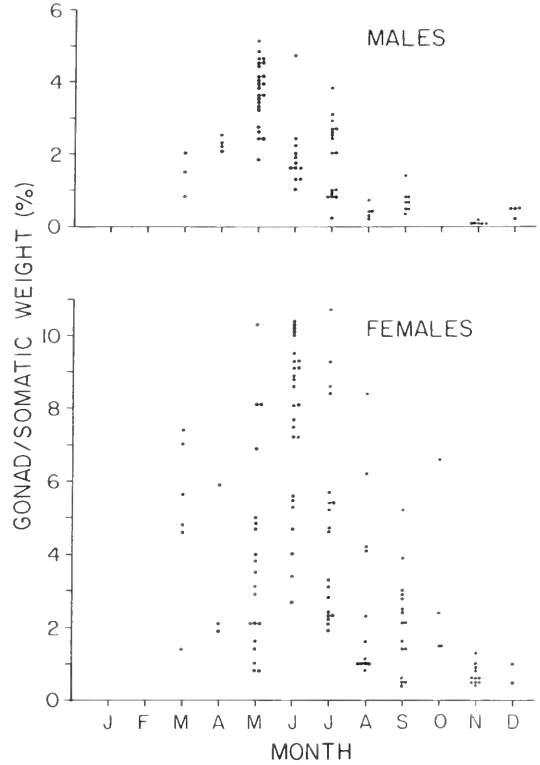

FIGURE 3.—Relationship between gonad/somatic weight and month of capture for adult (>80 mm SL) male and female *Herklotsichthys quadrimaculatus*, Kaneohe Bay, Oahu.

in Kaneohe Bay in all months. The juveniles, however, were decidedly more abundant and more frequently recorded during the summer and fall as would be predicted by a summer peak in spawning.

Our findings on ova development and size frequency in the gold spot herring are essentially the same as those of Nakamura and Wilson (1970) for the Marquesan sardine (see their figure 5). In addition to transparent ova less than ca. 0.10-0.15 mm in diameter, the ovaries of most adult female herring also contained partially yolked, semi-opaque ova ca. 0.16-0.30 mm and completely yolked, opaque ova >0.30-0.35 mm. Distinctly separated size-frequency modes of opaque ova were found from 0.30-0.40 mm to 0.60-0.90 mm. No larger, hydrated ova were found. The small, partially yolked ova were usually continuous with the smaller transparent ova; but in some fish, they formed a partially separated mode—often with opaque ova at the large end. Such modes, which were never completely separated from the smaller ova, were found in fish both with and without a separate mode of larger, opaque ova. Although a few females without a separate advanced mode had somewhat flaccid ovaries, we found no atretic ova nor any other evidence that these or any of the fish had already spawned. There was no indication of synchronous spawning or any short-term cycle; the large samples from the middle of the spawning season included females with ova in a wide range of sizes and stages of development.

In the 46 females (80-121 mm SL) with a separate advanced mode, the batch fecundity or number of ova in that mode ranged from 1,155 to 6,296 (Fig. 4). The relationships of batch fecundity to length or weight as determined by least squares linear regression were

$$F = 7{,}518.0 + 110.8\ \text{SL (mm)} \quad (r^2 = 0.84),$$
$$F = 172.0 + 218.4\ ww\ \text{(g)} \quad (r^2 = 0.79),$$
$$F = -10.2 + 795.6\ dw_t\ \text{(g)} \quad (r^2 = 0.80),$$
$$F = 21.8 + 842.1\ dw_s\ \text{(g)} \quad (r^2 = 0.77).$$

Fecundity was clearly correlated with some measure of size, but not very precisely with any of them. The appropriate equations predicted relative fecundities

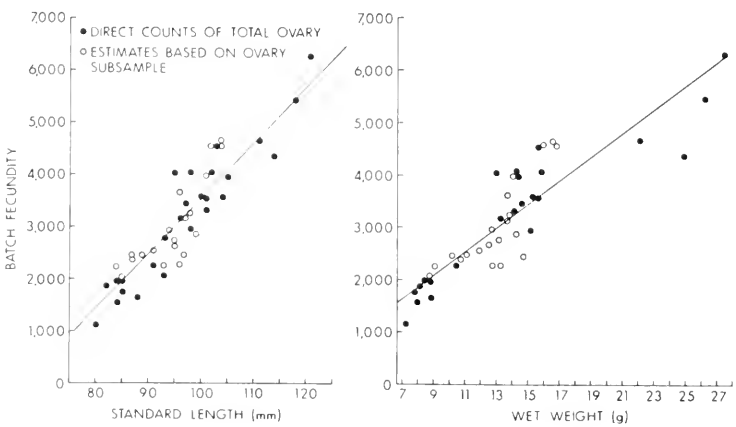

FIGURE 4.—Relationship between batch fecundity and length and wet weight of female *Herklotsichthys quadrimaculatus*, Kaneohe Bay, Oahu. Straight lines are drawn from regression equations (see text).

of 225-242 ova/g *ww* and 791-794 ova/g dw_t for the observed ranges of fish weights, while actual values ranged from 160-311 ova/g *ww* and 502-1,102 ova/g dw_t. There was no trend between relative fecundity and size.

Age and Growth

The holding experiments (Fig. 5, Table 1) provided strong evidence that growth increments on the otoliths are deposited daily. In the first experiment, there was a wide range of size and otolith ring counts in the initial and subsequent subsamples. Probably because of this, the increase in average number of rings agreed closely with the numbers of days elapsed for only two of the subsamples; otherwise, only a general trend for increase in average ring count was evident. In the second experiment, the fish were smaller and consisted primarily of two distinct groups separated by 3 mm SL and five otolith rings. These two groups were apparent in all the subsamples, and the increase for each in number of rings corresponded closely with the number of days elapsed. Since each group was about equally represented, the average difference in number of rings for the whole experiment also correlated closely with the number of days.

Both the fish and their otoliths grew faster in the third and fourth experiments, probably due to the higher feeding rate. The distance between rings was markedly greater and counts much easier to make than in the first two experiments. Fish in the initial subsample for the third experiment had a wide range of sizes and ring numbers, but a single group of fish with 26 rings dominated the initial subsample (16 of 41 fish). This group was apparent in most of the rest of the subsamples. The increase in number of rings in this group and differences in means for the subsamples corresponded closely with number of days. The results of the fourth experiment were similar. The subsample which deviated most from the predicted increase had a much narrower range of ring counts and was apparently made up mostly of the younger fish in the experiment.

Initial collections for the third and fourth experiments were made on consecutive days (31 July and 1 August 1979) from the same location and from what appeared to be the same school of transforming juveniles. In the initial subsample for the third experiment, the dominant group had 26 rings, while in that for the fourth, 13 of 39 had 27 rings (Fig. 5). Similarly, the lowest number of rings in the initial subsample for the third experiment was 23 (5 fish), and that for the fourth experiment was 24 (6 fish).

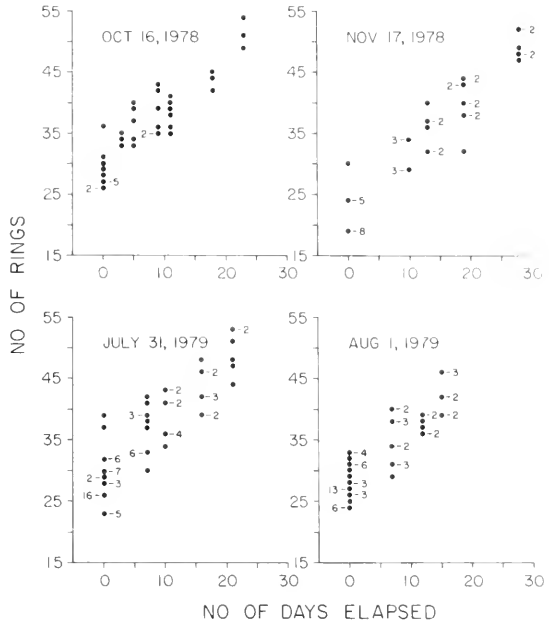

FIGURE 5.—Relationship between number of otolith rings and elapsed time for subsamples of juvenile *Herklotsichthys quadrimaculatus* from holding experiments started on four dates, 1978-79 (see text for details). Numbers of specimens are given for points representing more than one fish per subsample.

TABLE 1.—Number of days elapsed and mean increase in the number of otolith rings in subsamples of *Herklotsichthys quadrimaculatus* from holding experiments started on four different dates, 1978-79, at Kaneohe Bay, Oahu, Hawaii.

Starting date/ No. days elapsed	No. in subsample (Size range, mm SL)	Increase in mean increment count
16 October 1978		
0	12 (19.5-25.0)	0
3	3 (22.0-22.5)	5.6
5	5 (22.5-25.0)	8.2
9	6 (22.0-25.0)	9.9
11	6 (22.0-27.0)	9.8
18	3 (24.0-30.0)	15.4
23	3 (26.5-28.0)	22.9
17 November 1978		
0	14 (17.0-21.5)	0
10	6 (20.0-23.0)	9.9
13	6 (22.0-24.0)	14.1
19	9 (22.0-23.5)	18.7
28	6 (23.0-28.0)	27.8
31 July 1979		
0	41 (19.5-24.0)	0
7	14 (22.0-25.0)	7.9
10	9 (23.0-25.0)	10.6
16	8 (23.0-26.0)	14.9
21	6 (24.0-26.0)	21.3
1 August 1979		
0	39 (20.5-23.5)	0
7	11 (21.0-23.0)	7.8
12	6 (21.0-23.0)	9.5
15	7 (21.0-23.5)	14.9

Two fish in the initial subsample for the third experiment had higher counts than the maximum for the

fourth, 33 (4 fish), but the next highest value for the third was 32 (6 fish).

Although growth increments appear to be deposited daily, the age at deposition of the first ring is unknown because newly hatched gold spot herring were not available. Brothers et al. (1976) found that the northern anchovy, *Engraulis mordax*, deposits the first ring at 5 d and the grunion, *Leuristhes tenuis*, at 1 d after hatching. The otolith "age" or number of rings in the gold spot herring is probably only a few days less than the actual age, and the error for the former is substantial only for the youngest fish.

The ring counts from 106 gold spot herring 17-121 mm SL (Fig. 6) indicate that the smallest individuals were about 1-mo-old, both sexes mature at about 5-6 mo, and the largest fish was probably about 1-yr-old. Variability was high in length of fishes estimated to be older than 6 mo. There was no definite difference between males and females except that several females were both older and larger than any males.

Data suggest at least two growth cycles or stanzas. A two-cycle Gompertz-type model from Zweifel and Lasker (1976) was fitted to the data by a nonlinear least squares iteration. The equation was

$$L_t = 8.07e^{1.48\left(1-e^{-0.037A}\right)+1.37\left(1-e^{-0.013B}\right)}$$

where $A = \text{Min}(t, 59.6)$ and $B = \text{Max}(t - 59.6, 0)$ and t is the estimated age in days. The curve describes the data quite well for the fish < 80 mm, and the length at the break value for the two cycles of the curve, 59.6 d, is about 30 mm—identical to the size at which transformation appeared complete and subsequent growth more nearly isometric. The model predicts a length at time infinity of 119 mm—about the size of the largest male but well below that of the largest female. This indicates that the growth pattern for males is similar to that of juveniles, but a different curve or perhaps a third stanza may be required to describe the growth of females after maturity.

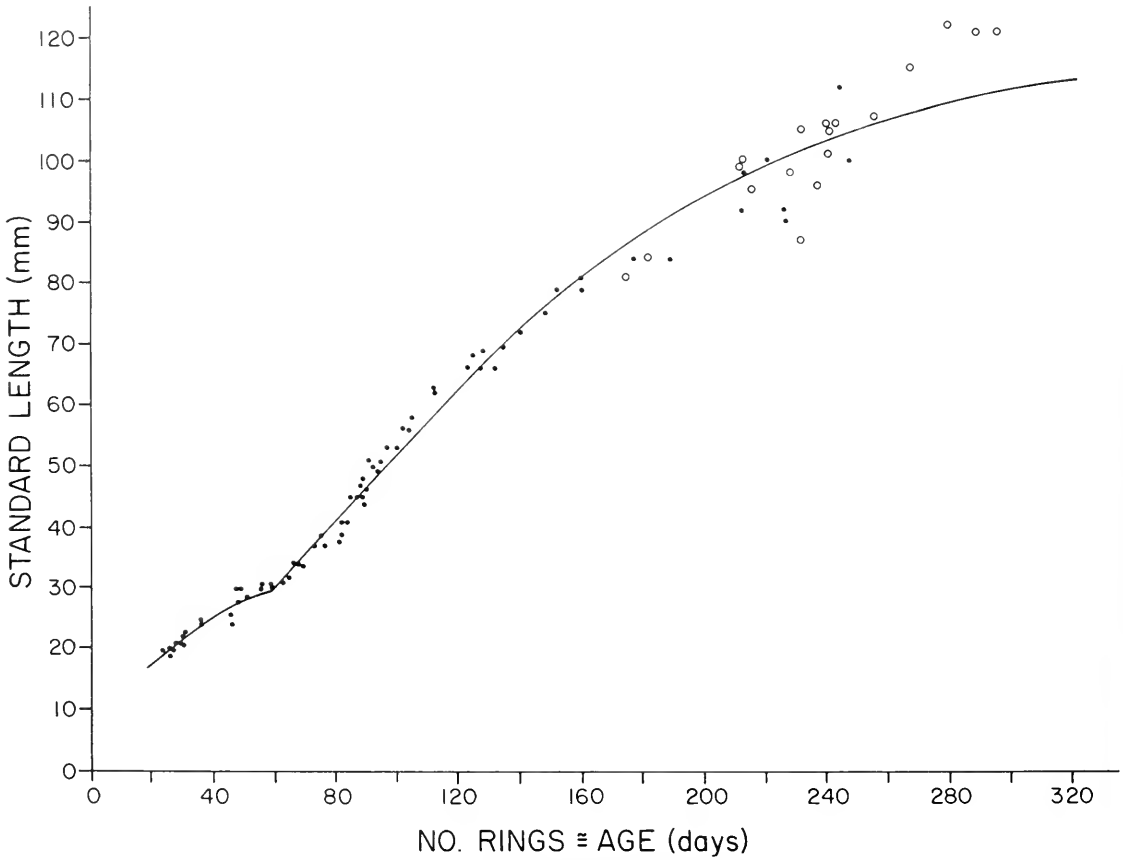

FIGURE 6.—Relationship between standard length and number of otolith rings or approximate age in days for 106 *Herklotsichthys quadrimaculatus* collected off Oahu, Hawaii. Females are indicated by open circles; solid circles represent juveniles (<80 mm SL) and males. Curve is drawn from a two-cycle growth model fitted to the data (see text).

DISCUSSION

The gold spot herring is an "annual" species which grows rapidly, but matures at an early age while small, and rarely lives more than a few months thereafter beyond maturity. Reproduction probably occurs all year, but there is a definite peak in the summer. Less extensive data on what is probably the same species[4] in the Marshall Islands (Hida and Uchiyama 1977) indicate the same life history pattern. Although seasonal changes in abundance and size composition observed in Kaneohe Bay were in part due to movements in and out of the bay, they correlate generally with the reproductive season and the 1-yr life cycle and are probably indicative of changes in the general population.

Few comparable data exist on other *Herklotsichthys* spp. or the closely related *Sardinella* spp. Maximum size in many, e.g., *H. punctatus* (Marichamy 1974) and *S. marquesensis* (Nakamura and Wilson 1970), is about the same as in *H. quadrimaculatus*. *Sardinella jussieui* (= *S. gibbosa*) and *S. brachysoma* (= *S. albella*) also appear to have a maximum age of about 1 yr (Nair 1960; Okera 1974). Other aspects of the life history of these small species may prove to be similar to those of *H. quadrimaculatus*. Within the tropics (and often cooccurring geographically with small clupeid species) some *Sardinella* spp., e.g., *S. longiceps* (Nair 1960; Ritterbush 1974) and *S. aurita* (Postel 1960), grow more than twice the length of *H. quadrimaculatus*, live for several years, and may reproduce more than one season. Such species are qualitatively more similar to the *Sardinops* spp. from higher latitudes than to the small tropical species. Following the arguments of Murphy (1968) and Leggett and Carscadden (1978), this indicates that reproductive success is more consistent in the smaller species and that even within the tropics, the basic population regulatory mechanisms of closely related species may be qualitatively different.

Data on ova development and fecundity of other species are also limited. The gold spot herring is very similar in these respects to *S. marquesensis* (Nakamura and Wilson 1970). Relative fecundity of *S. aurita* and *S. maderensis* (calculated from the respective data of Kwan-Ming 1960 and Ben-Tuvia 1960) is comparable with that of *H. quadrimaculatus*, but because of their larger size, batch fecundity in these species is much higher. *Sardinella longiceps*, however, is not only larger than *H. quadrimaculatus*, but has considerably higher relative fecundity (940-2,090 ova/g, calculated from Ritterbush 1974). These differences again indicate that reproductive success of the large species is lower or less predictable than in the small, less fecund species.

Neither our results nor those of Leary et al. (1975) on the Hawaiian anchovy offer any unequivocal evidence that these tropical clupeoids ever ripen and spawn more than one batch of eggs. The age-length data (Fig. 6) indicate that 90 mm SL gold spot herring, some of which appeared ready to spawn, are only about 1-mo older than clearly immature fish 75-80 mm SL and that females live 3-4 mo longer after reaching 90 mm SL. Thus the herring appear capable of spawning several times during their reproductive life span, but we have no evidence that they actually do so. The wide range in maximum size of ova found in herring >90 mm SL could result either from multiple spawning or variation in the size and age at which females begin to ripen ova for a single spawning. The absence of spent females indicates a single spawning and high mortality of spawners; however, no females with hydrated ova were observed either. Since spawning appears to occur away from the areas where we made our collections, it is possible that both hydration and recovery from spawning are so rapid that there is no trace of either in fishes about to leave for or just returned from spawning.

Our results, as well as those of the great majority of studies on clupeoid fishes in which appropriate data have been examined and presented, show that sex ratio of fish caught by a given gear and at a given time frequently deviates from 1:1. Assuming the actual sex ratio of adult gold spot herring is 1:1, the day-night differences in sex ratio indicate that males are more likely to move offshore at night and perhaps to remain there during the day. Such behavior is most likely related to spawning. The gold spot herring, like most other clupeoids, probably spawns at night, and Hunter and Goldberg (1980) have presented evidence that spawning schools of pelagic clupeoids are dominated by males.

Like many other clupeids, female gold spot herring appear to reach sizes larger than the largest male. Although there may be sexual differences in growth, our data indicate that female herring reach larger sizes because they live longer. If spawning incurs increased mortality due to either energy requirements or exposure to predation, the males may not live as long because they spawn more frequently than do females.

Discussion of the introduction and spread of *H. quadrimaculatus* in Hawaii is limited because we do

[4]Hida and Uchiyama identified their specimens as *H. punctatus*. W. J. Baldwin of the Hawaii Institute of Marine Biology has, however, examined numerous specimens collected from the Marshalls during Hida and Uchiyama's study and found them all to be *H. quadrimaculatus*.

not know (and probably never will) precisely when and how the species was introduced. Nevertheless, some speculations based on available data and very likely possibilities seem justified. First, it is almost certain that *H. quadrimaculatus* was not inadvertently introduced along with the *S. marquesensis* in the late 1950s. The former species is not known to occur in the Marquesas Islands, and the extensive study of Nakamura and Wilson (1970) would have likely detected it if it were actually present. The absence of any "sardines" generally and in our Kaneohe Bay samples prior to 1975, as well as the very rapid increase in abundance of *H. quadrimaculatus* between 1975 and 1976, both indicate that this species had probably not been in Hawaii very long before we collected our first specimens. Finally, the number of individuals released in Hawaii was almost certainly less than the 144,000 fish released when the Marquesan sardine was introduced (Hida and Morris 1963).

If the above speculation is close to the truth, *H. quadrimaculatus* appears to have increased from a small group of individuals to a widespread and very abundant species within a span of 2-3 yr. Even allowing for multiple spawnings per lifetime in females, the fecundity of *H. quadrimaculatus* is so low that survival from egg to adult during this period must have been extremely high. Since the population appears to have remained relatively stable since about 1976, some mechanism must have acted to lower survival rates. The most likely regulatory mechanism would be the increasing abundance of the gold spot herring themselves, i.e., intraspecific competition at some point in the life cycle. It is also possible that local predators have responded to the herring as a new resource and are presently regulating abundance.

The known differences between *Herklotsichthys quadrimaculatus* and *Sardinella marquesensis* seem unlikely to account for the former's greater success in Hawaii; to the contrary, the two species are very similar in morphology and ecology. Berry and Whitehead (1968) noted that in several respects *S. marquesensis* is more similar to the *Herklotsichthys* spp. than are other *Sardinella* spp. Fresh specimens of *H. quadrimaculatus* can be distinguished from *S. marquesensis* by the gold spots on the operculae; otherwise, close examination of the second supramaxilla, the imbedded portions of the body scales or the posterior anal rays (see Berry and Whitehead 1968) are required to separate the two species unequivocally. *Sardinella marquesensis* has higher gill raker counts than *H. quadrimaculatus*, but Nakamura and Wilson's (1970) diet data from the Marquesas indicate that, unlike most other *Sardinella* spp., *S. marquesensis* eats very little phytoplankton and, in fact, eats zooplankton equivalent to those recorded for *H. quadrimaculatus* in Hawaii. Other features of the life history of *S. marquesensis* considered by Nakamura and Wilson are almost identical to those of *H. quadrimaculatus*. Investigation of the physiology and larval ecology of the two species and, if still possible, of the ecology of *S. marquesensis* in Hawaii might better account for the greater success of *H. quadrimaculatus* in Hawaii and might also be pertinent to the broader problem of factors limiting natural distributions.

ACKNOWLEDGMENTS

We are indebted to W. J. Baldwin for correcting our initial misidentification of the topic species and to P. J. P. Whitehead for confirming the name used here. We thank T. D. Cooney for his assistance in fitting our age-length data to the growth model. This paper is based in part on V. R. Williams' Master of Science dissertation (Department of Oceanography, University of Hawaii). Partial support was derived from NSF OCE 77-09202 and from the Hawaii Institute of Marine Biology.

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AGE, GROWTH, AND SEXUAL MATURITY OF GREENLAND HALIBUT, *REINHARDTIUS HIPPOGLOSSOIDES* (WALBAUM), IN THE CANADIAN NORTHWEST ATLANTIC

W. R. Bowering[1]

ABSTRACT

Age composition of Greenland halibut, *Reinhardtius hippoglossoides*, in the eastern area ranged up to 14 years for males and up to 18 years for females; most fish, however, were less than 10 years old, with a predominance of older fish in the more northerly areas. In the Gulf of St. Lawrence, males beyond age 9 and females beyond age 12 were completely absent from the catch. It is not fully clear if this is the result of emigration of older fish from the area or mortality due to early maturity. The empirical growth curves for all areas show females growing faster than the males, particularly in the older ages, while the mean size at age indicates little difference up to ages 8-12. Statistical treatment of back-calculated growth curves up to age 5 indicated no difference between males and females. No statistical difference was found in the growth rate of fish of the Labrador and eastern Newfoundland areas. Fish from the Gulf of St. Lawrence exhibited the fastest growth rate and fish from Baffin Bank the slowest throughout the range.

Onset of maturity of female Greenland halibut from the Gulf of St. Lawrence occurred at a much smaller size and over a more narrow range of sizes than in other more northerly areas. In the Labrador-eastern Newfoundland area the onset of maturity occurred at smaller sizes, moving progressively northward. Since the growth rates of fish throughout this area are similar, this shift of the maturity curves is believed to be a result of mature fish migrating towards the spawning ground. The Baffin Bank maturity curve, on the other hand, is similar to that of Nain Bank in the mid-Labrador area. However, since Baffin Bank is so near the presumed spawning ground and heavily influenced by the cold polar current, most maturing fish are likely to be in deep warmer water outside the fishable range; consequently, the curve may be biased to the right. These inferences are supported by other investigations, particularly migration studies.

Greenland halibut, *Reinhardtius hippoglossoides*, are found in both the North Atlantic and North Pacific Oceans but absent from intervening Arctic waters (Hubbs and Wilimovsky 1964; Atkinson et al. 1981). Based on meristic and morphometric characters, Hubbs and Wilimovsky (1964) concluded that there is one species found in both oceans, not two as previously suggested (Andriyashev 1954). In the northwest Atlantic, Greenland halibut are widely distributed along the west Greenland coast and in the Davis Strait and are reported as far north as Smith Sound (lat. 78°N) by Smidt (1969) and Templeman (1973). In the Canadian far north they are found in abundance in the Baffin Island area (Templeman 1973; Bowering 1978b, 1979a) and in the Hudson Strait to Ungava Bay (Dunbar and Hildebrand 1952). They are most prevalent in deeper waters from northern Labrador to the deeper waters of the northern Grand Bank (Templeman 1973; Bowering 1977, 1978c, 1979b, 1980b; Bowering and Brodie 1981) with small numbers recorded in the vicinity of the Flemish Cap (Bowering and Baird 1980). Greenland halibut are found incidentally on St. Pierre Bank with a small localized concentration located in Fortune Bay (Bowering 1978a). Recent investigations (Bowering 1979c, 1980a, 1981) have shown that Greenland halibut have now become commercially abundant in this area with very little occurrence on the Scotian Shelf. The most southerly occurrence is Georges Bank where 20 specimens were reported caught (Schroeder 1955).

According to Smidt (1969), the main spawning for Greenland halibut in the northwest Atlantic occurs during winter in the Davis Strait area (lat. 67°N) at depths of 600-1,000 m. From here the young are believed to be carried by currents to west Greenland and eastern Canada where they colonize the banks and slopes of the continental shelf. Spawning also occurs in the Gulf of St. Lawrence in the Laurentian Channel, southwest of St. Georges Bay, during wintertime (Templeman 1973).

The commercial fishery for Greenland halibut in the Canadian northwest Atlantic is one of the most important groundfish fisheries in the region with landings averaging over 60,000 t annually during the last few years. It is of prime importance to such countries

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as Canada, U.S.S.R., Poland, German Democratic Republic, and Federal Republic of Germany, who have prosecuted this fishery for over 25 yr from Davis Strait to the northern Grand Bank and, more recently, the Gulf of St. Lawrence.

The only published information on age and growth of Greenland halibut in the northwest Atlantic was by Bowering (1978a), who reported growth in terms of arithmetic linear least squares regressions for selected areas where data were available. Walsh and Bowering (1981) presented information on the validity of field observations on sexual maturity in female Greenland halibut using histological techniques; the data, however, were confined to one area of northern Labrador. To my knowledge, this is the only available information on sexual maturity of Greenland halibut in the northwest Atlantic.

This paper presents a detailed account of the age and growth of Greenland halibut in the Canadian northwest Atlantic from Baffin Bank to the northern Grand Bank and into the Gulf of St. Lawrence. An analysis of sexual maturity data on female Greenland halibut throughout the region (except the northern Grand Bank) is also discussed.

MATERIALS AND METHODS

Age and Growth

For examination, the data were organized according to seven geographical areas: 1) Baffin Bank; 2) Saglek Bank; 3) Nain Bank; 4) Hamilton Bank; 5) Northeast Newfoundland Shelf; 6) northern Grand Bank; and 7) the Gulf of St. Lawrence, since these are discrete fishing areas where data were available (Fig. 1). All data were collected during random-stratified research vessel surveys for groundfish (Pinhorn 1972) stratified by depth. The Baffin Bank data were collected by the French research vessel *Cryos* in October 1977. This vessel is a stern trawler, 46 m long, which uses a Lofoten bottom otter trawl with a 5 mm small mesh liner in the cod end. All sets were of 30-min duration during daylight hours at a towing speed of 3.5-4.0 kn. Data from sets in which the gear was badly damaged or other reasons considered to interfere with normal retention of the catch were not used. All other data were collected by the Canadian research vessel *Gadus Atlantica*. The *Gadus Atlantica* is a stern otter trawler, 85 m long, which uses an Engels high-rise bottom otter trawl with a 12 mm small mesh liner in the cod end. All sets were of 30-min duration at 3.5-kn towing speed, and fishing was carried out on a 24-h basis.

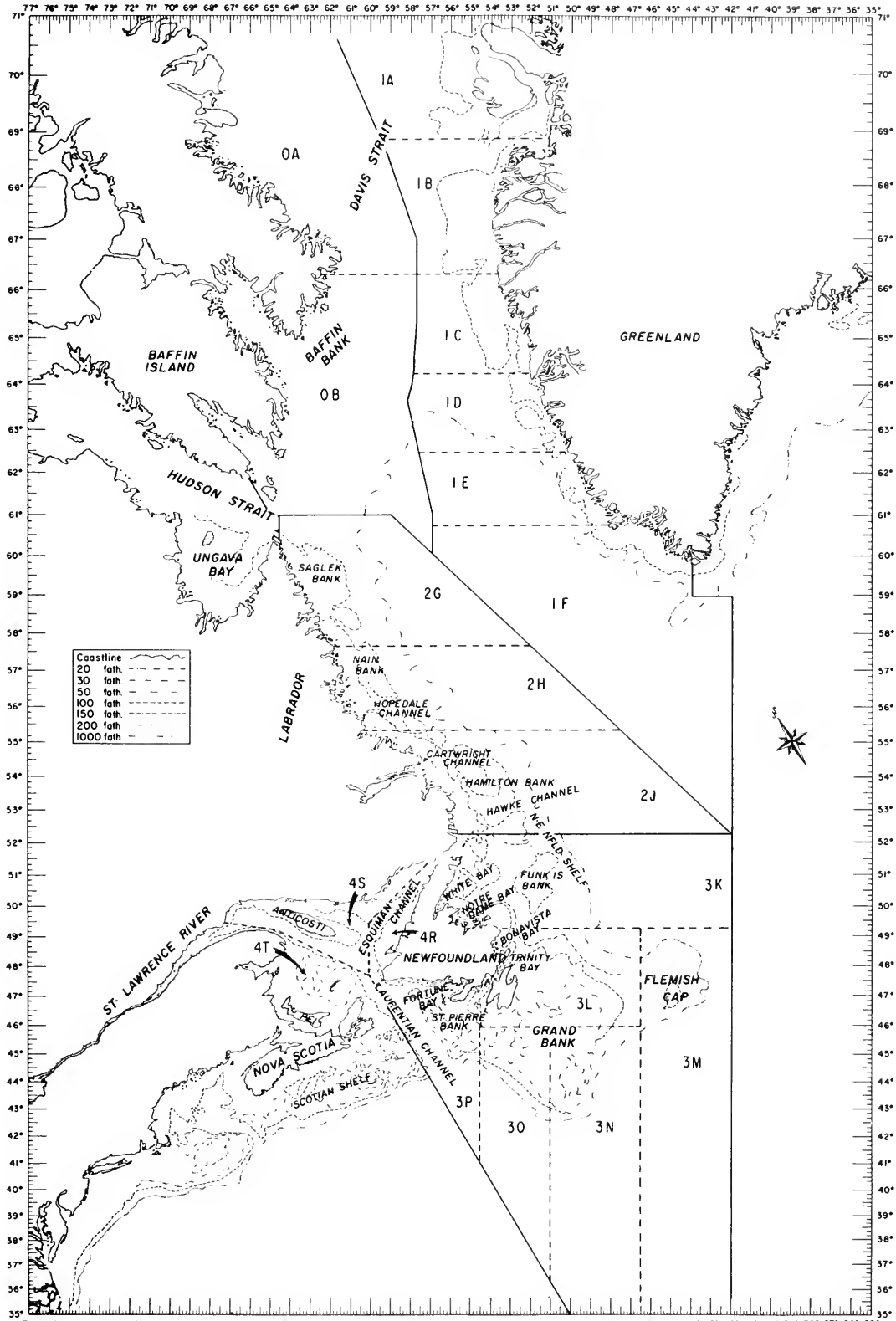
The fish ages were determined from the left sacculus otoliths which, in the case of Greenland halibut, were more suitable for age determination, since the annuli were spaced more evenly and were more distinct. Otoliths were ground on the convex surface exposing the center more clearly and were placed in a black watch glass containing ethanol in order to facilitate reading. Age frequencies were compiled for males and females separately using age-length keys for each area with the distributions calculated as numbers per thousand at age of the total catch.

For ease of statistical comparison, growth was expressed in terms of semilog curves (length $= a + b\ln$ age) similar to that used by Bowers (1960) for witch flounder and suggested in Roff (1980). Growth curves were computed separately by sex for each area. The growth curves were weighted by the number of observations at each age, since many of the older age groups were based upon as little as one observation, and the age reading of very large fish is often questionable (Lear and Pitt 1975).

Otoliths from 30 males and 30 females of the 1972 year class were selected from each area and examined to back-calculate length at age. Since the Baffin Bank data were collected in 1977 and the Gulf of St. Lawrence data were collected in 1980, only the 1972 year class was abundant enough in the samples for comparison. Subsequently, in order to standardize the number of ages for consideration, calculations could only be made up to age 5. Otoliths were measured by means of a drawing tube attached to a binocular microscope, using a technique similar to that described by Moores and Winters (1978). An annulus was considered to be the width described by an opaque (summer) zone and a translucent (winter) zone accounting for a growth increment in a particular year. The ratio of otolith length to total fish length was used to back-calculate the average length at each age, using the direct proportionality method described by Lea (1919). In order to validate the direct proportionality method as it applied to Greenland halibut, a linear least squares regression was performed on a random sample of 123 measurements of total fish length to total otolith length (3 measurements per 1 cm group from 10 to 50 cm).

A covariance analysis (Zar 1974) was performed on the back-calculated data for males versus females in order to determine if there were significant differences among the regression coefficients (slopes) or the adjusted means (y-intercepts). Where no differences between the sexes occurred the sexes were

FIGURE 1.—Map of study area with corresponding major names mentioned in text.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2J
3K
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4R
4S
4T
DAVIS STRAIT
BAFFIN ISLAND
BAFFIN BANK
GREENLAND
HUDSON STRAIT
UNGAVA BAY
SAGLEK BANK
NAIN BANK
LABRADOR
HOPEDALE CHANNEL
CARTWRIGHT CHANNEL
HAMILTON BANK
HAWKE CHANNEL
NEWFOUNDLAND SHELF
FUNK IS BANK
NOTRE DAME BAY
WHITE BAY
BONAVISTA BAY
TRINITY BAY
NEWFOUNDLAND
ESQUIMAN CHANNEL
ANTICOSTI
ST. LAWRENCE RIVER
FORTUNE BAY
ST PIERRE BANK
LAURENTIAN CHANNEL
GRAND BANK
FLEMISH CAP
NOVA SCOTIA
SCOTIAN SHELF

combined for each of the areas for further analysis. A covariance analysis was performed on these combined data to determine if there were any significant differences in the slopes of the fitted lines. Among the different areas, for areas where significant differences did not occur, the analysis was continued by using paired comparisons by *t*-tests to determine if differences occurred between the adjusted means (*y*-intercepts).

Sexual Maturity

Due to the difficulty and uncertainty connected with the determination of sexual maturity in male Greenland halibut, only sexual maturity data on female Greenland halibut were analyzed. Except for the Gulf of St. Lawrence data, only data collected during the same time of year were used to generate the maturity curves. Maturity conditions were determined by visual observations made at sea. Fish were considered mature if primary ova were visible in the ovary at any stage or if fish were in spawning or postspawning stages; otherwise, fish were considered immature.

The age or length when equal numbers of fish are mature and immature is known as the 50% maturity level or more commonly M_{50}. In assessing the effects of various dosages of poisons and vitamins on animals, Bliss (1952) devised a probit analysis method for calculating the 50% lethal dosage level (LD_{50}) which is the level where 50% of the animals are dead. Fleming (1960), Pitt (1966), and Bowering (1976) applied the same probit analysis method to determine the length at 50% maturity for cod, American plaice, and witch flounder, respectively. The only difference was that in fitting the provisional line (Bliss 1952), a closer fit was obtained by using log dosages which in the latter studies were the percentages of mature fish plotted against log length on probability paper. This modified probit analysis method was applied to the female Greenland halibut sexual maturity data from each of six areas where data were available. Since sexual maturity data for the northern Grand Bank area were so sparse, these were not included.

RESULTS

Age and Growth

Age Composition

Age composition of Greenland halibut from Baffin Bank in October 1977 showed a predominance of younger age-groups, particularly 3-5 yr olds, for both males and females (Fig. 2). Although fish were present in the catches up to age 14 for males and age 18 for females, very few fish were present beyond 8 yr old. In the Saglek Bank area, the opposite was the case with a strong predominance of fish beyond 5 yr old, although fish in the range of 3-5 yr olds were well represented (Fig. 2). Proportionally, there was a declining trend in the age-9+ groups of males from Saglek Bank to the northern Grand Bank with a marginal decline in the proportion of age-12+ females from Nain Bank to the northern Grand Bank. The most evident change in age composition over this range, however, is the abrupt change from the Northeast Newfoundland Shelf to the northern Grand Bank, particularly at ages 1 and 2. Age compositions for the Gulf of St. Lawrence data indicated very few fish less than age 4 for either sex (Fig. 2) with males absent beyond age 10 and females absent beyond age 12. The predominant age groups were 5-7 yr olds for males and 6-9 yr olds for females, all year classes of the early 1970's. It should be pointed out that since the Gulf of St. Lawrence data were collected in January and all other data collected late in the year, for comparison purposes, the Gulf of St. Lawrence data should be adjusted back by 1 yr.

Growth Curves from Observed Data

Female Greenland halibut have a longer life span than male Greenland halibut (Fig. 3). The difference in maximum age between males and females ranged from 2 yr in the Gulf of St. Lawrence to as much as 8 yr in the Saglek Bank area. It would appear from the curves (without considering mean size at age) that for all areas the overall growth rate of females is greater than that of the males. While the curves do not appear to fit the mean data points very well because of the weighting procedure, the correlation coefficients (r) were all greater than $r = 0.92$ and were all highly significant ($P > 0.001$). In almost all cases, however, the mean data points for the older ages are above the fitted lines (Fig. 3). This would suggest that if the observations were more numerous in the older ages, the computed growth rates would probably be higher than appear here, since more weight would be given to these points. As a consequence, the predicted size at age is probably only meaningful up to age 7 for males and age 10 for females. Beyond these ages, the mean size at age is increasingly higher than that determined from the fitted lines. In addition, the growth of males and females is identical up to age 7 for some areas and up to age 10 in others. It is clear that the weighting procedure underestimates relationships derived from the regression analyses compared with

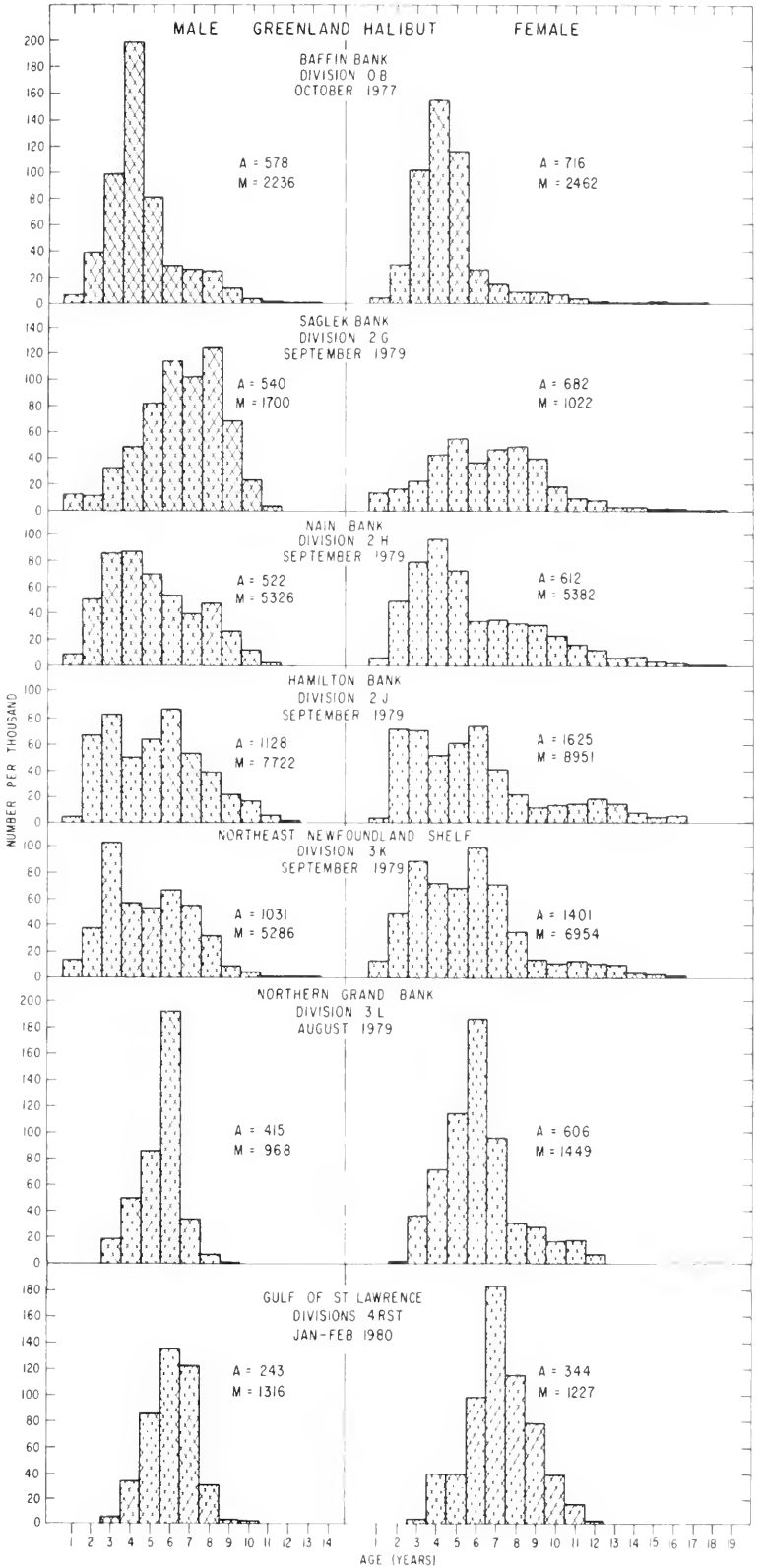

FIGURE 2.—Age composition of male and female Greenland halibut by area from Baffin Bank (NAFO Division 0B) southward to the northern Grand Bank (NAFO Division 3L) inclusive and the northern Gulf of St. Lawrence (NAFO Division 4RST).

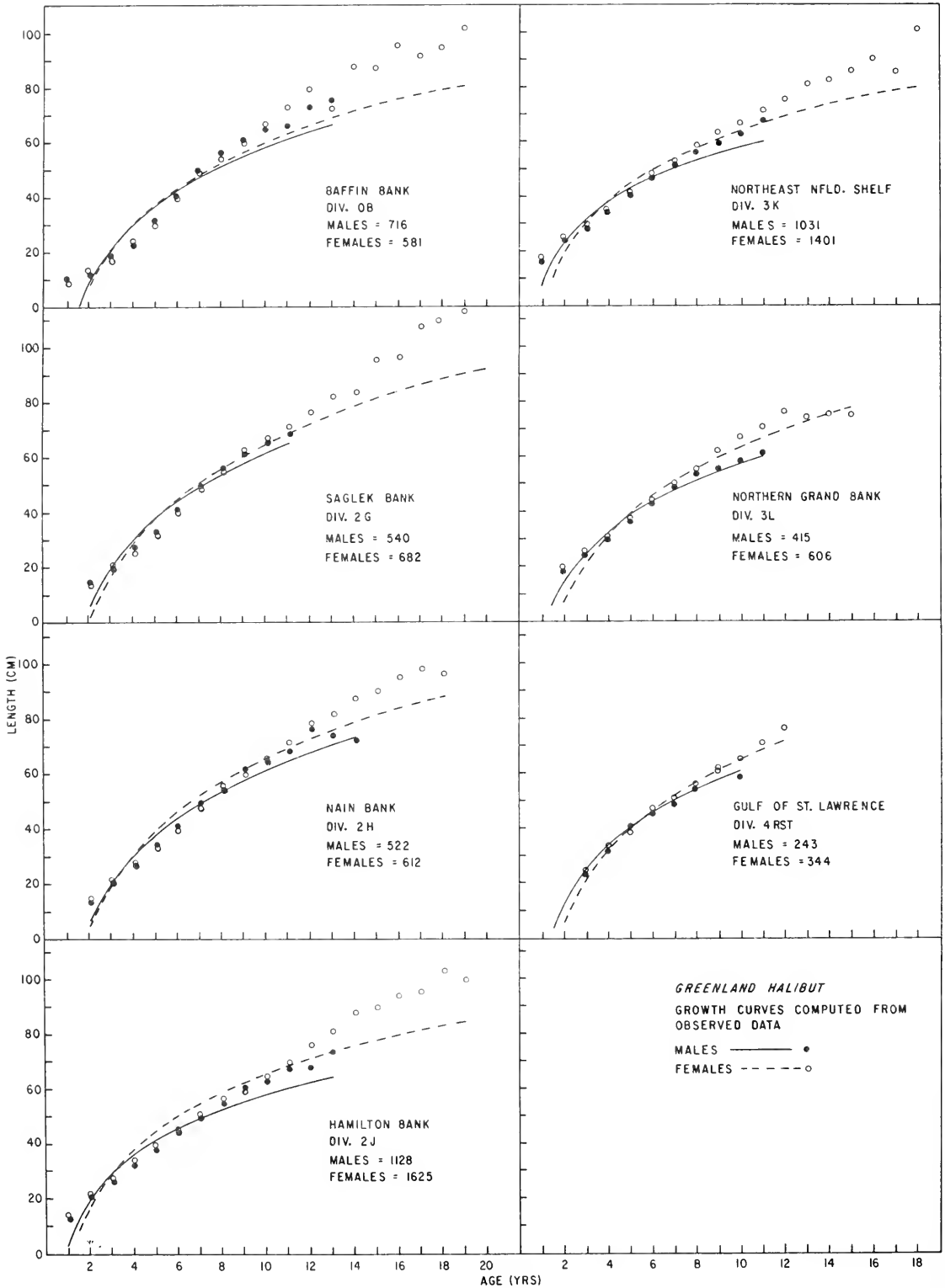

FIGURE 3.—Empirical growth curves of male and female Greenland halibut from seven areas of the Canadian northwest Atlantic.

the mean sizes at age, however, giving equal weight to each age may overestimate if given the lower numbers and questionable age readings in the very large fish.

Back-Calculated Growth Curves

The direct proportionality method (Lea 1919) for back-calculating size at age from otoliths appears valid for Greenland halibut (Fig. 4). The linear least squares regression for total fish length on total otolith length based on 123 observations yielded a correlation coefficient (r) of 0.98 and a t-value for r of 48.59 which is highly significant.

Back-calculated growth curves up to age 5 of the 1972 year class show very close agreement (Fig. 5) between males and females, particularly for the more southerly areas where the curves essentially coincide (Fig. 5). A covariance analysis of males versus females, however, indicated no significant difference in the males and females for both the regression coefficients (slopes) or adjusted means (y-intercepts) throughout the range under consideration ($P = 0.44$). The sexes, therefore, were combined. A covariance analysis on the slopes of the fitted lines for the sexes combined was performed and indicated that, with the exception of the Baffin Bank data, the regression coefficients (slopes) were not significantly different ($P > 0.05$). This would indicate that the growth rates in these areas were similar. Paired comparisons using t-tests to test for differences between the adjusted means indicated that both the Gulf of St. Lawrence data and the Nain Bank data were significantly different from those of all other areas. The Saglek Bank data differed from those of the Northeast Newfoundland Shelf but did not differ from either the Hamilton Bank data or the northern Grand Bank data. There were no significant differences amongst the adjusted means of the Hamilton Bank, Northeast Newfoundland Shelf, and the northern Grand Bank data. The combined back-calculated growth curves (Fig. 6) show the Baffin Bank growth rate to be the slowest with a considerably smaller size at age. The largest size at age is found in the Gulf of St. Lawrence with all other areas in the midrange.

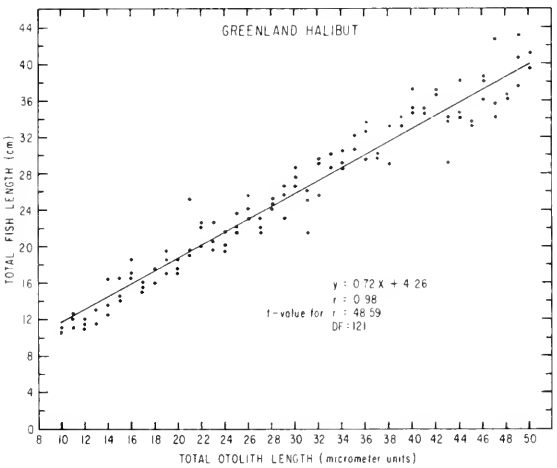

FIGURE 4.—Linear least squares regression of fish length against total otolith length of Greenland halibut.

Sexual Maturity

The sexual maturity curves (Fig. 7) indicate a clear shift to the right in the curves going from northern Labrador to southern Labrador with the Northeast Newfoundland Shelf and southern Labrador curves approximately the same. The curve for the Baffin Bank area falls near the middle (Fig. 7), close to that of the Nain Bank area. The Gulf of St. Lawrence curve, however, is well to the left and appears nearly isolated from all others.

The results of the probit transformation analysis of sexual maturity data, by area are shown in Table 1. All chi-square tests indicate acceptance of the fitted lines to the observed data at the 5% significance level. The length at the 50% maturity level, or M_{50},

TABLE 1.— Results of probit analyses of sexual maturity data for the Greenland halibut, by area, with results of χ^2 tests for acceptability of the fitted lines to the observed data.

Statistical parameter	Baffin Bank	Saglek Bank	Nain Bank	Hamilton Bank	Northeast Newfoundland Shelf	Gulf of St. Lawrence
Slope	0.1574	0.0733	0.0864	0.1118	0.1016	0.1574
y-intercept	−6.297	0.250	−1.312	−4.043	−3.086	−4.101
Length at M_{50}	71.76	64.80	73.05	80.86	79.58	57.83
χ^2 (Res. SS)	3.830	19.565	11.460	11.806	5.141	9 906
$\bar{x}$	70.57	60.70	69.82	78.85	72.52	56.07
SE M_{50}	0 2048	0.0613	0.0681	0.1237	1.7904	0.0684
SE M	0.0267	0.0058	0.0053	0.0208	0.0127	0.0127
No. fish	583	682	612	517	736	513
Age at M_{50}	10.6	9.6	10.8	12.0	12.0	7.8

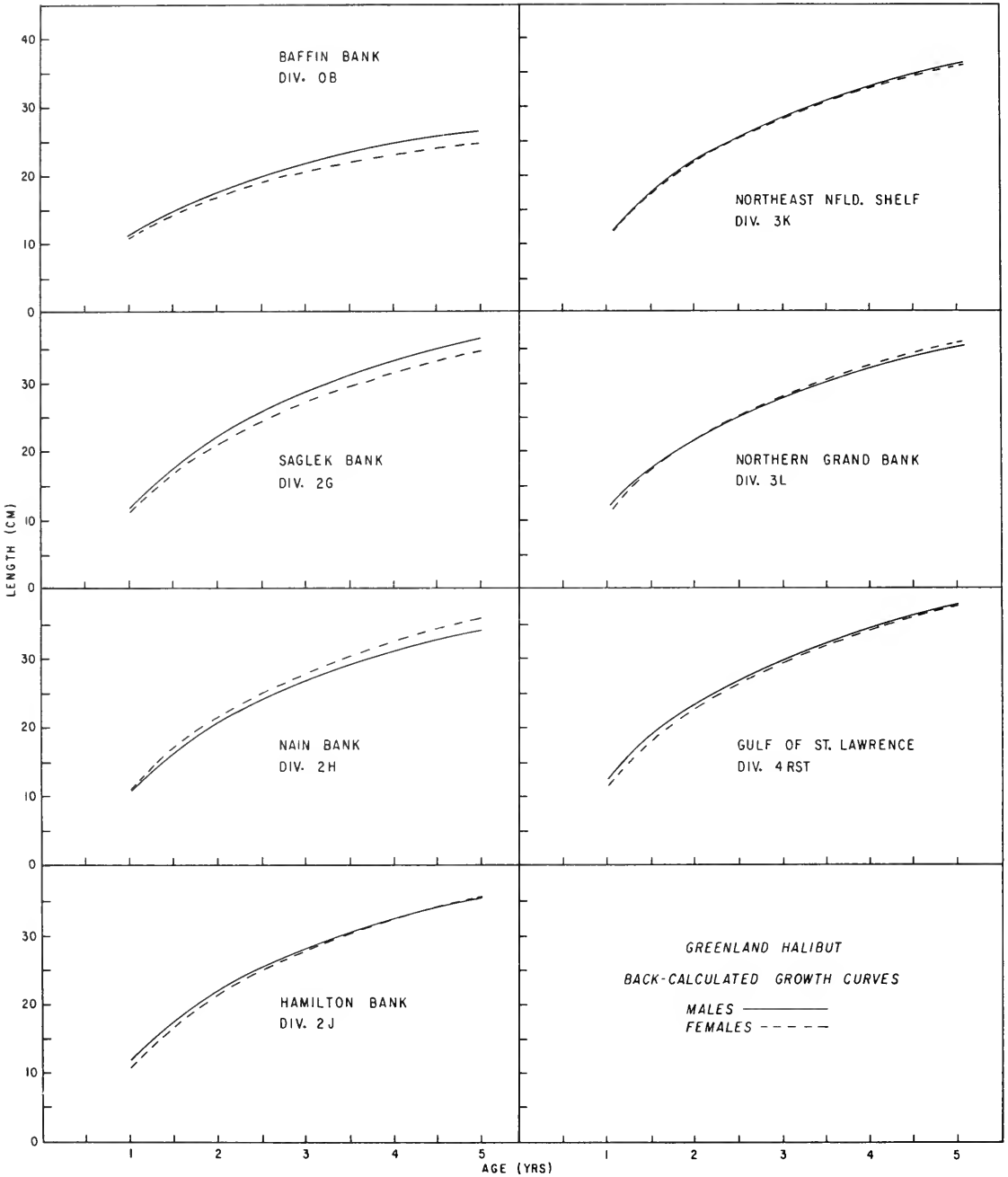

FIGURE 5.—Back-calculated growth curves (ages 1-5) of male and female Greenland halibut from seven areas of the Canadian northwest Atlantic.

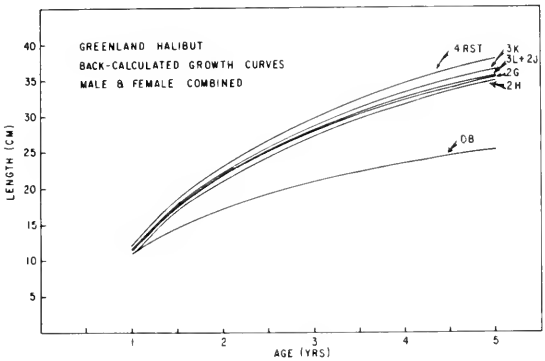

FIGURE 6.—Comparisons of back-calculated growth curves (ages 1-5) of Greenland halibut, sexes combined from seven areas of the Canadian northwest Atlantic.

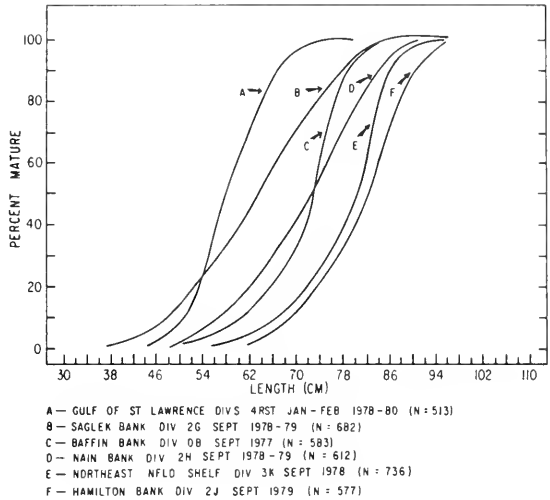

FIGURE 7.—A comparison of sexual maturity ogives of female Greenland halibut from six areas of the Canadian northwest Atlantic.

decreased from 71.8 cm in the Baffin Bank area to 64.8 in the Saglek Bank area; however, the length at M_{50} increased to 73.1 cm in the Nain Bank area and then to 80.9 cm in the Hamilton Bank area. The length at M_{50} for Northeast Newfoundland Shelf area was 79.6 cm, very similar to the Hamilton Bank value. The lowest length at M_{50} was 57.8 cm for the Gulf of St. Lawrence.

The ages at M_{50} calculated from the growth equations of Bowering (1978a) showed the same trends as did the lengths at M_{50}. The lowest age at M_{50} was 7.8 yr for the Gulf of St. Lawrence data to a maximum of 12 yr for both Hamilton Bank and Northeast Newfoundland Shelf. The results of the covariance analyses for testing the regression coefficients (slopes) and elevations (y-intercepts) of the fitted lines are shown in Table 2. The slope of the Baffin Bank data differed from that of Saglek Bank and Nain Bank but not from those of any other areas. The slope of the fitted lines for Saglek Bank, Nain Bank, Hamilton Bank, and Northeast Newfoundland Shelf did not differ significantly. Biologically, this means that the proportional increase of mature fish from one size group to the next were the same for these areas. The slope of the Gulf of St. Lawrence data differed significantly from those of all areas except Hamilton Bank and Baffin Bank. For paired comparisons which did not yield significant differences between the slopes of the fitted lines, statistical treatment of the elevations (y-intercepts) indicated highly significant differences between the intercepts for all pairs at the 1% significance level (Table 2). This means that although the proportional increase of mature fish from

TABLE 2.—Matrix of *t*-values for paired comparisons of sexual maturity data for Greenland halibut.

	Saglek Bank		Nain Bank		Hamilton Bank		Northeast Newfoundland Shelf		Gulf of St. Lawrence	
	0.0733 Slope	0.250 Int.	0.0864 Slope	−1.312 Int.	0.118 Slope	−4.043 Int.	0.1016 Slope	−3.086 Int.	0.1574 Slope	−4.101 Int.
Baffin Bank										
t	[1]2.404	N/A	[1]2.455	N/A	1.154	[2]−2.977	1.959	[2]−10.748	−0.0001	[2]−11.484
df	28	27	18	19	20	21	19	20		
Saglek Bank										
t			1.634	[2]8.311	1.877	[2]14.947	1.586	[2]13.824	[2]5.905	N/A
df			39	40	30	31	32	33	31	
Nain Bank										
t					1.394	[2]10.775	1.008	[2]7.958	[2]5.604	N/A
df					29	30	31	32	30	
Hamilton Bank										
t							0.426	[2]−4.619	1.918	[2]−6.643
df							22	23	21	22
NE Nfld. Shelf										
t									[2]2.923	N/A
df									23	

[1]Indicates rejection of H_0 at = 0.05.
[2]Indicates rejection of H_0 at = 0.01.

one size group to the next was the same, the range of the size groups themselves was different. In biological terms, this means that there is a significant difference in the size at M_{50} for all areas tested. Subsequently, the ages at which Greenland halibut reach the 50% maturity level are also different for these areas.

DISCUSSION

Age and Growth

Age composition of Greenland halibut varied throughout the range under consideration. It was apparent (although not greatly pronounced) from the age distribution that the older fish were proportionately more abundant in the more northerly areas and, according to Bowering (1978c), are more abundant in deeper waters. The large numbers of young fish in the Baffin Bank area suggest that this area may be a nursery area as indicated by Atkinson et al. (1981). However, the lower numbers of large Greenland halibut in the Baffin Bank survey may also be due to the ineffectiveness of the fishing gear at great depths (>500-700 m), since the vessel is comparatively small for fishing such depths. Chumakov (1975) found that the oldest individuals throughout the range studied here are located in waters >800 m deep in the northern region of Baffin Island (which he considered to be on or near the spawning grounds). Berth et al. (1979), in reporting results of a survey for Greenland halibut throughout the same area in December 1978, also found that young Greenland halibut increased in abundance with increased distance from the more northerly areas. Berth[2] also found that mature individuals are more abundant in the more northerly areas, suggesting a northward migration of maturing Greenland halibut for spawning. Subsequently, Templeman (1973) indicated that pelagic larvae are carried from there by the polar currents to the banks of west Greenland and eastern Canada.

The absence of Greenland halibut less than age 4 from the Gulf of St. Lawrence is difficult to explain. It may be that the young fish move to a different area than that surveyed in winter or, for some unknown reason, they are inaccessible to the fishing gear. It may be possible that if there is immigration into the Gulf of St. Lawrence from outside as suggested by Bowering (1980a, 1981), it may not include Greenland halibut in the very young age groups. The reporting of numerous 1-group Greenland halibut in summer of 1980 by Tremblay and Axelsen (1981) may in fact simply be the result of a very strong anomalous year class produced by a resident population of Greenland halibut within the Gulf of St. Lawrence. Furthermore, Bowering (in press) indicated that recruitment to the Gulf of St. Lawrence fishery was higher than that which could be expected from the stock of mature fish in the gulf. Therefore, most recruitment would have to come from elsewhere. Evidence from electrophoretic studies (Fairbairn 1981) also supports this hypothesis. Fairbairn (1981) concluded that Greenland halibut in the Gulf of St. Lawrence support a separate breeding stock with some gene flow (migration) between the Gulf of St. Lawrence area and the Northeast Newfoundland Shelf area, probably through the Strait of Belle Isle. It would appear then that the Gulf of St. Lawrence Greenland halibut population is composed of a small stock that spawns there and immigrants from the Labrador area that may emigrate to the north for spawning.

Growth Patterns

Differences in growth rate between males and females are generally the result of genetics which determine the physiology and behavior of the fish rather than the result of the environment (Alm 1959), since the males and females presumably are subjected to the same set of environmental conditions. These differences are generally the result of a diversion of energy towards the formation of the sex products with less energy available for growth, according to Alm (1959). Bowering (1978a) expressed growth of Greenland halibut in terms of linear least squares regression, since most fish in the study were immature and showed little or no diversion in growth patterns of males and females. Because of this, it was considered that the study only dealt with that section of the growth curve below the inflection point, and consequently estimates of L_∞ for the traditional von Bertalanffy growth equation were not realistic and could not be used. Results of back-calculated growth curves up to age 5 in this study resulted in no statistical difference between males and females, which in essence would support Alm (1959) and Bowering (1978a). Furthermore, the mean size-at-age points from the empirical data suggest that the difference in growth patterns between males and females would not be readily observed until in the range of 8-12 yr olds. These data suggest that, with the possible exception of the Gulf of St. Lawrence, the influence of sexual maturity on growth patterns in these areas was

[2]U. Berth, Senior Scientist, Institut fur Hochseefischerei and Fischverarbeitung, 251 Rostock-Marienehe, German Democratic Republic, pers. commun. October 1978.

negligible. Statistical comparisons could not be made with Bowering (1978a), since the data could not be standardized.

Covariance analyses on the back-calculated growth data indicated that the growth rate throughout the entire area, with the exception of the most northerly Baffin Bank area, was the same. The growth rate from the Baffin Bank data was considerably lower than all other areas. Analysis of the adjusted means (intercepts) indicated that the average size at age for the Gulf of St. Lawrence data was significantly higher than all other areas. Since the overall growth rate was the same as other areas, this would imply that the growth rate of the Gulf of St. Lawrence fish was substantially higher in the first year of life compared with other areas. While the size at age from Nain Bank was significantly different from all areas, it did not appear to vary greatly from the adjacent Labrador and eastern Newfoundland areas. Since differences between growth patterns from Saglek Bank and other areas are not totally variable, they may be a result of the location and behavior of the fish in the first year of life throughout the range.

Because there appears to be a general increase in average size at age from north to south, temperature would appear to be a contributing factor. Templeman (1964) indicated that the volume of warmer waters increased from north to south because of the direction of the Labrador Current so that temperature may have an influence on growth pattern. Any influence would have to be particularly related to the first year of life, since older Greenland halibut are known to migrate over long distances (Nizovtsev 1970; Chumakov 1970; Sigurdsson 1977), as well as vertically in the water column (Lear 1970; de Groot 1970), making them subject to a wide variety of temperatures. This may explain the high growth rate in the first year for the Gulf of St. Lawrence fish where temperatures are considerably higher than the eastern areas. It should be pointed out, however, that these growth patterns are based mostly upon immature individuals, and the difference in growth patterns of the immature individuals alone may simply be a result of conditions where they grew prior to maturity. Upon approaching maturity they could all still return to a common breeding area and be part of the same original stock.

Sexual Maturity

The commercial fisheries for Greenland halibut on the banks and slopes in the northwest Atlantic are mainly composed of immature fish (Chumakov 1975; Zilanov et al. 1976; Templeman 1973; Berth et al. 1979; Bowering 1977-81). The scarcity of mature fish in the commercial, as well as research, catches led to consideration of the possible misinterpretation of maturity condition of the ovaries, particularly by visual observation. Walsh and Bowering (1981) studied the problem histologically and concluded that while the accuracy of visual observations of sexual maturity of female Greenland halibut may be enhanced by histological analysis, for practical purposes, field observations on the onset of first maturity are adequate. Maturity of male Greenland halibut was not included in the analysis here, since it was extremely difficult to determine whether males with growing gonads were maturing for the upcoming spawning season or later. This uncertainty was probably a result of the timing of the surveys when milt was not present in the testes and previously spawned fish may have been fully recovered.

The results of probit transformation analysis indicated that the 50% maturity level (M_{50}) was reached at a much smaller size for the Gulf of St. Lawrence fish, whereas there was a trend of increasing size at M_{50} for fish from northern Labrador to the southern Labrador-Northeast Newfoundland Shelf area. Covariance analysis indicated that for the Labrador-eastern Newfoundland areas the rate of increase in the proportion of mature fish from one size group to the next was the same. The Baffin Bank and Gulf of St. Lawrence data differed from some areas but not from others. More importantly, however, were the significant differences in the intercepts of the fitted lines for all areas. In biological terms this indicates a significant difference in the sizes and ages of M_{50} for all areas.

Molander (1925), in studying European plaice and flounder in the Baltic, found that with increased growth rate, maturity occurred at a lower age but at a greater length. Bowering (1976) found similar results for witch flounder in the northwest Atlantic. Pitt (1975) indicated for American plaice that faster growing fish matured at an earlier age but all matured at approximately the same size, suggesting that sexual maturity is probably dependent on size, and indirectly on growth rate, rather than on age. From experimental research on sexual maturity of fishes, Alm (1959) concluded that "with an initially good growth rate maturity is reached at an earlier age than an initially poor growth rate. The metabolic processes are probably relatively fast with good growth rate. Consequently, differentiation processes in gonads and maturity apparently occur much earlier, the opposite being the result of poor growth rate."

The results reported here support in part the conclusions of Alm (1959). Greenland halibut from the

Gulf of St. Lawrence exhibit the highest growth rate and mature much earlier than fish from other areas. Conversely, the population of Greenland halibut from Baffin Bank exhibits the slowest growth rate, and maturity is reached at a later age than those from the Gulf of St. Lawrence. The initial growth rate of the Labrador-eastern Newfoundland areas has been shown to be very similar, occurring somewhere between those of the Baffin Bank and the Gulf of St. Lawrence. However, the size and age at maturity decrease significantly from south to north, contrary to the above theory. The reason for this may be explained if a northward spawning migration occurs. If this is the case, then it would be expected that the proportion of maturing individuals in catches at any particular size up to 100% mature would be greater, moving progressively northward. This would result in a shifting of the maturity curve to the left going north and subsequently producing lower values of M_{50}. This would further suggest that in the Labrador area the value of M_{50} for Saglek Bank may be in fact more representative of the entire Labrador-eastern Newfoundland area. The value of M_{50} for Saglek Bank falls between that of the Gulf of St. Lawrence and Baffin Bank data as does the initial growth rate. This would then be in agreement with Alm's (1959) theory of the relationship of maturity and initial growth rate.

Recent investigations by Chumakov (1982) also found that the abundance of larger mature fish increased moving northward. From tagging studies in eastern Newfoundland, Chumakov (1982) found that Greenland halibut migrated northward over long distances, from the southernmost parts of the area to the spawning grounds located in Davis Strait. He also indicated that having reached the spawning grounds, mature fish would not return to the areas where they had been dwelling before maturation. The proportions of mature fish in the more southerly areas would therefore be expected to be slowly moving southward, as shown in the data presented here. Furthermore, Bowering (1982) also studied migrations of Greenland halibut in the same area. For Greenland halibut tagged in White Bay, Newfoundland, (Fig. 1) the returns mostly came from deep waters along the continental slope of Labrador to as far north as the waters off Baffin Island near the known spawning grounds. This further suggests a northward migration of prespawning Greenland halibut.

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POWER PLANT IMPACT ASSESSMENT: A SIMPLE FISHERY PRODUCTION MODEL APPROACH

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ABSTRACT

The relative abundance of a cohort affected by power plant entrainment mortality as a fraction (R_c) of the abundance of that cohort in the absence of power plant impact can be calculated by $R_c = \exp(-E_i t_i)$ where t_i is the duration of life stage i, and E_i is the entrainment mortality rate at stage i. Rate E_i can be estimated by the ratio of nonsurviving entrained organisms during a given time interval to the mean standing crop of stage i organisms in the source water during that interval. An estimate of adult abundance allows calculation of equivalent adult losses. When insufficient information is available to determine the long-term effect on the population, the fishery "potential yield" formula provides an interim estimate. Relative equilibrium abundance of the affected population (R_e) is approximated by $R_e = 1 - (\Sigma E_i t_i + F_p + F_f)/2M$, where F_p is adult mortality rate due to power plant impingement, F_f is adult mortality rate due to fisheries, and M is adult natural mortality rate. As in the case of the "potential yield" formula, this approximation of long-term equilibrium impact should be discarded when better estimates can be developed.

In recent years considerable effort has been expended in evaluating the impact of fish removals by intake cooling water systems at power plants in the United States. Methods of impact assessment are as diverse as the power plant sites at which the studies have been conducted, but may generally be classified into those which, according to Hackney et al. (1980), 1) offer an "expert" opinion as to the presence or absence of impact, or 2) are fish population models in which the sensitivity of the source water fish populations are examined under varying impingement rates.

The first category of assessments generally attempts to compare losses of organisms owing to power plant operation with sport and commercial fishery harvests and/or estimates of standing stock (DeMartini 1979). For adults, which are subject to impingement, comparison is fairly straightforward. However, for eggs and larvae, which are subject to entrainment, meaningful comparison is less direct. Goodyear (1978) extended a method proposed by Horst (1975) for treating entrained larvae in terms of equivalent adult losses which may then be considered alongside losses because of impingement. The second category of assessments includes more complex models using Leslie matrices (Vaughan and Saila 1976; Horst 1977; Vaughan 1981), differential equations (Hackney et al. 1980), or stock-progeny-recruit models (Christensen et al. 1977).

Several problems are inherent in many of these methods. There is an absence of an impact "scale" which enables the investigator to judge objectively the significance or insignificance of fish removals relative to the source water stock and to removals by fisheries. Additionally, sophisticated methods such as Leslie matrices and Goodyear's (1978) calculation of equivalent adult losses require life history parameters (i.e., fecundity, survivorship), which are often unknown for the species in question, and require substantial expenditures of time and money to obtain. Finally, these models may be difficult to interpret. While the investigator may understand the subtleties of interpretation, agency reviewers often lack the technical background to evaluate the results of complicated models.

The approach presented in this paper will alleviate many of the above problems. The proposed methods draw on techniques and models used in fishery management in order to provide a criterion for significance of impact. Indeed, the objectives of fishery stock assessment are very similar to those of power plant impact assessment. In both cases, we wish to know the effect of removals relative to what the stock can sustain through its density-dependent or other compensatory mechanisms. The models we propose do not require detailed life history information, and are sufficiently simple that the assumptions are apparent and results can be interpreted accordingly.

The methods may be separated into two somewhat independent analyses. The first is short-term assessment, which estimates entrainment impact on a

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single cohort (e.g., year class) in the sense of Goodyear's (1978) equivalent adult mortality. The second analysis estimates the long-term equilibrium impact of combined removals, including entrainment and impingement by one or more power plants, and all other nonnatural removals, including fishery harvests.

SHORT-TERM IMPACT

In the natural state, where no spawning products are removed by entrainment, the adult abundance of a cohort, N'_c (at a reference age T), is given by

$$N'_c = Pe^{-\int_0^T \mu(x)dx} \quad (1)$$

where P is initial production of newly spawned eggs, x is age, and $\mu(x)$ is per capita natural mortality rate at age x, i.e., $-dN(x)/Ndx$.

A more convenient approximation of Equation (1) is

$$N'_c = Pe^{-\Sigma M_i t_i} \text{ and } T = \Sigma t_i \quad (2)$$

where t_i is the length of age interval i, and M_i is a per capita natural mortality rate, assumed to be constant over interval i.

In the presence of mortality due to entrainment, the adult abundance of the impacted cohort, N_c (again at reference age T) is given by

$$N_c = Pe^{-\Sigma(E_i+M_i)t_i} \quad (3)$$

where E_i is the per capita rate of entrainment mortality during age interval i.

The abundance of an impacted cohort relative to an unimpacted cohort is denoted R_c, and is given by

$$R_c = N_c/N'_c \quad (4)$$

and after substituting Equations (2) and (3), this simplifies to

$$R_c = e^{-\Sigma E_i t_i} \quad (5)$$

which is related to the conditional mortality rate (m) described by Ricker (1975: equation 1.9; here $m = 1 - R_c$). Note that T need not be specified, since we now need sum over only those age intervals in which E_i is nonzero. This is convenient since fish often cease being entrained at about the same time they cease being available to plankton sampling gear. More important is the fact that Equation (5) requires no knowledge of life history parameters. The main assumption here is that there is no compensatory change in the per capita rate of natural mortality during early life stages which offsets the added effect of entrainment mortality.

Equation (5) is similar in concept and derivation to recently published methods of calculating impact rate (e.g., Boreman et al. 1981; Jensen and Hamilton 1982). Those methods explicitly include water volumes and are especially appropriate to cases of highly fluctuating water flows. For the purposes of the assessment methods discussed in this paper, either method of calculating impact rate is applicable.

The entrainment mortality rates, E_i, are fairly easy to estimate. Larval mortality may be assumed to conform to a "Type 2 fishery" in the sense of Ricker (1975), wherein natural mortality occurs along with entrainment, and each occurs at a constant per capita rate during each age interval i. If power plant activity is fairly constant over the spawning season, each E_i is constant, and it is unnecessary to distinguish between Ricker's two types of recruitment. According to Ricker's (1975) equation 1.17, the quantity of larvae at stage i removed during a unit time by entrainment (L_i) is related to the mean abundance of larvae at stage i in the source water ($\bar{L}_i^*$) by the equation

$$L_i = E_i \bar{L}_i^* \quad (6)$$

Therefore, E_i may be estimated by the equation

$$E_i = L_i/\bar{L}_i^* \quad (7)$$

where L_i is a direct in-plant sample estimate of the quantity of stage i larvae entrained per day (or other convenient short time interval), and $\bar{L}_i^*$ is an estimate of the mean standing crop of stage i larvae over that same time interval in the source water, which may be estimated by quantitative plankton net tows. Note that entrainment rate E_i has units of inverse time according to the time interval used. Care must be taken to assure that time units are consistent throughout the analysis. Also note that i now refers to a stage, as it is generally most convenient to sort samples or planktonic larvae by size or stage categories. The length of time spent in each size category must also be determined. The most direct method may be to examine larval otoliths for daily growth rings (see Brothers et al. 1976) in order to ascertain the number of days (or other time unit employed) spent in stage i. Lacking this direct information on t_i, it may be necessary to assume that the larvae grow at the same

rate as does some better known similar species in a similar environment.

Equivalent adult loss from a cohort (A_c) may be defined as

$$A_c = N'_c - N_c. \tag{8}$$

However, a standing stock of adults often consists of several cohorts. Under the common fishery assumption that the age composition of the standing stock is at equilibrium, overall equivalent adult losses (A_e) from the stock are given by

$$A_e = N' - N \tag{9}$$

where N' denotes unimpacted stock abundance, and N denotes impacted stock abundance, given the same initial production of eggs. Although this equilibrium assumption is often violated, it is nonetheless the basis of management of many fish stocks. Since the quantity R_c describes the ratio for a cohort N_c/N'_c, under equilibrium it also describes the population ratio N/N', here denoted R. The latter may be substituted into Equation (9) to give

$$A_e = N' (1 - R) \tag{10}$$

or

$$A_e = N (\tfrac{1}{R} - 1). \tag{11}$$

Thus equivalent adult losses can be calculated if adult abundance has been estimated, and this does not require the extensive knowledge of life history parameters demanded by Goodyear's (1978) approach.

Equations (10) and (11) raise a dilemma with respect to short- and long-term impact. Estimation of short-term impact has been based on the assumption of a fixed initial production of eggs. However, when real data are used, preimpact abundance (N') will usually arise from a larger egg production than does postimpact abundance (N), for the very reason than N' is larger than N, and egg production is itself dependent upon adult abundance. For this reason, Equation (10) is misleading, and will tend to overestimate the amount of adult equivalent losses actually occurring from an impacted stock at equilibrium. However, in most cases, preimpact abundance is unknown, and sampling programs produce estimates of N, which require application of Equation (11). Moreover, Goodyear's (1978) equivalent adult losses are calculated for an impacted stock making Equation (11) appropriate. As will be seen below, our method of estimating long-term equilibrium impact does not require explicit calculation of equivalent adult losses, and avoids the above complications.

LONG-TERM IMPACT

Whereas short-term impact may be described in simple terms of adult equivalent losses, long-term impact is more difficult to quantify. Short-term loss of adults implies loss of reproductive potential (egg production), and this loss is compounded over several generations. If compensatory mechanisms were not present, the impacted population would decline exponentially to extinction, given that it was in equilibrium prior to the impact. Fortunately, there are many types of compensatory mechanisms that allow the population to augment its reproductive rate so that it reaches a new equilibrium in the presence of an increased mortality rate (see Goodyear 1980). For example, lowered adult abundance may lead to increased per capita fecundity, decreased age of first reproduction, and/or increased survivorship at various life stages. Unfortunately, the actual mechanisms are poorly known and can be seldom quantified even for well-studied species. Detailed knowledge cannot be expected in routine impact analyses. Rather, we need simple approximations that will require a minimum of data.

Fishery management has long been concerned with the effect of removal (harvests) rates on fish abundance. Most of the work has been concerned with long-term equilibrium, and many fishery models are directly applicable to impact analysis. In particular, the "production model" (see Ricker 1975, Chapter 13), by means of simplifying assumptions, requires minimal knowledge of life history parameters. One of the simplest production models is the Graham-Schaefer model, which is constructed on the assumption of logistic population growth. The model assumes that equilibrium stock abundance declines linearly with an increasing rate of harvest (fraction of stock removed per unit time). The maximum net productivity in terms of total harvest by a fishery is therefore assumed to be achieved at a stock size which is exactly one-half the virgin level of abundance or carrying capacity, K (Fig. 1).

Normally, the production model is useful when a long time series of catches and fishing efforts (rates of removal) is available. In such cases, the production curve can be estimated from the data by statistical regression. On the other hand, there are many fisheries for which there is no history of exploitation, or for which the required data were never collected. Here, we may draw on the "potential yield" formula, first proposed by Alverson and Pereyra (1969), promulgated by Gulland (1970, 1971), and critically reviewed by Francis (1974). This approximation assumes that net productivity is maximal when abun-

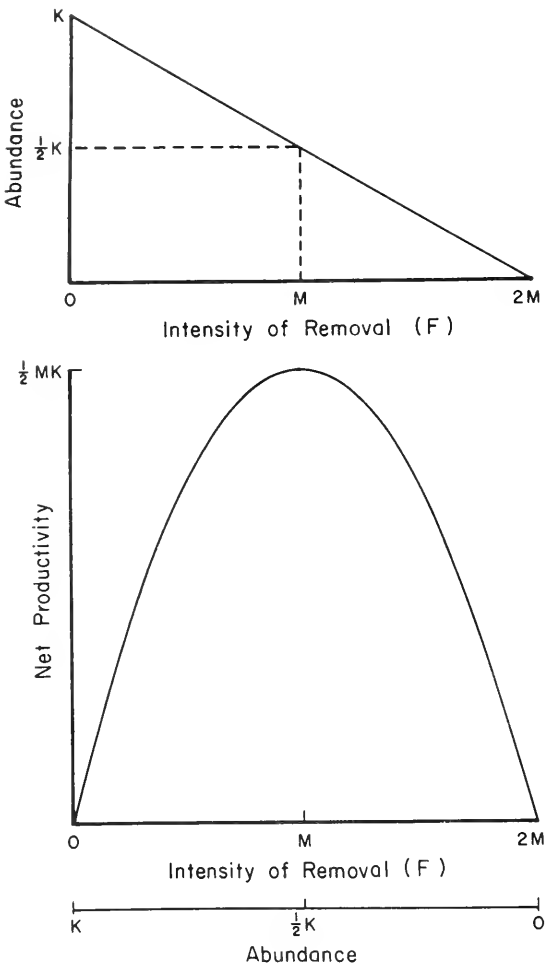

FIGURE 1.—The Graham-Schaefer production model scaled according to the "potential yield" formula (K is virgin abundance or carrying capacity, M is rate of natural mortality).

dance is at one-half the virgin level, and at this point the rate of fishery removals (F) is equal to the rate of natural mortality of adults (M). While many criticisms can be leveled at the potential yield formula, in actual practice it is often the only available basis of fishery management (e.g., North Pacific Fishery Management Council 1979a, b; Pacific Fishery Management Council 1982).

The production model corresponding to the potential yield formula is shown in Figure 1. The assumed relationship between equilibrium abundance (N_e) and rate of removal (F) is linear, giving the usual parabolic yield curve. Equilibrium abundance is at carrying capacity (K, denoted N'_e in this paper), when there are no removals. From inspection of Figure 1, the model predicts that equilibrium abundance falls to zero when the rate of removals is twice the rate of adult natural mortality (M). Thus, based on linearity, we have

$$N_e = N'_e\left(1 - \frac{F}{2M}\right) \tag{12}$$

which predicts long-term equilibrium abundance in the presence of removal rate F. In parallel with our treatment of short-term impact, the long-term equilibrium abundance of a harvested or impacted stock relative to the abundance of the virgin stock is denoted R_e, and is given by

$$R_e = N_e/N'_e \tag{13}$$

and according to Equation (12), we have the approximation

$$R_e = \left(1 - \frac{F}{2M}\right). \tag{14}$$

Equation (14) says that we can estimate the impact of all removals, given the total rate of removals and the rate of adult natural mortality.

The total rate of removals (F) includes entrainment (E) and impingement (F_p) by all power plants operating in the area of the stock, and all fisheries (F_f) exploiting the stock:

$$F = \Sigma E + \Sigma E_p + \Sigma F_f. \tag{15}$$

The removal rate due to entrainment (E) is estimated by the method presented in the previous section, i.e.,

$$E = \Sigma E_i t_i. \tag{16}$$

Impingement (F_p) and fishing (F_f) mortality rates may be estimated by a method similar to Equation (7):

$$F_p = I/\bar{N}^* \tag{17}$$

and

$$F_f = C/\bar{N}^* \tag{18}$$

where I is the number of adults impinged in a year, C is the annual fishery harvest, and $\bar{N}^*$ is the mean abundance of the stock over the year.

The natural mortality rate is a difficult parameter to estimate. Ricker (1975) reviewed many of the methods. In some cases it may be necessary to assume a value of M, based on comparison with better known species. One useful method, based on comparative growth and environmental parameters, has been described by Pauly (1980). If a mortality rate can be es-

timated, for example, based on age frequency, the estimate will often be the total mortality rate of adults (Z), where

$$Z = M + \Sigma F_p + \Sigma F_f. \quad (19)$$

The natural mortality rate can be obtained from

$$M = Z - \Sigma F_p - \Sigma F_f. \quad (20)$$

If fish are being removed from the stock by several power plants and fisheries, the impact by a single entity cannot be considered in isolation. Our proposed method of long-term impact assessment allows an integrated assessment of impact, but also allows dissection into individual contributions to the total impact. Equation (15) states that the total rate of removals (F) is the sum of the individual instantaneous rates of removal. Since Equation (15) is a linear function, the fraction of the total impact which is attributable to any particular entity is the ratio of the sum of its contributions to total F from all sources as in Equation (15).

CRITERIA FOR IMPACT EVALUATION

Removal of fish from a stock, whether by a fishery or by a power plant, will usually lead to lowered equilibrium abundance. The previous section has presented a method for estimating the approximate reduction in abundance which has taken place. We must now determine whether this impact is "acceptable." In the case of a fishery where tangible values can be assigned to the catch and the stock, optimal catch rates and population sizes can be defined (Roedel 1975; Clark 1976). However, losses to a power plant produce no direct consumptive benefit, and, in many cases, the impacted stock is not subject to a fishery and therefore has no conventional value.

Fortunately, there exists a precedent for evaluating impacts on nonvalued species. The Marine Mammal Protection Act, enacted by the United States in 1972, requires that marine mammals be managed for optimum sustainable population size (OSP). Subsequently, the term was given a working definition: "Optimum sustainable population is a population size which falls within a range from the population level of a given species or stock which is the largest supportable within the ecosystem to the population level that results in maximum net productivity. Maximum net productivity is the greatest net annual increment in population numbers or biomass resulting from additions to the population due to reproduction and/or growth less losses due to natural mortality." (Gehringer 1976).

While power plants clearly do not directly impact marine mammals, the principle of optimum sustainable population size as defined above may be extended to fish and invertebrates as well. Since OSP is defined to fall within a range, impact is unacceptable when it causes population size to fall below the lower limit of that range, which is the point of maximum net productivity. In the logistic model assumed by our long-term impact assessment, maximum net productivity occurs at one-half the virgin, unimpacted population size. This gives a simple criterion for acceptable impact: Abundance should not be driven below one-half of its unimpacted level. In terms of the long-term impact model and its assumptions, this criterion is equivalent to saying that the rate of removal should not exceed the adult rate of natural mortality.

EXAMPLE APPLICATION

This example is based on data collected during 1978 for the purpose of estimating power plant impact on topsmelt, *Atherinops affinis*, inhabiting a California estuary.[4] Topsmelt is a bay-dwelling species with demersal eggs and a short (2-3 mo) spawning period. Topsmelt eggs hatch to produce 6 mm larvae, and larvae >15 mm are not entrained. Larvae were categorized by two length stages, 6-10 mm and 11-15 mm. Based on laboratory growth rate experiments for a closely related atherinid, the California grunion, *Leuresthes tenuis*, duration of these two stages is about 14 d each.

Standing stock and entrainment data (Table 1) are averages for the 3-mo spawning period based on biweekly sampling. Since larvae are concentrated near the surface during daylight hours, larval standing stock estimates are determined based on daytime surface larval densities sampled by a neuston net. These density values are extrapolated to the area of the estuary and a depth of 1 m. The mean entrainment rates are adjusted for variation in cooling water flow during each of the sampling periods. All entrained larvae are assumed to die. The short-term impact of the power plant is estimated to reduce recruitment strengths to 98% of their unimpacted value. Based on seine catches, the standing stock of adult topsmelt in the estuary was 5.4×10^5 fish. Since the power plant has long been operational, equi-

[4]Because the power plant impact study has not completed the official review process, the proprietor wishes not to be identified at this preliminary stage.

TABLE 1.—Example calculation of short-term impact by entrainment of topsmelt larvae. n.e. indicates not estimated.

Stage	Entrainment (L_t) larvae/day	Standing stock (L_t^*) larvae	Entrainment rate (E_t) per day	Stage duration (t_t) days	$E_t t_t$
Eggs	0	n.e.	n.e	n e	0
Larvae					
6-10 mm	4.0×10^4	5.3×10^7	7.5×10^{-4}	14	1.1×10^{-2}
11-15 mm	2.0×10^3	3.0×10^6	6.7×10^{-4}	14	0.9×10^{-2}
16 + mm	0	n.e	n.e	n.e.	0
Sum					2.0×10^{-2}

Equation (5): $R_c = \exp(-2.0 \times 10^{-2}) = 0.98$.
Equation (11): $A_e = 5.4 \times 10^5 (0.98^{-1} - 1) = 1.1 \times 10^4$ fish.

valent adult losses are estimated by Equation (11) and are 1.1×10^4 fish.

Estimation of long-term impact requires information on all sources of mortality. The annual estimate of adult impingement by the power plant, based on 360 d of sampling, is 5,147 fish. According to California Department of Fish and Game records, there were no commercial landings of topsmelt in 1978, and recreational fishermen landed <1,000 topsmelt in this area (we use 1,000 fish for this example). Total mortality rate was estimated by regressing log abundance against age (Ricker 1975), giving an instantaneous total mortality rate (Z) of 1.8. Nonnatural mortality rates of adults were negligible (Table 2), giving a natural mortality rate of $M = 1.8$. Application of the long-term impact approximation (Equation (14)) indicates that topsmelt may be near 99% of their unimpacted abundance despite impacts by both power plants and fisheries. The majority of impact on the local resource is probably due to power plant operation, with entrainment impact being about twice as large as impingement impact. In any case, this estimated small reduction in long-term abundance indicates that there is no cause for concern with regard to power plant impact on topsmelt abundance in this estuary.

TABLE 2.—Example calculation of long-term impact from all sources of topsmelt mortality.

Source of impact	Catch (fish)	Mean standing stock (fish)	Coefficient of mortality
Impingement	5,147	5.4×10^5	1.0×10^{-2} (F_p)
Fishery	1,000	5.4×10^5	0.2×10^{-2} (F_f)
Entrainment	(see Table 1)		2.0×10^{-2} ($\Sigma E_t t_t$)
Sum			3.2×10^{-2}

Equation (20): $M = 1.8 - 1.0 \times 10^{-2} - 0.2 \times 10^{-2} = 1.8$.
Equation (14): $R_e = 1 - (3.2 \times 10^{-2}/3.6) = 0.99$.

DISCUSSION

This approximation of long-term impact is not intended to be a substitute for proper studies of population dynamics. Rather, just as in the case of fishery management, it is intended to be a working approximation which should be discarded as more definitive information and analyses become available. In the case of impact assessment there will always be a suite of organisms, particularly invertebrates, which undoubtedly are impacted, but lack sufficient "status" to justify the expense of close monitoring and study. For these organisms, approximation is the most that reasonably can be asked. In this respect the potential yield approximation is well established in fishery management and should therefore be an equally applicable approximation for power plant impact assessment.

It is likely that the bases of the approximation can be improved in two ways. First, organisms may be classifiable into types with various productivity curves, of which the logistic is a special case. For example, Fowler (1981) observed that species with high reproductive rates and short life-spans show most density-dependent compensation at low population levels, whereas species with low reproductive rates and long life-spans show most of their density-dependent compensation near carrying capacity. Thus, it may be possible to specify the shape of the curves in Figure 1 as a function of observable or measurable traits of specific organisms. The second improvement consists of developing better scaling criteria for the production curve, once its shape has been established. A survey of population growth rates of many species could form the basis of an empirical estimator of compensatory capacity; the use of natural mortality rate may not be appropriate in many cases. Clearly, an improved approximation method would be of value both to fishery management and to power plant impact assessment.

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NOTES

THE SIZE AT SEXUAL MATURITY OF BLUE KING CRAB, *PARALITHODES PLATYPUS*, IN ALASKA[1]

The blue king crab, *Paralithodes platypus*, is similar in size and general morphology to the better known and commercially more important red king crab, *P. camtschatica*. Unlike the red king crab, which is generally distributed throughout most of coastal Alaska, the blue king crab only occurs in small isolated populations. The principal fisheries for blue king crab occur in the eastern Bering Sea, where most populations are associated with offshore islands; minor, but locally important, fisheries occur south of the Alaska Peninsula, where populations are found in a number of widely scattered, enclosed bays.

Harvest of both species of king crab is restricted to males larger than minimum size. For red king crab, the minimum size is set at the average size of a male 3 yr after reaching sexual maturity in an attempt to assure that each male will have at least one opportunity to mate before becoming available for harvest (North Pacific Fishery Management Council 1981). For blue king crab, however, the size at maturity is not well known, and in some areas the minimum size limit is set at the same size as red king crab.

In this paper we estimate the size at maturity of female and male blue king crab in each of four populations. For females, the size at sexual maturity is based on the change in the presence of eggs or egg remnants on the pleopod setae as a function of size. For males, the size at maturity is based on chela allometry, using a new computer technique to estimate the size at which chela growth increases relative to carapace growth.

Materials and Methods of Collection

Samples of blue king crab were collected from each of four populations: St. Matthew Island, Pribilof Islands, Olga Bay, and Prince William Sound (Fig. 1). Sampling methods differed somewhat between populations. The populations from St. Matthew Island and Pribilof Islands were sampled with bottom trawls on cruises conducted by the National Marine Fisheries Service during the months of June and July of each year from 1976 to 1981. Sampling depths ranged from 30 to 180 m. The Olga Bay population was sampled by scuba divers and with hand operated ring nets in March, June, and October 1980 and January 1981. Sampling depths ranged from 1 to 50 m. The Prince William Sound population was sampled with bottom trawls in September 1980 and with commercial king crab pots in September 1979 and December 1980. Sampling depths ranged from 80 to 150 m.

Carapace length of both sexes and the major (righthand) chela height of males were measured to the nearest 1 mm using sliding jaw calipers (see Wallace et al. 1949 for definitions of these measurements). Reproductive condition of females was classified as either

virgin—no eggs or egg remnants attached to the pleopod setae,

attached eggs—eggs attached to the pleopods, or

hatched eggs—egg remnants, consisting of egg membranes and egg funiculi, attached to the pleopod setae.

Female Size at Maturity

Female blue king crab mate and extrude eggs quite soon after every adult molt (a pathological exception to this is discussed in Somerton and MacIntosh[2]); therefore, females can be classified as mature or immature based on the presence or absence of eggs or egg remnants on the pleopods. Using this classification criterion, the percent of females that were mature was calculated for each 3 mm size interval. Percent mature is plotted against carapace length in Figure 2.

The size at 50% maturity (SM50) was chosen as an appropriate measure of the size at maturity [see Somerton (1981) for a discussion of the strengths and weaknesses of this particular measure]. SM50 was estimated for each population by fitting a logistic equation to percent mature by size, using weighted nonlinear least squares (Somerton 1980a), then

[1]Contribution No. 625, College of Fisheries, University of Washington, Seattle, WA 98195.

[2]Somerton, D. A., and R. A. MacIntosh. In prep. Reproductive biology of the blue king crab, *Paralithodes platypus*. Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle, WA 98195.

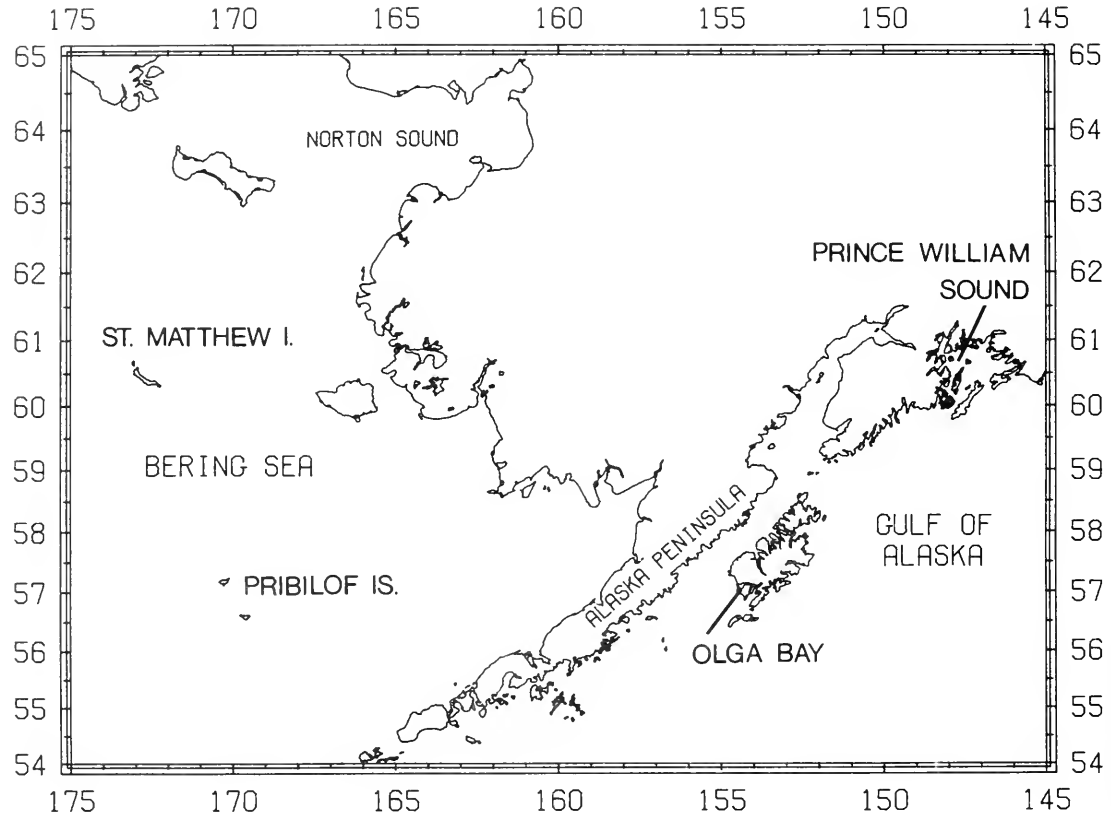

FIGURE 1.—Locations of the four blue king crab populations: St. Matthew Island, Pribilof Islands, Olga Bay, and Prince William Sound.

evaluating the fitted equation to find the size corresponding to 50% maturity. Variance of SM50 was estimated using the technique described in Somerton (1980a). Estimates of SM50, standard deviations, and 95% confidence intervals are shown in Table 1.

TABLE 1.—Female size at 50% maturity (SM50), standard deviation, and 95% confidence intervals for each of the four blue king crab populations studied.

Area	SM50 (mm)	Standard deviation	95% confidence interval
St. Matthew Island	80.6	0.6	79.4-82.6
Pribilof Islands	96.3	0.3	95.7-96.9
Olga Bay	93.7	0.4	92.9-94.5
Prince William Sound	87.4	0.5	86.4-88.4

Male Size at Maturity

Male blue king crab do not display external features that unambiguously indicate maturity; however, at maturity the growth of the major chela may increase relative to the growth of the carapace. Although this relationship has not been established for blue king crab, for tanner crab, *Chionoecetes bairdi*, the size of maturity based on chela allometry was almost identical to that based on a change in reproductive tract weights (Brown and Powell 1972). If this is also true for blue king crab, then the size at maturity can be estimated by the size at which chela growth increases.

When chela measurements are plotted against carapace measurements on log-log axes, the data assume a pattern consisting of two straight lines. These lines describe the juvenile and adult phases of relative growth (Hartnoll 1978). For some species of crab, especially brachyuran crabs, the two lines have similar slopes but different intercepts. Somerton (1980a) described a technique for estimating the size of maturity for species with this pattern of relative growth. For other species, including blue king crab, the two lines have different slopes and intersect at the size at maturity. In this case, the problem of estimating the size at maturity is one of estimating the intersection point of the two phase lines.

The intersection point can be estimated from morphometric data by finding the best fit of a model

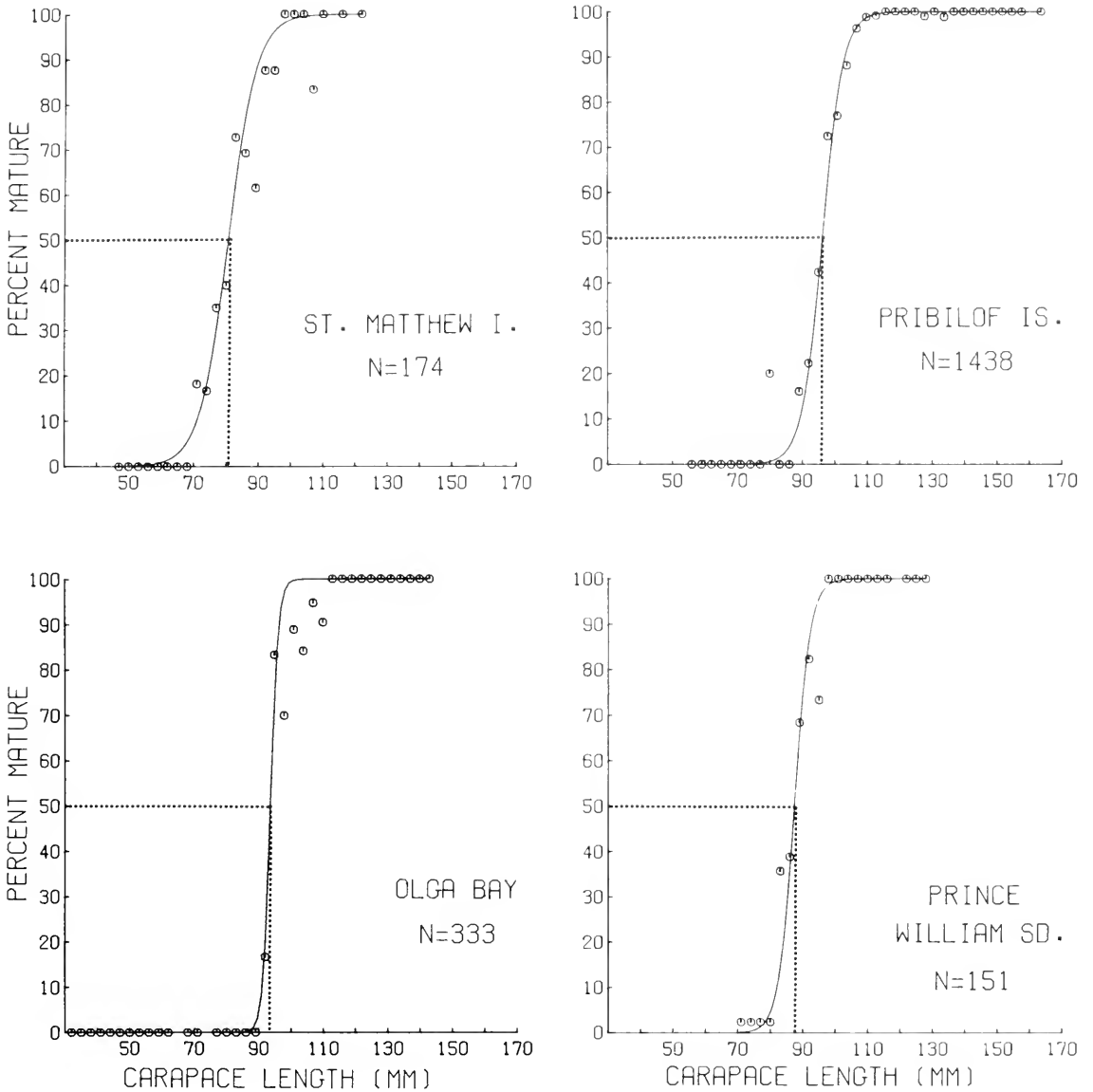

FIGURE 2.—Percent of blue king crab females that were mature, within 3 mm size intervals, as a function of size. Dotted lines indicate the carapace lengths corresponding to the 50% maturity levels on the fitted logistic functions (solid lines). Sample sizes (N) are indicated.

which describes a pair of intersecting straight lines and has the intersection point as a parameter. One such model, which has been previously used (Somerton 1980b) to describe the relation between premolt and postmolt carapace size, is

$$Y = A + BX \qquad X \leq X^*$$
$$Y = Y^* + C\,(X - X^*) \qquad X > X^*$$

where Y and X are the logarithms of chela height and carapace length, X^* is the intersection point on the X axis, and Y^* is the intersection point on the Y axis, ($Y^* = A + BX^*$). The model has four parameters. A, B, C, and X^*.

This model was fit to morphometric data using an iterative computer technique (FORTRAN program MATURE2 is available from the senior author). First, a lower and an upper bound of an interval on the X axis are chosen such that the intersection point is contained within the interval. Second, X^* is set

equal to the lower bound and linear regression is used to fit a lower line ($X \leq X^*$), then an upper line ($X > X^*$) to the data. Third, X^* is increased by some small amount and the model is fit to the data iteratively until X^* equals the upper bound. The size of sexual maturity is then equal to the antilog of the X^* value, which produced the minimum residual sum of squares about the model. Chela and carapace measurements and the best fitting pair of lines are shown in Figure 3.

Although this technique will always find the best fit of the model, the fit may not be statistically significant, that is, the fit of the two line model may not be significantly better than the fit of a single straight line. Therefore a single straight line was fit to the data and the residual sum of squares (RSS) of the two line model was tested against the RSS from the single line using a partial F test (Draper and Smith 1981). The partial F test was significant ($P<0.05$) for all four sets of blue king crab data. In cases where the fit of the two

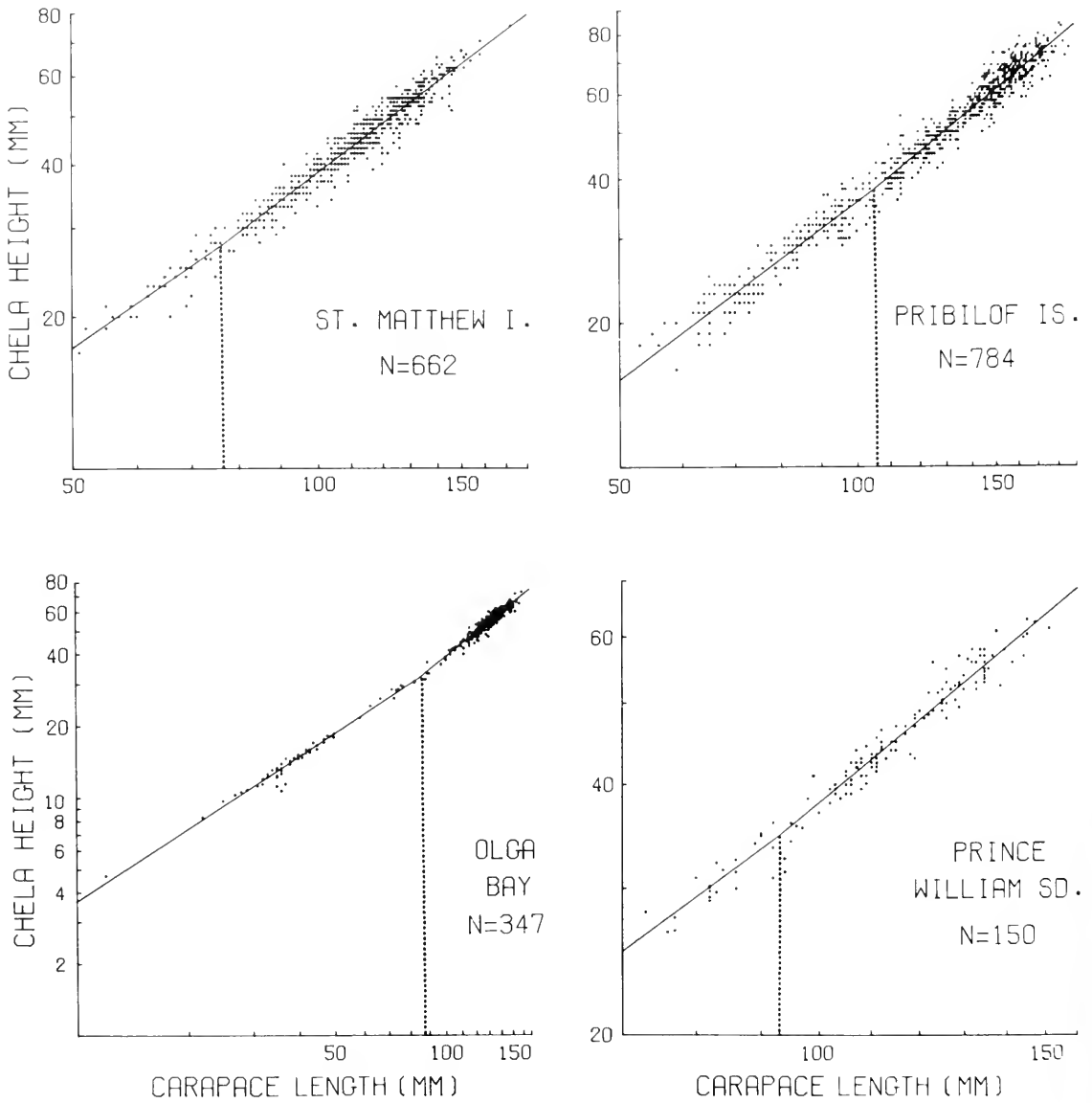

FIGURE 3.—Male chela heights and carapace lengths of the blue king crabs. The X axis intersection points of the two line model, or the estimated sizes of maturity, are shown by dotted lines. Sample sizes (N) are indicated.

line model is not significantly better than the fit of a single line, either more data or a broader size range of data is needed or some other procedure for estimating the size of maturity should be considered.

The standard deviation of X^* was estimated using Monte Carlo simulation (Hammersley and Handscomb 1964), which, in this particular application, consisted of 1) generating sets of synthetic morphometric data, 2) estimating X^* for each data set by fitting the two line model, and 3) calculating the standard deviation between the estimates of X^*. Each synthetic data set was constructed by generating a new chela measurement for each carapace measurement in the original sample. The new chela measurement was computed as

$$Y = E(Y) + Z \cdot SD$$

where Y is the logarithm of chela height, $E(Y)$ is the expected value of log chela height given carapace length and the parameters of the appropriate phase line, Z is a randomly generated standard normal deviate, and SD is the standard deviation about the appropriate phase line. For carapace widths $\leq X^*$, the parameters and SD for the juvenile phase line were used; for carapace widths $> X^*$, the parameters and SD for the adult phase line were used. Thirty samples of morphometric data were generated for each population. X^* was estimated for each sample and the standard deviation among the 30 independent estimates of X^* was calculated. The estimates of X^*, standard deviations, and 95% confidence intervals are shown in Table 2.

Samples from the populations of St. Matthew Island and Pribilof Islands contained some chela measurements that were unusually small compared with other measurements from crabs with similar carapace lengths (Fig. 4). These atypical measurements were probably obtained from crabs in the process of regenerating lost chelipeds. For crabs which are bilaterally symmetric, the inadvertent measurement of partially regenerated chelae should not be a problem, because the sizes of left and right chelae can be compared in the field, and, if different, the measurement can be rejected. For crabs, such as blue king crab, which are not bilaterally symmetric, partially regenerated chelae are harder to detect and thus are likely to be included in the sample. For red king crab, the

TABLE 2.—Male size at maturity, standard deviation, and 95% confidence intervals for each of the four blue king crab populations studied.

Area	Size at maturity (mm)	Standard deviation	95% confidence interval
St. Matthew Island	77.0	9.8	57.8-96.2
Pribilof Islands	108.0	12.8	82.9-133.1
Olga Bay	87.0	7.2	72.9-101.1
Prince William Sound	93.0	13.9	65.7-120.2

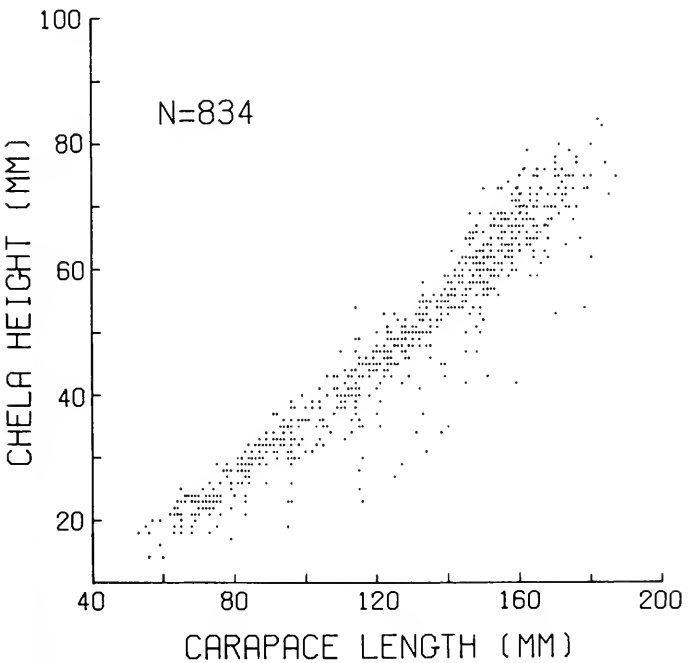

FIGURE 4.—Male chela height and carapace length measurements of the blue king crab from the Pribilof Islands before date deletion. Measurements of chela height which appear unusually small relative to the carapace length probably were obtained from crabs in the process of regenerating lost chela.

length of a limb after each of the five molts required for complete regeneration is 27, 45, 65, 85, and 100% of the length of a normal limb (Edwards 1972). Limbs in the last stages of regeneration are the hardest to detect.

Since measurements from regenerating chelae can be quite deviant from normal measurements, they can have a pronounced effect on the estimate of X^* and therefore must be detected and eliminated from the sample. The method we used for eliminating such outliers consisted of fitting a single straight line to the logarithms of chela height and carapace length (fitting the two line model is preferable if computer cost is not a consideration) then excluding the datum with the largest negative deviation. This is repeated iteratively until the mean square residual (MSR) is reduced to some level.

Two criteria were examined as a means of determining when MSR had been reduced sufficiently. The first criterion considered the change in MSR resulting from the deletion of each successive datum. Typically the change in MSR was initially large, then decreased almost asymptotically as additional data were deleted (Fig. 5). Elimination of regenerating chela measurements was assumed to be complete when the change in MSR became nearly constant. For the Pribilof Islands population, data deletion was halted after 50 values (6% of the sample) were removed (Fig. 6).

The second criterion was based on a comparison of the MSR of the contaminated sample with the MSR of a sample assumed to be free of regenerating chela measurements. Deletion was halted when the MSR of the contaminated sample was not significantly different from the uncontaminated sample, based on an F ratio, at some probability level. Although this criterion is more objective than the first, it requires an uncontaminated sample and it assumes that the true variance is identical between populations. For the Pribilof Islands data, to achieve an MSR that was not significantly different from the average MSR for the Olga Bay and Prince William Sound data (both of these data sets did not contain regenerating chelae measurements) at the 0.001 probability level, 114 values (14% of the sample) had to be excluded (Fig. 7). Even with this low probability level, the deletion of data was too severe, because the distribution of chela measurements about the fitted line appeared to have a positive skew. Since we believe that the true variance is probably less in the Olga Bay and Prince William Sound populations than in the Pribilof Islands population, the first criterion was used to determine when the deletion of data should be halted.

The number of data deleted by these methods may be too large, that is, some crabs with small, but otherwise normal, chela may have been excluded. In one study of limb regeneration in male red king crab, 14.7% of the adults and 25.6% of the juveniles had

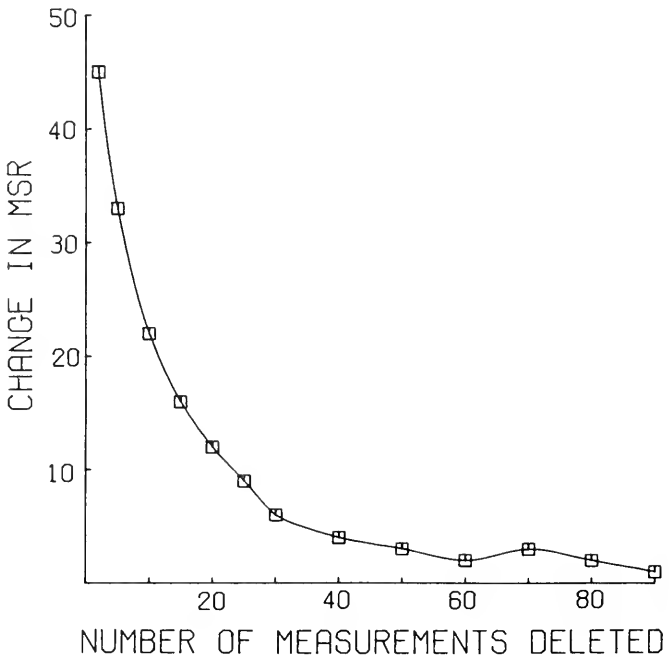

FIGURE 5.—Change in mean square error (MSR) about a single straight line fit to the data of the blue king crab from the Pribilof Islands as a function of the number of values deleted. Note that the change in MSR becomes nearly constant after deleting 50 values.

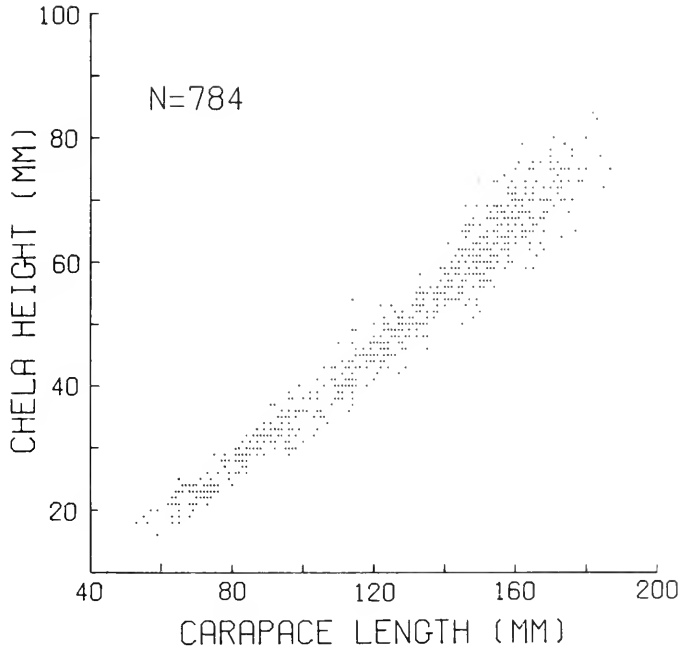

FIGURE 6.—Chela height and carapace length data of the blue king crab from the Pribilof Islands after the deletion of 50 values.

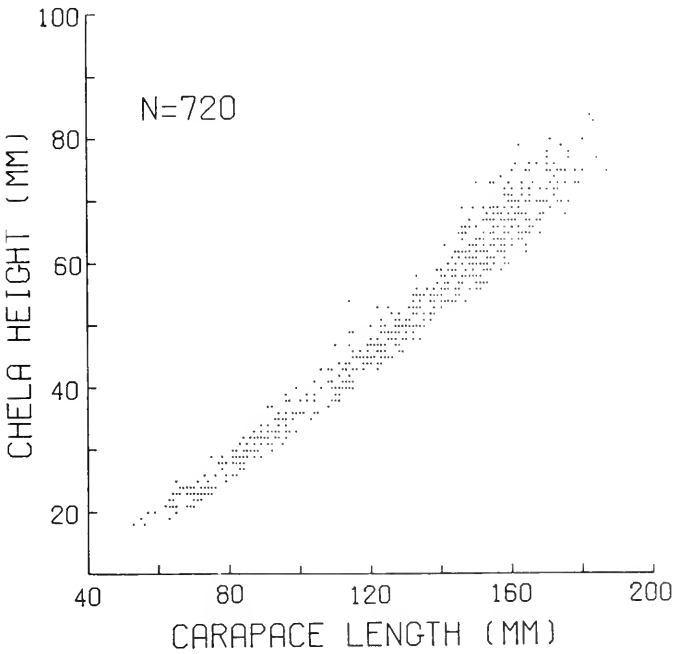

FIGURE 7.—Chela height and carapace length data of the blue king crab from the Pribilof Islands after the deletion of 114 values.

missing or regenerating limbs and 8.4% of the missing or regenerating limbs were the right cheliped (Edwards 1972). Thus 1.2% of all adult males and 2.2% of all juvenile males had missing or regenerating right chela. For the Pribilof Islands sample, 6.0% of the total sample was deleted. Although some valid measurements may have been rejected, the loss of these measurements should bias the estimate of X^* less

than the inclusion of measurements from regenerating chela.

Results and Discussion

For both sexes of blue king crab, estimates of the size at sexual maturity were largest at Pribilof Islands, smallest at St. Matthew Island, and intermediate between these extremes at Olga Bay and Prince William Sound (Tables 1, 2). Precision in the estimates of the size at maturity of blue king crab differs markedly between sexes. For females, the average standard deviation was 0.45 mm, whereas, for males, the average standard deviation was 10.93 mm, about 24 times larger. Because of this difference, the estimates for females differed significantly (Z test, $P<0.5$) between all areas, but the estimates for males did not differ between areas even though their range was nearly double that of females.

Much of the imprecision in the estimates of male size at maturity is the result of the pattern of relative growth. Standard deviation of an estimate of male size at maturity depends largely on the angle at which the two phase lines meet. As the included angle increases, uncertainty in the position of each phase line is progressively magnified in the uncertainty of the estimate of the size of maturity. Species, such as blue king crab, which exhibit a large angle between phase lines, inherently have a large standard deviation.

Future studies of male crabs with a similar pattern of relative growth should insure that samples include a broad range of sizes, because this will minimize the standard deviation of the estimates of size at maturity. The relationship between size range and standard deviation is exemplified by the two extreme cases examined here. The Olga Bay sample, which produced the smallest standard deviation, included individuals as small as 12 mm, whereas the Prince William Sound sample, which produced the largest standard deviation, included no individuals smaller than 72 mm.

Acknowledgments

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FOOD HABITS OF PACIFIC WHITING, *MERLUCCIUS PRODUCTUS*, OFF THE WEST COAST OF NORTH AMERICA, 1967 AND 1980

The Pacific whiting, *Merluccius productus*, forms a major groundfish resource off the west coast of North America. According to Nelson and Larkins (1970) it is "one of the most abundant species of fish in the northeastern Pacific Ocean." Fishing effort on the Pacific whiting stock has increased dramatically since 1965 when it became the target of the United States and Soviet fishermen (Grinols and Tillman 1970). The stock is now the basis of a large U.S. joint-venture and domestic fishery. Management of this stock requires more detailed information on the major prey of Pacific whiting throughout its distribution.

Previous studies have shown that Pacific whiting feed primarily on euphausiids, but at certain times commercially important fish or pandalid shrimp may constitute an important item in the diet (Gotshall 1969a, b; Alton and Nelson 1970; Outram and Haegele 1972). Indirect evidence of nocturnal feeding by Pacific whiting has also been presented by Alton and Nelson (1970) and by Outram and Haegele (1972). Although these studies contain useful baseline information, they are not complete enough to describe quantitatively the predatory interactions of Pacific whiting, with the exception of Gotshall's (1969a, b) study which focused only on the impact of whiting predation on the commercially important pink shrimp, *Pandalus jordani*.

The objective of the present study is to provide a quantitative account of the predatory patterns of Pacific whiting by identifying their major prey items, determining whether size-selective predation occurs, examining diel feeding behavior, and calculating daily ration.

Collection and Processing of Samples

Stomachs of adult Pacific whiting were collected in 1967 off the Oregon and Washington coasts (Livingston and Alton 1982) and in 1980 off Oregon, Washington, and Vancouver Island (Fig. 1). Also, samples of juvenile Pacific whiting taken off the California coast in the fall of 1980 were saved for stomach analysis (Table 1). Samples were obtained during resource assessment surveys using either bottom or midwater trawls. Only vessels operating during daylight hours used bottom trawls to survey whiting which were mostly on the sea bottom. Midwater trawls were used on those vessels with both day and night operations so that the net could be set at depths of greatest whiting concentration. Stomach samples were taken opportunistically at standard resource assessment stations. In 1967, most stations were at bottom depths of <100 m, while in 1980 bottom depths ranged from 77 to 298 m. Stomachs were taken randomly from the entire catch in 1967, but were stratified in 1980 by 10 cm whiting length groups.

A 15-h time series of stomach samples was taken in 1967 at a station off the Washington coast to detect

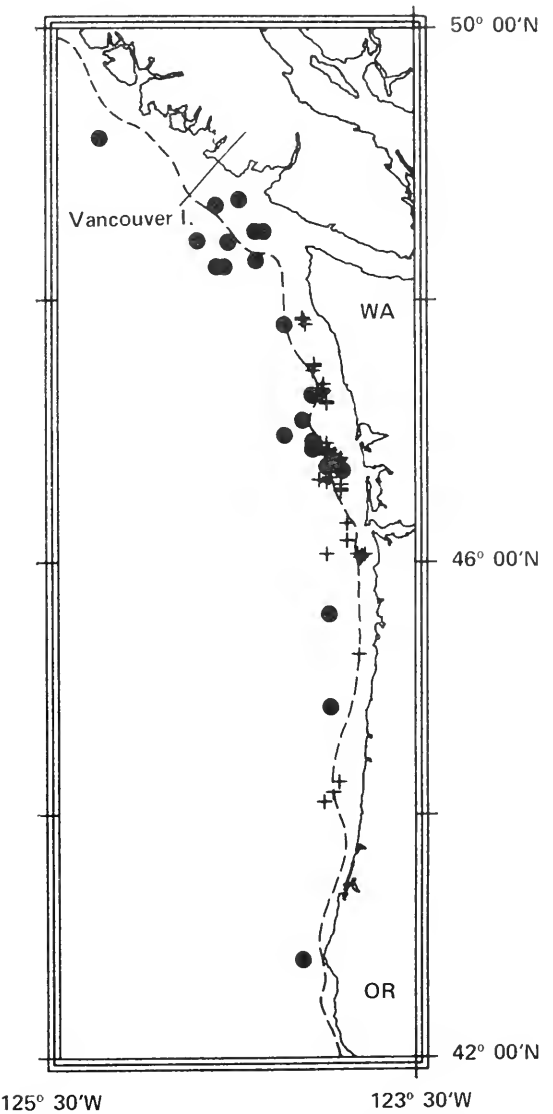

FIGURE 1.—Sampling locations for Pacific whiting, *Merluccius productus*, in 1967 (+) and 1980 (·) in relation to the 100 m depth contour (---).

TABLE 1.—Dates, locations, station information, and sample sizes of stomach samples of Pacific whiting taken from the northwest Pacific Ocean, 1967 and 1980.

Vessel	Location	Sampling period	Tows		Bottom depth range (m)	No. of stomachs collected[3]
			Number[1]	Type[2]		
RV *John M. Cobb*	Oregon	Apr.-July 1967	6 (2)	MW	84-126	104 (86)
RV *Commando*	Oregon	June 1967	1 (1)	MW	144	7 (8)
MV *Baron*	Oregon	June 1967	4 (0)	MW	49-77	91 (5)
RV *John M. Cobb*	Washington	May-July 1967	30 (2)	MW	53-156	785(108)
MV *Baron*	Washington	June 1967	8 (0)	MW	62-75	191 (56)
MV *Recruit*	Washington	June 1967	1 (0)	MW	75	9 (2)
MV *St. Michael*	Washington	June-July 1967	9 (0)	MW	55-84	243 (54)
RV *Tikhookeanskiy*	Oregon	Apr.-May 1980	3 (3)	BT	120-200	53 (13)
RV *Miller Freeman*	Washington-Vancouver I., B.C.	Aug.-Sept. 1980	6 (6)	MW	111-298	34 (–)
MV *Pat San Marie*	Washington-Vancouver I., B.C.	Sept. 1980	14(10)	BT	77-293	77 (–)
RV *Poseydon*	California	Oct. 1980	2 (2)	BT	130-160	40 (12)

[1]Number of tows at bottom depths >100 m are given in parentheses.
[2]MW = midwater trawl, BT = bottom trawl.
[3]Stomachs containing food. Number of empties in parentheses.

feeding discontinuity. A total of 258 stomachs were collected at seven different times of day (Table 2).

Fish showing signs of regurgitation were discarded from samples. Lengths were recorded for fish with stomachs containing food. The stomachs of adult fish were then excised and placed in muslin bags with a specimen card containing fish length and station information. Juvenile fish were placed whole in muslin bags for later stomach excision in the laboratory. All samples were preserved in a 10:1 seawater/formaldehyde mixture.

Because of incomplete records of numbers of empty stomachs sampled on two cruises in 1980, that data set could not be used for daily ration calculations. In 1967, however, numbers of empty stomachs at each station were recorded along with corresponding fish lengths.

Fish lengths were converted to weights using the weight-length relationship for Pacific whiting, sexes combined (Traynor[1]):

$$w_g = 0.004774 \ \ l_{cm}^{3.0947}.$$

[1]J. Traynor, Fishery Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112, pers. commun. December 1982.

TABLE 2.—Summary of a diel series of Pacific whiting stomach samples obtained on RV *John M. Cobb*, 14-15 July, 1967 off the Washington coast lat. 47° 19'N, long. 124° 33'W at a bottom depth of 65 m.

Time of day (P.S.T.)	No. of stomachs		Total weight of stomach contents (g)	Mean fish length (mm)
	With food	Empty		
1800	30	1	557.9	486
2100	34	2	474.8	429
2300	36	0	215.6	509
0100	61	1	348.2	524
0300	35	1	373.8	500
0400	17	2	83.9	533
0900	38	0	403.3	484
	251	7		

Stomachs were analyzed individually in the laboratory, with the exception of the fall 1980 samples which were analyzed by composite groups. Prey items were identified to the lowest practical taxon, and damp weight and number of each prey taxon per stomach or composite of stomachs were recorded. In 1967, there was some loss of information on the number of prey in some taxa because no attempt was made to count certain prey items when they showed a fair degree of digestion.

Food of Pacific Whiting

Euphausiids, including *Thysanoessa spinifera* and *Euphausia pacifica*, were the dominant food of Pacific whiting in 1967, constituting 72.2 and 90.2% by weight of the diet of Pacific whiting taken off Oregon and Washington, respectively (Table 3). In 1980, euphausiids were also the predominant item in the diets of Pacific whiting <200 mm in length off California (100% by weight) and of Pacific whiting 350-449 mm long off Oregon (99.6% by weight).

Schooling fish were also important dietary components for Pacific whiting. Northern anchovy, *Engraulis mordax*, comprised 16.4% by weight of the diet of Pacific whiting in summer 1967 off Oregon. In spring 1980 off Oregon, eulachon, *Thaleichthys pacificus*, comprised 22% by weight of the diet of 450-549 mm Pacific whiting and 79.6% by weight of the diet of 550+ mm fish. Pacific herring, *Clupea harengus pallasi*, dominated the diets of Pacific whiting taken in summer 1980 off Washington and Vancouver Island, constituting 54.2 and 67% by weight of the 450-549 mm and 550+ mm whiting size groups, respectively.

Other fish items were predominantly flatfish and rockfish, *Sebastes* sp. Pandalid shrimp, including *Pandalus jordani*, comprised <5% by weight of the

TABLE 3.—Percentage by weight of prey items in the stomachs of Pacific whiting, 1967 and 1980, off the west coast of North America and summary of average stomach content weight (not including empty stomachs)[1].

	Summer 1967		Fall 1980	Spring 1980			Summer 1980	
	Oregon	Washington	California	Oregon			Wash.-Vancouver I.	
	Mean predator size (mm)		Predator-size group (mm)					
Prey item	491	503	<200	350-449	450-549	550+	450-549	550+
Crustacea								
Euphausiids								
T. spinifera	21.1	35.3	72.5	6.2	9.1	T	19.0	1.7
E. pacifica	1.7	0.3	6.8	93.0	26.9	1.0	4.2	3.0
Unidentified	49.4	54.6	20.7	0.4	23.4	0.2	6.6	2.7
Crab megalops larvae	1.1	0.1						
Mysidacea	T	T	T	—	—	—	—	T
Pandalidae (unidentified)	0.3	0.3	—	—	3.7	4.5	3.0	0.3
Pandalus jordani	—	—	—	—	—	—	0.7	1.7
Sergestes similis	—	T	—	—	—	—	0.1	0.2
Pasiphaea pacifica	—	—	—	—	—	—	—	0.1
Spirontocaris sp.	—	—	—	—	—	—	—	T
Crangon sp.	0.2	0.2	—	—	—	—	0.4	—
Caridea (unidentified)	0.1	0.4	—	—	—	—	0.1	—
Gonatus sp.	—	—	T	—	0.1	0.2	—	—
Pisces								
Engraulis mordax	16.4	0.1	—	—	—	—	—	—
Clupea harengus	—	—	—	—	—	—	54.2	67.0
Thaleichthys pacificus	—	—	—	—	22.0	79.6	3.3	9.4
Osmeridae	0.7	0.8	—	—	7.8	—	1.0	2.3
Sebastes sp.	—	T	—	—	—	—	4.1	0.1
Liparis fucensis (larvae)	—	—	—	—	—	—	0.2	—
Agonidae	—	—	—	—	—	—	0.5	—
Gadidae	—	1.3	—	—	—	—	0.2	—
Pleuronectidae (unid.)	—	T	—	—	6.8	6.3	0.6	—
Citharichthys sp.	—	—	—	—	—	—	0.6	—
Porolinus rothrocki	—	—	—	—	—	—	0.7	—
Icichthys lockingtoni	—	—	—	—	—	—	—	8.9
Zoarcidae	—	0.5						
Unidentified	8.8	5.7	—	0.4	0.2	8.1	0.5	2.5
Number of Stomachs	202	1,228	40	16	17	20	70	41
Total weight of stomach contents(g)	2,403.8	10,560.8	13.65	133.7	86.74	607.3	849.1	934.6
Mean stomach content weight (g)	11.9	8.6	3.3	8.4	5.1	30.4	12.1	22.8
Mean fish length (mm)	491	503	132	380	506	587	529	591
Percentage body weight of stomach contents	1.46	0.96	23.57	2.27	0.57	2.14	1.18	1.57

[1]T indicates trace amounts of food, i.e. <0.1% by weight of the diet.

Pacific whiting diet in all cases. Other shrimp eaten included *Cragon* sp., *Pasiphaea pacifica*, and *Sergestes similis*. Other invertebrates were predominantly crab megalops larvae.

In terms of general prey categories, Pacific whiting in 1967 off Oregon ate proportionally more fish, especially northern anchovy, than did whiting in 1967 off Washington (Fig. 2). The diets of similar-sized Pacific whiting (450-549 mm) taken in 1980 off Oregon and Washington-Vancouver Island, however, contained an even greater proportion of fish (Fig. 3), but of different species. A shift in major dietary component from euphausiids to fish occurred as the length of Pacific whiting increased during spring and late summer of 1980. Diets of Pacific whiting >550 mm consisted of 90.2% fish by weight.

To illustrate the switch in food from euphausiids to fish as the length of Pacific whiting increased, the percentage frequency of occurrence of Pacific herring in Pacific whiting stomachs was plotted against Pacific whiting length for the late summer 1980 samples (Fig. 4). A steady increase in the occurrence of Pacific herring is noticeable up to the 561-580 mm whiting length interval. Thereafter, the curve

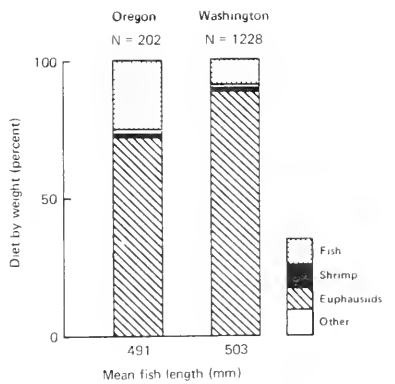

FIGURE 2.—Percentage by weight of major prey categories in the diet of Pacific whiting, *Merluccius productus*, taken off Oregon and Washington, summer 1967.

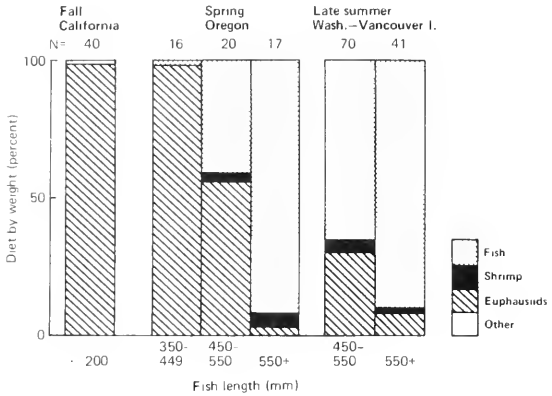

FIGURE 3.—Percentage by weight of major prey categories in the diet of Pacific whiting, *Merluccius productus*, for different length groups of whiting at various locations in 1980.

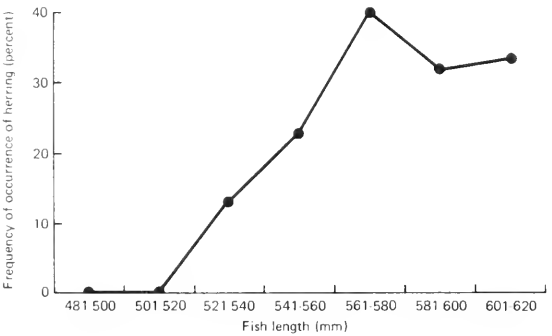

FIGURE 4.—Percent frequency of occurrence of Pacific herring, *Clupea harengus pallasi*, in stomachs of different length groups of Pacific whiting, *Merluccius productus*, taken late summer 1980 off Washington and Vancouver Island.

appears to level off at a 30% occurrence of Pacific herring.

The difference in Pacific whiting diets between the years 1967 and 1980 is mainly seen as a greater percent consumption of fish in 1980 by whiting >450 mm. No clear explanation is available because sample size in 1980 was small and samples were obtained further offshore than in 1967. The most distinct relationship noted in these results is the tendency of Pacific whiting to consume prey species which occur in patches or schools, usually euphausiids and pelagic fishes such as eulachon, northern anchovy, and Pacific herring which also prey on euphausiids (Wailes 1936; Barraclough 1964; Barraclough et al. 1968). Likewise, the majority of the invertebrate prey of Pacific whiting (e.g., pandalid, sergestid, and pasiphaeid shrimp) are documented predators of euphausiids (Renfro and Pearcy 1966; Pearcy 1970; Judkins and Fleminger 1972). Thus, euphausiids appear to be the unifying factor, their presence attracting not only the Pacific whiting but also other organisms which then become available prey for Pacific whiting.

Alton and Nelson (1970) reported the main food items of Pacific whiting off northern Oregon and Washington to be euphausiids, eulachon, and pandalid shrimp. Similarly, Outram and Haegele (1972) found euphausiids, pandalid shrimp, and schooling fish (such as Pacific sand lance, *Ammodytes hexapterus*; Pacific herring; and eulachon) most frequently in stomachs of Pacific whiting sampled off Vancouver Island. They also found Pacific herring to be a more important component in the diet of large Pacific whiting. Off California, Gotshall (1969a) discovered pandalid shrimp, euphausiids, flatfish, and schooling fish constituted most of the whiting's food. Although Gotshall (1969a, b) showed that on the average pandalid shrimp dominated the Pacific whiting diet, in some months fish or euphausiids were found to be the primary food items. This seasonal change in diet may have resulted from the changing size composition of the Pacific whiting population in the study area due to northward migration of adults in spring.

Predator-Prey Size Relationship

An examination of the relationship between a fish predator's size and its choice of prey sizes may aid in understanding, interpreting, and quantifying a predator's feeding habits (Ursin 1973; Werner 1974; Agger and Ursin 1976; Werner and Hall 1977; Hahm and Langton 1980). Calculation of the frequency distribution of predator weight to prey weight ratios, as described by Ursin (1973), quantifies a predator's food size preference through central tendency measures of its distribution. These measures can then be used directly as input parameters to models such as Andersen and Ursin's (1977) multispecies Beverton and Holt model or the various multispecies VPA models (Helgason and Gislason 1979; Sparre 1980).

The basic method of calculating predator-prey size ratios utilizes the total weight in grams (W_j) and total number (ΣN_j) of each prey type j in a collection of predator stomachs. The individual mean weight of each prey type ($\bar{w}_j$) is calculated and compared with the mean predator weight ($\bar{w}_i$). Ursin (1973) discovered that for benthic-feeding fish the frequency distribution of the ratios of predator weight to prey weight ($\bar{w}_i/\bar{w}_j$) was approximately log-normal in shape. Therefore, a plot of ln ($\bar{w}_i/\bar{w}_j$) vs. ΣN_j should be a normally shaped curve.

This methodology was applied to the 1980 Pacific whiting stomach data. There was a total of 204 Pacific whiting in this sample, ranging in length from 116 to 645 mm, with $\bar{w}_i$ of 862 g. These Pacific whiting consumed a total of 8,940 food items $[\Sigma(\Sigma N_j)]$ with individual $\bar{w}_j$ ranging from 0.002 g for amphipods to 83 g for a medusafish, *Icicthys lockingtoni*.

The solid lines in Figures 5-7 represent the shape of the predator-prey size curves resulting from the analysis of 1980 data when separated into three predator size groups. However, these curves do not necessarily represent the prey-size preference of Pacific whiting. Lawlor (1980) stated that the proportion of a food item in the diet of a predator is a function not only of the predator's choice for that item but also of the item's availability. Only when abundances of all prey items are equal, do the observed proportions of prey items in a predator's stomach reflect the predator preference.

To determine the prey-size preference of Pacific whiting, we may examine a theoretical situation in which equal numbers of each prey size are offered to the Pacific whiting. Assuming the numbers of each prey type in the environment to be inversely proportional to the prey type's weight (Ursin 1973), this situation can be created by multiplying total ΣN_j by $\bar{w}_j$. To adjust for predator size, this quantity is divided by $\bar{w}_i$. The dashed lines in Figures 5-7 depict the theoretical results of offering equal numbers of each prey size to the whiting.

Pacific whiting <200 mm, whose diet consisted mainly of euphausiids, have a very narrow prey-size selection curve (Fig. 5) which reflects their choice of a narrow size range of food. The dashed line of the pre-

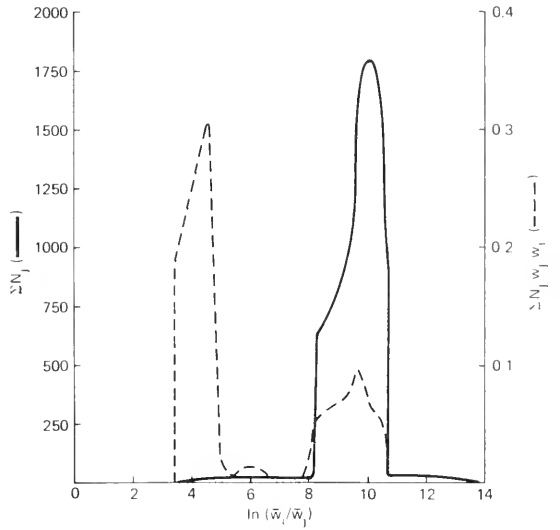

FIGURE 6.—Frequency distribution of predator-prey size scores for Pacific whiting, *Merluccius productus*, predators 350-549 mm long with an average weight ($\bar{w}_i$) of 876.2 g, under natural (—) and simulated (---) conditions.

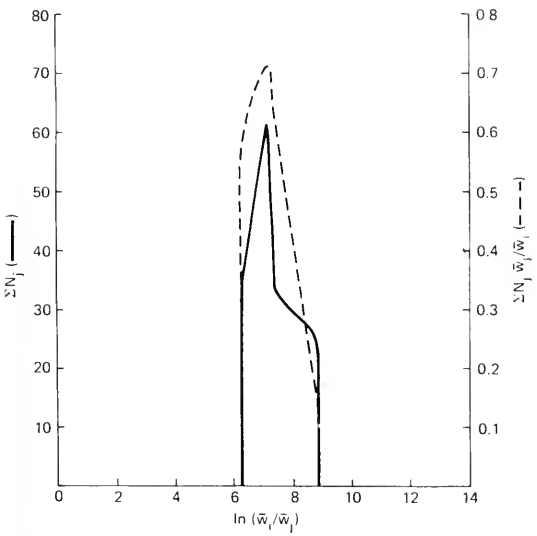

FIGURE 5.—Frequency distribution of predator-prey size scores for Pacific whiting, *Merluccius productus*, predators <200 mm long with an average weight ($\bar{w}_i$) of 13.2 g, under natural (—) and simulated (---) conditions.

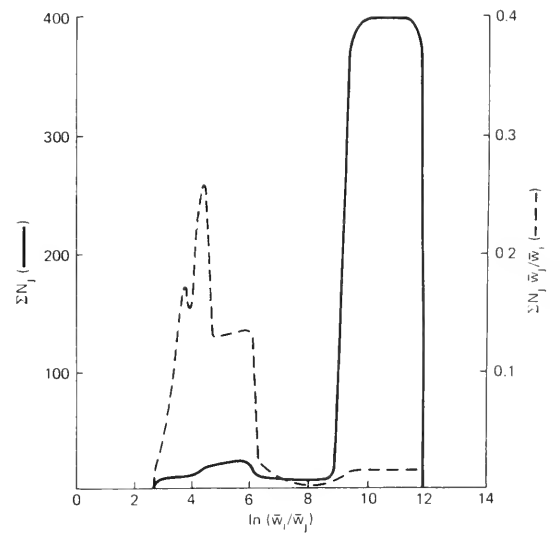

FIGURE 7.—Frequency distribution of predator-prey size scores for Pacific whiting, *Merluccius productus*, predators 550+ mm long with an average weight ($\bar{w}_i$) of 1,441.3 g, under natural (—) and simulated (---) conditions.

ference curve for the small Pacific whiting closely follows the selection curve in which euphausiid-sized prey dominated.

The selection curve for the middle-sized group of Pacific whiting, 350-549 mm, also peaks sharply but with long, trailing ends indicating that euphausiids dominated the diet in numbers although small numbers of prey items, both smaller and larger than euphausiids, were eaten (Fig. 6). The preference curve is bimodal with the largest mode corresponding to a predator-prey size ratio of about 100:1, while the second mode reflects a continuing preference for euphausiid-sized items.

The largest size group of Pacific whiting, 550+ mm, have an actual prey-size curve which depicts the numerical dominance of euphausiids in their food by the sharp peak at $\ln(\bar{w}_i/\bar{w}_j)$ value of about 10.5 (Fig. 7). There is also a pronounced hump in the left tail of the curve in the region of a predator-prey weight ratio corresponding to a large Pacific whiting predator and a Pacific herring-sized prey. The preference curve shifts completely away from the selection curve for these Pacific whiting. The mode for euphausiid prey is dampened almost completely and the most prevalent predator-prey size ratio is about 130:1, equivalent to the ratio of a large Pacific whiting predator to a Pacific herring-sized prey.

Thus, it appears that the diets of Pacific whiting <200 mm long reflect a preference for euphausiid-sized prey. Although the 350-549 mm size group of Pacific whiting shows a dominant prey-size preference of 100:1, the calculated preference curve deviates from the predicted normal shape due to a second mode in the region corresponding to euphausiid-sized prey. Deviations from normality can be caused when the abundance of a naturally occurring prey item is not inversely proportional to its weight as assumed or when the prey occur in such dense patches that the predator consumes more than one prey item at a time (Ursin 1973). The latter case is a likely description of Pacific whiting predation on euphausiids, though this would have to be verified through direct observation. The largest size group of Pacific whiting shows a preference for Pacific herring-sized prey with a median predator-prey size ratio of about 130:1. This is similar to Ursin's (1973) calculation of an average predator-prey size ratio of 160:1 for Atlantic cod, *Gadus morhua*.

The prey-size preference of Pacific whiting is reasonably described by Ursin's model. The major parameters which define the shape of the prey-size preference curve are the mean ($\bar{x}$) and variance (s^2) of the frequency distribution of predator-prey size scores (Table 3) when equal numbers of prey sizes are offered to the predator. These parameters are $\bar{x} = 7.16$, $s^2 = 0.42$ for <200 mm fish; $\bar{x} = 6.48$, $s^2 = 7.18$ for 350-549 mm fish; and $\bar{x} = 4.88$, $s^2 = 2.40$ for 550+ mm fish.

Diel Feeding Pattern

A total of 258 Pacific whiting stomachs (7 of which were empty) were taken at 7 different times of day during a 15-h period at a location off the Washington coast in July 1967. To detect any discontinuity in feeding during this period, a one-way analysis of covariance was performed using the model

$$y = \mu + a_i + bx_i,$$

where y is the weight of the stomach contents and x is the Pacific whiting weight. If the stomachs are grouped by time, i, then the test of among-time variation in the weight of stomach contents after adjustment for Pacific whiting weight is the test of the equality of the intercepts, a_i, given a common slope, b (Jenkins and Green 1977). The F-ratio for this test is the among-group variance estimate divided by the within-group variance estimate.

Figure 8 plots mean stomach content weight as a percentage of Pacific whiting weight for samples taken during the 15-h period in July 1967. Stomach content weight per fish weight is highest at 1800 h, with a value of 2.5%, and slightly increases between 0100 and 0300 h and between 0400 and 0900 h. Despite the great variability among all time periods, the analysis of covariance of the data rejects the null hypothesis of no difference between group means of stomach content weight at the 0.01 level of significance [$F(6,243\ \text{df}) = 7.83$]. Therefore, feeding by Pacific whiting was discontinuous during the sampling period.

Stomach fullness was highest in early evening (1800 P.S.T.), with some increases after midnight (0300 P.S.T.) and morning (0900 P.S.T.). These fullness peaks coincide with the times of euphausiid, *Thysanoessa spinifera*, concentration in the same portion of the water column where the Pacific whiting are concentrated—nearbottom at evening and morning and nearsurface after midnight (Alverson and Larkins 1969; Alton and Blackburn 1972).

Hickling (1927) noted that stomachs of European hake, *Merluccius merluccius*, were fullest at midnight. He also suggested that European hake migrate vertically in search of euphausiids. Silver hake, *Merluccius bilinearis*, of the northwest Atlantic also feed nocturnally, starting their feeding activity after dusk and actively feeding until midnight (Bowman and Bowman 1980). Thus, fish of the genus *Merluccius*

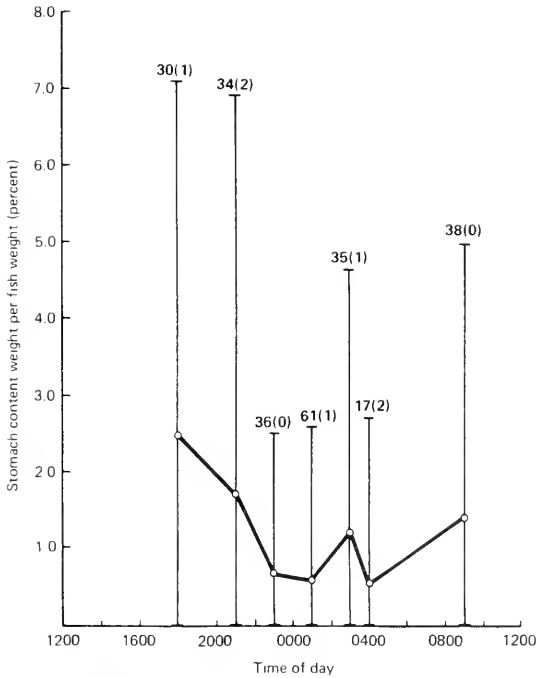

FIGURE 8.—Mean stomach content weight as a percentage of Pacific whiting, *Merluccius productus*, weight over part of a 24-h period at a diel sampling location off the Washington coast in July 1967 (vertical bars indicate the range of values in a given time period). Numbers of stomachs containing food are noted above each time period, with numbers of empty stomachs in parentheses.

have similar nocturnal feeding habits, although the timing of peaks in stomach fullness is not identical.

Daily Ration

An estimate of the average food intake by a fish predator is needed to evaluate predation mortality rates of prey species in some models (Majkowski and Waiwood 1981). Daily ration is a useful measure of food intake and can be calculated from field data if there exists an estimate of the gastric evacuation rate (Eggers 1977; Elliott and Persson 1978). The total 1967 Pacific whiting data set, containing 1,749 stomach samples, is used here to compute daily ration, since it includes a large number of samples taken at many different times of day and records of the number of empty stomachs present in the samples which is necessary for daily ration calculation.

The Elliott and Persson (1978) model which assumes an exponential, temperature-dependent evacuation rate, R, is applied to the data set for the daily ration computations. If stomach samples are collected at intervals of t hours, the mean stomach content weight as a percentage of fish weight, S_i, in each interval i is calculated for a total of m intervals over the 24-h period. According to Elliott and Persson (1978) the daily ration in terms of percentage body weight, ΣC_t, can then be evaluated by the following expression:

$$\Sigma C_t = \frac{Rt}{1 - e^{-Rt}} \sum_{i=1}^{m} S_i (1 - e^{-Rt}) = 24\bar{S}R \qquad (1)$$

where $\bar{S} = \Sigma S_i/\mathrm{m}$. Durbin and Durbin (1980) found that the relationship between R and water temperature T for marine fish eating small food organisms was

$$R = 0.416e^{0.105T}. \qquad (2)$$

This Equation (2) was used to calculate R here, since most prey eaten by Pacific whiting in 1967 were small organisms, mainly euphausiids. Some error is introduced at this point because part of the diet consisted of fish which are evacuated at a slower rate than small crustaceans (Durbin et al. 1980). Water temperature was assumed to be 8.2°C, the approximate monthly mean temperature for July at 60 m below surface in the Washington-Oregon coastal region (Robinson 1976) where most of the fish were collected.

The calculated daily ration of Pacific whiting, using Equations (1) and (2) on the 1967 data, is equal to 2.5% body weight/d for an average Pacific whiting size of 500 mm. Although this estimate is probably high, due to the use of the evacuation rate only for small crustaceans, it is comparable to other estimates. Daily ration estimates for a similar fish—adult silver hake in the northwest Atlantic—range between 0.6 and 2.7% body weight/d (Durbin et al. 1980; Cohen and Grosslein 1981; Pennington 1981). The present estimate is reasonable but should be verified further before it is used in calculating energy budgets for Pacific whiting.

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FOOD OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, IN AN EMBAYMENT OF SOUTHEASTERN ALASKA

The walleye pollock, *Theragra chalcogramma* Pallas, is commercially and ecologically one of the most important fishes in Alaskan waters. In recent years, it has predominated by weight in the catches of commercial groundfish and in demersal trawling surveys of the Bering Sea and the Gulf of Alaska (North Pacific Fishery Management Council 1979a, b; Pereyra et al. 1976[1]; Ronholt et al. 1978[2]). It is similarly abundant in the inside waters of southeastern Alaska (Carlson et al. 1977[3]), where recent attempts have been made to establish a commercial fishery for walleye pollock. Walleye pollock are also an important component of the food web, primarily as forage for seabirds, marine mammals, and fish. In the eastern Bering Sea, walleye pollock is the most important species in the diet of many seabirds (Hunt et al. 1981) and is a major food of seals, *Phoca* spp. (Lowry and Frost 1981); whales (Frost and Lowry 1981); and northern fur seals, *Callorhinus ursinus* (Harry and Hartley 1981). In southeastern Alaska, juvenile walleye pollock are one of the most common foods of troll-caught Pacific salmon, *Oncorhynchus* spp. (Wing 1977).

Despite the importance of walleye pollock, their diet has been little studied. The food of adults and juveniles from the eastern Bering Sea has been investigated during the spring, summer, or fall (Takahashi and Yamaguchi 1972; Mito 1974; Bailey and Dunn 1979), but no single study covered more than one season in a given area. There are no published data on the food of walleye pollock in the eastern North Pacific Ocean south of the Bering Sea except for one report of their feeding upon salmon fry in southeastern Alaska (Armstrong and Winslow 1968). In this report, I document the foods and seasonal changes in the diet of walleye pollock for 1 yr in an area of the inside waters of southeastern Alaska.

Methods

During each of the four seasons, stomachs were collected from walleye pollock in two adjacent bays, Auke Bay and Fritz Cove, near Juneau, Alaska (Table 1; Fig. 1). The two bays make up a larger embayment of Stephens Passage, a prominent fjord in the inside waters of southeastern Alaska. Depending upon the availability of research vessels, fish were caught with three types of bottom trawls: A 400-mesh (27 m) Eastern otter trawl, a standard 40-ft (12 m) Gulf shrimp trawl, and a 12-ft (3.7 m) balloon-type otter trawl. All trawling was done during daylight. The trawls were dragged from deeper to shallower water during each haul, so the exact depth at which fish were captured could not be determined. Trawling depths averaged 46 m (range 16-60 m) in Auke Bay and 90 m (range 55-110 m) in Fritz Cove. It was necessary to collect walleye pollock from both bays to obtain a broad size range of fish in each season. When a single tow produced large numbers of walleye pollock, the catch was arbitrarily sampled to obtain about 40 fish in each 100 mm size category; otherwise, all walleye pollock were retained. Standard length (SL) of each retained fish was measured, sex determined when possible, and stomachs removed and preserved in 5% buffered Formalin[4]. Walleye pollock used for the stomach samples were mostly between 150 and 450 mm SL, and ranged from 106 to 585 mm SL. Most of these fish were probably juveniles or young adults because walleye pollock mature at lengths between 290 and 350 mm FL (fork length) (Hughes and Hirschhorn 1979).

A number of authors have discussed various techniques for analyzing stomach contents of fish (see Windell 1971), and it appears that any single method

[1]Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Processed rep., 619 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

[2]Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1978. Demersal fish and shellfish resources of the Gulf of Alaska from Cape Spencer to Unimak Pass 1948-1976, a historical review. Processed rep., 4 vols., 955 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

[3]Carlson, H. R., R. E. Haight, and K. J. Krieger. 1977. Species composition and relative abundance of demersal marine life in waters of southeastern Alaska, 1969-77. Processed rep., 69 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, 2725 Montlake Boulevard E., Seattle, WA 98112.

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

TABLE 1.—Summary of walleye pollock stomach samples collected each season, by date and location of collection, Auke Bay and Fritz Cove, southeastern Alaska, 1979-80.

Season	Dates of collection	Number of trawl hauls	Number of stomachs collected		
			Auke Bay	Fritz Cove	Total
Summer	July, August 1979	11	105	62	167
Fall	October, November 1979	6	64	113	177
Winter	January 1980	4	81	67	148
Spring	April 1980	2	39	46	85
Totals			289	288	577

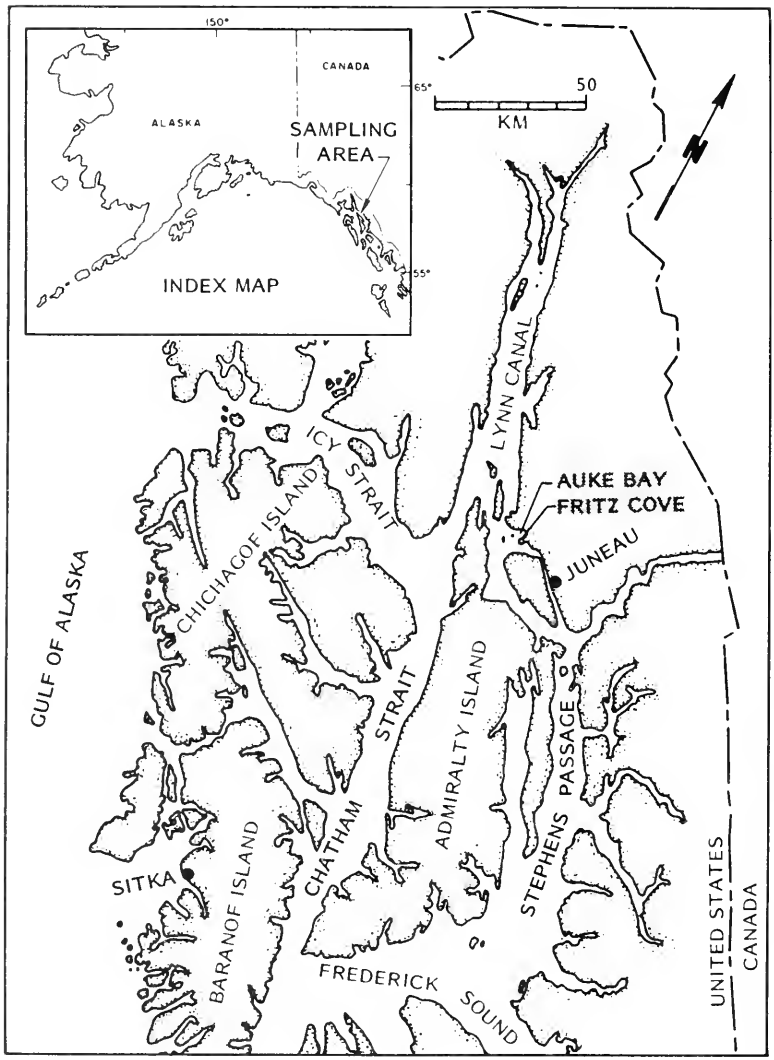

FIGURE 1.—Location of Auke Bay and Fritz Cove, southeastern Alaska, where stomachs were collected from walleye pollock in 1979-80.

has its biases. Therefore, I chose to analyze the stomach contents of walleye pollock in two ways: 1) Percent by volume of major food categories to show the contribution in biomass of the foods, and 2) percent frequency of occurrence to show the diversity of foods at lower taxonomic levels.

To determine percent by volume, I either measured or estimated the volume of major food categories (e.g., mysids, shrimp, or fish) in each stomach, depending upon the amount of food present. In walleye pollock with stomach contents about ≥ 0.5 ml, the displacement volume of food in each major category was measured in a graduated cylinder and then expressed as a percentage of the total volume of the stomach contents. In fish with stomach contents <0.5 ml, food was divided by categories into piles of uniform height in a petri dish and placed over a grid. The number of grid squares covered by each pile was used to estimate the volume percentage of each food category. I then pooled percent-volume measurements and estimates for all fish and calculated mean percentages for each food category. Walleye pollock with empty stomachs or with stomachs containing only a trace of food were excluded from these calculations. Many stomachs contained a large percentage of flocculent, digested matter or an indistinguishable mixture of crustacean parts; these items were termed "unidentified digested matter" and "unidentified crustacean fragments," respectively.

To determine the frequency of occurrence of foods, each item present in a stomach was identified to the lowest practical taxon. Percent frequency of oc-

currence for the food item was calculated by dividing the number of stomachs that contained the item by the total number of walleye pollock stomachs. Stomachs with a trace of food were included in this analysis, but empty stomachs were not.

The volumetric data were categorized by size and sex of walleye pollock and by season of year (for dates, see Table 1) to determine if these factors influenced the diet. To compare types of food eaten by different sizes of walleye pollock, the fish were arbitrarily divided into three length groups: Small, <250 mm; intermediate, 250-349 mm; and large, >349 mm SL. The percent of empty stomachs was also calculated for each season and size category as an indicator of seasonal feeding activity. Because the size of walleye pollock was generally different in each bay during the same season, the foods of the fish in the two bays could not be compared. Consequently, data for the two bays were pooled for all analyses. Differences in feeding at different depths also could not be analyzed because, as previously noted, the precise depth where fish were caught was unknown.

Results and Discussion

When data from all samples of walleye pollock were combined (regardless of size, sex, or season), crustaceans were the major food. Of the crustaceans, euphausiids and mysids had the highest percent volumes and frequencies of occurrence (Tables 2, 3). *Thysanoessa raschii* was the most frequently eaten euphausiid; *Acanthomysis pseudomacropsis* and *Neomysis kadiakensis* were the most frequently eaten mysids. The percent volume of shrimp was nearly as high as the percent volume of euphausiids and mysids; however, shrimp were eaten less frequently. Most of the shrimp were either *Crangon* spp. (Crangonidae) or Pandalidae. Copepods, hyperiid and gammarid amphipods, and cumaceans were found in many of the stomachs (>20%), but their percent volumes were small (<3%). Often stomachs contained only one or two individuals that comprised a minute fraction of the contents. Copepods were mostly *Metridia* sp. and *Calanus* sp.; cumaceans were mostly *Eudorella* sp. Amphipods were generally not identified to species.

Fish and, to a lesser degree, polychaetes were the only other foods present in amounts greater than a trace. They were found less frequently than crustaceans and were usually identifiable only to class. However, compared with crustaceans, fish found in the stomachs were relatively large and usually composed most of the volume of food in the stomachs, when they occurred.

The common food organisms in all of the studies of walleye pollock have been crustaceans and fish. In the eastern Bering Sea in summer 1970, walleye pollock fed almost exclusively on euphausiids, copepods, and fish (Takahashi and Yamaguchi 1972). In fall 1972, walleye pollock there ate euphausiids and fish (Mito 1974); and in summer 1974 and spring 1977, they ate mostly euphausiids, copepods, fish, and amphipods (Bailey and Dunn 1979). In southeastern Alaska in 1979-80 (my study),

TABLE 2.—Mean percent volume of major categories of food in walleye pollock stomachs from Auke Bay and Fritz Cove, southeastern Alaska, 1979-80. (Table does not include empty stomachs or those with only a trace of food.)

Food category	All fish (%)	By length (SL) category of fish			By sex of fish[1]	
		<250 mm (%)	250-349 mm (%)	>349 mm (%)	Males (%)	Females (%)
Euphausiids	17.1	16.6	21.4	8.5	19.3	18.8
Mysids	14.8	21.4	9.9	6.5	11.7	10.2
Shrimp.	14.3	7.7	13.8	35.6	15.5	18.3
Pandalids	7.3	1.7	7.1	25.2	8.7	9.6
Crangonids	5.3	4.7	5.0	7.6	4.0	7.0
Hippolytids	0.6	0.9	0.5	0.1	0.2	1.3
Unidentified shrimp	1.1	0.4	1.2	2.7	2.6	0.4
Fish	5.7	3.7	4.6	14.7	5.7	6.7
Cumaceans	2.8	3.8	2.4	0.8	2.2	1.5
Polychaetes	2.4	0.7	4.5	2.5	3.0	3.1
Copepods	2.2	4.0	0.6	0.5	0.3	1.4
Gammarid amphipods	1.6	1.9	1.3	1.4	1.9	1.3
Hyperiid amphipods	1.2	1.2	1.3	0.9	1.8	0.8
Unidentified crustacean fragments	9.7	10.6	8.8	9.3	9.0	7.2
Other foods	2.0	2.0	0.9	4.5	1.0	2.6
Unidentified digested matter	26.2	26.4	30.5	14.8	28.6	28.2
Mean length of pollock (mm)	261.3	193.9	292.0	394.9	283.8	283.2
Number of samples	431	204	161	66	150	190

[1]91 additional fish were examined for which sex could not be determined.

TABLE 3.—Frequency of occurrence of food items found in at least 1% of stomachs of 541 walleye pollock from Auke Bay and Fritz Cove, southeastern Alaska, 1979-80[1]. (Table does not include an additional 36 stomachs that were empty.)

Food item	Frequency of occurrence (%)
Mysids	54
Acanthomysis pseudomacropsis	19
Acanthomysis nephrophthalma	5
Neomysis kadiakensis	18
Neomysis rayii	3
Neomysis sp	1
Pseudomma truncatum	7
Unidentified mysids	9
Euphausiids	47
Thysanoessa raschii	31
Thysanoessa spinifera	1
Thysanoessa longipes	1
Unidentified euphausiids	17
Copepods	42
Metridia sp	20
Calanus sp	15
Euchaeta elongata	6
Aetidius sp	6
Centropages abdominalis	2
Unidentified copepods	6
Hyperiid amphipods	29
Parathemisto sp	6
Unidentified hyperiids	23
Shrimp	28
Pandalid shrimp	11
Pandalus borealis	3
Pandalus tridens	1
Unidentified pandalids	9
Crangonid shrimp	14
Crangon communis	2
Crangon dalli	2
Crangon franciscorum	1
Crangon sp	6
Unidentified crangonids	4
Hippolytid shrimp	4
Eualus avinus	1
Unidentified hippolytids	3
Unidentified shrimp	5
Gammarid amphipods	25
Oetocerotidae	4
Cyphocaris challengeri	1
Unidentified gammarids	21
Cumaceans	21
Eudorella sp	16
Leucon sp	2
Unidentified cumaceans	3
Polychaetes (unidentified)	12
Fish	10
Theragra chalcogramma	1
Unidentified fish	8
Cephalopods	1
Pelecypods	1
Isopods	1
Larval shrimp	1
Larval brachyuran crab	1
Larval anomuran crab	1

[1]Also present at frequencies <1%: Mysids—*Pseudomma berkeleyi*, *Meterythrops* sp., *Holmesiella anomula*, *Stilomysis grandis*; pandalid shrimp—*Pandalopsis dispar*; crangonid shrimp—*Crangon alaskensis*, *Argis crassa*; fish—*Clupea harengus pallasi*, Osmeridae, Pleuronectidae, Stichaeidae; cumaceans—*Cumella* sp.; copepods—*Calanus cristatus*, *Pseudocalanus* sp., hyperiid amphipod—*Primno macropa*; cephalopod—*Octopus* sp.; unidentified gastropods; Paguridae—*Pagurus ochotensis*; brachyuran crab; barnacle cyprid; larval fish—*Thaleichthys pacificus*; Holothuroidea—*Molpadia intermedia*; algae.

walleye pollock consumed primarily euphausiids, mysids, shrimp, and fish. Thus, of the crustaceans, euphausiids were a major food in all studies, whereas the types of other crustaceans varied among the investigations. Shrimp, an important food for walleye pollock both in my study and near Kodiak Island[5], were found only in very small amounts in Bering Sea fish. In all studies, organisms that are strictly benthic (e.g., clams and crabs) were conspicuously scarce in the diet.

In fishes, the size of prey generally increases as the size of predators increases (Nikolsky 1963), and this appears to be true in walleye pollock. In my study, small walleye pollock ate mostly planktonic crustaceans, particularly euphausiids, mysids, and copepods; large walleye pollock generally ate larger prey, such as shrimp and fish (Table 2). Intermediate-sized walleye pollock were transitional in their diet and ate a combination of large and small foods. In the Bering Sea, juvenile walleye pollock (<350 mm) also ate mostly euphausiids or copepods, whereas larger walleye pollock ate larger foods, primarily fish (Takahashi and Yamaguchi 1972; Mito 1974; Bailey and Dunn 1979). Walleye pollock became increasingly cannibalistic with increase in size in the Bering Sea: More than half the food of fish >550 mm FL was smaller walleye pollock (Takahashi and Yamaguchi 1972). In my study, cannibalism was observed in only 1% of the stomachs (Table 3); however, few walleye pollock >450 mm SL were examined.

Sex of the fish had little effect on their diet (Table 2). The diets of male and female walleye pollock were nearly identical in percent volume of each food category.

Walleye pollock apparently fed year-round (Table 4): In any one season only 4-8% of all fish had empty stomachs. In any one size group, no more than 14% of the fish had empty stomachs in any season. In con-

[5]P. Livingston, Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, unpubl. data.

TABLE 4.—Seasonal feeding activity of walleye pollock shown by percent of fish with empty stomachs, Auke Bay and Fritz Cove, southeastern Alaska, 1979-80.

Size	Stomachs examined	Spring	Summer	Fall	Winter
All sizes	Total (no.)	85	167	177	148
	With food (no.)	82	158	162	139
	Empty (%)	4	5	8	6
<250 mm SL	Total (no.)	14	91	99	83
	With food (no.)	14	84	92	76
	Empty (%)	0	8	7	8
250-349 mm SL	Total (no.)	51	36	57	53
	With food (no.)	48	35	52	51
	Empty (%)	6	3	9	4
>349 mm SL	Total (no.)	20	40	21	12
	With food (no.)	20	39	18	12
	Empty (%)	0	3	14	0

trast, in a seasonal 1-yr study of food of adult walleye pollock off Hokkaido Island, Japan, the rate was much higher, particularly during the winter months when up to 80% of the stomachs were empty (Maeda et al. 1981). In an eastern Bering Sea study (Bailey and Dunn 1979), generally few walleye pollock had empty stomachs in summer 1974 (results similar to those of my study); however, a much higher percentage of fish had empty stomachs there in spring 1977 than in my study.

The diet of small walleye pollock varied widely from season to season in the percent volume of each food type (Fig. 2). Euphausiids were the predominant food of small walleye pollock in winter and spring (34% and 78%, by volume, respectively) but constituted <7% of the stomach contents in the summer and fall. Conversely, mysids were the predominant food in the summer and fall diets (36% and 22%, by volume, respectively) but were much less important in the winter and spring (<5%, by volume). Copepods were also an important food (11%, by volume) in the summer but were insignificant (<1%) in other seasons.

For each season, the diet of intermediate-sized

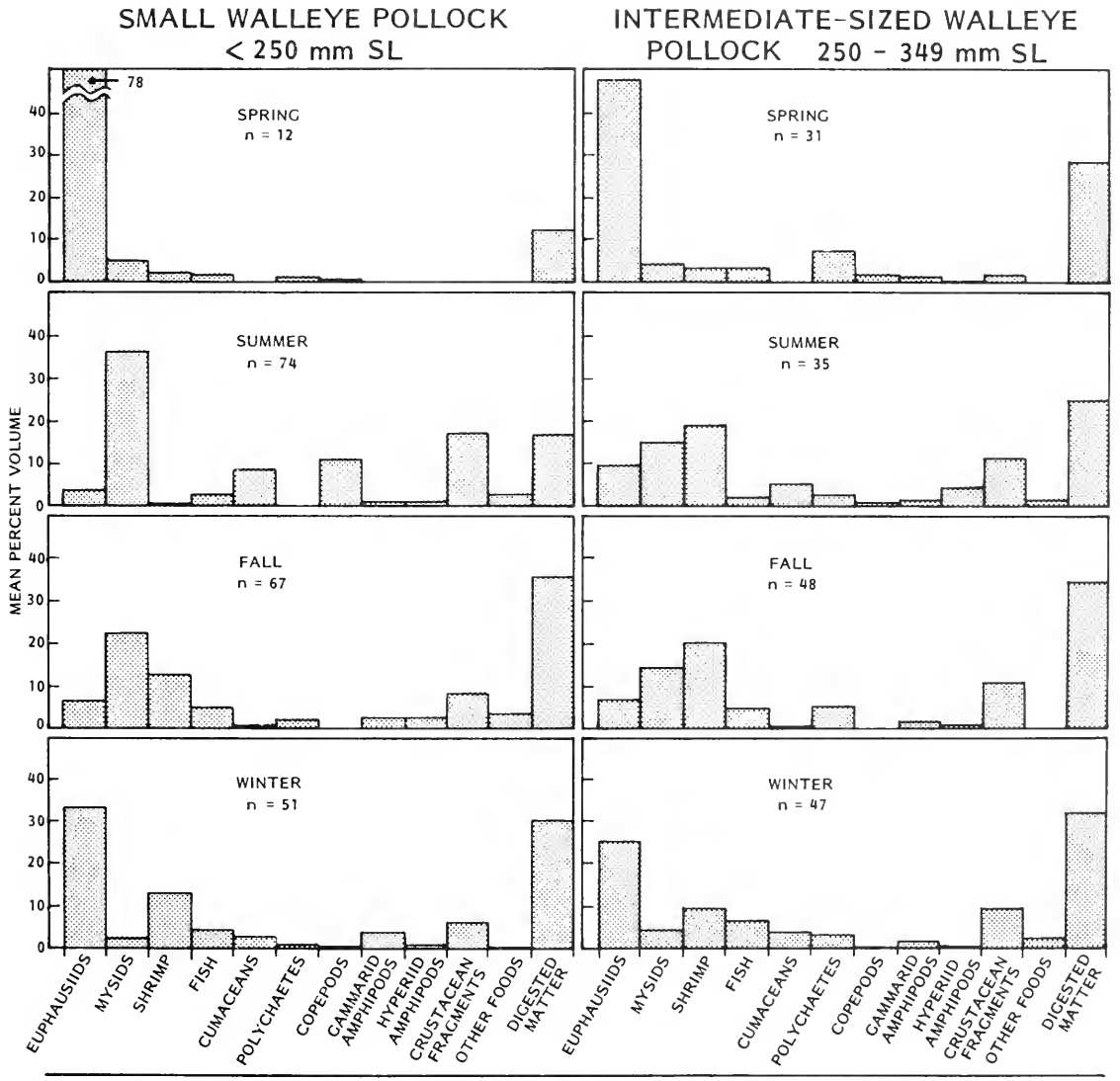

FIGURE 2.—Mean percent volume of major food categories in stomachs of small and intermediate-sized walleye pollock by season of year, Auke Bay and Fritz Cove, southeastern Alaska, 1979-80. (Figures do not include empty stomachs or those with only a trace of food.)

walleye pollock was similar to that of small walleye pollock (Fig. 2). Intermediate-sized fish also fed predominately on euphausiids in the winter and spring and more on mysids in the summer and fall. However, seasonal variability in diet was not as great as for small walleye pollock. Too few large walleye pollock were collected in three of the seasons to demonstrate seasonal changes in their foods.

Some of the seasonal differences found in foods of small walleye pollock may be explained by the availability of euphausiids and copepods. In two seasonal studies of zooplankton in the Auke Bay vicinity, 1962-64 (Wing and Reid 1972) and 1973-75 (Carlson 1980), euphausiids (excluding small larval forms) were least abundant and copepods were most abundant during the late spring and summer. Similar seasonal patterns were found in the foods of small walleye pollock: The percent volume of euphausiids was lowest in the summer, whereas copepods were a significant food only during the summer. However, results of the zooplankton studies also differ in some respects from my results: In 1973-75, euphausiids were most abundant in plankton in the fall (Carlson 1980), but in my 1979-80 study, they were relatively scarce in the stomach samples during the fall. Concurrent studies of walleye pollock foods and zooplankton abundance are needed to better understand the causes of seasonal variations in the diet of small walleye pollock.

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SUMMER FOODS OF TEXAS COASTAL FISHES RELATIVE TO AGE AND HABITAT

Age and habitat are often ignored as factors which simultaneously influence the diets of demersal fishes. Studies of fish foods by age (size) or habitat (depth of capture, substrate) either summarize foods over all sizes and depths (Henwood et al. 1978), construct several size or depth groupings to equalize sampling effort (Overstreet and Heard 1978; Mericas 1981), or establish arbitrary size or capture depth ranges for ontogenetic or depth-related analyses (Rogers 1977; Divita et al. 1983). In this paper, we analyze the stomach contents of seven species of Texas coastal fishes with respect to both age and habitat.

Materials and Methods

Fishes examined in our study were taken from trawl catches by the NOAA RV *Oregon II* and the Texas Parks and Wildlife Department RV *Western Gulf* between sunset and sunrise in waters 7-73 m deep along the entire Texas coast. Each vessel towed a 12.2 m semiballoon trawl with tickler chain at 5-6 km/h. The species collected from the family Sciaenidae are sand seatrout, *Cynoscion arenarius*; silver seatrout, *C. nothus*; spot, *Leiostomus xanthurus*; and Atlantic croaker, *Micropogonias undulatus*; from the family Sparidae, longspine porgy, *Stenotomus caprinus*; and from the family Trichiuridae, Atlantic cutlassfish, *Trichiurus lepturus*. Fishes were collected by depth ranges (7-17, 18-44, or 45-73 m) and preserved in 3.7% formaldehyde-seawater. These depth ranges correspond to distinctive habitats (substrates) as reported by Grady (1971), Flint and Rabalais (1980), and Gallaway and Reitsema (1981): sand or muddy-sand (7-17 m), sand-silt-clay (18-44 m), and silty-sand or silty-clay (45-73 m).

In the laboratory, fishes from each depth range were measured (standard length, SL, or total length, TL, where applicable) and further separated into either age-0 or age-I classes, based upon data summarized by the Gulf of Mexico Fishery Management Council (1980) or upon unpublished personal data on gonadal maturation. Fishes were presumed to have reached age I at the following lengths: longspine porgy, 75 mm SL; spot, 100 mm SL; Atlantic croaker, 125 mm SL; sand and silver seatrouts, 150 mm SL; hardhead catfish, 200 mm SL; and Atlantic cutlassfish, 400 mm TL. No age II individuals were collected. For each species, the stomach contents of all individuals in a given age/depth category were combined and washed through sieves to separate similar-sized food items (Carr and Adams 1972), which were identified and enumerated microscopically and then dried at 80°-90° C for 24 h. The dry weights of the various food items were calculated from their numerical proportions and converted to percentages of total food dry weight. Stomach contents were identified to broad but exclusive categories such as sand, diatoms, shrimps, or fishes. Fish bones and scales without associated flesh were often found in hardhead catfish stomachs and were thus given a category. Animal fragments not distinctly referable to any taxon were also categorized. Fine organic matter not referable to any other category was termed detritus. Prey fishes, shrimps, and crabs were identified to family or genus when possible. Within each species, diet similarities among age/depth categories were compared by the Spearman rank correlation coefficient, r_s (Fritz 1974).

Results

The stomach contents of the four sciaenid fishes are summarized in Table 1, and those of the other three species in Table 2. Intraspecific diet similarities are given in Table 3. The effect of depth of capture on diets of spot and Atlantic cutlassfish could not be evaluated, since the majority of individuals were collected from a single depth range (7-17 m and 18-44 m, respectively). Correlations between diets of age-0 and age-I spot ($r_s = 0.069$) and between diets of age-0 and age-I Atlantic cutlassfish ($r_s = 0.399$) were not significant. Age-0 spot consumed more infaunal organisms, such as polychaetes and nematodes, and nearly twice as much detritus as age-I spot, which captured proportionately more epifaunal prey such as fishes, amphipods, and shrimps. While both age classes of Atlantic cutlassfish preyed primarily upon fish, age-I individuals also exploited squids. Small sample size (three stomachs) for the age-0 Atlantic cutlassfish is probably responsible for the lack of diet correlation.

Sand and silver seatrouts fed both in the water column and near the bottom. Diets of three of the four age/depth categories of sand seatrout were significantly correlated, primarily because fishes and shrimps were the favored prey. The exception was the diet of age-0 sand seatrout in 18-44 m waters in which squids were the primary prey. The most frequently identified sand seatrout prey taxa were anchovies, *Anchoa*, and roughback shrimp, *Trachypenaeus* sp. Silver seatrout also preyed upon fishes and shrimps, but only the age-0 diets in the two inhabited depth ranges were correlated. The data on

age-I silver seatrout from 7-17 m waters, indicating shrimps as the primary food, were based on only two stomachs. Age-I silver seatrout from 18-44 m depths consumed relatively large proportions of squids and stomatopods, unlike any other age/depth category. The most often noted prey taxa in silver seatrout stomachs were *Anchoa* and unidentified caridean shrimps.

Atlantic croaker, hardhead catfish, and longspine porgy were benthic feeders. No significant correlations in diet were found among the four age/depth categories of Atlantic croaker. Although the

TABLE 1.—Stomach contents of sand seatrout, silver seatrout, spot, and Atlantic croaker collected from Texas coastal waters between 4 June and 3 July 1981, expressed as percentages of total food dry weight by age and depth of capture. A "+" indicates presence in the diet but <0.1%. Fish lengths are mm SL, depth ranges in meters.

		Sand seatrout				Silver seatrout				Spot		Atlantic croaker			
Stomach	Age	0		I		0		I		0	I	0		I	
contents	Depth	7-17	18-44	7-17	18-44	7-17	18-44	7-17	18-44	7-44	7-44	7-17	18-44	7-17	18-44
Diatoms		—	—	—	—	—	—	—	—	0.6	0.9	—	—	—	—
Nematodes		+	—	—	—	—	—	—	—	3.8	0.4	0.1	—	—	—
Polychaetes		0.4	—	—	—	0.1	—	—	—	7.3	3.9	61.2	35.9	4.3	36.1
Bivalves		—	—	—	—	—	—	—	—	1.8	1.2	—	—	—	—
Squids		—	47.5	—	—	—	—	—	19.7	—	—	0.2	—	—	—
Copepods		+	—	—	—	—	—	—	—	5.2	0.6	+	+	+	—
Stomatopods		+	—	+	—	0.3	0.2	—	11.4	—	—	—	—	—	—
Mysids		0.5	—	+	—	3.0	0.1	0.6	—	1.4	—	0.7	—	—	0.6
Cumaceans		—	—	—	—	0.1	—	—	—	0.8	2.0	—	—	—	—
Isopods		—	—	—	—	0.2	—	—	—	—	—	—	—	—	—
Amphipods		0.2	—	—	—	+	—	0.3	—	2.2	4.3	0.2	—	—	—
Crabs		0.9	—	7.2	4.4	4.3	—	1.2	+	—	—	5.9	0.3	76.5	—
Shrimps		2.0	24.7	59.5	40.3	6.7	16.8	88.9	12.9	4.8	6.6	8.6	35.6	9.0	16.3
Holothurians		—	—	—	—	—	—	—	—	—	—	—	9.4	6.7	—
Tunicates		—	—	—	—	—	—	—	—	—	—	—	—	—	30.0
Lancelets		—	—	—	—	—	—	—	—	—	3.0	—	—	—	—
Fishes		87.0	27.7	24.4	52.3	76.5	82.9	9.1	55.9	0.1	17.0	0.9	—	—	—
Animal fragments		3.2	—	8.0	1.5	8.9	—	—	—	8.2	9.9	10.4	9.4	0.9	8.4
Detritus		5.7	—	0.8	1.5	—	—	—	—	62.4	37.6	8.4	9.3	2.6	8.7
Sand		—	—	—	—	—	—	—	—	1.4	12.6	3.3	—	—	—
Number examined		126	11	9	31	35	38	5	25	103	17	136	47	12	12
Number empty		27	6	1	13	6	18	3	8	53	9	17	24	4	6
Mean weight/stomach (g)		0.051	0.035	0.664	0.353	0.036	0.149	0.058	0.450	0.007	0.012	0.017	0.021	0.058	0.024
Length range		51-139	33-74	152-225	163-250	92-145	92-149	153-173	150-172	75-99	100-159	83-121	95-124	126-152	125-159

TABLE 2.—Stomach contents of hardhead catfish, longspine porgy, and Atlantic cutlassfish collected from Texas coastal waters between 4 June and 3 July 1981, expressed as percentages of total food dry weight by age and depth of capture. A "+" indicates presence in the diet but <0.1%. Fish lengths are mm SL, except Atlantic cutlassfish which are mm TL. Depth ranges are in meters.

		Hardhead catfish				Longspine porgy				Atlantic cutlassfish	
Stomach contents	Age	0		I		0		I		0	I
	Depth	7-17	18-44	7-17	18-44	18-44	45-73	18-44	45-73	7-73	7-73
Nematodes		—	0.1	—	0.9	0.2	—	0.2	—	—	—
Polychaetes		4.5	+	—	—	33.0	60.9	47.0	45.6	0.6	—
Bivalves		0.7	—	—	—	0.1	—	—	—	—	—
Gastropods		—	—	—	—	—	6.4	—	—	—	—
Squids		—	—	—	—	—	—	—	—	—	28.8
Copepods		0.2	—	—	—	4.0	4.9	0.2	—	—	—
Stomatopods		0.1	40.1	38.0	85.7	0.6	—	1.3	—	—	0.1
Mysids		—	—	—	—	—	—	—	—	0.8	—
Cumaceans		0.1	—	—	—	—	—	—	—	—	—
Amphipods		—	—	—	—	0.7	—	1.0	3.2	—	+
Crabs		34.1	26.4	29.9	1.1	0.8	3.7	15.7	6.8	0.6	—
Shrimps		37.8	11.2	0.9	12.2	6.7	3.2	4.9	12.7	1.6	0.8
Holothurians		10.0	3.5	11.8	—	—	—	—	—	—	—
Tunicates		—	2.8	—	—	—	—	—	—	—	—
Fishes		1.6	—	9.0	—	1.0	—	2.3	—	81.3	66.6
Fish bones/scales		1.2	9.3	0.5	—	—	—	—	—	—	—
Animal fragments		7.6	2.5	—	—	25.6	7.8	11.0	15.7	10.5	1.3
Detritus		1.9	4.0	9.9	—	25.9	13.2	12.7	16.1	3.4	2.3
Sand		0.5	—	—	—	1.5	—	3.6	—	1.1	—
Number examined		24	13	7	3	127	8	13	42	5	33
Number empty		1	0	1	0	67	0	7	28	2	13
Mean weight/stomach (g)		0.157	0.323	0.967	0.785	0.007	0.005	0.018	0.003	0.070	0.399
Length range		137-192	169-192	202-255	222-255	25-74	40-51	84-94	78-127	229-399	400-595

TABLE 3.—Spearman rank correlation coefficient matrices comparing age and depth-specific diets within species of Texas coastal fishes collected between 4 June and 3 July 1981. Significant correlations indicated by * at 0.05 or ** at 0.01 levels. Depth ranges in meters.

	Age		0		I	
Species		Depth	7-17	18-44	7-17	18-44
Sand seatrout	0	7-17	—	0.215	0.831**	0.847**
		18-44		—	0.484	0.516
	I	7-17			—	0.940**
Silver seatrout	0	7-17	—	0.687*	0.605	0.371
		18-44		—	0.746	0.732
	I	7-17			—	0.555
Hardhead catfish	0	7-17	—	0.186	0.232	0.131
		18-44		—	0.689*	0.697*
	I	57-17			—	0.545
Atlantic croaker	0	7-17	—	0.460	0.346	0.389
		18-44		—	0.569	0.482
	I	7-17			—	0.135

	Age		0		I	
Species		Depth	18-44	45-73	18-44	45-73
Longspine porgy	0	18-44	—	0.590*	0.762**	0.758**
		45-73		—	0.469	0.741*
	I	18-44			—	0.655*

favored prey in three of four categories, polychaetes comprised more than half the diet only in age-0 Atlantic croaker in shallow waters. Age-I Atlantic croaker in shallow waters preferred crabs (mainly *Albunea*). Alpheid and other caridean shrimps formed one-third of the age-0 Atlantic croaker diet in 18-44 m waters, while age-I individuals at these depths consumed large amounts of tunicates. The prey of hardhead catfish was mainly stomatopods, crabs, and shrimps. The diets of age-I hardhead catfish in both inhabited depth ranges were correlated with the age-0 diet in 18-44 m, where the primary food was stomatopods. Age-0 hardhead catfish in shallow waters did not consume stomatopods but concentrated on crabs and shrimps. Crabs comprised at least 25% of the diets of all age/depth categories except the age-I hardhead catfish from 18-44 m depths, probably due to the small number of stomachs (3) analyzed. Identifiable prey taxa were mainly brown shrimp, *Penaeus aztecus*; rock shrimp,

Sicyonia sp.; and the crabs *Albunea* and *Pinnixa*. All comparisons of longspine porgy diets were significantly correlated, except between age-0 in 45-73 m waters and age-I in 18-44 m waters. Polychaetes were the primary food in all age/depth categories, and animal fragments and detritus were also abundant. The main differences between age classes were that age-0 longspine porgy consumed more copepods but less crabs than age-I individuals.

Discussion

The major foods identified in this study are generally similar to the foods of these seven species described by other investigations in the Gulf of Mexico. Gunter (1945), Knapp (1949), and Darnell (1958) reported that hardhead catfish consumed crabs, shrimps, and detritus in estuaries, but provided neither age nor habitat-related analyses of their data. Divita et al. (1983), using samples collected at the same time as ours but analyzing diets by percent frequency of occurrence, reported differences between age-0 and age-I hardhead catfish diets in 9-17 m waters. They found that, in comparison with age-0 individuals, age-I fish consumed holothurians, fishes, bivalves, shrimps, and detritus more frequently and crabs, stomatopods, and polychaetes less frequently. Our results (based on percent dry weight) contrast in that, for the age-I catfish diet, shrimps were less important and stomatopods were more important than in the age-0 diet in 7-17 m waters.

Two studies have investigated the diet of longspine porgy, the results of which generally agree with ours. Henwood et al. (1978), summarizing data over a 130 m depth range and ages 0 and I, found polychaetes, shrimps, and crabs were the most abundant foods. Rogers (1977) analyzed longspine porgy diets in four arbitrary size classes (two each in ages 0 and I) and three arbitrary depth zones (3-18, 19-55, and 56-200 m), but not by age/depth combinations. He found that both ages preferred polychaetes and that age-0 porgy stomachs contained more animal fragments and detritus than did age-I porgy stomachs, as we report. In contrast, though, Rogers noted that age-I longspine porgy preyed extensively on fishes causing midshelf diets to differ from outer shelf diets. The differences between our reports are probably due to Rogers' year-round sampling over a wide area (Texas, Louisiana, and Mississippi shelf).

The diets of sand and silver seatrouts were also examined by Rogers (1977). His three size classes of sand seatrout were all age-0 fish (26-100 mm SL) which consumed fishes, shrimps, and squids, preyed mainly upon fishes in shallow waters and squids in moderate depths, thus agreeing with our data. His largest size class of silver seatrout (76-175 mm SL, ages 0 and I combined) was piscivorous and is comparable to our findings, but no age/depth data were given.

We found the Atlantic croaker diet was influenced by both age and depth of capture. This is the likely reason for the variety of primary foods previously reported for this species. Chen (1976) examined age-0 and age-I Atlantic croaker (data summed over 9-73 m depths) and reported similar diets of primarily organic and inorganic matter with lesser amounts of crabs, shrimps, and stomatopods. Although the influence of depth was not discussed, she proposed that diet variations were substrate-related. Rogers (1977) noted that polychaetes and stomatopods were the main foods of age-0 Atlantic croaker in shallow and moderate depths. Overstreet and Heard (1978) documented both size and depth of capture as factors independently affecting Atlantic croaker diets: small individuals (76-195 mm SL) consumed more polychaetes and fewer molluscs, crustaceans, and fishes than did large individuals (200-351 mm), and fish from shallow water (11-29 m) consumed more polychaetes and fishes and fewer crustaceans than fish from deep water (30-90 m). However, their comparisons apparently included two age classes in each size range, formed arbitrary depth zones, and did not examine age/depth as a combined influence. Divita et al. (1983) found detritus to be the most frequently observed item in both age-0 and age-I Atlantic croaker stomachs from both shallow- and midshelf, and observed no differences in diets among age/depth categories. The available data thus indicate that Atlantic croaker are highly opportunistic in their feeding strategy, which is readily influenced by age, depth, season, and, probably, site.

Our results agree with previous reports concerning offshore spot and Atlantic cutlassfish diets. Chen (1976) examined age-I spot from 9-27 m depths and found inorganic and organic matter, polychaetes, and shrimps were the primary foods. Mericas (1981) noted Atlantic cutlassfish were piscivorous from late age 0 into age III.

We conclude that the degree to which age and depth of capture simultaneously affect fish diets depends upon the species examined: Atlantic croaker are highly influenced and longspine porgy are only slightly influenced. This variation between species may have been due to the age/depth distributions of the fishes during the limited collecting period, and thus seasonal collections should be compared. It is also possible that fishes had fed in one depth zone and moved into the adjacent depth zone prior to capture.

We know of no data concerning swimming speeds of the species examined, but an individual moving completely across one depth zone would cover 6-35 km in southern and up to 20-90 km in northern Texas coastal waters.

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LIFE HISTORY OF SPLITTAIL (CYPRINIDAE: *POGONICHTHYS MACROLEPIDOTUS*) IN THE SACRAMENTO-SAN JOAQUIN ESTUARY[1]

The Sacramento-San Joaquin estuary is the largest on the west coast of North America. Because of its comparatively young geologic age, <8,000 yr (Atwater 1979), its fish fauna is a mixture of native freshwater and marine species, to which numerous exotic species have been added in the past 100 yr (Moyle 1976). The ranges of two extant species, the delta smelt, *Hypomesus transpacificus*, and the splittail, *Pogonichthys macrolepidotus*, are restricted to the estuary. Both species are abundant but their biology is nevertheless poorly known, since most fisheries research in the estuary has concentrated on species of major economic importance, especially the introduced striped bass, *Morone saxatilis* (Stevens 1980; Collins 1982).

The fish communities of the estuary are changing, however, as new species are introduced and as conditions change in response to upstream water projects, water diversions, such as increased use of the water for cooling power plants, and pollution. Given the restricted ranges and habitats of these two species (Moyle 1976), their abundance could decline rapidly if environmental conditions become unfavorable for them, possibly making them candidates for listing as threatened species. This paper is concerned with the life history of the splittail, a species of

[1]Contribution No. 351 from the New York State Museum, Albany, N.Y.

interest for reasons besides its status as a potentially threatened endemic: 1) It is consistently one of the most abundant species in many of the brackish sloughs of the estuary (Moyle and Daniels unpubl. data; Caywood 1974), 2) most other cyprinids are exclusively freshwater species, rarely found in brackish waters, 3) its life history patterns reflect adaptation to an environment in which drought and flood occur episodically, and 4) it supports a small but locally important hook-and-line fishery (Caywood 1974).

Methods

Fishes were collected in the Suisun Marsh between January 1979 and January 1982, using 2.5 m otter trawls (mesh at cod end 6 mm bar) and 3 mm bar beach seines. The Suisun Marsh is the largest contiguous tidal marsh on the eastern Pacific coast (Fig. 1). It comprises 34,000 ha of marshland, sloughs, and shallow bays (Moyle et al. 1982a). At each locality, salinity (‰), water temperature (°C), secchi depth, and turbidity were recorded. Standard length (SL) was measured on all fish captured; for most months a random sample of splittail was preserved in 4% formaldehyde solution. In the laboratory, preserved specimens were measured and weighed. Scales were removed from 210 randomly selected fish, from the area above the lateral line, caudad to the posteriormost point of the pectoral fin. These scales were mounted on glass slides and projected on a microfiche reader screen. Measurement and back-calculation follow Tesch (1968). A condition factor ($K = \text{wt}/\text{SL}(3 \times 10^6)$) was calculated for each fish (Tesch 1968). Gonads were removed and weighed; fecundity was determined by weighing three subsamples from each prespawning ovary, counting the number of ova present in each subsample, averaging, and multiplying by total gonad weight. Stomachs were removed; contents were separated, identified, and weighed. When possible, the total length of prey items was measured. In April 1979, fish were collected over a 24-h period for a feeding habit study. Fullness indices (Windell 1968) were calculated for each fish as an indirect measure of activity.

Several statistical techniques were used. One-sided *t*-tests were used to compare means between two groups; one-way analysis of variance was used to

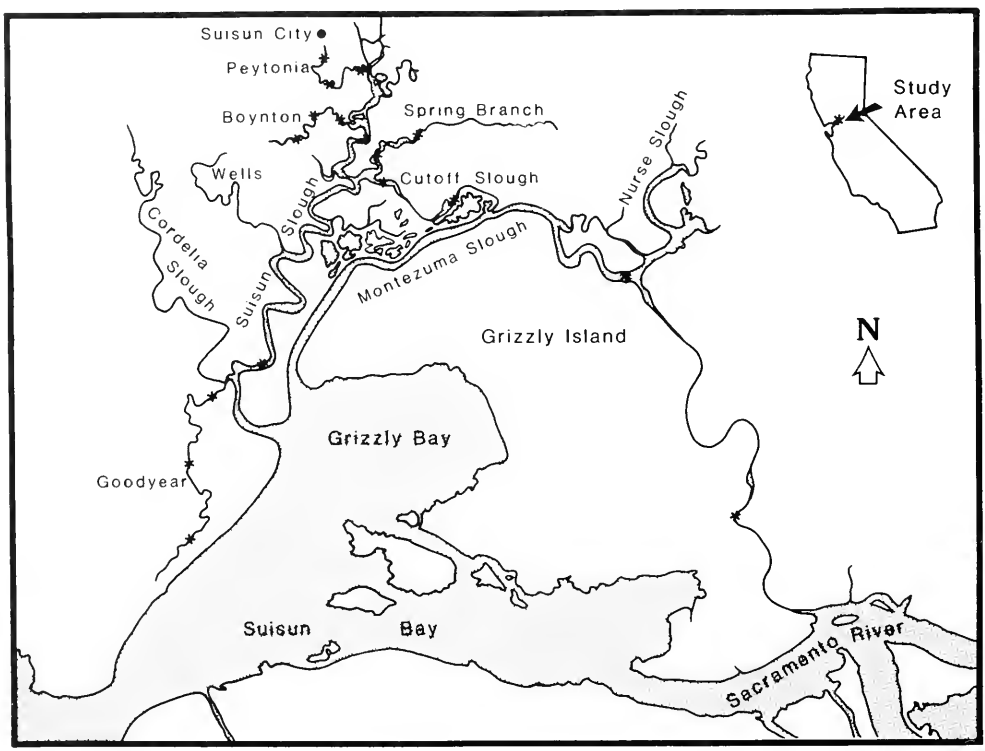

FIGURE 1.—Suisum Marsh, Sacramento-San Joaquin Estuary, Calif. Samples were taken from all sloughs identified. Monthly (1979) or bimonthly (1980-81) sample sites are designated (*). Each site represents two tows.

compare means among three or more groups (Remmington and Schork 1970). Wilcoxon sum of ranks or Kruskal-Wallis tests were used to compare indices (Sokal and Rohlf 1981). Regression lines were compared using techniques in Neter and Wasserman (1974).

Results and Comparisons

Age, Growth, and Condition

Young-of-the-year splittail appeared in samples in late May 1980 and early June 1981 with a mean of 32 mm SL in both years (Fig. 2). Lengths ranged from 23 to 54 mm. The back-calculated length for scale formation was 22 mm. Splittail grew at about 20 mm/mo through September, then that rate decreased to <5 mm/mo through February. In March fish began to grow again and added about 10 mm/mo during the next growing season. During the remaining 3 yr, fish added 5-7 mm/mo in length. These results were corroborated by back-calculating fish length from scales (Table 1). Annuli were formed in March 1979 and in late February 1980 in most specimens. Back-calculated growth rates were similar within the first and second age groups in 1979 and 1980 [age group 0: $F = 2.78 < F_{(0.95;2,12)}$; age group 1: $F = 0.8 < F_{(0.95;2,18)}$] but differed in the third age group [$F = 20.7 > F_{(0.95;2,16)}$]. Growth increments determined from back-calculation also were not significantly different between drought years (1976-77) and wet years (1978-80) in the first two age groups (age group 0: $t = 0.2 < t_{0.95}$; age group 1: $t = 1.0 < t_{0.95}$). These growth rates are similar to those found by Caywood (1974) in the upper Delta. The largest fish encountered in this study was 387 mm SL, which is approximately the

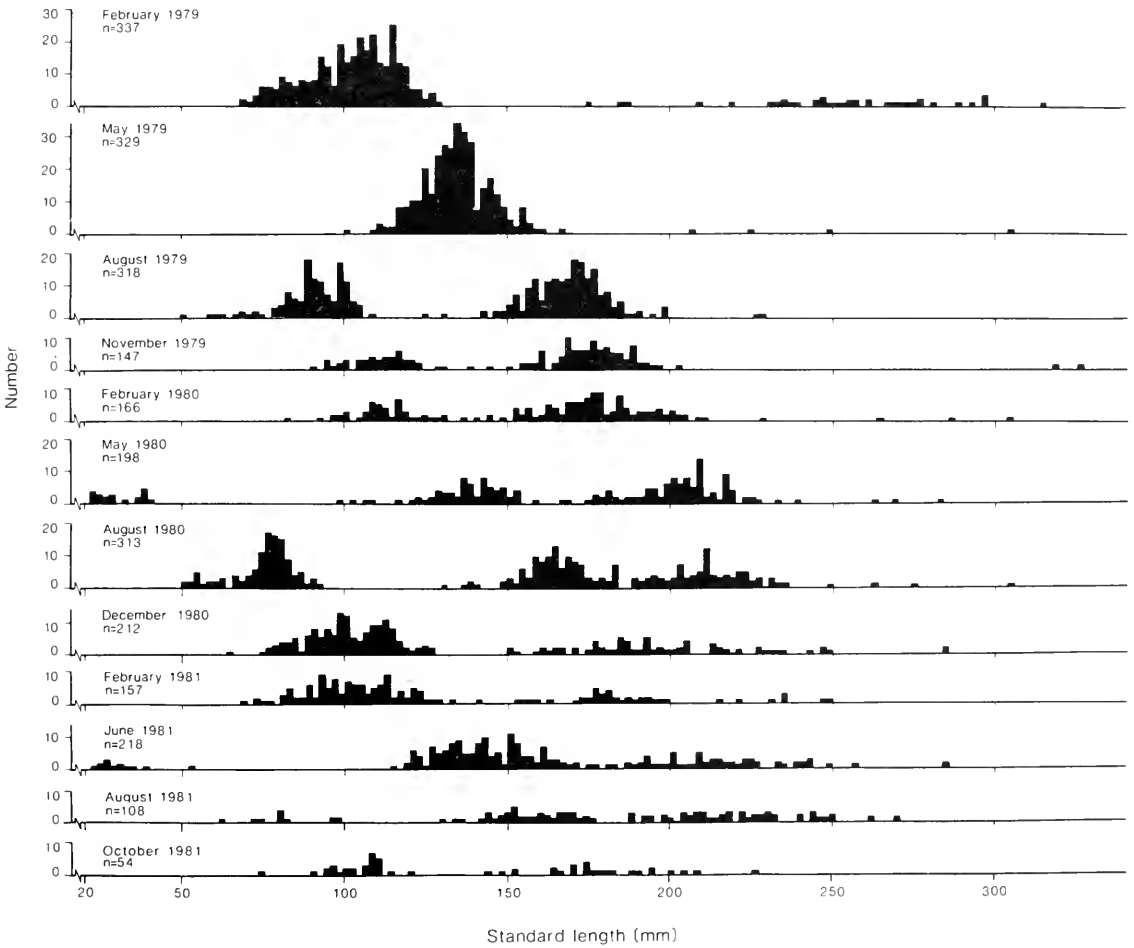

FIGURE 2.—Length (SL) frequency histograms of splittail samples, Suisun Marsh, Calif., 1979-81.

TABLE 1.—Mean back-calculated standard length (mm) and 95% confidence intervals at successive annuli for splittail taken in the Suisun Marsh, Calif., 1979-80.

Age group	n	I	II	III	IV	V
0	11					
1	86	111.8±2.7				
2	56	109.6±4.1	175.3±5.0			
3	29	110.8±4.5	170.2±5.3	218.9±5.0		
4	20	115.7±8.3	162.4±9.0	211.1±6.4	249.7±6.2	
5	8	109.4±12.2	167.3±15.2	213.4±12.4	253.1±14.1	286.8±12.4
Total	210					
$\bar{x}$		111.4	171.2	215.4	250.6	286.8
Increment		59.8	44.2	35.2	36.2	

same maximum size encountered by Caywood (1974). No sex-related differences in growth were detected (t-test, $\alpha = 0.05$).

Monthly mean condition factors of mature fish varied little throughout the year (Table 2). Mean condition factors were significantly higher in females during the months preceding spawning (t-tests, $\alpha = 0.05$); sex-related differences were not significant in other months. The condition factors of immature fish generally were not significantly different from those of mature fish (t-tests, $\alpha = 0.05$). Between-year differences in mean condition factors were not significant in mature fish. However, immature fish of the 1978 year class (immediately postdrought) had mean condition factors significantly higher than those of the 1979 year class in March ($t = 4.81 > t_{0.99}$) and April ($t = 1.73 > t_{0.95}$).

TABLE 2.—Mean monthly condition factors of splittail from Suisun Marsh, Calif., 1979-80. No data are available for December.

Month	Female	Male	Immature
January	23.0	20.4	19.9
February	22.1	21.5	19.7
March	20.5	19.1	20.9
April	20.7	19.6	20.4
May	20.1	17.7	19.5
June	19.2	19.6	19.2
July	19.5	19.9	21.2
August	20.8	19.1	20.2
September	19.8	19.9	19.4
October			18.7
November	21.0	20.5	21.5

Reproductive Biology

Sacramento splittail were mature by their second winter, at minimum lengths of 180-200 mm; both males and females matured at the same age. Caywood (1974), however, noted that a small percentage of the males became sexually mature at the end of their first year and a small percentage of the females did not become mature until their third year. Gonadal growth began to increase in the autumn at about the same time somatic growth declined. Ovaries increased in size until April when they account for 18% of the body weight; testes reached their greatest size in March, April, and May, but never accounted for more than 2% of body weight. Splittail spawned in late April or early May in the marsh. Caywood (1974) found that spawning in the upper Delta occurred between early March and mid-May (in 1973 and 1974). Young-of-the-year fish appeared in our collections in late May or early June at 22-40 mm SL; at this size they had absorbed the yolk sac and were free swimming.

The fecundity (F) of 20 fish >175 mm SL collected from January through March ranged from 17,500 to 266,000 ova. Mean number of ova per gram body weight (Wt) was 408; in this sample the relationship between number of ova and body weight was $F = 457(\mathrm{Wt})^{0.91}$ (log-log transformation $r = 0.546$; $F = 7.64 > F_{1,18}$ at $P = 0.05$). They averaged 600 ova/mm SL. The relationship between fecundity and SL was $F = 0.01(\mathrm{SL})^{2.92}$ (log-log transformation $r = 0.536$; $F = 7.25 > F_{1,18}$ at $P = 0.05$). Fecundity increases with length and weight; both adequately predict fecundity.

The onset of spawning appears to be associated with increasing water temperatures and increasing day length; during the spawning period there were no changes in turbidity or salinity. The success of the spawn was correlated with river outflow (Table 3). Caywood (1974) captured ripe splittail in the upper end of a freshwater slough, in association with recently flooded vegetation. It is possible that splittail spawn on vegetation.

Year Class Strength

The percent of each year class in the catch varied (Fig. 3). The 1978 year class was extremely strong and dominant through the 1980 summer. The 1979 year class was never strong and never clearly dominated a monthly sample. Instead it remained

TABLE 3.—Splittail reproductive success, outflows of the Sacramento River at Chipps Island, Calif., and the correlations between them (* = $P < 0.05$, ** = $P < 0.01$). Abundance index is based on the strength of the year class, by percentage of sample (1 = weak, 3 = strong). The index is derived from the collection data of this study, from California Department of Fish and Game unpublished records, and Caywood (1974).

Year	Abundance index	Monthly mean flows at Chipps Island (in cubic feet per second × 10^3)												Annual total
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	
1969	3	5	11	26	123	159	94	69	65	47	13	12	20	644
1970	2	19	20	46	193	111	56	11	11	6	5	8	15	501
1971	2	13	26	85	64	34	32	37	26	21	12	13	20	383
1972	1	14	14	24	21	22	18	7	5	3	6	6	10	150
1973	2	12	26	27	11	102	77	22	12	7	5	6	11	318
1974	3	14	60	76	139	59	78	109	26	17	9	13	21	621
1975	2	19	24	28	17	57	67	35	29	23	11	10	13	333
1976	1	17	18	20	9	7	8	9	4	4	4	5	3	108
1977	1	4	4	4	4	5	3	3	4	3	3	3	3	43
1978	3	2	4	9	64	54	84	60	41	9	4	6	12	349
1979	2	10	11	9	30	44	37	14	13	5	5	4	5	187
1980	3	8	12	19	118	122	99	29	21	15	11	4	10	468
1981	1	6	5	12	13	20	21	10	9	5	5	2	4	112
Correlation of flow with index		−0.215	0.316	0.285	0.655*	0.720**	0.924**	0.786**	0.765**	0.600**	0.553*	0.511	0.682*	0.864**

relatively constant, representing 30-50% of the catch. The 1980 year class did not begin to dominate monthly samples until the disappearance of the 1978 year class in November 1980. The 1980 year class remained dominant from that date to the end of the study. The importance of the 1978 year class was indicated by the significant negative correlation ($P < 0.01$) between catch per minute and number of months that had elapsed since the beginning of our study.

Data for 1969 through 1974 from Caywood (1974) and for 1972 through 1978 from the California Department of Fish and Game (CDFG) (D. Kohlhorst unpubl. data) also show strong and weak year classes in splittail. These data sets are not strictly comparable with ours because different methods were used to capture the fish and because Caywood's samples were not from the Suisun Marsh. However, the consistency of the patterns in the data from two sources on the same years (1972-74, 1977-78) allowed us to rank year class strength from weak to strong, on a 1 to 3 scale (Table 3). Although the use of such a scale is likely to bias an analysis against finding significant correlations (Thorndike 1978), strong positive correlations ($P < 0.01$) were nevertheless found between year class strength and outflows in February, March, April, and May, as well as with total outflows. Splittail may spawn on flooded vegetation in March and April. Thus, wet years, such as 1974 and 1978, show extremely large year classes that remained abundant for several successive years. During drought years, such as 1976 and 1977, nearly complete year class failures occurred. CDFG collected only one young-of-the-year in 1976 and none in 1977. Our samples in January-March of 1978 yielded only large adults, none of which was from the 1976 or 1977 year classes.

Feeding

Splittail prey upon a variety of organisms but detritus dominates gut contents (Table 4). A small part of the gut content was unidentifiable animal matter. *Neomysis mercedis* was the dominant prey item, and crustaceans accounted for almost 85% by volume of the animal portion of the diet. *Neomysis mercedis* dominated the diet seasonally and through a diel cycle. Annelids, molluscs, insects, and fish completed the prey list; all were relatively unimportant components. These results are in contrast to those of Caywood (1974) who analyzed three collections of splittail from the upper Delta. He found the dominant animal matter in the stomachs to be clams (*Corbicula manilensis*), amphipods (*Corophium* spp.), copepods, and dipteran larvae and pupae. In a sam-

TABLE 4.—Prey items taken by 635 splittail collected from the Suisun Marsh, Calif., 1979-80.

Item	Frequency of occurrence (%)	Volume (%)	Volume less detritus/substrate (%)
Detritus/substrate	74	57	—
Polyclads	1	<1	<1
Polychaetes	3	2	3
Oligochaetes	1	<1	1
Molluscs	1	<1	<1
Crustaceans		35	
Harpacticoid copepods	15		7
Other copepods	7		2
Ostracods	6		<1
Cladocerans	1		1
Corophium	8		9
Other amphipods	1		2
Isopods	<1		1
Neomysis	37		59
Crangon	3		1
Palaemon	<1		<1
Insects		1	
Collembola	1		<1
Coleoptera	1		<1
Diptera	1		<1
Fish	1	2	3
Unidentified	6	3	7

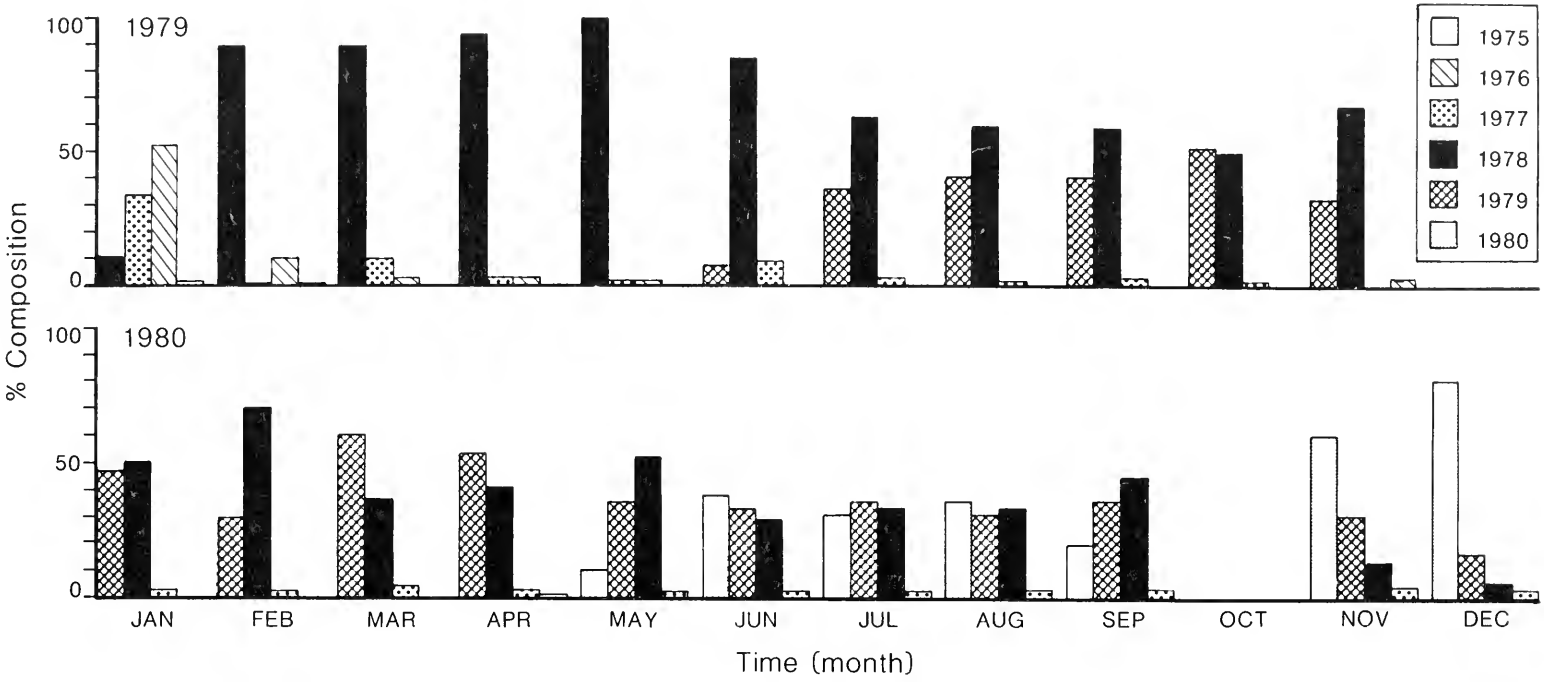

FIGURE 3.—Year class strength of splittail as percentage of sample, Suisun Marsh, Calif., 1979-80.

ple of splittail taken in a flooded pond, however, the main food was earthworms (*Lumbricus* sp.). The types of prey consumed indicate that splittail are bottom feeders. Feeding activity, inferred from fullness indices, was greatest during morning and early afternoon. The mean fullness index for fishes collected from 0600 to 1400 was 5.4, the mean index for fishes collected at 1800 and 2200 was 2.3. There was a seasonal difference in fullness indices of fishes collected midday (Kruskal-Wallis $\chi^2 = 28.9 > \chi^2_{0.99}$). The greatest mean index (2.8) was calculated from fishes collected during the summer. Mean autumn, winter, and spring indices ranged from 1.3 to 1.8.

Discussion

Sacramento splittail is a major component of the Sacramento-San Joaquin estuary fish association. Although abundant within its range, Sacramento splittail is now confined to the lower Delta and the main channel of the Sacramento River, a fraction of its former distribution (Moyle 1980). Population size fluctuates drastically from year to year and year class strength varies annually.

Within the Suisun Marsh, Sacramento splittail is dominant, by number, in the small cul-de-sac sloughs where it is associated with other native fishes (Moyle et al. 1982b). It is a benthic feeder with a limited range of prey types. *Neomysis mercedis*, the primary, nondetritus/substrate component of its diet, is abundant throughout the marsh and serves as a major food source of most other fishes in the marsh as well (Moyle and Daniels unpubl. data).

Sacramento splittail grows to moderate size, lives a relatively long life, and produces a large number of eggs per year. This is typical of native California cyprinids, particularly those found in the larger rivers and lakes (Moyle et al. 1982b). Such a pattern allows this annual spawner to fail to reproduce during environmentally unfavorable years. Unfavorable conditions, which, in the case of splittail, may include high salinities, low water levels, and/or high temperatures, are (or were) periodic and predictable. Particularly dry years occurred in 1972, 1976, and 1977. During these years splittail either failed to spawn or the spawn failed to develop; however, adults were present in the sloughs. A similar relationship between year class strength and outflows has been demonstrated for striped bass for the years 1959-76, although since then the relationship has not been as strong (Stevens 1980).

The small shallow sloughs lined with emergent vegetation inhabited by splittail offer protection from larger piscivorous fish and provide abundant sources of food. The periodic fall in water level simultaneously concentrates prey in the remaining shallow water and excludes large predatory fishes. Avian and mammalian predators are thwarted in all but the most shallow water by its turbidity.

Tolerance to relatively high salinities is unusual in cyprinids although tolerances similar to that of splittail have been recorded for carp, *Cyprius carpio*, and peamouth, *Mylocheilus caurinus* (Scott and Crossman 1973). It is likely that salinity tolerance in splittail increases somewhat with size, as many large (200 mm SL +) adults were collected from the more saline areas (>8‰).

Acknowledgments

In a project that lasts many years and includes over 100 sampling days, many people are responsible for its success. We thank all the individuals, mostly volunteers, who helped in the field. We are particularly grateful to D. M. Baltz, B. L. Herbold, and L. M. Brown for continued assistance in the field and laboratory and for reviewing the manuscript. We also thank R. L. Brown, who was instrumental in securing the resources necessary to complete this project, and D. Kohlhorst of CDFG, who allowed us to examine and report unpublished information collected over a 7-yr period. This work was supported by grants from the California Department of Water Resources.

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LIFE HISTORY AND EXPLOITATION OF *MACROBRACHIUM FAUSTINUM* IN A TROPICAL HIGH-GRADIENT RIVER

Macrobrachium spp. are widely distributed in tropical freshwaters where they often support commercial or artisanal fisheries (Holthuis and Rosa 1965; Holthuis 1980). Studies of exploited *Macrobrachium* stocks have been carried out in large, low-gradient rivers in Liberia (Miller 1971), India (Rajyalakshmi and Ranadhir 1969), and the Philippines (Rasalan et al. 1969), but do not provide the bionomic information necessary for a quantitative assessment of the response of the stocks to exploitation. We know of no such study of a wild population of *Macrobrachium* species.

Macrobrachium faustinum inhabits freshwaters throughout the Caribbean area and in Florida (Chace and Hobbs 1969). In Jamaica it is the most common, eurytopic, freshwater shrimp, inhabiting both slow-flowing rivers and marshes in low lying areas, and fast-flowing streams in hilly regions (Hunte 1978). In the former, *M. faustinum* supports trap fisheries; in the latter it is fished either by hand or by turning over stones and allowing the shrimps to be washed into baskets. Although this fishery is pursued part time by children and men after work, these and other shrimps from small rivers are an important dietary component in an area where protein is scarce and expensive. In this paper we describe the bionomics of *M. faustinum* in a high-gradient stream (Cane River, Jamaica), and assess the effects of fishing on yield and population fecundity.

Description of Study Area

Cane River (lat. 17°58'N, long. 76°44'W) flows into the Caribbean Sea on an exposed south shore (Fig. 1). There is no protected bay at the river mouth, and the estuary is small. Altitude at the source is about 650 m, total length about 10.2 km, overall mean width 2.3 m, and mean depth about 9.4 cm. The width and depth vary markedly with seasonal rainfall. Cane River is a characteristic high-gradient stream in Jamaica. The water is clear and fast-flowing with a high oxygen content and a rocky bottom devoid of macrovegetation. Mean oxygen concentration along the river was 8.5 mg/l, mean pH 7.3. Mean temperature at the extreme lower limit of the river was 25.4°C with a mean daily range of 8.6°C and a mean seasonal range of 4.2°C. Corresponding temperature values at the extreme upper limits were overall mean 21.7°C, mean daily range 3.7°C, and mean seasonal range 3.4°C. The river bed consisted of stones, pebbles, gravel, sand, and mud over rock.

Materials and Methods

Shrimps were collected using a combined Surber sampler (Moffett 1936; Surber 1936) and Box sampler (Berg 1938). It consisted of a square frame of 0.25 m^2 with four legs protruding 5 cm below the frame and 40 cm above it. Net (1 mm square mesh) enclosed the sampler on three sides. Flaps of net under all four sides of the frame served as a seal between the frame and the substrate. On the fourth (downstream) side, there was a detachable collecting net 80 cm long with a mouth 50 × 40 cm (1 mm square mesh).

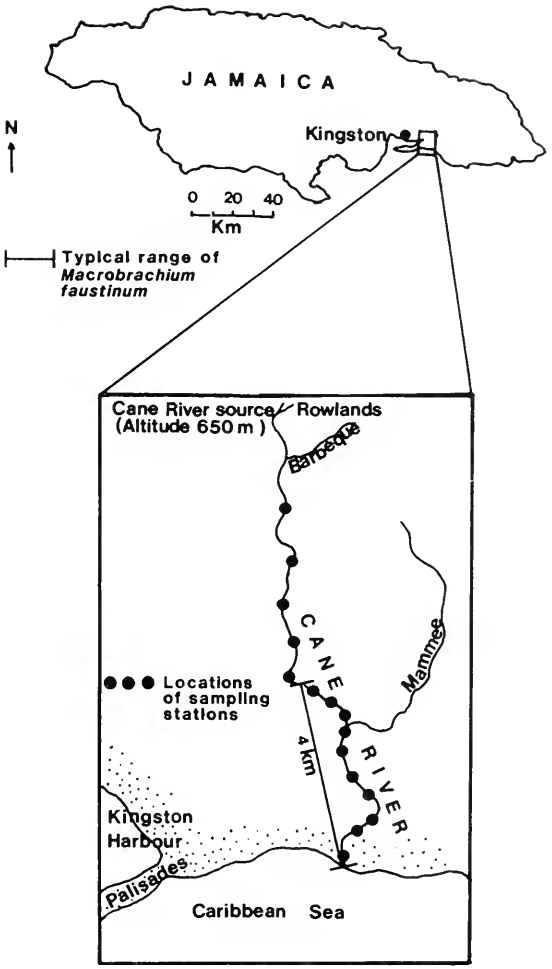

FIGURE 1.—Map of study area and its location in Cane River, Jamaica.

To sample, the legs were forced into the substrate and the net flaps pinned around by stones. The collecting net was attached to the frame, and its bottom side held firmly down by the operator's feet. All stones within the sample area were then removed and the shrimps swept into the collecting net by the current.

During a 20-mo period (February 1973-September 1974), 10 samples, randomly chosen, were taken monthly at each of 15 stations along the length of the river. Areas of the stream bed which were devoid of stones were not sampled since they were known to be without shrimps (Hunte 1976). Samples were taken during the day when the shrimps are inactive and hide under stones.

Each specimen of *M. faustinum* was sexed, and its total length measured (from the tip of the rostrum to the tip of the telson) to the nearest 0.5 mm for adults and 0.1 mm for juveniles. Specimens subsampled from each month's catch were weighed to the nearest 10 mg for adults and the nearest 1 mg for juveniles. Growth and mortality were estimated from monthly length-frequency histograms.

The catch of fishermen was sampled opportunistically throughout the period of sampling in the river. On each occasion the shrimps in the catch were measured and the resulting length-frequency distribution converted to a catch curve using the age-length relationship.

Yield per recruit (Y/R) for various levels of fishing mortality (F) was estimated for males and females combined by the method of Thompson and Bell (Ricker 1975), using an APL algorithm (Rivard 1980). The parameters required for the input are b, age of the youngest age-group fished; m, age of the oldest age-group fished; w_i, weight (g) at age i; r_i, the partial recruitment to fishing mortality at age i; and M, the instantaneous rate of natural mortality. Then

$$Y/R = \sum_{i=b}^{m} w_i N_i F_i \frac{(1 - e^{-Z_i})}{Z_i},$$

where $F_i = r_i F$, $Z_i = F_i + M$, and $N_i = N_{i-1}\, e^{-Z_{i-1}}$. The sequence of N_i for each age-group in the fishery is calculated assuming $N_b = 1$.

The partial recruitment to fishery mortality (r_i) is the proportion of the fishing mortality which can be allocated to age-group i. These values increase throughout recruitment to a maxium of 1 for fully recruited age-groups. In this study r_i was estimated as the ratio of the proportions of age-group i in the catch and population survey, standardized to a maximum of 1 by dividing each ratio by the largest one (Winters 1978).

The number of eggs produced per female recruit (E/R) was estimated for various levels of fishing mortality.

$$E/R = \sum_{i=a}^{m} E_i N_i$$

where a is the age of first maturity for females and E_i is the number of eggs per female at age i. For postrecruits ($i > b$), N_i were as defined above for the estimation of Y/R. For prerecruits ($i < b$), N_i were backcalculated assuming $N_b - 1$, and $Z = M$. The number of eggs per female at each age was determined from the fecundity-length and age-length relationships.

Results

Cane River does not flow through to the sea for much of the year (January-August). As the larvae of *M. faustinum* must develop in the sea (Hunte 1980a, b), juveniles enter the river during a short period each year. Consequently, length-frequency histograms showed distinct modes which were useful for growth and mortality analyses (Fig. 2).

Juveniles entered the river between September 1973 and January 1974, and again in September 1974 (Fig. 2). The weighted mean time of entry of the 1973 cohort was in early December, and was assumed to be early December for all cohorts. At this time shrimps were about 3 mo of age. The peak of the breeding season is about 3 mo earlier (see Fig. 4). Larval development in the laboratory takes about 95 d (Hunte 1980a) after which the length of the juveniles (Hunte 1980b) is similar to that of juveniles entering the river.

Monthly growth for males and females (Fig. 3) was estimated from changes in mean length of cohorts (Fig. 2). Sex could not be distinguished before about 10 mo, when all members of a cohort are longer than 20 mm. Males grew slightly faster than females (Fig. 3).

The wet weight/length relationship for males was $\log W = 3.15 \log L - 2.02$, and for females $\log W = 3.23 \log L - 2.20$. The regression coefficients do not differ significantly, but are significantly >3, indicating allometric growth ($b > 3$; for males $t = 2.64$, $P < 0.01$; for females, $t = 5.14$, $P < 0.001$).

Females composed 49% of adult shrimps caught (i.e., those >20 mm). This was not significantly different from a 1:1 sex ratio ($\chi^2 = 0.81$, $P > 0.25$).

No females smaller than 26 mm (about 9 mo old) bore eggs. This is therefore an estimate of the minimal size (age) at sexual maturity. Of the females in the 26-28 mm size class, 39% were berried, compared with 51% for all mature classes combined. This suggests that most females mature in the 26-28 mm size range, with little variation in size at sexual maturity.

Eggs were oval, about 0.54 by 0.42 mm when laid, and about 0.70 by 0.53 mm prior to hatching. Egg size was independent of female length. Eggs were counted on females carrying eggs in advanced developmental stages, and the fecundity/length relationship was $\log F = 3.52 \log L - 2.47$.

Monthly percentages of mature females carrying eggs (berried) showed that spawning was continuous but peaked between June and November (Fig. 4), just before or during the months of heaviest rainfall in Jamaica.

Total mortality for the *M. faustinum* stock is estimated from the decline in monthly catch of the four year classes sampled in this study (Fig. 5). The percentage contribution of each age-group to the fishermen's catch shows the age of first capture to be 16 mo and full recruitment to the fishery to be at 24 mo (Fig. 4). There is a distinct increase in mortality at, or just before, the age of complete recruitment. We estimate the instantaneous rate of natural mortality (M) as equal to the instantaneous rate of total mortality (Z) for the prerecruits (ages 5-15 mo). Fishing mortality (F) is taken as equal to Z-M for the fully recruited age groups (25-34 mo). The estimates of M and F are 0.13 and 0.15, respectively, and the former is used in the estimation of Y/R.

The information used to calculate the partial recruitment values is given in Table 1. The ratios of proportion in catch to proportion in the survey indicate that F increases steadily with age and size. However, as there are relatively few individuals in the older age-groups, we felt it more appropriate to consider recruitment as complete at age 24 and to assign $r_i = 1$ to all older age-groups. Therefore, all values of r_i for $i < 24$ are relative to the catch survey ratio at age 24.

The relationship between Y/R and F (Fig. 6) appears to be asymptotic; therefore, no F for maximum yield could be computed. However, beyond an F of about 0.5 the returns in terms of Y/R for increased F are minimal. Both the mean weight of shrimp in the catch and the index of catch per unit effort change most rapidly at values of F less than about 0.5.

The relationship between fishing mortality and the number of ripe eggs produced per recruit shows that

TABLE 1.—The calculation of partial recruitment to fishing mortality at each age for *Macrobrachium faustinum* in Cane River, Jamaica.

Age (months)	Percent in catch	Percent in survey	Ratio catch/survey	R_i used in Y/R estimates
16	1.1	10.0	0.11	0.048
17	1.1	10.1	0.11	0.048
18	3.2	10.7	0.30	0.130
19	2.3	9.8	0.23	0.100
20	5.9	8.6	0.69	0.300
21	3.6	7.3	0.49	0.210
22	9.0	6.7	1.35	0.59
23	11.1	6.7	1.66	0.72
24	14.7	6.4	2.30	1
25	9.5	5.6	1.70	1
26	6.5	4.7	1.38	1
27	6.1	3.8	1.60	1
28	6.1	2.8	2.18	1
29	5.3	2.2	2.41	1
30	2.3	1.4	1.64	1
31	3.8	1.3	2.92	1
32	3.4	0.9	3.78	1
33	3.4	0.7	4.86	1
34	1.9	0.3	6.33	1

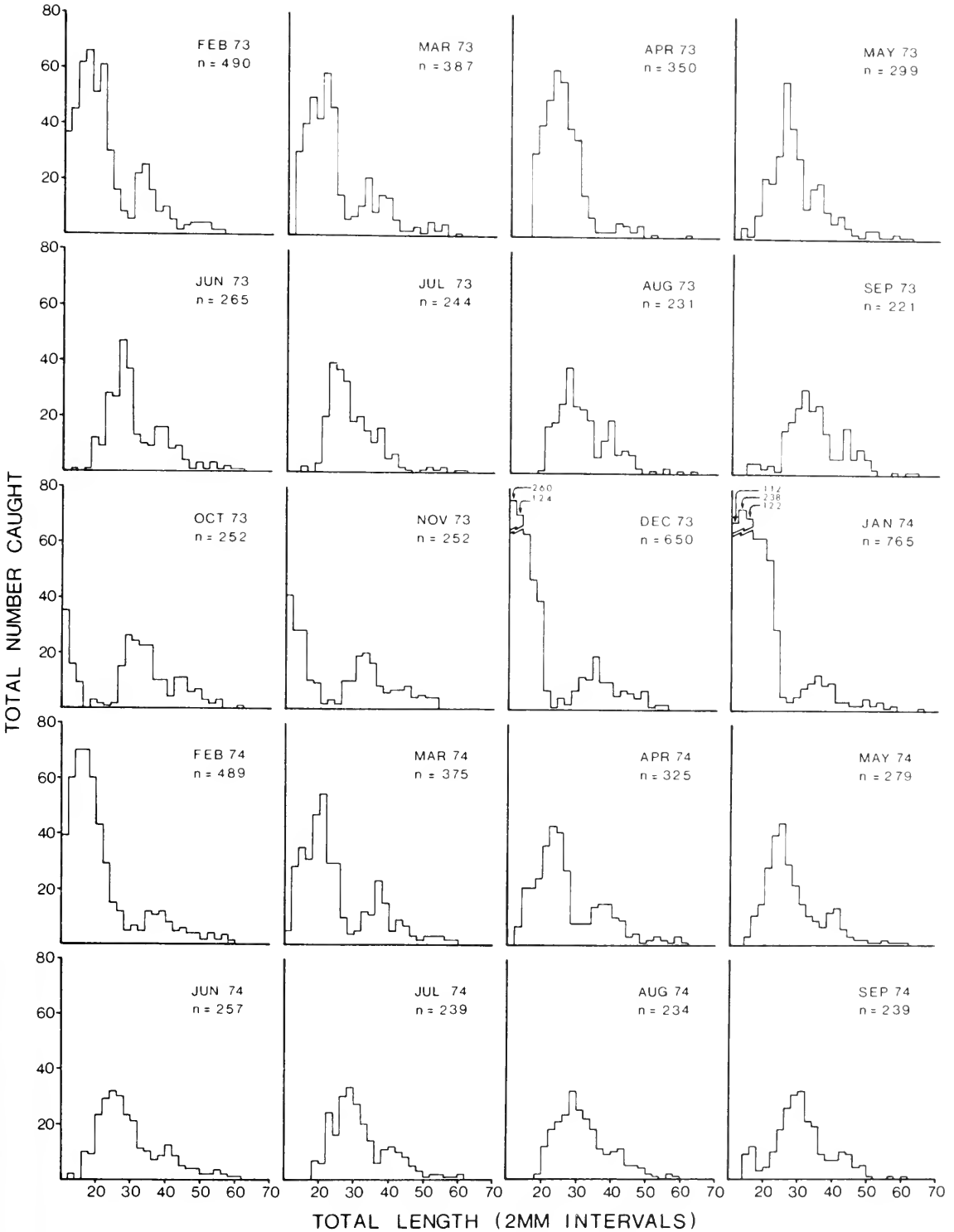

FIGURE 2.—Monthly length-frequency histograms for *Macrobrachium faustinum* in Cane River.

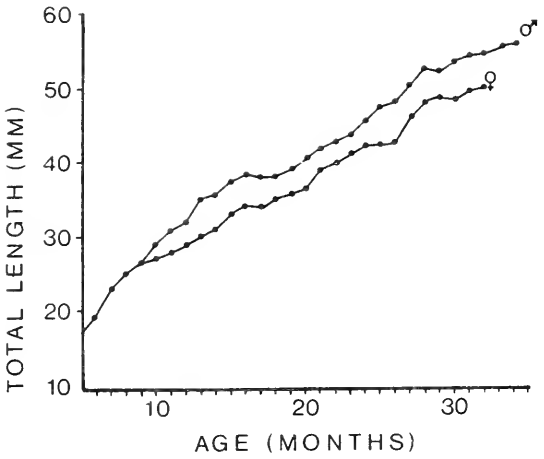

FIGURE 3.—Growth of *Macrobrachium faustinum* in Cane River.

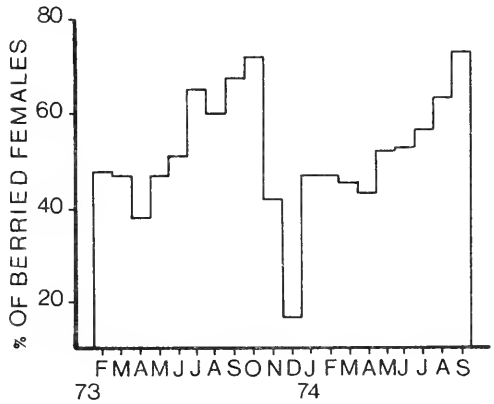

FIGURE 4.—Seasonal variation in the percentage of berried *Macrobrachium faustinum* in Cane River.

even at relatively high values of fishing mortality ($F = 2.0$) egg production is only 37% less than at $F = 0.1$ (Fig. 7).

Discussion

Macrobrachium faustinum and other small shrimps support important subsistence fisheries in the hilly regions of Jamaica and throughout the Caribbean. Management of a resource so widely and diffusely distributed throughout the countryside is difficult. Consequently, to assess the need for management it is important to have some understanding of the likely effects of increased exploitation on these shrimps.

The asymptotic relationship between Y/R and fishing mortality suggests that the shrimps are unlikely to be overfished from the viewpoint of optimal yield of biomass. At the present level of fishing mortality ($F = 0.15$) there would be substantial gains in yield from small increases in fishing effort (Fig. 6). However, sharp reductions in catch per unit effort and in the mean size of shrimp captured would be expected to accompany increased exploitation. *Macrobrachium faustinum* is already small, and we expect that, except in the event of extreme food shortage, the reduction in mean size and catch per unit

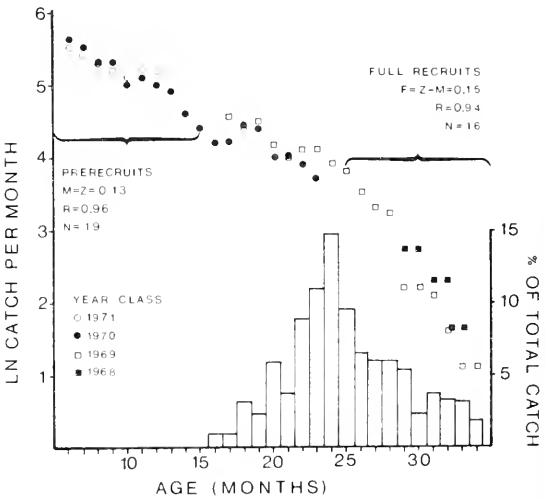

FIGURE 5.—Mortality of *Macrobrachium faustinum* in Cane River as indicated by decline in abundance of year classes (catch per month), and the age composition of the fishermen's catch (percent of total catch).

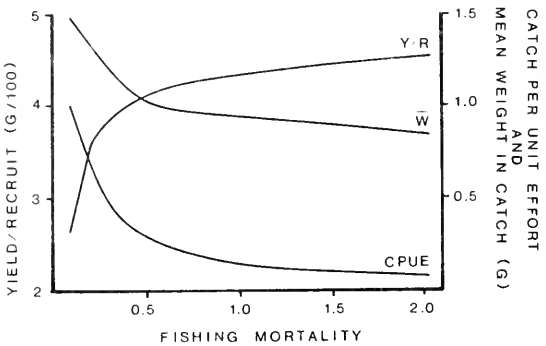

FIGURE 6.—The relationship of yield per recruit (Y/R), mean weight of shrimp caught ($\bar{w}$), and the index of catch per unit effort (CPUE) to fishing mortality for *Macrobrachium faustinum* in Cane River.

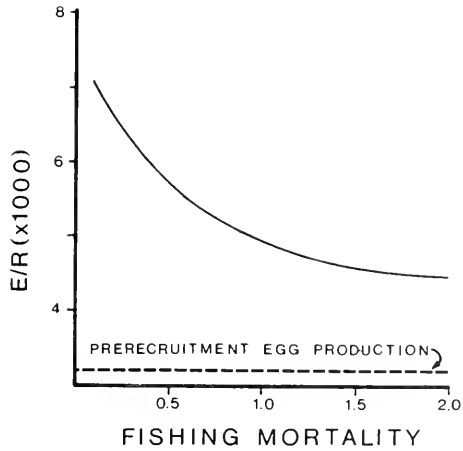

FIGURE 7.—The relationship between fishing mortality and the number of eggs produced per recruit for *Macrobrachium faustinum* in Cane River.

effort of shrimp will self-regulate the fishery. The low level of F suggests that this effect is currently operative.

Even though yield (growth) overfishing is unlikely, the possibility of recruitment overfishing (Cushing 1977) must be considered. This too is unlikely, because *M. faustinum* mature early and a high proportion of egg production takes place before recruitment to the fishery (Fig. 7).

Animals which are small, highly fecund, and mature early are to be expected in a habitat where density-independent mortality prevails and is not stronger and/or more variable for juveniles than for adults (see Stearns 1977). In the rainy season Cane River is subject to flash floods which cause high density-independent mortality of shrimps (Hunte 1976). This is almost certainly true of all high-gradient streams in the Caribbean and the shrimps which inhabit them would be expected to have life history characteristics similar to *M. faustinum*. It appears likely then that such species, many of which support significant subsistence fisheries, will be resistant to overexploitation and that regulatory management need not be considered.

Acknowledgments

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INCIDENTAL CATCH OF HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.), IN HERRING WEIRS IN CHARLOTTE COUNTY, NEW BRUNSWICK, CANADA

In this report we examine the indirect exploitation of harbor porpoises, *Phocoena phocoena*, by the weir fishery for herring (*Clupea harengus*) in Charlotte County, New Brunswick, in the lower Bay of Fundy. This fishery is of considerable economic importance to the region; the landed value averaged 2.2 million dollars annually from 1974 to 1979 (table 11 in Iles 1979). Although herring constitute 50% of the harbor porpoise diet (Smith and Gaskin 1974), the level of competition and conflict between *P. phocoena* and the fishery is unknown.

The harbor porpoise is taken accidentally by several commercial fisheries throughout the world (Mitchell 1975), including a pound net fishery in Denmark (Andersen 1974) similar to the weir fishery of eastern Canada. In Canadian waters, harbor porpoises have been caught frequently in Newfoundland cod traps (Sergeant and Fisher 1957) and an unknown number are killed annually in gill nets in the Gulf of St. Lawrence (Laurin 1976). In addition to the indirect catch in the Bay of Fundy, harbor porpoises have been hunted for food and oil by native people and fishing families from at least the 19th century to the present (Gilpin 1878; Leighton 1937; Prescott et al. 1981). An unknown number of animals were also used as mink food in the 1950s (Fisher and Harrison 1970).

As part of a continuing study of *P. phocoena*, we had the opportunity to examine 48 specimens trapped in herring weirs since 1969. Eleven were tagged or equipped with radio-telemetry packs and released (Gaskin et al. 1975). The remainder were routinely autopsied and ages of 30 specimens were estimated from dentinal growth layers (Gaskin and Blair 1977).

Since no formal reporting system exists, we attempted to assess the annual rate of entrapment by mailing questionnaires to all 214 members of the Fundy Weir Fishermen Association in 1980. A total of 49 questionnaires were returned, of which 36 (16.8%) were of a usable nature.

Specimens Examined from Herring Weirs

The 48 harbor porpoises examined between 1969 and 1982 consisted of 22 females and 26 males. Harbor porpoises became trapped in weirs from May to December with the majority (36) taken in July and August. Ages ranged from 0 to 8 yr, with a disproportionate number of 1-yr-old animals. Over half (52%) of the aged sample ($n = 25$) taken from 1969 to 1973 consisted of 1-yr-old harbor porpoises, while yearlings constituted only 18.9% of a sample of 95 animals collected by shotgun from the free-ranging population during the same time period (Fig. 1).

This catch bias may be a consequence of the inexperience of 1-yr-old harbor porpoises in echolocation, navigation, and prey capture. *Phocoena phocoena* has a lactation period of only 8 mo (Gaskin et al. 1981), short in comparison with other odontocete species. Brodie (1969) suggested that prolonged lactation in odontocetes is attributable to the

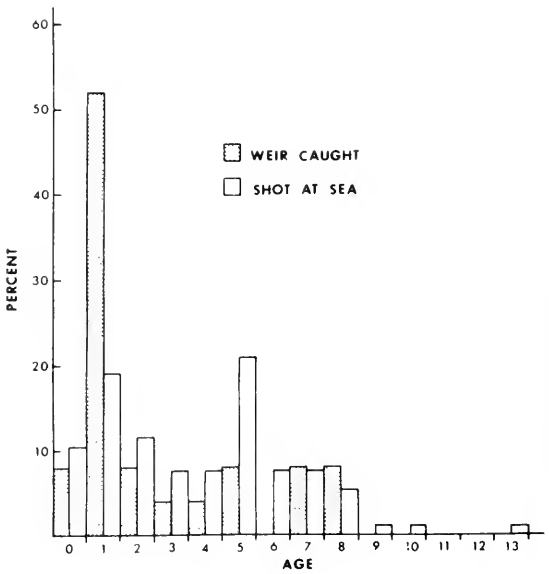

FIGURE 1.—Frequency histogram of age classes (estimated from dentinal growth layers) of harbor porpoises collected in the Bay of Fundy, 1969-73, expressed as percentage of totals captured by two methods: Weir-caught ($n = 25$) and shot at sea ($n = 95$).

sophisticated navigational training required by young animals.

Andersen (1974) concluded, on the basis of parasitic infestation, that about 90% of the 50 harbor porpoises he examined from Danish pound nets were "sick." Most of the yearlings autopsied from our weir sample were only lightly parasitized and appeared to be in good health. Older harbor porpoises were heavily infected with pseudaliid lung worms and campulid liver flukes, but in our experience this is typical of the adult population in general (Arnold and Gaskin 1974).

Many of the harbor porpoises we examined had empty stomachs, indicating either a lack of available fish in the weir or refusal to feed while trapped. Harbor porpoises observed inside weirs usually appeared to be stressed, breathing rapidly and swimming quickly (1.5 m/s) in a regular circular or figure-eight pattern. These animals rarely demonstrated any behavior that might have been interpreted as feeding or foraging activity.

Weir Entrapment Questionnaire

The 36 respondents reported 59 trapped harbor porpoises over the 5-yr period, 1975-79. Of these animals, 23 (39%) were shot or died accidentally, usually by drowning after becoming entangled in the seine net while being removed. The majority of weir fishermen (72%) indicated that they endeavored to release the animals unharmed, either by seining and releasing them, or by waiting for the animals to escape on their own. One respondent who shot entrapped harbor porpoises indicated that the meat was used for human consumption. In general, weir fishermen displayed a favorable attitude towards harbor porpoises, in contrast to their attitude towards harbor seals, *Phoca vitulina*. Harbor seals are generally considered pests, as they swim freely in and out of weirs and may chew holes in the netting.

Fourteen respondents indicated that harbor porpoises became trapped in weirs during the summer months (July-September), while only one reported entrapment at other times (September-October). This is in agreement with our own observations and reflects the seasonal abundance of both harbor porpoises and herring in inshore waters (Gaskin 1977).

Many responses (12 of 18) indicated that harbor porpoises usually entered herring weirs at night. This suggests that visual detection of the weir is important in avoiding entrapment. Busnel et al. (1965) found that a captive harbor porpoise using only echolocation had difficulty avoiding transparent nylon monofilament 3.5 mm in diameter. Since the netting on weirs is constructed from synthetic material, it may not be readily detectable by echolocating harbor porpoises.

Herring tend to be closer to the surface at night than during daylight hours (Brawn 1960) and thus are more susceptible to the weir fishery during this period. Harbor porpoises may follow schools of herring into the weirs and then become trapped. However, questionnaire respondents indicated that large numbers of herring were not always present when entrapment occurred. Some harbor porpoises, therefore, presumably became trapped as a result of foraging on small schools of herring or other prey species.

Impact of the Fishery on the Population

If the annual bycatch per weir (0.328) calculated from the questionnaire returns is representative of all 216 licensed weirs, some 70 harbor porpoises become trapped in Charlotte County each year. Of these animals, 27 die as a result of entrapment.

Gaskin (1977), using uncorrected sighting per unit effort data, estimated the harbor porpoise population in the lower Bay of Fundy as 4,000 during mid-August. Prescott et al. (1981) estimated the August population in the "western half of the Bay of Fundy" as 3,456, using aerial strip census methodology. The annual mortality inflicted on the harbor porpoise population by weirs in Charlotte County would appear to be $<1\%$ of these population estimates. An unknown number of individuals from this population are trapped in weirs in northern Maine (Prescott and Fiorelli 1980) and a few scattered weirs along the Digby, Nova Scotia, shore and in Saint John County, New Brunswick (incomplete data from questionnaire returns).

Subsistence hunting for harbor porpoises is at a very low level in Charlotte County at the present time, although one native hunter claimed to have taken approximately 50 animals in 1979 (Prescott et al. 1981). Based on our own observations, however, native hunters from Maine take only 5-10 harbor porpoises each summer in the area. Harbor porpoises used for human consumption by New Brunswick fishing families are almost invariably from herring weirs or gill nets.

Entanglement in gill nets has a much greater potential for impact on the *P. phocoena* population since there is no opportunity for live release. About 20 fishermen actively gill net in the county (A. B. Cross[1]), but we have little information on the level of

[1]A. B. Cross, Fisheries and Oceans Canada, Lord's Cove, Deer Island, New Brunswick, Canada E0G 2J0, pers. commun. August 1982.

incidental catch. Those interviewed by us reported catching 0-3 harbor porpoises/year. Prescott and Fiorelli (1980) suggested that the incidental catch by gill nets in the Gulf of Maine may be as high as 300 harbor porpoises/year. In Charlotte County, however, the mortality appears to be no greater than that inflicted by the weir fishery.

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A TECHNIQUE FOR TAGGING DEEPWATER FISH

Mark-recapture data have been used extensively in fishery science to estimate population size, survival/mortality rates, growth rates, and movement parameters. Many devices and methods have been used to tag fish (reviewed extensively by Laird and Stott 1978). Virtually all tagging methods necessitate bringing the fish to the surface for marking. For fishes with physoclistic swim bladders inhabiting deeper waters, raising them to the surface subjects them to rapid changes in hydrostatic pressure and, usually, temperature. Procedures used to obtain healthy fish for marking include venting of excess gases from the swim bladder and body cavity with a hypodermic syringe (Gotshall 1964) and raising the fish gradually to the surface to allow acclimatization to changing pressure. Additionally, Phillips (1968) attempted to mark California rockfish by using detachable hooks with "Peterson type" plastic discs fastened to the hooks with wire. However, these methods are at best only moderately successful, as well as time consuming, often expensive, and simply impractical in some situations.

In 1978 we began an investigation of the life history and population dynamics of tilefish, *Lopholatilus chamaeleonticeps*, in the Mid-Atlantic Bight. Reasonable interpretation of these data requires knowledge of tilefish movements. Because tilefish are caught on longlines from depths of 73-254 m along the outer continental shelf (Grimes et al. 1980), fishing operations usually kill or severely injure the fish, thus making conventional marking at the surface pointless. This note describes the design and evaluation of a technique we developed for tagging tilefish, and potentially other deepwater fishes, with tags designed to detach from a bottom longline, thus eliminating the problems of pressure and temperature changes caused by raising fish to the surface.

Methods

We intended to design a tag that could be lightly attached to a longline, so that when a fish took a baited tag the hook would become lodged in the jaw or lip, detach, and thus mark the fish. We designed and constructed tags similar to the snoods or branch lines used on commercial longline fishing gear (see Freeman and Turner 1977 for a description of the gear). These tags consisted of a 30 cm length of 23 kg test monofilament line inserted through red vinyl tubing. We crimped an 8/0 hook to one end of the tag, and the other end was looped, crimped, and attached to the longline groundline at 4 m intervals. No addresses or serial numbers were printed on the red vinyl tubing in these preliminary experiments because our only purpose was to determine if this tagging method was functional. No reward was offered, but tags were returned because we personally alerted most fishermen. This was possible because of the small size of the fishery (i.e., about 25 vessels with most operators already cooperating with our research program by maintaining catch and effort logs) and also because of the localized nature of the tilefish ports (i.e., only two ports landed significant numbers of fish). Because we intended to evaluate only the tagging procedure, we did not request biological data on tagged fish that were caught.

To determine the optimal tag design, we tested different hook types (straight and circle) and different strengths of monofilament (0.9, 1.8, 2.7 kg test) for attaching tags to the longline. The vinyl portion of each tag was knotted to indicate the strength of monofilament (i.e., no knot for 0.9 kg, one knot for 1.8 kg, and two knots for 2.7 kg test).

We attached tags to longlines in two different sequences or "series" (one and ten) of attachment strength and hook type. To prevent a patchy distribution of tilefish from biasing the frequency of removal of tags of various hook types and attachment strengths, the "one-series" tagging consisted of one tag with a particular sequence of attachment strength and hook type (e.g., one 0.9, one 1.8, and one 2.7 kg monofilament with straight hooks; one 0.9, one 1.8, and one 2.7 kg monofilament with circle hooks, etc.). To make identification of hook type and attachment strength easier when we observed tagging longlines from a research submersible, the "ten-series" consisted of 10 tags with a particular sequence of attachment strength and hook type (e.g., ten 0.9, ten 1.8, and ten 2.7 kg monofilaments with straight hooks; ten 0.9, ten 1.8, and ten 2.7 kg monofilaments with circle hooks, etc.).

Longlines fitted with detachable tags were coiled in galvanized tubs, transported to the fishing grounds, and set voluntarily on two occasions by cooperating commercial fishermen. On one tagging operation (at east Hudson Canyon, 23 August 1979, lat. 39°38′05″N, long. 72°16′35″W, 117 m) conducted simultaneously with a gear evaluation study (Grimes et al. 1982a), an onboard observer recorded the numbers of tags of various attachment strengths and hook types remaining on the longline after retrieval. On the other tagging operation (west Hudson Canyon, 17 September 1979, lat. 39°20′30″N, long. 72°26′30″W, 137 m), the longlines were set and retrieved by commercial fishermen who returned the gear for us to

count detached tags. Any tags fouled and detached on deck during setting were retained by the fishermen, returned to us, and counted. Thus our effort between tagging longline sets consisted only of counting detached tags and replacing them with new tags.

The results of experimentally setting tagged longlines (i.e., the variation in proportions of detached tags in relation to various attachment strengths, hook types, tagging locations, and series) were tested by analysis of variance (ANOVA) using the Statistical Analysis System (Barr et al. 1976).

Results and Discussion

A total of 1,156 detachable tags (687 of one-series and 469 of ten-series) were set with various hook types and attachment strengths on two separate occasions near Hudson Canyon (Table 1). Following retrieval of the longlines we determined that 384 detachable tags had been lost, 96 at the east Hudson location and 288 at the west Hudson site (Table 1).

ANOVA of the proportions of tags detached showed significant variations in detachment rate (Table 2). Significant or near-significant probability levels were calculated for variations in proportions of detached tags in relation to the following sources of variation: Tagging location (east or west Hudson); series (one or ten); tagging location-series interaction; attachment strength; hook type; and hook type-tagging location interaction (Table 2).

We know that some accidental tag loss occurred due to fouling, which was observed at the east Hudson site as the gear was being set. However, we believe that detachment rate data actually reflect the relative abundance of tilefish tagged. This is supported by observations made from a submersible at the same time and location (Grimes et al. 1982a); in a transect of commercial longline gear, tilefish were hooked on 42 of 227 hooks (0.19 hooking rate). This hooking rate was nearly identical to the 0.19 loss rate for all tags set at the east Hudson location (Table 3). Evidently, tag loss from fouling was a random event that occurred irrespective of hook type or attachment strength and thus did not affect the analysis, although it could be logically reasoned that weaker attachment strengths and curved hooks would foul most readily.

We know no obvious reason why 1) higher proportions of one-series than ten-series tags were detached, or 2) higher proportions of ten-series than one-series tags were detached at the east Hudson site (Table 3), causing the significance in the ANOVA of the series and tagging location-series interaction (Table 2). If tilefish were contagiously distributed, one might expect these results from the ANOVA and also expect overall tag loss to be contagiously distributed along longlines. A runs test (Sokal and Rohlf 1969) failed to demonstrate contagion in tag loss, and Grimes et al. (1982a) failed to demonstrate contagion for longline catches using the same statistical procedure. The significantly greater tag loss at the west Hudson site (Tables 2, 3) presumably reflects greater tilefish abundance there.

Attachment strength was deemed significant by the ANOVA because increasing proportions of tags were lost with decreasing attachment strength (Table 3). Apparently tilefish were able to detach most easily those tags with 0.9 kg monofilament, followed by 1.8 and 2.7 kg. Among tags returned, four were attached with 1.8 kg and two with 2.7 kg monofilament (Table

TABLE 1.—Numbers of detachable tags of various hook types and attachment strengths set, detached, and returned at east and west Hudson Canyon tagging locations, August and September 1979.

Attachment strength (kg)	Hook type	Set		Detached		Returned	
		East	West	East	West	East	West
0.9	Straight	81	82	22	43	—	—
1.8		80	81	12	39	—	—
2.7		81	80	12	30	—	—
		242	243	46	112		
Total no.		485		158			
0.9	Circle	78	147	19	67	—	—
1.8		81	140	14	55	—	4
2.7		81	144	17	54	—	2
		240	431	50	176		6
Total no.		671		226			[1]7
Total no. tags set and detached		1,156		384			
Total no. tags set, detached and returned		482	574	96	288		

[1]Includes one hook of unknown attachment strength.

TABLE 2.—Analysis of variance of the proportions of tags detached at east and west Hudson Canyon locations, August and September 1979.

Source of variation	df	Sum of squares	Mean square	F value	P>F
Tagging location	1	0.2724	0.2724	61.53	<0.01
Series	1	0.0486	0.0486	10.98	0.01
Tagging location-series	1	0.1059	0.1059	23.91	<0.01
Attachment strength	2	0.0379	0.0190	4.28	0.05
Attachment strength-tagging location	2	0.0039	0.0019	0.44	0.66
Attachment strength-series	2	0.0016	0.0008	0.18	0.83
Hook type	1	0.0154	0.0154	3.47	0.10
Hook type-tagging location	1	0.0212	0.0212	4.80	0.06
Hook type-series	1	0.0002	0.0002	0.04	0.84
Hook type-attachment strength	2	0.0123	0.0062	1.39	0.30
Standard error	9	0.0399	0.0044		
Total	23	0.5593			

1). Evidently 0.9 kg monofilament attachment did not offer sufficient resistance for the hook to pierce the jaw and tag the fish. Furthermore, it did not take an exceptionally large fish to detach a tag because the returned tag with 2.7 kg monofilament was removed from a 3.2 kg fish.

Hook type and the hook type-tagging location interaction approached the 0.05 significance level as sources of variation in the ANOVA (Table 2) because higher proportions of straight hooks were detached, except for tagging longlines set at the east Hudson site where slightly higher proportions of circle hooks were lost (Table 3). These results suggest that fish are more easily hooked by straight hooks. However, all tags returned had circle hooks (Table 1); thus, although straight hooks tagged more fish, they apparently did not remain in the jaws as well.

The returned tags (7) represent about 2% of the maximum number theoretically deployed (384). However, because an unknown number of tags were observed to be lost due to fouling during setting and retrieval, the true rate of return is >2%. This return rate is comparable with that reported for marine tagging studies on relatively deep-dwelling reef fishes using conventional tags applied at the surface (Grimes et al. 1982b). Our tagging technique appears to be useful over relatively long periods. Tagged fish were at liberty from 115 d (0.32 yr) to 577 d (1.6 yr) (Table 4). Similarly, Phillip's (1968) only detachable tag return was from a marked kelp bass at liberty about 2 yr. All of our returns suggest that tilefish in the vicinity of Hudson Canyon are relatively sedentary, which might be expected given that tilefish inhabit (and presumably construct) extensive burrows (Able et al. 1982).

This tagging procedure may represent one of the few workable procedures presently available for investigating deep-dwelling fish. Optimal tag design could be determined by a preliminary study, as we have demonstrated (e.g., the optimal detachable tag for tilefish is constructed with a circle hook, serially numbered and addressed, and attached with 1.8 kg test monofilament). Studies using this procedure could be relatively inexpensive because the major expense in most marine fish-tagging studies—vessel time—would be eliminated. However, problems with the detachable tagging technique may make its use questionable for determining population parameters other than movement. As with other tagging procedures, mortality of tagged animals may be increased, especially since tags are placed in the mouth and could impair feeding. However, all recaptured animals in our study were reported in good condition with no obvious scars, wounds, or other signs of stress. Gut hooking (swallowed hooks) may also cause additional tagging mortality. In a longline assessment study (Grimes et al. 1982a) about 4% of all hooked fish seen (42) from a submersible were gut-hooked.

Unlike conventional tagging procedures, the researcher using detachable tags does not know what species (and their relative numbers) were marked, other than the target species. This was not a problem in our tilefish study because this fishery is virtually monospecific; if detachable tags are administered via a fishery, as in the case we described, tagging data can be adjusted according to the relative abundance of species in the catch.

It may also be possible to use detachable tags to estimate other population parameters, such as total mortality, if sufficient return data are available and assuming that tags are not lost from fish over the experimental period. For example, mortality could be estimated either from the ratio of numbers of tagged

TABLE 3.—Weighted mean proportions of tags detached according to hook type, tagging location, series (see Methods section) and attachment strength.

	Hook type		Tagging location		Series		Overall mean
	Straight	Circle	East	West	One	Ten	
Attachment strength (kg)							
0.9	0.40	0.32	0.24	0.47	0.39	0.32	0.36
1.8	0.32	0.24	0.16	0.39	0.33	0.23	0.28
2.7	0.26	0.27	0.18	0.36	0.32	0.22	0.27
Tagging location (all attachment strengths)							
East Hudson Canyon	0.19	0.20			0.17	0.22	0.19
West Hudson Canyon	0.46	0.35			0.52	0.30	0.41

TABLE 4.—Returns from tilefish tagged in the west Hudson Canyon, 1979. n.a. = not available.

Tag	No. days at liberty	Retrieval site	Fish weight and condition
1	115	tagging site	5.5 kg (good)
2	256	tagging site	n.a.
3	256	tagging site	n.a.
4	257	tagging site	n.a.
5	257	tagging site	n.a.
6	365	tagging site	2.3 kg
7	577	1.9 km west of tagging site	3.2 kg (good)

individuals to total individuals caught over time, or from the number of tagged individuals caught per unit of fishing effort over a specified period of time (Jones 1976).

In conclusion, we believe this procedure can be of value to fishery biologists desiring to investigate migration and movement (and perhaps mortality) of deep-dwelling fishes not markable by more conventional methods.

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We initiated our studies of tilefish and their fishery largely through the urgings of our friend the late Lionel A. Walford. The project could not have succeeded without the cooperation of longline fishermen from Barnegat Light, N.J. Captains John Larson and Ron Minor, owner and operator, respectively, of the longliner *Lori L*, kindly allowed us to set and retrieve tagging longlines. Captains Mike and Augie Ciell set and retrieved tagging longlines from FV *Panther*. Captains Keith Larson, Richard Moch, Curt Blensinger, and Bob McKnight returned recaptured tags. Valuable statistical advice was provided by Richard J. Trout, Rutgers University.

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BIOCHEMICAL GENETIC POPULATION STRUCTURE OF YELLOWFIN SOLE, *LIMANDA ASPERA*, OF THE NORTH PACIFIC OCEAN AND BERING SEA

W. STEWART GRANT,[1] RICHARD BAKKALA,[2] FRED M. UTTER,[2] DAVID J. TEEL,[2] AND TOKIMASA KOBAYASHI[3]

ABSTRACT

The gene products of 31 protein-coding loci were examined electrophoretically in samples of yellowfin sole from the North Pacific Ocean and Bering Sea to assess genetic population structure. Four loci, *Ada-2*, *Gpi-1*, *Pep-2*, and *Pgd*, were polymorphic where the frequency of the most common allele was <0.95 and were used to test for allele-frequency differences within and between stock areas defined by life history and tagging data. A nested contingency-table analysis of allelic frequencies showed that there were no genetic subdivisions either within the eastern Bering Sea or within the Gulf of Alaska. At the next higher nested level, genetic heterogeneity was detected for the Japan-Bering Sea comparison at two loci and for the Japan-Bering Sea-Gulf of Alaska comparison at four loci. Genetic distances between pairs of samples within each of the genetic units averaged 0.0005 (±0.0003), but averaged 0.0049 (±0.0026) between samples from these groups. The results of a gene-diversity analysis showed that 95.7% of the total genetic variation was contained on average within populations and that 3.6% was due to differences between Japanese, Bering Sea, and Gulf of Alaska fish. The remaining 0.7% of the genetic diversity was due to differences between populations within these groups. The genetic differences between Bering Sea and Gulf of Alaska fish are due probably to genetic isolation and divergence caused by coastal glaciation in the Pleistocene Period.

Population genetic data of four additional flatfishes are summarized in the form of a gene-diversity analysis and compared with the genetic structure of yellowfin sole populations. There is generally very little genetic differentiation among flatfish populations separated by <1,000 km. The potential for mixing over this distance is great because of adult migration and passive drift of pelagic eggs and larvae.

Yellowfin sole, *Limanda aspera*, can be found from Vancouver Island in the eastern North Pacific Ocean to Japan in the western North Pacific Ocean. However, the greatest densities are found in the eastern Bering Sea where it is one of the major demersal fishery resources. In the late 1950's and early 1960's it was the primary target of Japanese and Soviet distant-water fisheries. During the period 1959-62, total catches ranged from 185,000 to 554,000 metric tons (t) annually (Wakabayashi et al. [4]) but have since declined to range from 42,000 to 167,000 t. In 1975 the biomass of yellowfin sole was estimated to be 23% (1,000,000 t) of all demersal fishes sampled by trawl survey covering the continental shelf region of the eastern Berin Sea (Pereyra et al. [5]).

Yellowfin sole migrate from wintering areas on the outer continental shelf to shallow water of the inner shelf in summer where they feed and spawn. There are two major winter concentrations in the eastern Bering Sea (Fadeev 1970; Wakabayashi[6]); the largest is located in the vicinity of Unimak Island and the second largest west of St. Paul Island. Other smaller wintering concentrations have been recognized by Fadeev (1970) and by Wakabayashi et al. (footnote 4), but the results of tagging studies (Wakabayashi et al. footnote 4) indicate that these concentrations are part of the Unimak Island group.

Tagging studies by Japan indicated that the west St. Paul Island and Unimak Island groups tended to

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[4]Wakabayashi, K., R. Bakkala, and L. Low, 1977. Status of the yellowfin sole resource in the eastern Bering Sea through 1976. Unpubl. manuscr., 21 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

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[6]Wakabayashi, K. 1974. Studies on resources of the yellowfin sole in eastern Bering Sea. I. Biological characters. Unpubl. manuscr., 77 p. Japan Fishery Agency, Far Seas Fisheries Research Laboratory, 5-7-1 Orido, Shimizu, Shizuoka, Japan.

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remain separate throughout the year (Wakabayashi footnote 6). These tagging data, together with distribution patterns and morphological differences between populations of the two main wintering concentrations, suggested that these groups may constitute independent northern and southern spawning stocks. Other evidence supporting a two-stock concept was 1) apparent differences in growth rate and length-weight relationships between samples from the two areas (Wakabayashi footnote 6), 2) differences in egg diameter between samples from north and south of Nunivak Island, where independent spawning areas for the two stocks might exist (Kashikina 1965), and 3) distribution patterns shown by research vessel surveys in spring and late summer (Chikuni 1971; Yamaguchi 1972), which indicated independent concentrations of fish in northern and southern stock areas.

However, results from other studies have not supported a two-stock concept. Fadeev (1970) found no significant differences in growth rates, length-weight relationships, body proportions, and meristic characters for samples from the two principal wintering groups near Unimak Island and west of St. Paul Island, and Wakabayashi (footnote 6) found no significant differences in the relationship between total body length and radius of the otolith for samples from the two areas. Moreover, winter concentrations of small yellowfin sole have only been found in Bristol Bay (Fadeev 1970), and tag recoveries since 1974 have shown more intermixing of fish between the proposed northern and southern stock areas than had earlier tagging data (Wakabayashi et al. footnote 4).

In the Gulf of Alaska, yellowfin sole are much less abundant and have not been targeted by directed fisheries. As a result much less is known about the geographic distributions of morphological and life history traits in this area.

In this paper, the geographic distributions of electrophoretically detectable protein variants was used to describe the genetic stock structure of yellowfin sole in the eastern Bering Sea and the Gulf of Alaska. Specifically, samples were collected in the inshore spawning areas of the eastern Bering Sea to determine whether the northern and southern stocks are genetically distinct. In addition to these data, the data from one sample of Japanese yellowfin sole provide an estimate of the amount of ocean-wide genetic differentiation among populations. Finally, the genetic population structure of yellowfin sole is compared with the genetic structures of four species of flatfish using the gene-diversity analysis as a summary statistic.

MATERIAL AND METHODS

Electrophoresis

Tissue samples or whole fish were collected at 12 locations in the southeastern Bering Sea, at 3 locations in the Gulf of Alaska, and at 1 location off Hokkaido, Japan, and shipped frozen to Seattle, Wash. (Table 1, Fig. 1). Samples were held at −25°C up to 5 mo until laboratory analysis. The tissues assayed for specific proteins using horizontal starch-gel electrophoresis were skeletal muscle, heart, stomach muscle, vitreous fluid of eye, brain, liver, spleen, kidney, gill, and gonad, but only skeletal muscle, heart, vitreous fluid, and liver were examined in all of the samples. Extraction procedures and electrophoretic methods followed May et al. (1979). Gels consisted of 13% hydrolyzed potato starch (Electrostarch, Madison, Wis., lot 307; Sigma starch, lot 39c-0459)[7]. The locations of specific enzymes were visualized in the gels using solutions described by Harris and Hopkinson (1976). The peptidase staining method A of Harris and Hopkinson (1976) was used to detect zones of activity of a number of peptidases, except that 0-dianisidine diHCl was used as a dye coupler. Three peptides, leu-ala, leu-gly-gly, and phe-pro were used as peptidase substrates.

Three buffer systems were used to achieve maximum resolution of the protein bands on the gels: (I) gel, TRIS 0.03 M, citric acid 0.005 M (pH 8.5), tray, lithium hydroxide 0.06 M, boric acid 0.3 M (pH 8.1) (Ridgway et al. 1970); (II) gel, 1:20 dilution of tray solution, tray, citric acid 0.04 M adjusted to pH 6.1

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

TABLE 1.—Locations (see also Figure 1) and collection dates of samples of yellowfin sole used for electrophoretic analysis.

Location	Lat. N	Long.	Date
Western North Pacific Ocean			
1. Hokkaido, Japan	42°40′	145°10′E	Aug. 1981
Bering Sea			
North stock area			
2. Norton Sound	63°48′	164°14′W	Aug. 1979
3. Nunivak I.	62°20′	167°28′W	Aug. 1979
4. Nunivak I.	59°21′	167°56′W	Aug. 1979
5. Nunivak I.	60°30′	168°00′W	Oct. 1975
6. St. Paul I.	58°10′	170°40′W	July 1977
7. St. Paul I.	57°00′	171°10′W	Feb. 1978
South stock area			
8. Kuskokwim Bay	59°00′	163°57′W	July 1979
9. Bristol Bay	57°20′	160°24′W	July 1979
10. Bristol Bay	57°59′	161°39′W	July 1979
11. Bering Shelf	56°50′	164°30′W	Sept. 1975
12. Unimak I.	56°10′	164°40′W	Sept. 1975
13. Strogonof Pt.	56°55′	159°30′W	Aug. 1977
Gulf of Alaska			
14. Chirikof I.	56°21′	154°25′W	June 1980
15. Kodiak I.	57°51′	152°44′W	July 1980
16. Kayak I.	59°52′	154°45′W	July 1980

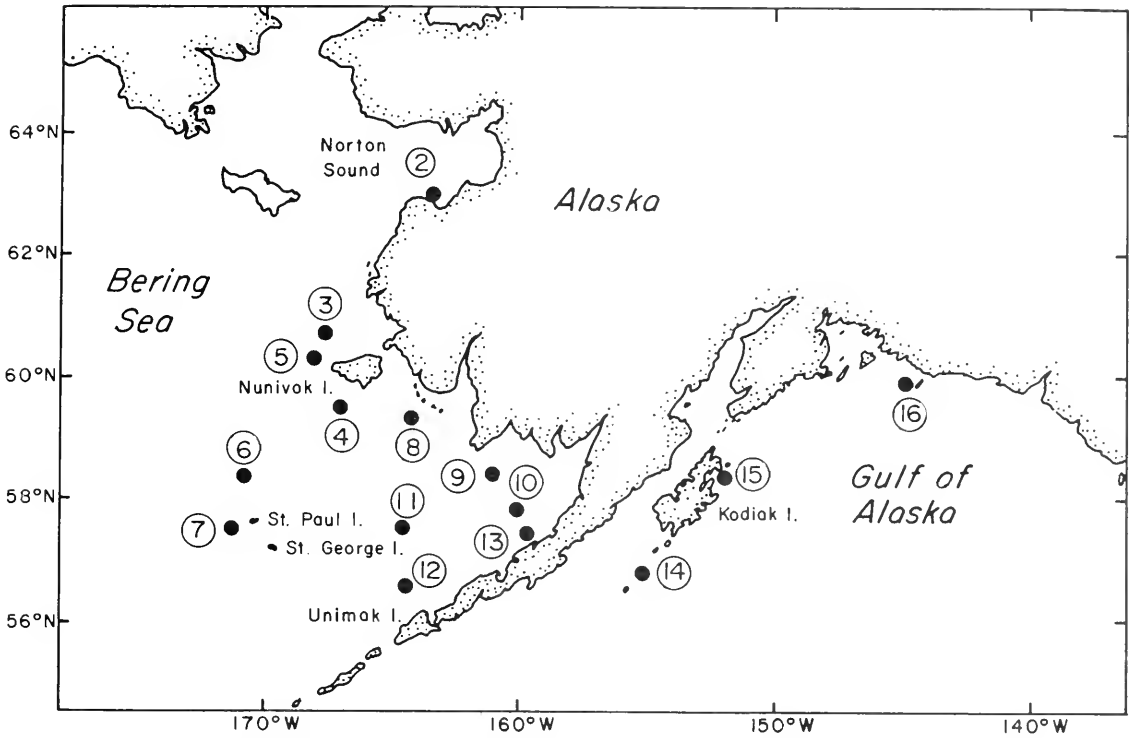

FIGURE 1.—Map of Bering Sea and Gulf of Alaska showing locations (see Table 1 for numbered locations) of samples of yellowfin sole used in this study.

with N(3-aminopropyl)-morpholine (Clayton and Tretiak 1972); (III) gel 1:4 dilution of tray solution, tray, TRIS 0.18 M, boric acid 0.1 M, EDTA 0.004 M (pH 8.7) (Markert and Faulhaber 1965).

The system of locus and allelic nomenclature suggested by Allendorf and Utter (1979) was used. Locus homologies with other fish (Whitt et al. 1975; Fisher and Whitt 1978) were designated with letters where they could be deduced from tissue distributions (Table 2). The enzymes examined in this study, their abbreviations, and Enzyme Commission (E.C.) numbers are listed in Table 2.

Statistical Procedures

Departures from Castle-Hardy-Weinberg proportions in each of the samples were detected using the log likelihood-ratio test for goodness of fit (Sokal and Rohlf 1969) with the degrees of freedom equal to the number of phenotypes minus the number of alleles for a codominant locus.

Stock structure was analyzed using a nested contingency-table analysis where the total heterogeneity among allelic frequencies at each locus was partitioned into orthogonal, regional comparisons in a manner analogous to ANOVA. The log likelihood-ratio test criterion, G, was used to test each comparison with the degrees of freedom equal to the number of alleles minus one, times the number of areas or samples minus one. Only loci having variant-allele frequencies of 0.05 or greater were used in this analysis to avoid low expected frequencies. Rare alleles at these loci were pooled into the next least-frequent allelic class until the pooled class reached a frequency of at least 0.05. The significance level of each comparison was modified to account for the increase in type I error, when multiple tests of the same comparison are made (Cooper 1968). Comparisons at each locus were considered significant if G exceeded the value in a chi-square table associated with a probability of $0.05/4 = 0.012$, where n was the number of polymorphic loci. In this way the overall probability of rejecting H_0 by chance was $1 - (1 - 0.05/4)^4 \approx 0.05$. Only data of samples taken in 1979, 1980, and 1981 were used in all of the statisical analyses, because the six earlier samples were not all taken from spawning areas and because not all of the loci were examined in these samples. However, allelic

TABLE 2.—Protein-coding loci surveyed in yellowfin sole. Multiple loci are numbered beginning at the cathodic end of a gel. Letter designations after locus abbreviations show homologies with proteins in other teleosts. Tissue abbreviations: M = skeletal muscle, H = heart, L = liver, E = vitreous fluid of eye, B = brain, Sp = spleen, K = kidney, St = stomach muscle, Gi = gill, Go = gonad.

Protein (Enzyme Commission number)	Locus abbreviation	Used for study	Buffer	Tissue
Adenosine deaminase (3.5.4.4)	*Ada-1*		III	Sp
	Ada-2	X	III	H, M
Adenylate kinase (2.7.4.3)	*Ak*	X	II	M, Gi
Alcohol dehydrogenase (1.1.1.1)	*Adh*	X	II	L
Creatine kinase (2.7.3.2)	*Ck-1* (C)		II	H, St
	Ck-2 (A)	X	III	M
	Ck-3 (D)		III	Go
	Ck-4 (B)	X	III	B, E
General protein	*Gp*	X	I	M
Glucosephosphate isomerase (5.3.1.9)	*Gpi-1*	X	I	M
	Gpi-2	X	I	H, E, M
Glutamate dehydrogenase (1.4.1.3)	*Gdh*	X	III	L
Glyceraldehyde phosphate dehydrogenase (1.2.1.12)	*Gap-1*	X	II	M, H, B
	Gap-2	X	II	E, H, B
Glycerole-3-phosphate dehydrogenase (1.1.1.8)	*G3p-1*	X	II	L, M
	G3p-2		II	M
	G3p-3		II	L
Isocitrate dehydrogenase (1.1.1.42)	*Idh-1*	X	II	H, M
	Idh-2	X	II	L
Lactate deydrogenase (1.1.1.27)	*Ldh-1* (B)	X	I	M, B
	Ldh-2 (A)	X	I	M, H, B
	Ldh-3 (E)	X	I	E
Malate dehydrogenase (1.1.1.37)	*Mdh-1*	X	II	L
	Mdh-2	X	II	L, E, St
	Mdh-3	X	II	M
Malic enzyme (1.1.1.40)	*Me-1*	X	II	M
	Me-2		II	H, M, Go
Mannosephosphate isomerase (5.3.1.8)	*Mpi*	X	III	M
Peptidase (3.4.11)	*Pep-1*[1]		III	M
	Pep-2[1]	X	III	M, H, B
	Pep-3[2]	X	III	M, K, H
	Pep-4[3]	X	III	M
	Pep-5[2,3]	X	III	M
Phosphoglucomutase (2.7.5.3)	*Pgm-1*	X	I	M
	Pgm-2	X	I	H, L
Phosphogluconate dehydrogenase (1.1.1.44)	*Pgd*	X	II	M, H, K, Go
Superoxide dismutase (1.15.1.1)	*Sod*	X	I	L
Xanthine dehydrogenase (1.2.3.2)	*Xdh*	X	III	L

[1] Substrate: Phenylalanyl-proline
[2] Substrate: Leucyl-glycyl-glycine
[3] Substrate: Leucyl-alanine

frequencies in the six earlier samples were compared with allelic frequencies of the samples taken from the same general areas in 1979 using the contingency-table analysis.

The standard genetic distance, D, (Nei 1972) and its standard error (Nei and Roychoudhury 1974) were calculated for each pair of samples which were examined for all 31 loci. D is an estimate of the number of codon differences in DNA between each pair of samples.

Total gene diversity (H_T) of allelic frequencies, pooled over samples, was partitioned into its components at three levels of population subdivision, regions (R), stocks (S), and populations (P) such that

$$H_T = H_I + D_{PS} + D_{SR} + D_{RT}$$

where H_I is the average heterozygosity over samples, D_{PS} is the diversity due to differences between populations within stocks, D_{SR} is the diversity due to differences between the north and south Bering Sea stocks, and D_{RT} is the diversity due to differences between the western North Pacific Ocean, the Bering Sea, and the eastern North Pacific Ocean. Genetic differentiation relative to H_T was estimated for each subdivision. Thus, $G_{SR} = D_{SR}/H_T$ was the proportion of gene diversity due to subdivision into stocks within regions. The model of population subdivision for both the gene-diversity and the contingency-table analyses is presented in Table 3.

TABLE 3.—Model of population subdivision in yellowfin sole used for contingency-table and gene-diversity analyses. Location codes correspond to numbers in Table 1 and Figure 1.

Total	1	2	3	4	8	9	10	14	15	16
Regions	1	2	3	4	8	9	10	14	15	16
Stocks	1	2	3	4	8	9	10	14	15	16
Populations	1	2	3	4	8	9	10	14	15	16

RESULTS

Electrophoretic Variation

Nineteen protein systems were examined, and 31 zones of enzymatic activity appeared to represent gene products of single locus, which could be reliably scored for population data (Table 2). In the absence of breeding data, the Mendelian nature of the electrophoretic variants may be inferred from the banding patterns. Four guidelines were useful in formulating genetic models: 1) Banding patterns had to be consistent with the subunit structures of homologous proteins in related teleosts, 2) models were formulated by considering gene expression in other teleosts, 3) whenever the same locus was expressed in two or more tissues, the banding patterns of the variants had to be consistent among tissues, and 4) the frequencies of the phenotypes had to fit Castle-Hardy-Weinberg proportions in most of the spawning-area samples. This last criterion has been criticized by Fairbairn and Roff (1980) because of the low power of statistical tests to distinguish among alternative hypotheses (e.g., random distribution of phenotypes) with samples sizes normally used in population studies.

Twenty-one invariant bands appeared on the gels and each was interpreted to reflect the gene products of a monomorphic locus. Although these loci provided no information about differences among populations, they were routinely scored to provide a basis for computing average heterozygosities and genetic distance, both of which require a large sample of randomly selected loci. The following proteins were controlled by one or more polymorphic loci.

Adenosine Deaminase (Ada)

Two loci with different tissue expressions were observed. The last anodal locus, *Ada-2*, had a number of single- and double-banded phenotypes which reflected homozygotes and heterozygotes of seven alleles (Fig. 2). Double-banded heterozygotes suggest that the subunit structure of this enzyme is monomeric. Similar phenotypes have been observed in Pacific herring (Grant 1981) and in North Atlantic pliace, *Pleuronectes platessa* (Ward and Beardmore 1977).

Glucosephosphate Isomerase (Gpi)

The most common phenotype of *Gpi* had three bands reflecting the gene products of two loci where the central band represented the heterodimeric product between the two loci (Fig. 2). Several single- and triple-banded phenotypes were observed at each locus along with corresponding interlocus heterodimeric bands.

Isocitrate Dehydrogenase (Idh)

Two zones of activity having different tissue distributions appeared to reflect the products of two loci where heterodimeric bands between the loci did not form (Fig. 2). The more anodic oocus, *Idh-2*, was expressed predominantly in liver was invariant. *Idh-2* had a number of single- and triple-banded phenotypes reflecting the products of four alleles.

Malate Dehydrogenase (Mdh)

The following genetic model of *Mdh* is based on the observation of several low-frequency variants (Fig. 2). The most common phenotype consisted of four bands, the least anodic of which is designated as the homodimeric band of *Mdh-1*. The products of this locus do not form heterodimeric bands with the products of other *Mdh* loci. An analogous locus appears in salmonids (May et al. 1979) and in Pacific herring (Grant 1981) and is considered to be mitochondrial. The next anodic band of the common phenotype reflects the products of a single locus, *Mdh-2*, having single- and triple-banded variants. The third band of the common phenotype represents a heterodimeric band between *Mdh-2* and *Mdh-3*. At *Mdh-3* there were triple- and broad-banded heterozygotes with corresponding heterodimeric bands with *Mdh-2*.

Mannosephosphate Isomerase (Mpi)

One zone with rare two-banded heterozygotes was observed for this monomeric enzyme.

Peptidase (Pep)

Three polypeptide substrates were used to detect the products of five peptidase loci. *Pep-2* was segregating for five alleles that produced single-banded homozygotes and triple-banded heterozygotes (Fig. 2). The remaining peptidase loci appeared to be monomorphic.

Phosphoglucomutase (Pgm)

There appeared to be two loci with different tissue expressions. The locus, which was predominantly expressed in skeletal muscle tissue, had several different single- and double-banded phenotypes reflecting the products of seven alleles (Fig. 2). *Pgm-2*, which was best visualized with extracts of heart and liver tissues, was monomorphic.

Phosphogluconate Dehydrogenase (Pgd)

The products of *Pgd* were interpreted to be coded by a single locus having five alleles. Heterozygotes were triple- or broad-banded depending upon the relative mobilities of the variant alleles (Fig. 2).

Population Structure

The proportion of polymorphic loci was similar to that observed for other teleosts. The frequency of the most common allele was 0.99 or less for 10 loci (32%), including 4 loci—*Ada-2*, *Gpi-1*, *Gpi-2*, and *Pgd*—which were polymorphic at the 0.95 frequency criterion. The allelic frequencies of these 10 polymorphic loci are presented in Table 4. A complete set of data was not available for samples collected between 1975 and 1978, so these data were only used to test for differences between these samples and those collected in the same areas in the eastern Bering Sea in 1979 and 1980. The remaining statistical analyses were applied only to data collected in 1979,

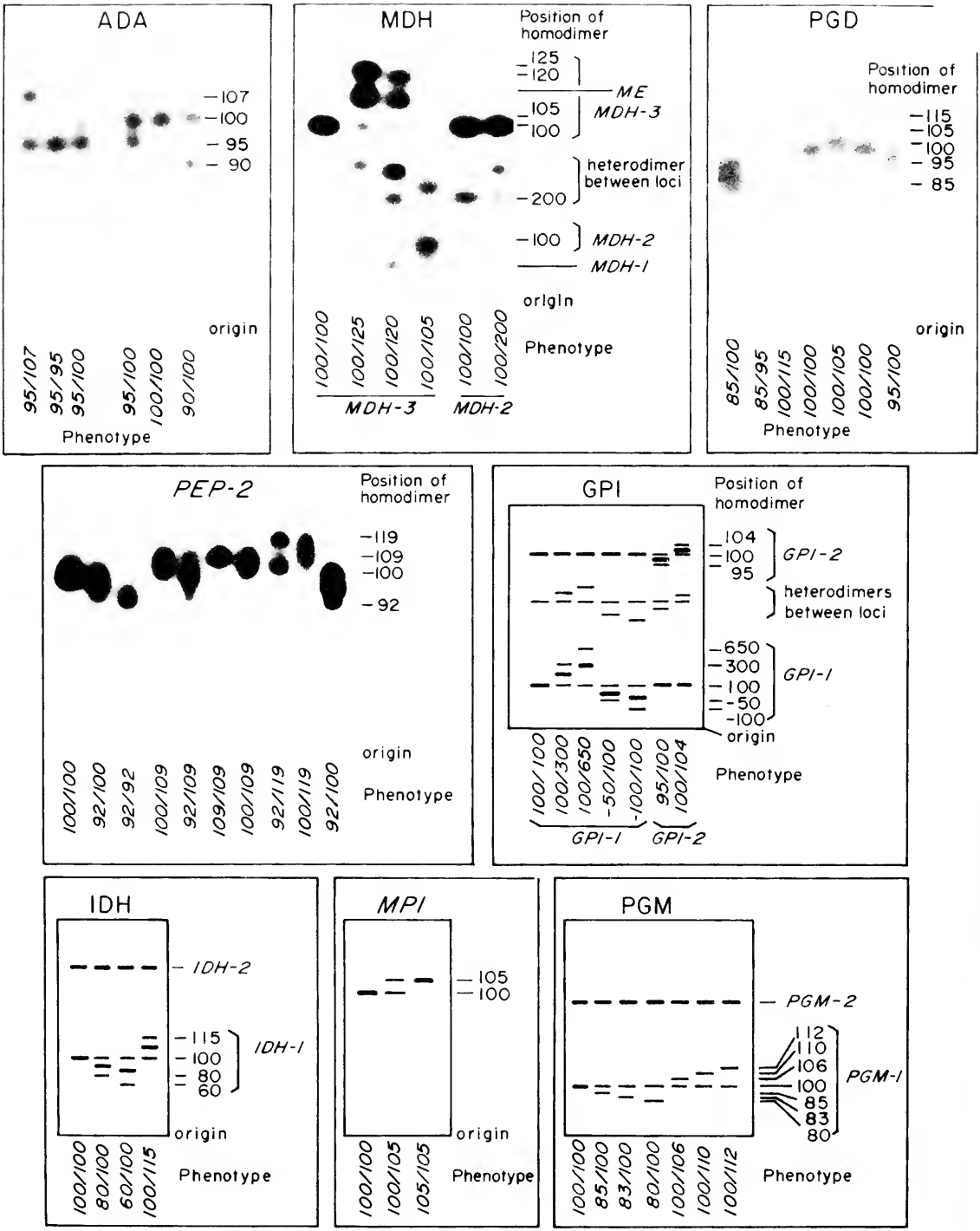

FIGURE 2.—Photographs and diagrammatic representations of electrophoretic gel banding patterns of yellowfin sole.

TABLE 4.—Allelic frequencies of protein variants in samples of yellowfin sole of the North Pacific Ocean and Bering Sea. Sample numbers correspond to location numbers in Table 1 and Figure 1.

		Japan	Bering Sea												Gulf of Alaska		
Locus	Allele	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Ada-2	80	0.007	—	—	—				—	0.008	—				—	—	—
	90	0.051	0.033	0.030	0.046				0.010	0.025	0.020				0.031	0.023	0.040
	93	—	—	—	—				0.021	—	—				0.011	0.011	0.040
	95	0.246	0.325	0.370	0.375				0.365	0.358	0.420				0.213	0.157	0.080
	97	—	—	—	0.011				—	0.017	—				—	—	0.020
	100	0.609	0.575	0.580	0.534				0.583	0.542	0.500				0.745	0.809	0.820
	107	0.087	0.067	0.020	0.034				0.021	0.050	0.060				—	—	—
	N	69	60	50	44				48	60	50				47	89	25
Gpi-1	−150	0.007	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	−100	0.053	0.025	0.050	0.023	0.082	0.022	0.071	0.021	0.025	0.010	0.020	0.065	0.034	—	—	—
	− 50	0.027	—	—	—	0.015	0.008	—	—	0.008	0.010	—	—	0.011	—	—	—
	100	0.733	0.750	0.770	0.796	0.796	0.848	0.772	0.896	0.808	0.770	0.870	0.740	0.764	0.958	0.949	1.000
	250	0.007	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	300	0.160	0.208	0.180	0.182	0.107	0.112	0.157	0.083	0.142	0.210	0.110	0.193	0.185	0.042	0.051	—
	650	0.013	0.017	—	—	—	0.006	—	—	0.017	—	—	—	0.006	—	—	—
	N	75	60	50	44	98	189	35	48	60	50	50	85	100	48	[1]89	25
Gpi-2	95	0.027	0.017	0.010	0.057				0.042	0.050	0.020				—	—	—
	100	0.967	0.975	0.990	0.943				0.958	0.950	0.980				0.989	0.959	0.980
	104	0.006	0.006	—	—				—	—	—				0.011	0.041	0.020
	N	75	60	50	44				48	60	50				47	86	25
Idh-1	60	—	—	—	—	—	—	—	—	—	—	—	—	—	0.010	—	—
	80	—	0.025	—	0.011	—	—	0.014	0.021	0.017	0.020	—	—	—	—	—	—
	100	0.986	0.950	0.990	0.955	1.000	1.000	0.986	0.969	0.975	0.970	1.000	1.000	1.000	0.990	1.000	1.000
	115	0.014	0.025	0.010	0.034	—	—	—	0.010	0.008	0.010	—	—	—	—	—	—
	N	69	60	49	44	98	189	35	48	60	50	50	85	100	48	89	25
Mdh-2	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	200	—	0.008	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	N	75	60	50	44	98	189	35	48	60	50	50	85	100	48	89	25
Mdh-3	60	—	—	—	—	0.005	—	0.015	—	—	—	—	0.006	—	—	—	—
	100	0.974	1.000	0.990	0.977	0.980	1.000	0.971	0.990	0.992	0.990	0.990	0.982	0.960	1.000	1.000	1.000
	105	0.013	—	—	—	—	—	—	—	—	0.010	—	—	—	—	—	—
	120	0.013	—	0.010	0.023	0.015	—	0.014	—	0.008	—	0.010	0.012	0.020	—	—	—
	125	—	—	—	—	—	—	—	0.010	—	—	—	—	0.020	—	—	—
	N	75	60	50	44	98	189	35	48	60	50	50	85	100	48	89	25
Mpi	100	1.000	0.992	1.000	1.000				0.990	0.992	0.980				1.000	0.994	1.000
	105	—	0.008	—	—				0.010	0.008	0.020				—	0.006	—
	N	75	60	50	44				48	60	50				48	89	25
Pep-2	92	0.132	0.148	0.180	0.114				0.125	0.178	0.120				0.073	0.062	0.080
	100	0.772	0.708	0.720	0.761				0.792	0.712	0.800				0.635	0.640	0.660
	102	0.007	0.008	—	—				—	—	—				—	—	—
	109	0.073	0.092	0.090	0.114				0.073	0.093	0.080				0.292	0.287	0.260
	116	0.015	0.008	0.010	0.011				0.010	0.017	—				—	0.011	—
	N	74	60	50	44				48	59	50				48	89	25
Pgm-1	80	0.014	0.008	—	—	—	—	—	—	—	—	0.010	0.012	0.018	—	—	—
	83	—	—	—	—	—	—	—	0.010	—	—	—	—	—	—	—	—
	85	0.021	—	0.010	—	0.005	0.006	—	0.021	0.017	0.030	0.030	0.039	—	—	—	—
	100	0.917	0.950	0.960	0.966	0.964	0.964	0.971	0.948	0.958	0.940	0.940	0.947	0.976	0.958	0.994	1.000
	106	0.034	0.008	—	0.011	—	—	—	—	—	—	—	—	—	—	—	—
	110	0.014	0.025	0.030	0.023	0.026	0.024	0.014	0.021	0.025	0.030	0.020	0.012	0.006	0.042	0.006	—
	112	—	0.009	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	N	73	60	50	44	98	189	35	48	60	50	50	85	100	48	89	25
Pgd	85	0.013	0.025	0.040	0.114	0.056	0.014	0.029	0.063	0.067	0.030	0.070	0.010	0.037	0.196	0.191	0.292
	95	—	—	—	—	—	—	—	—	0.008	—	—	—	—	—	—	—
	100	0.987	0.967	0.960	0.863	0.908	0.969	0.957	0.917	0.900	0.950	0.920	0.990	0.944	0.804	0.803	0.708
	105	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.006	—
	115	—	0.008	—	0.023	0.036	0.017	0.014	0.021	0.025	0.020	0.010	—	0.019	—	—	—
	N	75	60	50	44	98	189	35	48	60	50	50	85	100	46	89	24
H%		0.055	0.056	0.050	0.060				0.049	0.058	0.053				0.044	0.043	0.041

[1] Deviation from Castle-Hardy-Weinberg proportions, $P < 0.01$.

1980, and 1981. One significant ($P < 0.05$) departure from Castle-Hardy-Weinberg proportions was detected for *Gpi-1* in sample number 15 collected in the Gulf of Alaska.

Contingency-Table Analysis

The results of the nested contingency-table analysis are presented in Table 5. Within the eastern Bering Sea, the allelic frequencies of *Gpi-1* and *Pgd* for samples collected from 1975 to 1978 were not significantly different from samples collected in 1979 from the same stock areas. Likewise, no significant allele-frequency differences were detected for *Ada-2*, *Gpi-1*, *Pep-2*, and *Pgd* for either the within- or between-Bering Sea stock comparisons. Similarly,

TABLE 5.—Contingency-table analysis of allelic frequencies of yellowfin sole of the North Pacific Ocean and eastern Bering sea. Parentheses indicate non-orthogonal tests not included in the totals.

Source of variation	*Ada-2* df	*Ada-2* G	*Gpi-1* df	*Gpi-1* G	*Pep-2* df	*Pep-2* G	*Pgd* df	*Pgd* G	Sum df	Sum G
Total	18	[1]73.63	9	[1]79.21	18	[1]70.61	9	[1]94.00	54	[1]317.45
Among Bering Sea, Gulf of Alaska, Japan	4	[1]60.29	2	[1]68.89	4	[1]63.74	2	[1]81.62	12	[1]274.54
(Between Japan and Bering Sea)	(2	[1]10.36)	(1	2.74)	(2	0.49)	(1	[2]6.32)		
Between Bering Sea stocks	2	0.45	1	2.74	2	1.08	1	0.43	6	4.70
Within Northern stock	4	2.66	2	0.60	4	2.41	2	7.68	12	13.75
(Between years)		—	(1	3.73)		—	(1	0.43)		—
Within Southern stock	4	2.87	2	5.95	4	3.19	2	2.02	12	14.03
(Between years)		—	(1	0.09)		—	(1	3.98)		—
Among Gulf of Alaska stocks	4	7.36	2	1.03	4	0.19	2	2.25	12	10.83

[1] $P<0.01$
[2] $0.05 \geq P \leq 0.01$.

none of the among-sample comparisons for the Gulf of Alaska were significant. At the next nested level, the allelic frequencies of *Ada-2* and *Pgd* were significantly different ($P<0.05$) between the pooled Bering Sea samples and the sample from Japan. The three-way comparison between the pooled frequencies of the Bering Sea, the Gulf of Alaska, and Japan was significant ($P<0.01$) for each of the four polymorphic loci.

Genetic Distance

Among the Bering Sea and Japanese samples, D ranged from 0.0002 to 0.0012 and averaged 0.0005 with an average standard error of 0.0003 (Table 6). Similarly, for the Gulf of Alaska samples D ranged from 0.0002 to 0.0008 and averaged 0.0005 with an average standard error of 0.0003. However, the D's between the samples from these two areas were much greater than those within each region; they ranged from 0.0029 to 0.0086, averaged 0.0049, and had an average standard error of 0.0026.

Gene-Diversity Analysis

The results of the gene-diversity analysis are presented in Table 7. The average within-population diversity (heterozygosity) ranged from 0.041 to 0.056 and averaged 0.051. This represented 95.7% of the total gene diversity. Of the remaining gene diversity, 3.6% was due to regional differences between the Gulf of Alaska, the Bering Sea, and the Japanese samples. The proportion of the total gene diversity due to differences among populations within each stock was 0.6% and that due to differences between the north- and south-stock areas in the Bering Sea was 0.1%.

DISCUSSION

The results of this study show that there is little genetic structuring of yellowfin sole populations within the eastern Bering Sea or within the Gulf of Alaska. Although tagging studies in the eastern Bering Sea reported by Wakabayashi et al. (footnote 4) demonstrated that fish from the northern and southern stock areas largely remained separated during their annual inshore-offshore migration, there appears to be sufficient migration between these areas to prevent genetic differentiation. A similar degree of migration between areas in the Gulf of Alaska can be inferred from the lack of allele-

TABLE 6.—Standard genetic distance (below diagonal) and standard errors (above diagonal) between samples of yellowfin sole based on 31 protein-coding loci. Location numbers correspond to those in Table 1 and Figure 1.

1	—	0.0002	0.0004	0.0006	0.0007	0.0004	0.0008	0.0021	0.0021	0.0035
2	0.0004	—	0.0002	0.0004	0.0006	0.0001	0.0003	0.0020	0.0023	0.0037
3	0.0006	0.0002	—	0.0002	0.0004	0.0001	0.0001	0.0018	0.0022	0.0036
4	0.0011	0.0007	0.0006	—	0.0003	0.0002	0.0002	0.0017	0.0024	0.0033
8	0.0012	0.0010	0.0007	0.0006	—	0.0002	0.0006	0.0016	0.0021	0.0030
9	0.0008	0.0004	0.0003	0.0003	0.0004	—	0.0002	0.0016	0.0023	0.0033
10	0.0010	0.0005	0.0005	0.0005	0.0008	0.0005	—	0.0026	0.0033	0.0048
14	0.0041	0.0040	0.0037	0.0032	0.0029	0.0032	0.0051	—	0.0002	0.0005
15	0.0044	0.0046	0.0044	0.0040	0.0035	0.0039	0.0060	0.0002	—	0.0004
16	0.0068	0.0071	0.0069	0.0059	0.0054	0.0060	0.0087	0.0008	0.0006	—
	1	2	3	4	8	9	10	14	15	16

TABLE 7.—Gene-diversity analysis of yellowfin sole of the North Pacific Ocean and Bering Sea.

H_P Mean within population diversity (SE)	D_{PS} Between populations within stocks (SE)	D_{SR} Between Bering Sea stocks (SE)	D_{RT} Between regions (SE)	H_T Total (SE)
Average absolute gene diversity				
0.0507 (0.0223)	0.0003 (0.0001)	0.00005 (0.00001)	0.0019 (0.0009)	0.0530 (0.0233)
Average relative gene diversity				
0.9575 (0.0065)	0.0057 (0.0013)	0.0009 (0.0003)	0.0359 (0.0049)	1.0000

frequency differences among the samples from that region. In addition to adult migration, the passive transport of pelagic eggs and larvae may also contribute to gene flow between stocks within these two regions.

In contrast to the genetic homogeneity within these regions, significant allele-frequency differences were detected for the four polymorphic loci between the Bering Sea and the Gulf of Alaska. This genetic subdivision across the Alaska Peninsula was also reflected in the genetic distances between samples and in the gene-diversity analysis.

The reason for the observed genetic structure of yellowfin sole populations cannot be due to isolation by distance, because the greatest genetic differences were detected between nearby populations and not between more distantly separated populations. The two major genetic groups most likely reflect past periods of isolation and genetic divergence caused by coastal glaciation during the Pleistocene. The first of four major glacial periods in Alaska began about 2 million yr ago and the last major period of glaciation ended only 11,000 yr ago (Ericson and Wollin 1964; Péwé and Roger 1972). During most of these periods glacial ice covered the coastline of the Alaska Peninsula and central Alaska. Since yellowfin sole are rarely found at depths >100 m (Hart 1973) and since juveniles use shallow bays and estuaries as nursery areas, populations would be greatly influenced by coastal glaciation. There are similar genetic subdivisions across the Alaska Peninsula or across the Bering Sea for Pacific herring, *Clupea pallasi* (Grant in press); walleye pollock, *Theragra chalcogramma* (Iwata 1975; Grant and Utter 1980); and Pacific cod, *Gadus macrocephalus* (Grant et al.[8]).

How similar is the genetic population structure of yellowfin sole to that of other flatfishes? Two statistics can be used to make this comparison, genetic distance and relative gene diversities. The former statistic cannot be used for most of the available flatfish data because only a few loci were examined in these studies. The gene-diversity analysis is more appropriate in cases where only a few loci have been examined because the analysis can be computed for each locus. Nonetheless, the best estimates of population structure are averages over loci because random effects can produce different results for different loci, even though each locus experiences the same population events. Caution must be used when comparing the results of these analyses between species because the results depend, in part, on the geographic extent of the study and, hence, on the number of genetic subdivisions included in the data. A summary of all of the available biochemical data for five species of flatfishes is presented in Table 8 in the form of a gene-diversity analysis.

Thirteen loci (2 polymorphic loci) were examined in Greenland halibut, *Reinhardtius hippoglossoides*, collected from four coastal areas of eastern Canada and from the Bering Sea (Fairbairn 1981a). If only the Canadian samples are considered, 99.93% of the gene variation was contained within populations, and

[8]Grant, W. S., C. I. Zhang, and T. Kobayashi. 1982. Biochemical genetics of *Gadus*: II Population structure of Pacific cod (*Gadus macrocephalus*). Processed rep., 27 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

TABLE 8.—Summary of relative gene diversities in five species of flatfishes.

Species	No. of polymorphic loci	Geographic range of samples (km)	Within population diversity	Between populations within areas	Between areas within regions	Between regions within seas	Between seas	References
Atlantic Ocean								
Greenland halibut, *Reinhardtius hippoglossus*	2	1,000 (+Bering Sea)	0.9993 0.9308	— —	0.0001 0.0001	0.0006 0.0004	— 0.0687	Fairbairn (1981a)
Witch, *Glyptocephalus cynoglossus*	2	1,500	0.9923	0.0011	0.0066	0.0001	—	Fairbairn (1981b)
Plaice, *Pleuronectes platessa*	5	1,000	0.9959	—	—	0.0013	0.0018	Ward and Beardmore (1977); Purdom et al. (1976)
Pacific Ocean								
Pacific halibut, *Hippoglossus stenolepis*	17 1	6,200 2,000	0.9871 0.9962	— 0.0039	— —	0.0040 0.0009	0.0089 —	Grant et al. (in press); Tsuyuki et al. (1969)
Yellowfin sole, *Limanda aspera*	10	6,200	0.9597	0.0057	0.0009	—	0.0359	This paper

0.07% was due to differences between the Gulf of St. Lawrence and the shelf populations, and to population differences on the continental shelf. No significant allele-frequency differences were detected among these samples. When the Bering Sea sample is included in the analysis, 6.9% of the gene diversity was due to subspecific differences between the two areas.

Also in eastern Canada, the gene products of 15 loci (2 polymorphic loci) were examined in samples of witch flounder, *Glyptocephalus cynoglossus*, (Fairbairn 1981b). The gene-diversity analysis of these data also shows low levels of genetic differentiation among witch flounder populations; 99.2% of the total gene diversity was contained on average within populations and 0.8% was due to all population differences combined. In spite of the low level of genetic differentiation among populations, significant allele-frequency differences were detected between some of the areas. Tag-and-recovery and distribution data show that adults tend to be sedentary and that populations tend to be separated by weak barriers to migration such as the cold shallow waters of the Grand Bank (Bowering 1976; Bowering and Misra 1982). However, the potential gene flow at the egg and larval stages is great (Evseenko and Nevinsky[9]) and no doubt counters genetic divergence of the partially isolated adult populations.

For plaice, *Pleuronectes platessa*, in the eastern North Atlantic Ocean, there are data for the five loci in common in the studies of Ward and Beardmore (1977) and Purdom et al. (1976). Allele-frequency differences were not detected either within the Irish Sea, within the North Sea, or between these seas for these loci. The results of the diversity analysis reflected this degree of homogeneity; 99.6% of the total gene diversity was contained within populations and only 0.4% was due to differences between populations.

Grant et al. (in press) examined the gene products of 17 polymorphic loci in three widely separated samples of Pacific halibut, *Hippoglossus stenolepis*, in the North Pacific Ocean and Bering Sea. The gene-diversity analysis showed that 98.7% of the gene diversity was contained within populations, that 0.4% was due to differences between the Bering Sea and the Gulf of Alaska, and that 0.9% was due to trans-Pacific Ocean differences. Tsuyuki et al. (1969) examined genetic variation at one locus in samples from 10 locations in the Bering Sea and in the eastern North Pacific Ocean. The gene-diversity analysis of these results estimated the within-population diversity to be 99.6%, that due to differences between regions to be 0.09%, and that due to differences among populations within regions to be 0.04%. This high degree of genetic homogeneity which was detected in both studies reflects the long distance migrations that Pacific halibut are known to make. For instance, tagging studies have demonstrated migrations of at least 3,200 km (Skud 1977).

The results of these studies show that there is very little genetic differentiation among populations of flatfishes located over areas of about 1,000 km. For Pacific halibut, areas of genetic homogeneity appear to be even larger because of its ability to migrate long distances. These areas of genetic homogeneity probably cannot be considered randomly mating populations in the strict sense, because it is unlikely, for example, that fish located on one edge of a genetic unit have an equal chance of mating with fish on the other side of the genetic unit. Rather, these units reflect long-term processes that influence population size and migration over several generations. The division of yellowfin sole into two genetic groups by coastal glaciation in the Pleistocene is an excellent example of the importance of interpreting present-day allele-frequency distributions in terms of past population events.

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YIELD PER RECRUIT MODELS OF SOME REEF FISHES OF THE U.S. SOUTH ATLANTIC BIGHT

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ABSTRACT

Yield per recruit models for red porgy, *Pagrus pagrus*; vermilion snapper, *Rhomboplites aurorubens*; white grunt, *Haemulon plumieri*; red snapper, *Lutjanus campechanus*; black sea bass, *Centropristis striata*; gag, *Mycteroperca microlepis*; scamp, *M. phenax*; snowy grouper, *Epinephelus niveatus*; and speckled hind, *E. drummondhayi*, the most important species to both recreational and commercial fishing off North Carolina and South Carolina, are strikingly similar, and suggest that there is a single strategy for managing reef fishes in the South Atlantic Bight. For all species, yield per recruit at median recruitment ages increased rapidly in response to increasing F (instantaneous fishing mortality rate) until $F = 0.3$-0.4. Thereafter, only small increases in yield resulted from large increases in F. Major gains in yield at all but very small values of F ($F \leq 0.15$), resulted if recruitment to the fishery was delayed to age 3 or older. The value of M (instantaneous natural mortality rate) affected the magnitude of yield/recruit but had little effect on the shape of the response surfaces.

The annual total recreational and commercial catches of reef fishes provides a preliminary estimate of maximum sustainable yield if the following assumptions are accepted: 1) $F \geq 0.3$, 2) recruitment ages approximate those required to produce maximum yield per recruit, and 3) recruitment is sufficient to saturate the available habitat. Preliminary estimates of the relative fishing power (per day) of different components of the fishery are headboats, 1.0; commercial handline boats, 1.3-1.5; and reef trawlers, 3.8-5.2.

In this paper we examine the implications of yield per recruit models to management of the reef fishery in the South Atlantic Bight. We examined models for each of the several important species in this fishery to determine if there was a single pattern of yield response that, in turn, would allow development of a coherent management philosophy.

The Fishery

Warm Gulf Stream-influenced water and irregular rocky substrates allow occupancy of the outer continental shelf of the U.S. South Atlantic Bight (Cape Hatteras to Cape Canaveral) by a community of primarily Caribbean, deep reef fishes. Principal species include groupers (*Mycteroperca* and *Epinephelus*), snappers (*Lutjanus* and *Rhomboplites*), porgies (*Calamus* and *Pagrus*), and grunts (*Haemulon*) (Huntsman 1976a). The black sea bass, *Centropristis striata*, is abundant at more temperate reefs nearer shore.

Reef fishes support both recreational and commercial fisheries in the area. About 40 headboats, about 260 charter boats (usually six passengers or fewer), and numerous private boats operate in the recreational fishery. The last two groups exert a greater fraction of the fishery effort in Georgia and Florida than in the Carolinas. The commercial fishery has two main segments—handline vessels and trawlers. Traps are also used occasionally, especially for black sea bass. Handline fishing is with hook and line retrieved by hydraulic or electric reel. Trawling is relatively new in the area and had little acceptance until Sea Grant programs in South Carolina and Georgia introduced the "high-rise" trawl in 1975 (Ulrich et al. 1977). When used by knowledgeable snapper fishermen skilled in fathometer reading, the high-rise trawl can be exceptionally effective in taking reef fish.

The magnitude of the recreational catch is only partly known. Headboats landed about 773 t annually from 1972 through 1974 at North Carolina and South Carolina ports (Huntsman 1976a), and the catch for the entire bight averaged 972 t from 1976 through 1980.[3] Catches by charter and private boats are unknown, except for an estimate by Manooch et al. (1981) of the 1978 charter boat catch in North Carolina (about 91 t).

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The offshore commercial catch cannot be accurately calculated from commercial fishery statistics. In the Carolinas in 1973 and 1974 the headboat catch of snappers and groupers appeared to be 3 or 5 times greater (depending on the inclusion of vermilion snapper) than the commercial catch (Huntsman 1976b). Beginning in 1975 the commercial landings in the Carolinas increased greatly and were 836 t of snappers and groupers in 1980. Commercial snapper-grouper landings for the entire bight were 1,308 t for 1980.[4]

Both commercial and recreational fishermen prefer groupers and any of three species known in the trade as red snapper—*Lutjanus campechanus*, *L. vivanus*, and *L. buccanella*. Recreational fishermen and trawlers usually take whatever species is most available, but commercial handline fishermen often leave white grunts or red porgies and seek red snappers and groupers. Since 1976, however, commercial handline fishermen have responded to an improved market for small species by being less selective.

Potential Management Problems

Public Law 94-265 requires that fisheries within the United States extended jurisdiction zone (the area between 3 and 200 mi seaward of the U.S. coast) be managed so that an optimum yield is attained. Optimum yield is an allocation of the yearly harvest to recreational, commercial, and nonexploitive users that is usually equal to, or less than, the maximum sustainable yield (MSY). Minor conflicts and polarized viewpoints have arisen between the various users, primarily because of differing goals and differing methods of fishing. At present there is no objective way of allocating the catch among the various groups, because there is an insufficient understanding of stock productivity. Institutional provisions for the allocation of the catch exist, but the understanding of stock productivity necessary for the allocation is lacking.

Insight into stock productivity may be achieved through mathematical models. But neither the dynamic pool (Beverton and Holt 1957) nor the surplus-yield (Schaefer 1957) population models is presently useful to us because both require data that do not exist. The dynamic pool model requires parameter estimates (such as the relationship of stock size to recruitment) that are unavailable for the stocks involved and the surplus yield model requires a fairly long series of annual catch and effort measurements.

Despite initiation of fishery censuses in 1880, there is a lack of interpretable records of annual commercial catches for the South Atlantic snapper-grouper fishery. Serious problems in the data series include, among others:

1) Missing or faulty species distinctions. At least 10 species of grouper are listed only as grouper, and porgies include both inshore estuarine-dependent and oceanic reef species. The red snapper listing includes at least three species of *Lutjanus* and, depending on the year, may or may not include vermilion snapper, *Rhomboplites aurorubens*.
2) Missing records, often covering decades, in the series of records begun in 1880.
3) Catches reported by area of landing instead of by area of fishing (e.g., snappers landed on Florida's east coast may have come from North Carolina or the Bahamas).
4) No useful or reliable effort data.

Matching catch and effort data available for the headboat fishery from 1972 to 1980 in North Carolina and South Carolina (Huntsman 1976a, b; footnote 3) and from 1976 to 1980 in Georgia and North Florida, (footnote 3) are nearly useless for yield-model construction without concurrent commercial data.

Enough information is available to develop an abbreviated version of the full dynamic pool model—the yield per recruit model (Beverton and Holt 1957). The yield per recruit model, which can be used for partial analysis, is especially useful if one must prepare management schemes from incomplete information. An advantage of the yield per recruit model is that it has minimal requirements of parameter estimates but allows easy evaluation of the response of yield to changes in fishing mortality and recruitment age. Even if the exact relationship between effort and fishing mortality is unknown, one can derive general information on which to base management regulations.

The yield per recruit model predicts the ratio of the weight or numbers of fish caught during the life span of a cohort to the initial number of individuals of the cohort that enter the fishing grounds. It expresses these yields as a surface responding to the independent variables F (instantaneous fishing mortality rate) and t_r (age at recruitment to the gear). The growth rate, natural mortality rate, and longevity of the species are the principal parameters influencing the shape of the surface.

[4]Unpublished data, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, Miami, FL 33149-1099.

Yield per recruit models may be especially appropriate to the snapper-grouper fishery, because carrying capacity and growth, rather than recruitment, are apparently the principal limiting factors (Ehrlich 1975). Since reef habitat occupies a relatively small proportion of the outer continental shelf (Parker and Colby in press), recruitment is probably always sufficient to replace losses from fishing mortality and natural mortality. New reefs, such as wrecks and artificial fishing reefs, are almost immediately colonized (Anonymous 1971; Stone et al. 1979; Stone[5]).

MATERIALS AND METHODS

Species Studied

Species were selected on the basis of their importance to the recreational and commercial catch and, to a lesser extent, on the amount and quality of information available. Huntsman's (1976a, b) and Huntsman and Dixon's (1976) descriptions of the headboat fishery, and Ulrich et al.'s (1977) description of the handline and trawl fisheries suggested the inclusion of:

1) red porgy, *Pagrus pagrus*;
2) vermilion snapper, *Rhomboplites aurorubens*;
3) white grunt, *Haemulon plumieri*;
4) red snapper, *Lutjanus campechanus*;
5) black sea bass, *Centropristis striata*;
6) *Epinephelus* groupers (the important species are the speckled hind, *E. drummondhayi*, and snowy grouper *E. niveatus*);
7) *Mycteroperca* groupers (gag, *M. microlepis*, and scamp, *M. phenax*, are the most important species).

Estimates of Growth and Mortality Parameters

In general, reliable estimates of growth parameters are available (Table 1) from both published and unpublished sources. Reliable estimates of M (instantaneous natural mortality rate) are not available. Determining M is a difficult but common problem solved by many authors by assuming single (Low 1981) or multiple (Houde 1977a, b; Chittenden 1977; Breiwick et al. 1980; Lenarz et al. 1974) values. M can be reasonably estimated by computed estimates of Z (instantaneous total mortality rate), which provide maximum estimates of M, and by the relationship of growth parameters to M, described generally by Beverton and Holt (1959) and more specifically by Pauly (1980-81).

For most species we provided two or more estimates (Table 1), one of which was, or was very close to, the Pauly estimate. For three groupers (scamp, snowy grouper, and speckled hind), we used only the Pauly estimate because the other analyses indicated that changing M had little effect on the pattern of yield response.

Yield Per Recruit Computations

Computer program BM007,[6] which requires a relatively small amount of memory, is written in FORTRAN and can be used on most computer systems for calculating yields per recruit. The program output is tabular and must be transposed by hand to graph paper if isometric yield lines are to be drawn.

$$Y/R = FW_\infty \left(\frac{1 - e^{-Z\lambda}}{Z} - \frac{3e^{-Kr}(1 - e^{-(Z+K)\lambda})}{Z+K} + \frac{3e^{-2Kr}(1 - e^{-(Z+2K)\lambda})}{Z+2K} - \frac{e^{-3Kr}(1 - e^{-(Z+3K)\lambda})}{Z+3K} \right)$$

and
- t_r = age at recruitment to the gear
- t_0 = theoretical age at length "0"
- t_λ = maximum age in fishery
- F = instantaneous rate of fishing mortality
- M = instantaneous rate of natural mortality
- Z = instantaneous rate of total mortality, $M + F$
- L_∞ = asymptotic length of a fish
- W_∞ = asymptotic weight of a fish
- K = growth coefficient from von Bertalanffy growth equation for length
- r = $t_r - t_0$, theoretical age of cohort entering fishery
- λ = $t_\lambda - t_r$, amount of time cohort is in fishery
- Y = yield in weight
- R = number of recruits at t_r
- Y/R = yield per recruit.

[5]R. B. Stone, Office of Fisheries Management, National Marine Fisheries Service, NOAA, Washington, DC 20235, pers. commun. 1975.

[6]Written by John E. Hollingsworth, Southeast Fisheries Center Beaufort Laboratory, NMFS, NOAA, Beaufort, NC 28516-9722 and Larry L. Massey, Southeast Fisheries Center, NMFS, NOAA, Virginia Key, Miami, FL 33144-1099.

TABLE 1.—Parameter estimates for yield per recruit models.

Species	von Bertalanffy parameters												
	K	L_∞ (mm)	t_0 (yr)	Source	a	b	Source	M	Source	t_r (yr)	Source	t_λ (yr)	Source
Red porgy, *Pagrus pagrus*	0.096	763	−1.88	Manooch and Huntsman 1977	2.524×10^{-8}	2.8939	Manooch and Huntsman 1977	0.35	Catch curves (Manooch and Huntsman 1977)	1	Manooch and Huntsman 1977	13	Manooch and Huntsman 1977
								0.20	Relationship to K				
Vermilion snapper, *Rhomboplites aurorubens*	0.198	627	0.13	Grimes 1978	1.722×10^{-8}	2.9456	Grimes 1978	0.25	Relationship to K	1	Grimes 1978	10	Grimes 1978
								0.40	For sensitivity analysis				
								0.50	Catch curve minimum				
White grunt, *Haemulon aurolineatum*	0.108	640	−1.01	Manooch 1977	1.452×10^{-8}	3.0214	Manooch 1977	0.57	Catch curves	2	Manooch 1977	13	Manooch 1977
								0.30	Choice of lower values for sensitivity analysis				
Red snapper, *Lutjanus campechanus* *L. vivanus* *L. buccanella*	0.160	975	0.00	Nelson and Manoch 1982	315×10^{-7}	2.887	Nelson and Manooch 1982	0.16	Relationship to K	1	Nelson and Manooch 1982	16	Nelson and Manooch 1982
								0.25	Higher value sensitivity analysis				
								0.34	Pauly 1980-81				
								0.40	Higher value for sensitivity analysis				
Black sea bass, *Centropristes striatus*	0.219	350	0.183	Mercer 1978 (Based on standard length[1])	2.654×10^{-8}	3.024	Cupka et al. 1973	0.30	Relationship to K and T_λ	1	Cupka et al. 1973	10	Cupka et al 1973
								0.50	For sensitivity analysis				
Speckled hind, *Epinephelus drummondhayi*	1,100.088	1,105	−1.92	Matheson and Huntsman[2]	1.1×10^{-8}	3.073	Matheson and Huntsman[2]	0.20	Pauly (1980-81) estimate Matheson and Huntsman[2]	1	Matheson and Huntsman[2]	25	Matheson and Huntsman[2]
Snowy grouper, *Epinephelus niveatus*	0.063	1,350	−2.32	Matheson and Huntsman[2]	7.0×10^{-8}	2.755	Matheson and Huntsman[2]	0.13	Pauly (1980-81) estimate Matheson and Huntsman[2]	1	Matheson and Huntsman[2]	25	Matheson and Huntsman[2]
Gag, *Mycteroperca microlepis*	0.112	1,290	−1.13	Manooch and Haimovici 1978	12×10^{-7}	2.996	Manooch and Haimovici 1978	0.20	Relationship to K	1	Manooch and Haimovici 1978	13	Manooch and Haimovici 1978
								0.35	Higher value for sensitivity analysis				
Scamp, *Mycteroperca phenax*	0.067	1,090	−3.91	Matheson et al.[3]	2.400×10^{-8}	2.910	Matheson et al.[3]	0.17	Pauly (1980-81) estimate Matheson et al.[3]	1	Matheson et al.[3]	25	Matheson et al.[3]

[1] TL = −11.2 + 1.34 SL (Cupka et al. 1973).

[2] R. H. Matheson, and G. R. Huntsman. 1983. Growth, mortality, and yield per recruit models for speckled hind, *Epinephelus drummondhayi*, and snowy grouper, *E. niveatus*, from the U.S. South Atlantic Bight. Unpubl. manuscr., 13 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

[3] R. H. Matheson III, C. S. Manooch III, and G. R. Huntsman. 1983. Growth, mortality, and yield per recruit models for the scamp, *Mycteroperca phenax*. Unpubl. manuscr., 14 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

Parameters t_0 and K are derived from the von Bertalanffy (1938) growth equation, and W_∞ is estimated as the weight corresponding to the asymptotic length (L_∞) based on a length-weight regression. Growth was assumed to be isometric.

The Beverton and Holt model implies instantaneous or "knife edge" recruitment with respect to age. Knife edge recruitment is not an apparent attribute of the hook-and-line fishery for at least two reasons. First, relatively large variation in size of fish of a single nominal age (resulting in part from long spawning seasons, e.g., vermilion snapper, Grimes and Huntsman 1980) makes it difficult to specify the initial age of capture. Second, the probability of a fish being taken by hook appears to increase somewhat more gradually with size than do probabilities associated with other gears.

Specifying an age at first recruitment is critical to determining the yield being taken from a stock. We believe that the mean age of recruitment provides a practical estimate of recruitment age for species which enter fisheries gradually.

Determination of Mean Age at Recruitment

Computation of mean age at recruitment occurs in three steps:

1) A minimum size at which fish first become vulnerable to the gear is determined from inspection of catch length frequencies. We designated the lower limit of the first class interval containing substantial numbers (usually five or more) of observations as the minimum size of vulnerability. This designation was usually unambiguous, but for species where it was not we evaluated more than one size.
2) The probability that a fish of a given age will equal or exceed the minimum size of vulnerability is determined on the assumption of a normal distribution of lengths about the mean length at age.
3) The probability for each age is multiplied by the numerical age value (e.g., 0.5×3). The products and probabilities are summed over all ages and the sum of the products is divided by the sum of the probabilities. The success of this treatment depends on exclusion from the calculations of ages beyond the first age at which all ($P \geq 0.99$) fish are vulnerable.

The estimation described here should be successful if the specified minimum size at vulnerability is accurate and if the relationship between size and recruitment is strong.

RESULTS

Regardless of the estimate of M, all models had a strikingly similar response to F (Table 2, Figs. 1-18). For median recruitment ages there was a rapid increase in yield as F increased, then an abrupt change as the rate of increase in yield declined at about $F = 0.3$, and finally a broad plateau of yield near the maximum. In general the absolute maximum yield per recruit was attained at a very high F relative to that needed to achieve 80 to 90% of the maximum yield. At the lowest estimate of M for all species examined, about 87%, on the average, of the maximum yield could be taken with an $F = 0.3$, which is

TABLE 2.—Summary of yield per recruit (Y/R) models for South Atlantic reef fish. M = instantaneous rate of natural mortality; F = instantaneous rate of fishing mortality; t_r = age at recruitment to the gear.

Species	For the model with M =	Maximal Y/R (g)	Where F =	and t_r =	At F =	and t_r =	Y/R is (g)	Percent max Y/R	At F =	and t_r =	Y/R is (g)	Percent max Y/R	Fig no.
Red porgy	0.35	150	0.80	2.9-4.0	0.50	≤5.5	130	87	0.50-0.30	1.0-5.6	110	73	1
	0.20	300	0.50	5.5-7.3	0.10	3.0-7.5	225	75					2
Vermilion snapper	0.50	100	1.75	3.5-4.0	0.70	2.5-4.0	90	90	0.40	2.5-4.0	80	80	3
	0.40	140	1.50	4.0-4.5	0.65	1.5-3.5	130	93	0.45	1.5-3.5	120	86	4
	0.25	250	0.55	4.5-5.0	0.30	2.5-5.5	200	80					5
White grunt	0.30	180	0.60	4.0-5.0	0.30	2.5-5.0	160	88	0.20	2.0-5.0	140	78	6
	0.57	30	0.55	4.5	0.25	2.7-5.0	25	83					7
Red snapper	0.16	1,600	0.50	6.5-8.0	0.30	5.5-7.5	1,500	94	0.20	4.0-7.5	1,300	81	8
	0.25	900	0.50	≥5.0	0.30	4.0-5.0	800	88	0.20	3.0-6.5	700	78	9
	0.34	550	0.60	4.0-4.5	0.38	3.5-4.5	500	91	0.20	2.0-5.0	400	73	10
	0.40	400	0.45	3.0-4.5	0.20	2.0-5.0	300	75					11
Black sea bass	0.50	50	0.90	2.5-3.5	0.30	2.5	40	80	0.20	1.0-3.5	30	60	12
	0.30	100	0.70	4.0	0.30	2.5-5.0	80	80					13
Speckled hind	0.20	1,200	0.50	5.0-7.0	0.25	4.0-7.0	1,100	92	0.19	3.0-7.0	1,000	83	14
Snowy grouper	0.13	1,300	0.38	9.0-11.0	0.20	7.0-10.0	1,200	92	0.15	5.0-11.0	1,100	85	15
Gag	0.35	900	3.25	4.5	0.70	3.5	850	94	0.30	2.0-4.8	700	78	16
	0.20	1,875	2.20	7.0	0.70	5.5-7.0	1,800	96	0.35	4.0-7.0	1,600	85	17
Scamp	0.17	900	0.72	6.5	0.23	3.0-7.0	800	89	0.15	1.0-8.0	700	78	18

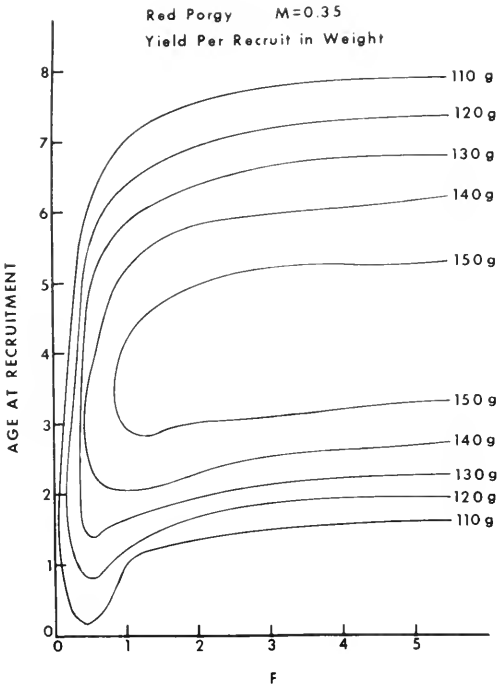

FIGURE 1.—Yield per recruit in weight of red porgy where M = 0.35.

less than half the average F needed to take the maximum. At the lower estimates of M for white grunt, vermilion snapper, red porgy, and black sea bass—those species that supply the greatest numbers and most weight to the headboat catch—86, 80, 92, and 80%, respectively, of the maximum yield can be taken with an $F = 0.3$. This is only 50, 55, 60, and 43% of F

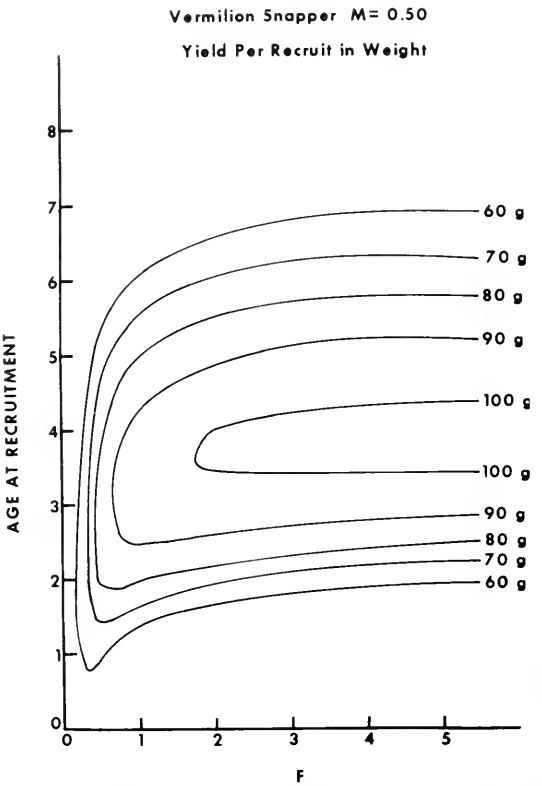

FIGURE 3.—Yield per recruit in weight of vermilion snapper where M = 0.50.

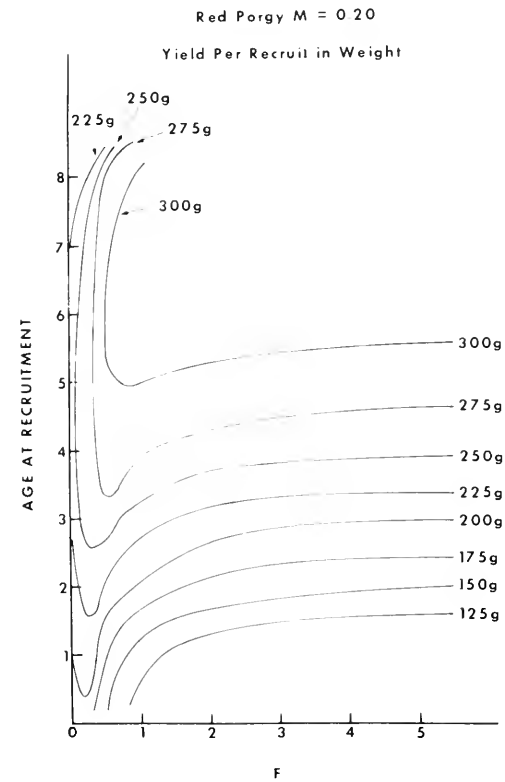

FIGURE 2.—Yield per recruit in weight of red porgy where M = 0.20.

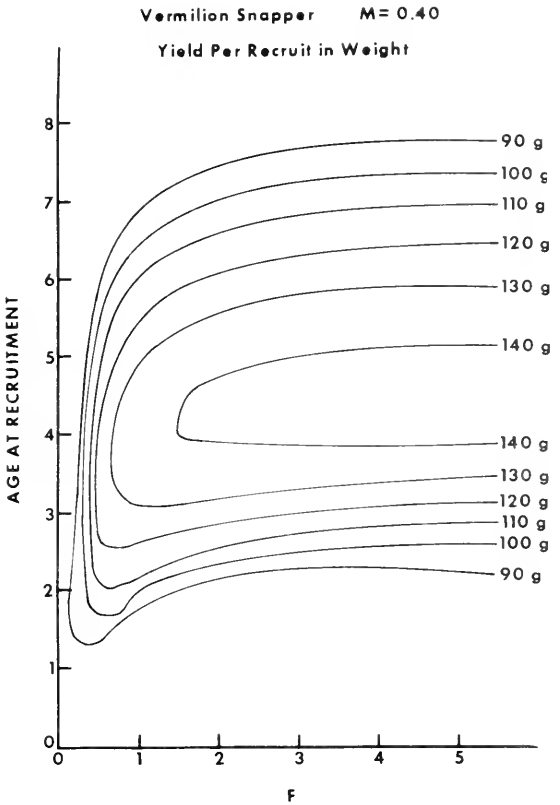

FIGURE 4.—Yield per recruit in weight of vermilion snapper where M = 0.40.

needed to take the maximum. At the highest estimates of M, 73, 60, 83, and 90% of maximum yield can be taken with an F of 0.3, which is 55, 17, 38, and 33%, respectively, of the effort needed for maximum yield.

For less numerous, larger species, conservative harvest strategies would be even more successful than for smaller fishes. For instance, for speckled hind, snowy grouper, scamp, and for gag and red snapper at their lowest M estimates, 94, 95, 89, 94, and 78% of the maximal yield per recruit can be taken if $F = 0.3$ which is 60, 79, 42, 14, and 60% of the F required to take that maximum. Even at the high estimate of M for gag and red snapper, 78 and 88% of the maximal yield per recruit are available if $F = 0.3$. This F is only 9 and 42% of that needed to take the maximum.

While the absolute relationship of recruitment age to yield varies according to species, it is true for all species that the lower the fishing mortality, the greater the range of recruitment ages at which the highest available yield may be taken. At $F = 0.3$, recruitment age, regardless of M, could range over 4 or more years for 9 of the 18 models without substantial loss of yield; for the remaining models it could range over 3 yr.

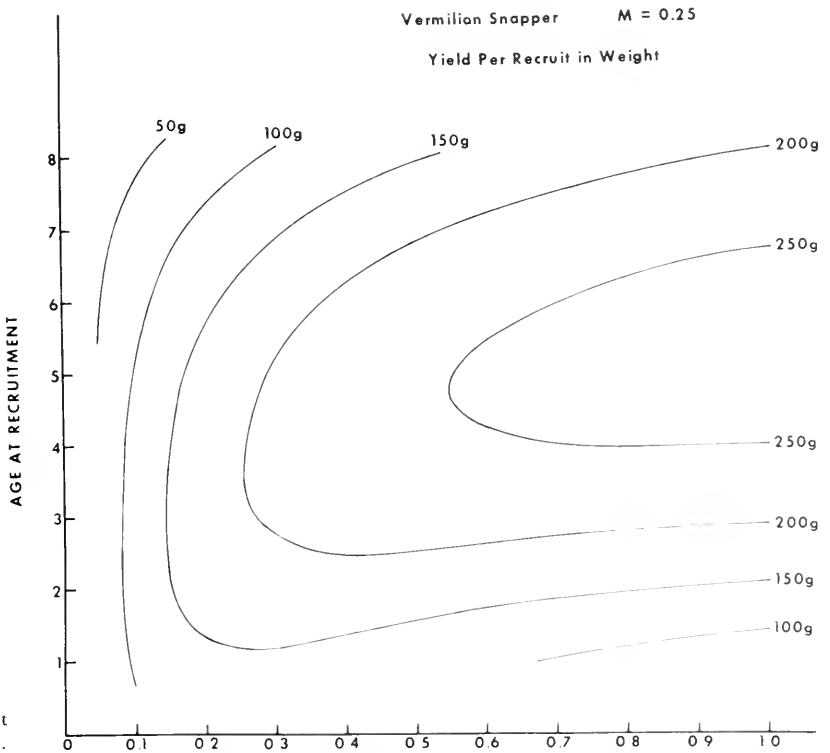

FIGURE 5.—Yield per recruit in weight of vermilion snapper where M = 0.25.

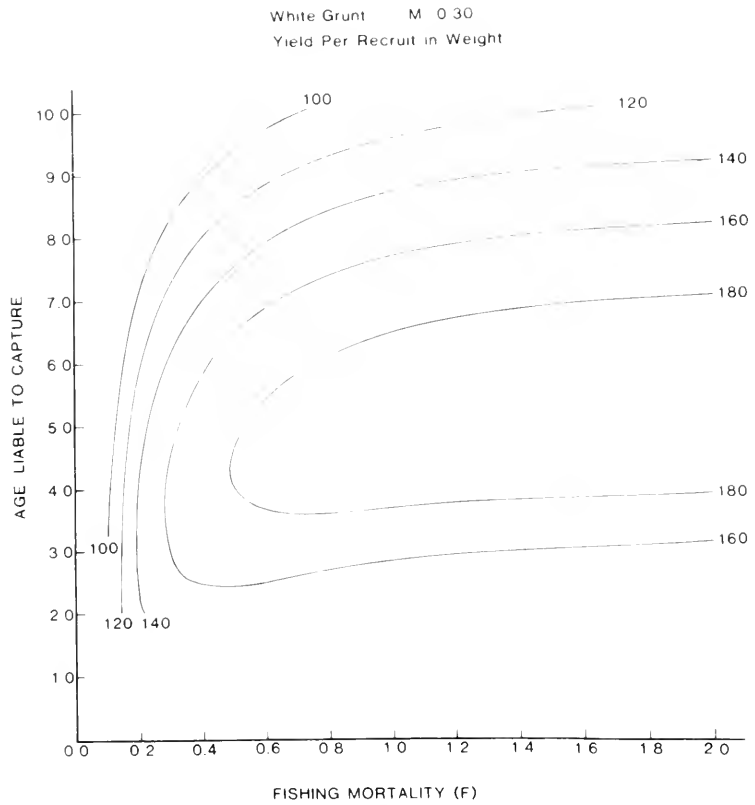

FIGURE 6.—Yield per recruit in weight of white grunt where M = 0.30.

It is apparent that on a yield per recruit basis the fishery response to an increase in F is a nonlinear decrease in catch per unit effort (CPUE). The CPUE decreases most rapidly after F exceeds about 0.3 for most species. Further, the range of recruitment ages at which any given yield is available increases rapidly as F decreases.

STATUS OF THE FISHERY

Despite slight differences in the periods when each species was studied, reasonable generalizations can be made about the state of reef fish stocks off North Carolina and South Carolina in the mid to late 1970's.

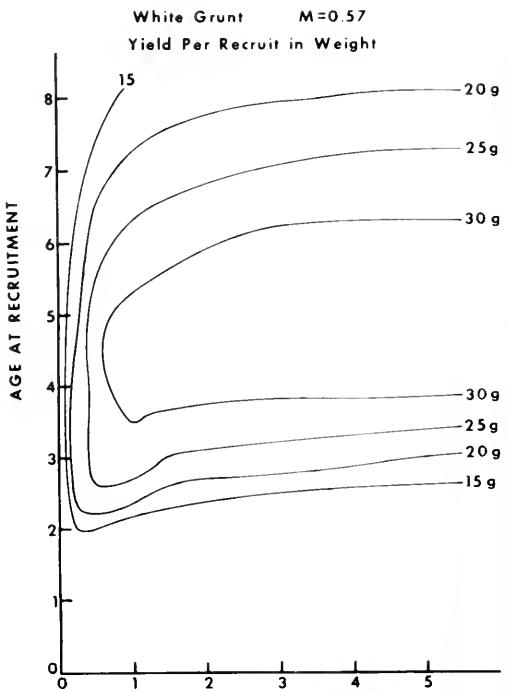

FIGURE 7.—Yield per recruit in weight of white grunt where M = 0.57.

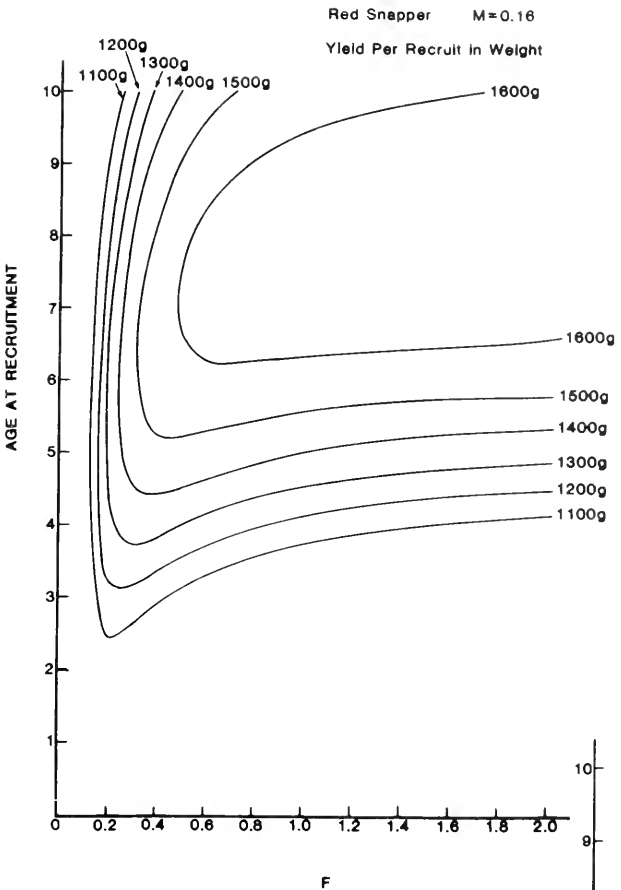

FIGURE 8.—Yield per recruit in weight of red snapper where M = 0.16.

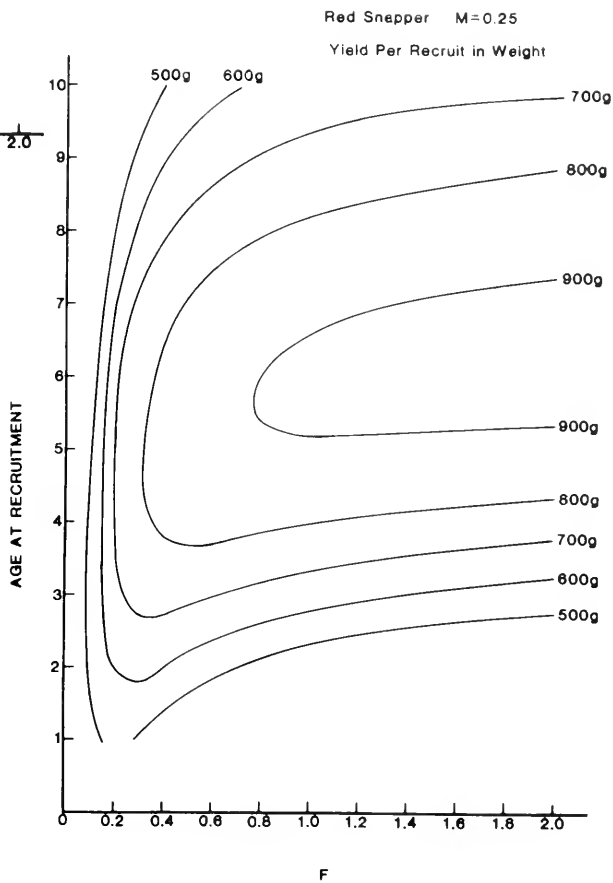

FIGURE 9.—Yield per recruit in weight of red snapper where M = 0.25.

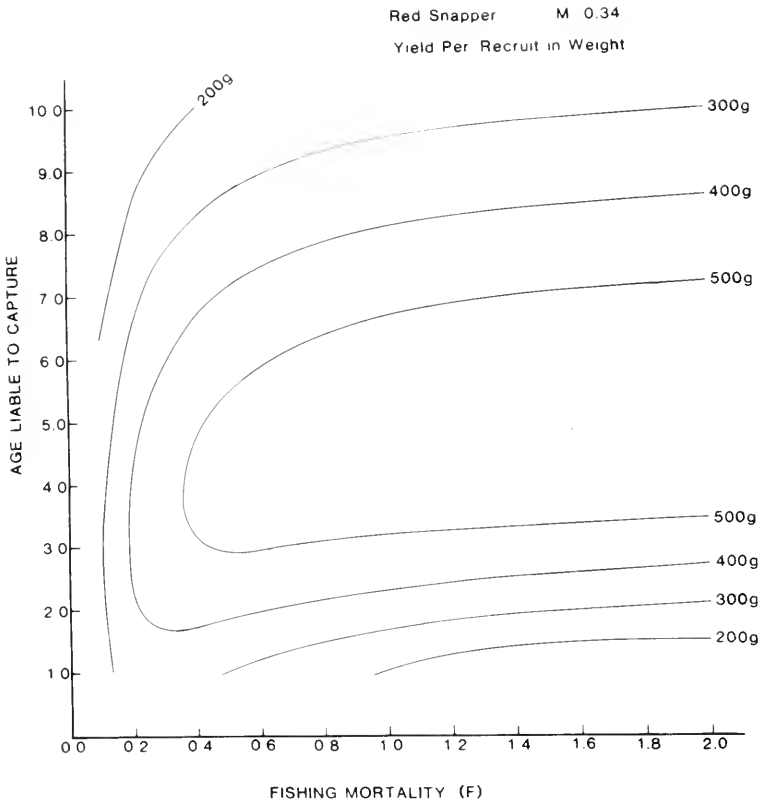

FIGURE 10.—Yield per recruit in weight of red snapper where M = 0.34.

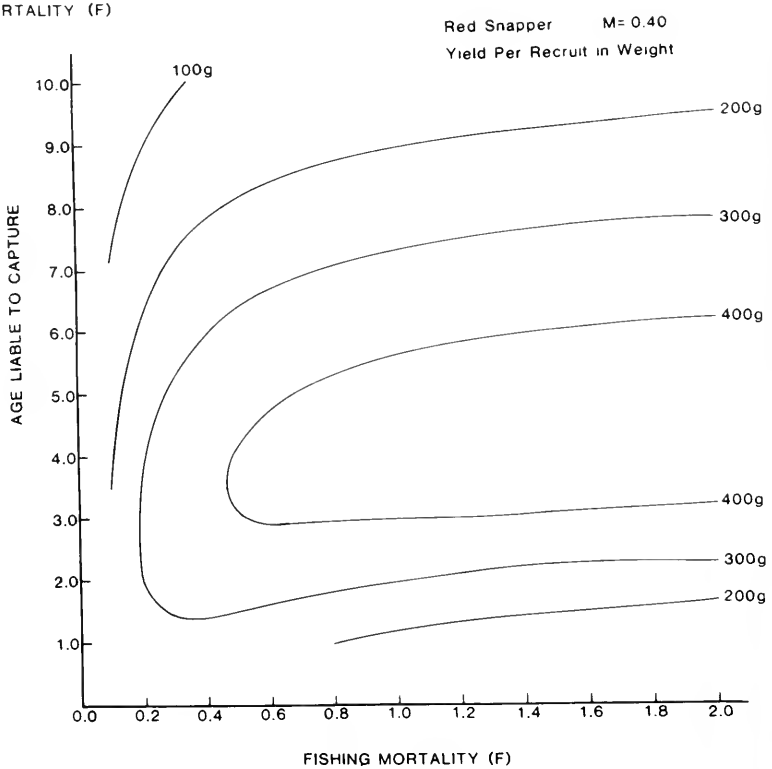

FIGURE 11.—Yield per recruit in weight of red snapper where M = 0.40.

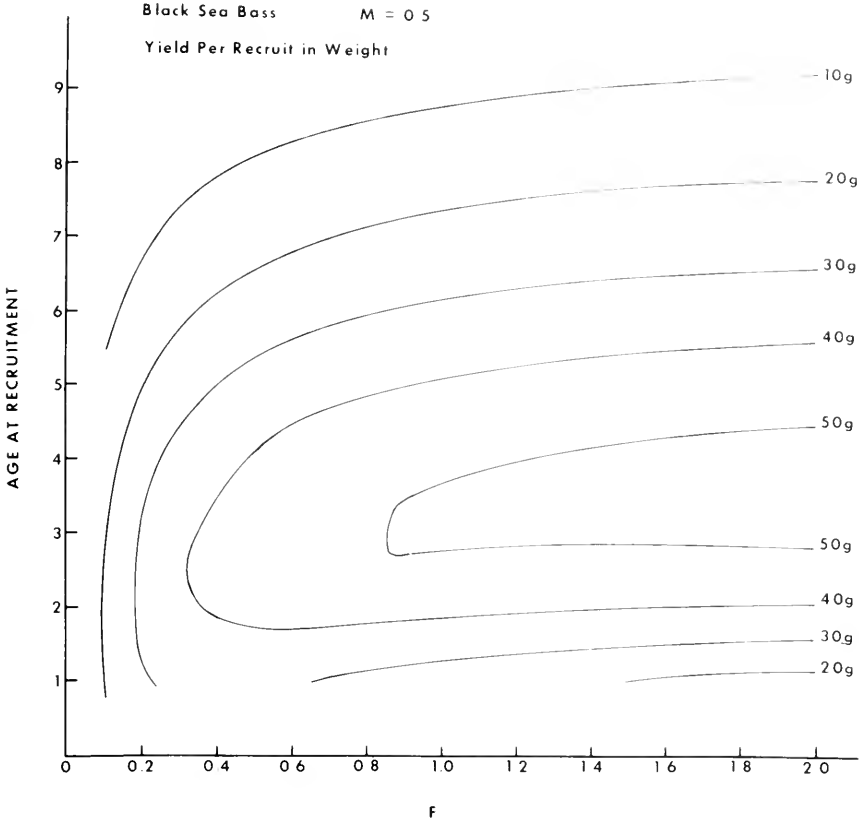

FIGURE 12.—Yield per recruit in weight of black sea bass where M = 0.5.

Regardless of the M estimates chosen, of the recruitment ages specified, or of whether the recreational or commercial fishery is discussed, it is apparent that most of the important species in the headboat fishery were providing the bulk of their readily available yield per recruit (Table 3). At the lowest M estimates all species studied (except deep water black sea bass) were subjected to sufficient fishing mortality on the headboat grounds to provide at least 70% (mean = 87%) of the maximal yield per recruit. Even at the estimates provided by the highest M values and least favorable recruitment ages, 50% or more (mean = 68%) of the maximal yield per recruit was taken for all species except red snapper (40%).

Stocks available to the commercial fishery (including those on the headboat grounds) were similarly exploited. At the lowest M estimates, at least 70% of the maximal yield per recruit was harvested for all species (black sea bass and white grunt were not taken commercially) except speckled hind for which 50% was taken. The mean for all species was 81%. At the high M estimates, 40% was the minimum taken (for red snapper) and the mean for all commercial species was 67%.

It appears that by the late 1970's most of the practically available yield was being taken from the grounds fished at that time. Several species were incurring sufficient F to provide virtually all the yield per recruit possible while F for most others was at the level beyond which increased yield per recruit comes only with very large increases in effort and concomitant large decreases in CPUE.

DISCUSSION

Any value of our models lies in their utility to management of reef fish stocks. Some information about management can be derived directly from the models without resort to adjunct information; for instance, the models alone reveal that if recruitment age can be kept moderately high, yield per recruit will stay high regardless of how great F becomes. Thus protection of yield per recruit can be obtained without having to know what F is, or without having to

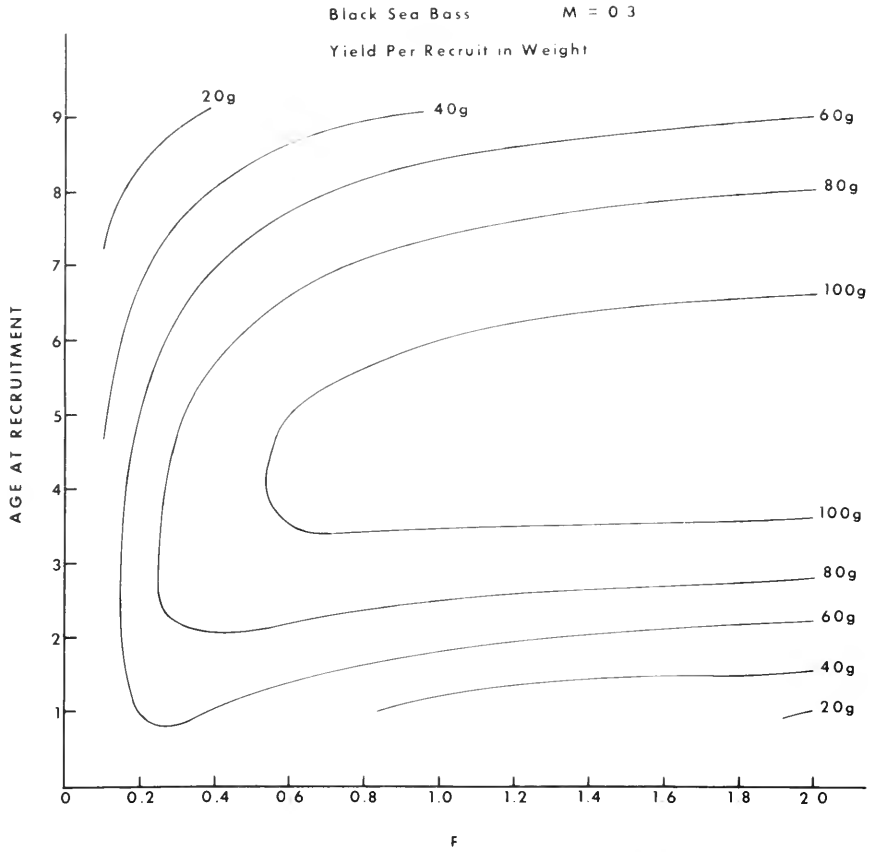

FIGURE 13.—Yield per recruit in weight of black sea bass where M = 0.3.

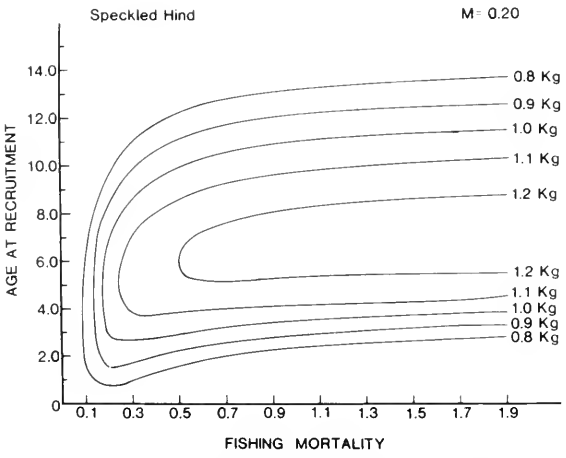

FIGURE 14.—Yield per recruit in weight of speckled hind where M = 0.20 (from Matheson and Huntsman, see Table 1).

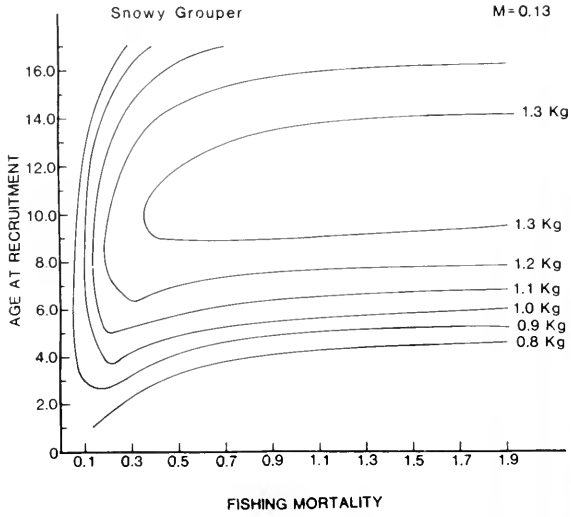

FIGURE 15.—Yield per recruit in weight of snowy grouper where M = 0.13 (from Matheson and Huntsman, see Table 1).

TABLE 3.—Status of fishery. M = instantaneous rate of natural mortality; F = instantaneous rate of fishing mortality; $Z = F + M$ instantaneous rate of total mortality; Y/R = yield per recruit.

Species	M estimates	Z Value	Z Period	Z Source	Fishery	Recruitment size (mm)	Age (yr)	Y/R available at F =	Y/R available g	Percent max Y/R
Red porgy	0.20	0.65	1972-74	Manooch and Huntsman 1977	Headboat	300	4.1	0.30	120	80
	0.35					or		0.45	280	93
						325	4.3	0.30	120	80
							4.1	0.45	290	97
					Commercial handline	300		0.30	120	80
							2.1	0.45	280	93
					Commercial trawl	200		0.30	125	83
						or	2.6	0.45	225	75
						250			125	83
									250	83
Vermilion snapper	0.25	0.67	1972-73	Grimes, pers commun.[1]	Headboat	225	3.5	0.32	225	90
	0.40					or		0.27	100	71
	0.50					250		0.17	60	60
							3.8	0.32	225	90
								0.27	100	71
								0.17	60	60
					Commercial Handline	300	4.5	0.32	225	90
								0.27	100	71
								0.17	60	60
					Commercial trawl	200	3.3	0.32	225	90
								0.27	100	71
								0.17	60	60
White grunt	0.30	0.73	1972-75	Manooch 1977	Headboat	250	4.4	0.43	175	92
	0.57					or		0.16	15	50
						300	5.9	0.43	170	90
								0.16	15	50
					Commercial handline and trawl	species rarely taken				
Red snapper	0.16	0.38	1974-78	Nelson and Manooch 1982	Headboat and commercial handline	500	6.0	0.22	1,300	81
	0.25							0.13	575	64
	0.34							0.04	200	40
	([2])									
					Commercial trawl	450	5.0	0.22	1,300	81
								0.13	500	56
								0.04	200	40
Black sea bass	0.30	0.83 (depth <40m)	1978	Low 1981	Headboat	400	4.0	0.53 shallow	98	98
								0.30 deep	80	80
		0.60 (depth >40M)			Commercial handline and trawl	species rarely taken				
	0.50				Headboat	40	4.0	0.33 shallow	35	70
								0.10 deep	10	20
Speckled hind	0.20	0.35	1976-79 headboat	Matheson and Huntsman[3]	All fisheries	365	3.3	0.15	950	79
		0.25	1976-79 commercial handline					0.05	600	50
Snowy grouper	0.13	0.38	1976-79 headboat	Matheson and Huntsman[3]		365	3.3	0.25	950	73
		0.24	1976-79 commercial handline					0.11	920	70
Gag	0.20	No estimate[4]		Manooch and Haimovici 1978	Headboat	—	1.0	[4]0.36	1,050	58
					Commercial handline	750	6.6	[4]0.68	1,800	100
						800	8.0	[4]0.68	1,700	94
	0.36		1978-79 commercial handline		Headboat	—	1.0	[4]0.36	650	67
					Commercial handline	—	6.6	[4]0.68	650	72
							8.0	[4]0.68	480	53
Scamp	0.17	0.53	1976-79 headboat	Matheson et al.[5]	Headboat 1972-75	500	5.4	0.36	850	94
					Headboat 1977-79	350	3.1	0.36	800	89
		0.85	1976-79 commercial handline		Commercial handline	400	4.0	0.68	900	100

[1] Churchill B. Grimes, Department of Horticulture and Forestry, Rutgers University, P.O. Box 231, New Brunswick, NJ 08903

[2] M of 0.40 omitted because it was greater than estimated F.

[3] R. H. Matheson, and G. R. Huntsman. 1983. Growth, mortality, and yield per recruit models for speckled hind (*Epinephelus drummondhayi*) and snowy grouper (*E. niveatus*) from the U.S. South Atlantic Bight. Unpubl. manuscr. 13 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

[4] F for gag assumed to be same as for scamp which occupies same habitat and is taken simultaneously with same gear.

[5] R. H. Matheson III, C. S. Manooch III, and G. R. Huntsman. 1983. Growth, mortality, and yield per recruit models for the scamp, *Mycteroperca phenax*. Unpubl. manuscr., 14 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

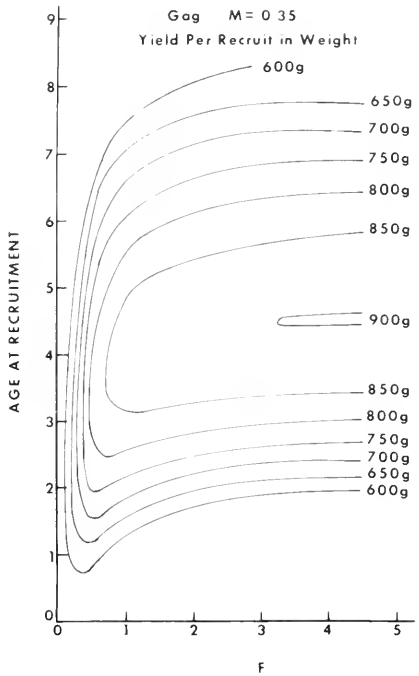

FIGURE 16.—Yield per recruit in weight of gag where M = 0.35.

deal with the technically and politically troubling problems of restricting F. However, much of the knowledge required for management requires information in addition to knowledge of the yield per recruit responses. Currently much of this additional information is imprecise.

Despite missing and imprecise information, concern about reef fish stocks has been sufficiently great to foster creation of reef fish management plans by the South Atlantic, Gulf of Mexico, and Caribbean Fishery Management Councils. The basis of these plans has been use of "the best available information" as prescribed in the Fishery Management and Conservation Act. In the remainder of this discussion we proffer some uses and interpretations of our yield per recruit models and other information about reef stocks that are not necessarily precise but may, indeed, be the "best available information."

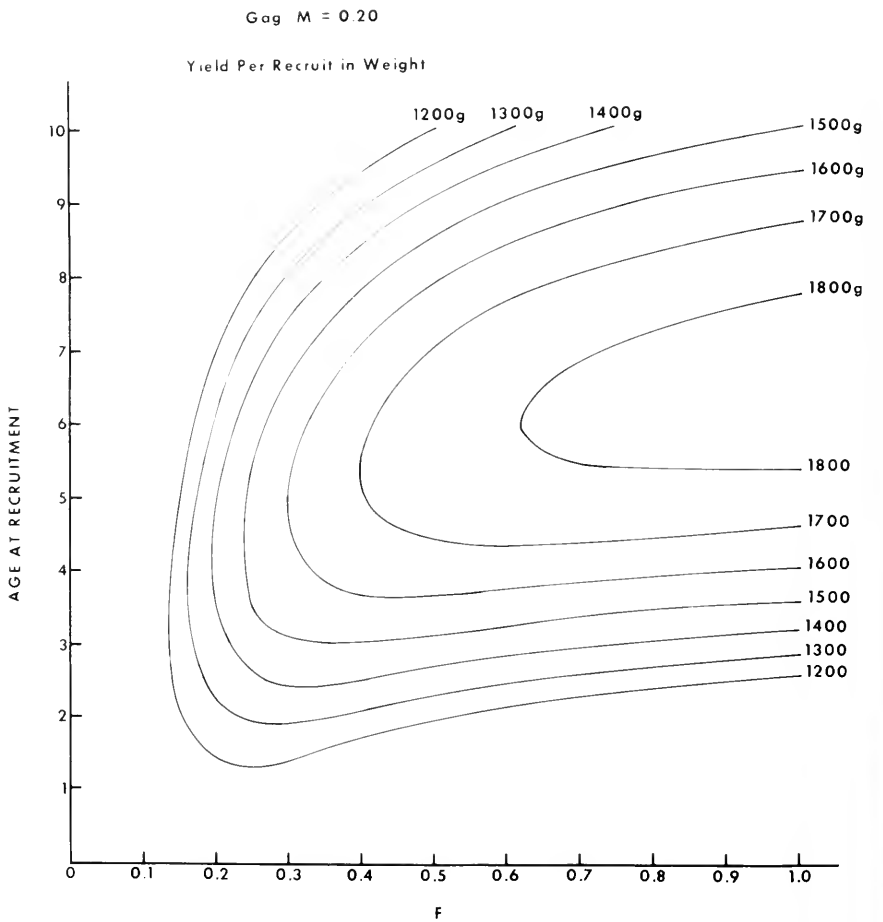

FIGURE 17.—Yield per recruit in weight ,of gag where M = 0.20.

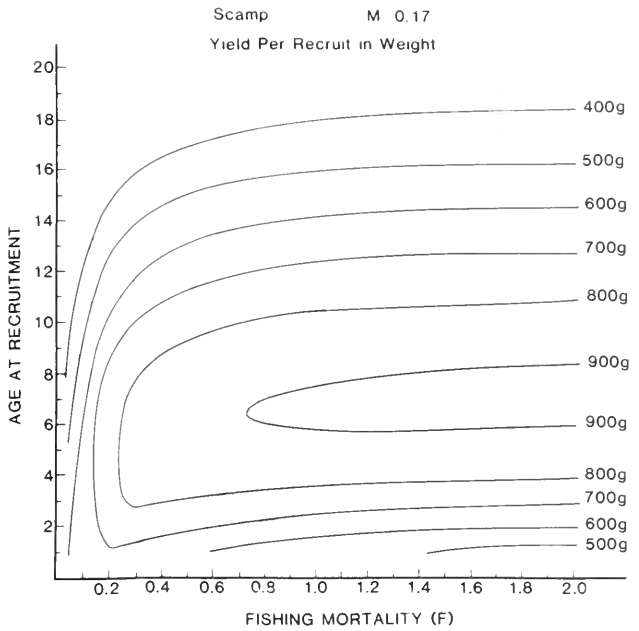

FIGURE 18.—Yield per recruit in weight of scamp where M = 0.17 (from Matheson, Manooch and Huntsman, see Table 1).

For instance, we believe that our yield per recruit models allow preliminary estimates of MSY, estimates required in fishery management plans promulgated under the Fishery Conservation and Management Act. Current catches are an estimate of MSY if three fairly safe assumptions, concerning fishing effort, amount of recruitment, and recruitment ages, are fulfilled. The first is that current effort is sufficient to take most of the yield. As early as 1975, F for most important species was great enough that 70 to 85% of the maximum yield was taken. The most cursory observation would reveal that commercial fishing has increased an enormous amount since 1976. Consequently F should now be more than sufficient to take all the yield practically available. The second assumption is that recruitment was sufficient to fully populate the reefs. The major factor limiting reef fish abundance is the scarcity of habitat (Ehrlich 1975), rather than scarcity of recruits. Reef fishes in general have long-lived larval stages allowing replenishment of local populations from distant spawning stocks. Observations of natural and artificial reefs suggest that recruits are almost always abundant (e.g., Anonymous 1971; Stone et al. 1979). The third assumption is that recruitment ages remain within a range that will allow maximum yields. It appears that current recruitment ages for major species either are within, or close to, this range.

Allocation of the catch to various sectors of the fishery may eventually become important. Allocators will need to understand the relative impact of various types of gear on the stock and the relationship between effort and mortality. To provide a preliminary estimate of relative impact, we calculated a crude measure of the relative fishing power of the three most important vessel types in the Carolina area. Handline vessels operating from South Carolina ports averaged 321 kg/d (Ulrich et al. 1977), "high-rise" trawlers took 958 kg, and headboats caught 208 to 250 kg (Huntsman 1976b; Huntsman et al 1978). Thus handline boats were about 1.3 to 1.5 times as effective and trawlers about 3.8 to 5.2 times as effective as headboats. We cannot perfectly equate the three types, however, because each takes different species (Ulrich et al. 1977).

The disparity in species vulnerability might allow partitioning the resource without conflict—red snapper to trawlers; groupers to handliners; porgies, grunts, and vermilion snapper to headboats. But we do not believe such partitioning is desirable. Large trophy fish constitute only a small portion of the headboat catch but are probably extremely important in motivating the fishermen. Further we believe pursuit of large fish catalyzes the taking of smaller and more abundant species in offshore areas. Only about 30,000 groupers and red snapper (totaling about 182 t) were taken annually by headboats in North Carolina and South Carolina from 1972 to 1974, compared with some 400,000 individuals of other species (excluding black sea bass) totaling

about 409 t (Huntsman 1976b). If the opportunity for catching large fish were removed, anglers might prefer to patronize smaller and less expensive boats that fish inshore where large catches of smaller fish can also be made.

Relating fishing mortality to fishing effort is difficult because we lack a long series of concurrent effort and mortality estimates. Catch curves for red porgy, vermilion snapper, and white grunt suggest that if M is indeed low, F through 1974 was about 0.3 to 0.4 and was mostly attributable to headboats. Headboat activity for North Carolina and South Carolina was reported as 48,989 angler days in 1972, 59,515 in 1973, and 85,608 in 1974 (Huntsman 1976a). Because we know effort was underestimated, we used the 1975 data to determine the percentage of vessels omitted in earlier years. Our adjusted estimates for 1972, 1973, and 1974 were 71,902, 85,561, and 88,513 angler days, respectively. The 3-yr mean was 81,922, corresponding to about 2,350 headboat trips (using the 1974 average of 34.87 anglers/trip). We suggest than an F of about 0.35 was generated by this effort.

Because F on the headboat grounds was quite likely 0.3 to 0.4 in the period 1972-74, the annual catch (450 to 600 t exclusive of black sea bass) for that period should be an estimate of MSY. This catch could be taken with about 2,350 headboat trips (1 d), 1,679 handline vessel days (1.0 handline vessel day = 1.4 headboat day), 522 d of trawling (the range is 452 to 618 d depending on the coversion factor selected), or with some combination of these vessel efforts. Additionally, a headboat fishery at the 1972-74 level should take about 273 t of black sea bass, if the trap fishery remained at the 1972-74 level.

It should not be surprising that near-maximum yields could be taken by a small and apparently inefficient fishery. Historically, reef fish stocks have been vulnerable even to primitive fisheries. Munro et al. (1971) described Jamaica's reef fish stock as overexploited. Brownell and Rainey (1971) reported that inshore reef fishes in the U.S. Virgin Islands were heavily fished, even though handlines and primitive traps fished from unpowered vessels were the only gear. The hook-and-line red snapper fishery in the northern Gulf of Mexico has been sustained by constant expansion of the fishing grounds rather than by continued good catches on existing grounds (Crowley 1983).

Continued laissez-faire management of the snapper-grouper fishery may result in a disproportionate allocation of the catch. If the trawl and handline sectors reduce the abundance of large species to such a level that an acceptable CPUE of trophy fish cannot be experienced by headboat fishermen, the headboat fishery might be weakened. During hundreds of hours spent mingling with the public while sampling headboat catches, we have observed that large (>10 kg) snappers and groupers are very important in promoting headboat ticket sales. Many headboat operators use mounted specimens of large fish to attract customers. Headboat fishing is arduous and expensive ($40-$50/d in 1982) and large catches of small fish can usually be made easily and cheaply from piers and small boats in the Carolinas.

In this paper we have employed yield per recruit models to suggest guidelines for managing the South Atlantic Bight reef fishery. We believe that we have shown that large and intensive fisheries probably are not needed to fully harvest reef fish in the South Atlantic Bight and that the Carolina headboat fishing grounds are probably fully exploited. A low intensity fishery should take most of the yield available, produce large, high value fish, and allow a sufficient number of fish to live to ages of maturity and sexual transition to allow sustained high yields.

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HARD CLAM, *MERCENARIA MERCENARIA*: SHELL GROWTH PATTERNS IN CHESAPEAKE BAY[1, 2]

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ABSTRACT

Dark bands in the middle homogenous layer of *Mercenaria mercenaria* shells, formed each summer and early fall in lower Chesapeake Bay experimental and wild populations, were used to determine age. Distinct growth cessation marks caused by low winter water temperatures were present in some annual increments, but were not formed each year by each individual. This was due primarily to differences among age groups in seasonal band formation. *Mercenaria mercenaria* younger than 8 years tended to form light bands in fall and spring, which were bisected by distinct winter growth cessation marks. Older individuals tended to form light bands only in spring; thus, winter growth cessation marks were masked by dark bands deposited from summer through winter. These results differ from *M. mercenaria* shell growth patterns found elsewhere along its range, suggesting that time of annulus formation varies with latitude.

One microgrowth increment in the prismatic layer was formed during each solar day of activity (growth). From a 106-day monitored growth experiment in summer 1980, the slope of the regression describing the relationship between the number of increments formed (Y) and days (X) was not significantly different from 1.00 ($t_s = 1.23, P > 0.20, r = 0.98$). Inactive periods, represented by growth cessation marks, became longer and/or more frequent with increasing age and length of monitored growth periods. Both factors, increasing age and length of monitored growth periods, contributed to decreased increment-to-day ratios.

There has been considerable research on the periodicity of line, band, zone, and increment formation in bivalve shell microstructure since Barker's (1964) initial description (see Lutz and Rhoads 1980). Annual shell increments have been identified in shells of many species, including *Arctica islandica* (Thompson et al. 1980), *Mya arenaria* (MacDonald and Thomas 1980), *Spisula solidissima* (Jones et al. 1978), and *Geukensia demissa* (Lutz 1977; Lutz and Rhoads 1978[5]; Lutz and Castagna 1980). In shells of the hard clam, *Mercenaria mercenaria* (Linneaus, 1758), annual increments have been described in two distinct ways: 1) Regions of narrow and wide microgrowth increments in the outer prismatic layer resulting from seasonal changes in growth rate (Pannella and MacClintock 1968; Rhoads and Pannella 1970) and 2) a single pair of translucent and opaque zones in the middle homogenous layer (as viewed in thin radial section; Clark 1979). However, these definitions are not mutually exclusive, since translucent zones are associated with narrower microgrowth increments (or slower growth rates) than opaque zones (Clark 1979).

The season of slow shell growth by *M. mercenaria* varies along its latitudinal range (Gulf of St. Lawrence to Gulf of Mexico; Franz and Merrill 1980). In the north-central part of its range (Connecticut, Massachusetts, and New Jersey), reduced growth rates and growth cessations occur during winter, microgrowth increments being between 2 and 100 times narrower than those formed in summer (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Kennish and Olsson 1975). Conversely, *M. mercenaria* in the southern part of its range (Georgia) grow slowly in summer and early fall when translucent zone formation occurs (Clark 1979). *Mercenaria mercenaria* in Georgia may also grow throughout winter, since no winter growth cessation marks have been observed in shell microstructure (Clark 1979). Thus, latitudinal variation may preclude the universal application of defined annual shell increments to all populations along the range of the hard clam. Shell growth patterns of local populations must be analyzed to determine its unique features.

There have been no previous stiudies of microstructural shell growth patterns of *M. mercenaria* in lower Chesapeake Bay. Hard clams used in this study to

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determine annual shell increments were from experimental growth lots established by Loesch and Haven (1973). Monitored growth periods of hard clams in these lots, as long as 13 yr, are the longest of any bivalve shell growth study in the literature.

MATERIALS AND METHODS

Sources of *Mercenaria mercenaria*

Mercenaria mercenaria were obtained from three sources for use in this study: 1)Four long-term experimental growth lots, 2) two short-term experimental growth lots, and 3) natural population or wild stock. Long-term studies lasting a maximum of 13 yr were initiated in 1967 and 1969 at four subtidal locations in the lower James and York Rivers [Table 1; see also Loesch and Haven (1973) for a description of long-term growth lots]. Hard clams in each group were numbered individually (using an indelible ink pen) and measured (shell length—greatest distance along the anterior-posterior axis—to the nearest 0.1 mm) prior to placement directly in the substrate by scuba-equipped divers. As many hard clams as possible were retrieved, measured, and replanted at the lot location each fall through 1972. From fall 1972 to the dates of final collection between 1976 and 1980, each group remained in the substrate continuously. Shell height (greatest distance from umbo to ventral edge) was not measured from 1967 to 1972. After final collection, however, shell length measurements obtained each fall were used to identify growth rings on the shell exterior of each hard clam. Shell height was measured at each of these growth rings to yield a size-time relationship along the height axis, along which valves were cut for microstructural analyses.

Short-term growth studies began on 16 October 1979 and continued for 20 mo (Table 1). Age 2+ *M. mercenaria* were obtained from the Virginia Institute of Marine Science hatchery on Virginia's Eastern Shore (Castagna and Kraeuter 1977). Each individual was numbered, measured (shell length and height), and transplanted to a subtidal location in the York River. Collections of four hard clams each were made from this T series group at approximately monthly intervals. Shell growth did not resume until April 1980, probably due to the combined effects of salinity difference between the Eastern Shore (28-30 ppt) and York River (16-18 ppt) and low winter water temperatures. Because of this, the exact date of growth resumption in spring 1980 was unknown.

The TI series was composed of T series hard clams in which a growth cessation mark was induced in spring 1980 (Table 1). This was used as a baseline for determining the periodicity of formation of prismatic microgrowth increments. Growth cessation marks in shell microstructure were induced by the thermal shock method of Richardson et al. (1979). On 29 May 1980, 16 T series hard clams were collected, measured, renumbered, and placed in a moist incubator at 4°C for 24 h to disrupt shell growth. TI series hard clams were replanted on 30 May 1980 in a segregated area of the T series location. Three TI series hard clams were collected and measured on 22 June, 18 July, 8 August, and 13 September 1980.

Mercenaria mercenaria from the natural population of lower Chesapeake Bay and its tributaries ($N = 24$) were collected during winter, spring, and summer of 1978 and 1980. Shell height and length of each hard clam were measured.

TABLE 1.—Experimental groups of *Mercenaria mercenaria* used in long-term and short-term studies.

Study and lot no.	Location	Date of lot establishment	*N*	Date of final collection
Long-term study:				
I	York River	9/67	16	12/76
			1	6/80
			1	7/80
II	York River	9/67	15	8/76
			10	1/78
			8	2/78
XI	James River	1/69	26	7/79
XIV	York River	9/69	6	8/76
			6	1/76
Short-term study:				
T series	York River	10/16/79	71	Monthly to 6/27/81
TI series	York River	5/30/80	12	Monthly to 9/13/80
Total			172	

Preparation of Acetate Peels

Acetate peels of polished and etched radial shell surfaces were prepared from single valves of each experimental and wild hard clam according to the methods of Stewart and Taylor (1965) and Pannella and MacClintock (1968). Valves were cleaned and air-dried for several days prior to being embedded in liquid casting plastic[6] and cut from ventral edge to umbo along the height axis with a geological saw. One of the sectional surfaces was ground and polished with optical quality grits and cerium oxide on glass plates and a cloth-covered disc polisher. Polished surfaces were etched in either 1% or 5% HCl for 20-60 s and dried completely. Clear acetate sheets (0.003-in thick) were carefully melted on each etched

[6]American Handicrafts, Inc., Fort Worth, Texas (reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA).

surface with acetone and air-dried for at least 1 h, after which they were stored between glass microscope slides.

Analysis of Shell Microstructure—Terminology and Methods

Clark (1979) described a series of translucent and opaque zones in the middle homogenous layer of thin sections of *M. mercenaria* shells. These zones were associated with narrow and wide prismatic microgrowth increments, respectively (Table 2). In this study, acetate peels of etched radial sections, rather than thin sections, were used. Regions of low and high light transmittance through acetate peels corresponded exactly with "dark" and "light bands," respectively, in the middle homogenous layer of polished shell sections (Table 2; see Figure 2). For convenience, we refer to regions of low and high light transmittance through acetate peels as dark and light bands. Clark's description of translucent zones in thin sections could also be correctly applied to dark bands in acetate peels, since both were associated with narrow microgrowth increments. However, regions of the middle homogenous layer associated with narrow increments appear translucent in thin sections, but optically dense or "dark" in acetate peels. Conversely, opaque zones in thin sections appear transparent or "light" on acetate peels (Table 2). Since Clark's terminology from analyses of thin sections does not strictly apply to middle homogenous layer growth patterns observed on acetate peels, we have used the new terms "dark" and "light bands," as outlined in Table 2. However, translucent zones and dark bands, and opaque zones and light bands describe the same growth pattern in shell microstructure.

Acetate peels were analyzed on a compound microscope at 100× magnification with nonpolarized light. Known annual shell increments formed between 1967 and 1972 by experimental hard clams in lots I, II, XI, and XIV were analyzed for annually produced patterns. Similarly, total shell increments deposited between 1972 and the date of final collection by each experimental hard clam in the four lots should contain the same number of annual increments as there were years in the period. Annual increments were defined primarily in the middle homogenous layer due to the simplicity of its growth pattern (dark and light bands) compared with the outer prismatic layer (microgrowth increments). Band color at the shell margin was catalogued by season of collection in both experimental and wild hard clams to determine time of year of dark and light band formation. To increase the number of fall observations, band color was also observed dorsal (toward the umbo) to each disturbance mark in shell microstructure of long-term experimental hard clams caused by measurements in 1967-72. Observations of band color in each season were catalogued by three age groups defined by Kennish (1980): Young—under 3 yr of age; mature—3 to 8 yr; old—over 8 yr.

Microgrowth increments in the prismatic layer (their average width and number) were used to describe bands in the middle homogenous layer. Individual increments were traced through the prismatic to the middle layer to identify single increments corresponding to the dorsal (toward the umbo) and ventral (toward the shell margin) surfaces of each band. Band width was measured along the surface of maximum growth (SMG) in the prismatic layer (Pannella and MacClintock 1968) using an ocular reticle with an estimated accuracy of ±1 reticle unit (10.8 μm at 100×). Microgrowth increment counts were made only in shell regions bracketed by growth disturbance marks of known formation time or one growth disturbance mark and the shell margin (collection date). This allowed determination of the periodicity of increment formation. All microgrowth increment counts in bands or annual shell increments were averages of three trials. Guidelines suggested by Crabtree et al. (1979/1980) were used to distinguish and count microgrowth increments. Least squares linear regressions (Sokal and Rohlf 1969) of increment counts on days in monitored growth

TABLE 2.—Terminology used to describe growth patterns in the middle homogenous layer of *Mercenaria mercenaria*.

			Descriptive terms for pattern associated with:	
Reference	Technique	Light	Narrow microgrowth increments	Wide microgrowth increments
Clark (1979)	Thin section	Transmitted	Translucent zone	Opaque zone
This study	Acetate peel	Transmitted	Low light transmittance region	High light transmittance region
This study	Polished shell section	Reflected	Dark band	Light band

periods were used to support conclusions on the periodicity of increment formation. Comparisons of regression coefficients were done using either a t-test (t_s) if the comparison was between a calculated coefficient and its expected value, or an F-test (F_s) if the comparison was between two calculated coefficients (Sokal and Rohlf 1969). To ascertain effects of age on number of increments formed in annual shell increments, microgrowth increments were counted between each pair of fall measurement disturbance marks (MDM) in long-term experimental hard clams (lot XI) formed 1 yr apart. Each count was divided by the number of solar days between measurements, yielding the percent agreement (Richardson et al. 1979) between increments and days. Data were pooled by absolute hard clam age.

RESULTS

Annual Shell Increments—Light and Dark Bands

The series of fall MDM divided the shell microstructure of 89 long-term experimental hard clams into 177 known years of shell growth formed between 1967 and 1972 (Table 3). A single dark band in the middle homogenous layer had been formed within each known annual shell increment (see Figure 2). Furthermore, dark bands were located dorsal to the MDM, suggesting that they had been formed each summer. To confirm this observation, the number of complete summers from fall 1972 to the date of final collection in each hard clam was compared with the number of completed dark bands observed in shell microstructure formed in these periods (Table 4). Complete dark bands were defined as those which were not at the shell margin. Ninety-four percent (84/89) of the hard clams examined contained the same number of completed dark bands as there were complete summers, while the remaining 6% (5/89) formed one fewer dark band than years. This is regarded as the error estimate (6%) of this procedure for determining age of *M. mercenaria*.

TABLE 3.—Total numbers of known years of shell growth between 1967 and 1972 and dark bands in the middle homogenous layer observed in the known shell increments of long-term experimental *Mercenaria mercenaria*

Lot no.	No. of clams analyzed	Total no. of known years for all clams[1]	Total no. of dark bands
I	18	35	35
II	33	43	43
XI	26	86	86
XIV	12	13	13
Totals	89	177	177

[1]Many of the hard clams from each lot were added to it after the lot had been established. Because of this, the number of known years of shell growth for all hard clams in each lot is always less than the number of hard clams analyzed multiplied by the maximum number of known years of shell growth in each hard clam from 1967 to 1972 (5 yr).

Analysis of shell margin growth bands of all experimental and wild hard clams collected seasonally also revealed that dark band formation occurred during summer (Table 5; Fig. 1). The percentage of all ages of hard clams collected in summer which had a dark band at the shell margin (91%) was over twice that of hard clams collected in winter (40%). However, a significant proportion of hard clams collected in fall had a dark band at the shell margin (78%), indicating that the period of dark band formation also extended into fall.

Further examination of Figure 1 reveals differences among age groups in color of shell margin bands in fall and winter. The percentage of hard clams in all age groups with a dark band at the shell margin in summer ranged between 88 and 100% (Table 5; Fig. 1). However, in fall and winter, differences between age groups began to appear. In fall, 100% of old and 75% of mature hard clams had dark bands at the shell margin (Table 5; Fig. 1). The percentage with dark bands in winter declined in both age groups, but was still larger in old (44%) than mature (17%) hard clams. Thus, light band formation began sooner

TABLE 4.—Number of long-term experimental *Mercenaria mercenaria* with expected number of complete dark bands in the middle homogneous layer in known years of shell growth between 1972 and dates of final collection.

Lot no.	Date of final collection	Complete summers	Expected no. of complete dark bands	No. of clams analyzed	No. of clams with expected no. of dark bands
II	8/76	1973-75	3	15	15
XIV	8/76	1973-75	3	6	5
I	12/76	1973-76	4	16	16
II	1/78	1973-77	5	10	8
XIV	1/78	1973-77	5	6	6
II	2/78	1973-77	5	8	8
XI	7/79	1973-78	6	26	24
I	6/80	1973-79	7	1	1
I	7/80	1973-79	7	1	1
Totals				89	84

(after the summer dark band was completed) in a greater percentage of mature than old hard clams. This could also have been due to a lack of growth by old hard clams in fall and winter, leaving the summer dark band at the shell margin.

Enlargements of acetate peels in Figure 2 further illustrate the time of dark band formation each year. Figure 2A-C form a representative summer-to-winter series of shell margin bands formed by mature (T and TI) hard clams. Dark bands were at the shell margin in hard clams collected in summer (Fig. 2A), while in hard clams collected in fall and winter, dark bands became separated from the margin by light bands with increasing numbers of microgrowth increments (Fig. 2B, C). Light bands continued to be formed through spring and early summer but appear differently in the two hard clams pictured (Fig. 2D, E). Eighty-five percent (23/27) of the hard clams collected during or after winter 1980 (from December 1980 to June 1981) had a growth cessation mark within the shell margin light band formed during winter (Fig. 2D). This mark, termed a distinct winter growth cessation mark, was a thick microgrowth increment boundary in the light band with narrow microgrowth increments dorsal and ventral to it. It was also separated from the dark band by a light band representing growth in fall. Thus, one annual shell increment in these hard clams consisted of a dark band formed in summer and a light band formed in fall through spring which was bisected by a distinct winter growth cessation mark. This was the typical seasonal growth pattern of mature hard clams (Fig. 1). The remaining 15% (4/27) of the hard clams collected during this period did not have distinct winter growth cessation marks within the light band (Fig. 2E). This does not mean, however, that these hard clams grew throughout winter. In order for a winter growth cessation mark to be distinct, a light band formed in fall must separate it from the summer dark band. Consequently, lack of a distinct winter mark was more likely caused by lack of light band formation in fall. One annual increment in these hard clams consisted of a dark band formed in summer and fall and a light band formed in the following spring. This seasonal growth pattern was similar to that described for old hard clams (Fig. 1). Thus, there can be significant variation even among individuals in a single year class in seasonal shell growth patterns. Dark bands formed in summer and fall, however, were the only annually produced and universal component of the shell growth pattern of *M. mercenaria* in lower Chesapeake Bay.

TABLE 5.—Summary of seasonal shell margin growth bands in long-term experimental and wild *Mercenaria mercenaria* (in summer, winter, and spring collections) and those dorsal to each fall measurement disturbance mark in 1968-72. Group collected in each season was subdivided by age according to Kennish (1980; see legend to Figure 1).

Season	Months	Age	N	Light band		Dark band	
				N	%	N	%
Spring	Mar.-Apr.	Mature	5	5	100	0	0
		Old	3	0	0	3	100
Total			8	5	62	3	38
Summer	June-Sept	Young	3	0	0	3	100
		Mature	18	1	6	17	94
		Old	34	4	12	30	88
Total			55	5	9	50	91
Fall	Oct.-Nov.	Mature	139	35	25	104	75
		Old	17	0	0	17	100
Total			156	35	22	121	78
Winter	Dec.-Feb.	Mature	6	5	83	1	17
		Old	39	22	56	17	44
Total			45	27	60	18	40

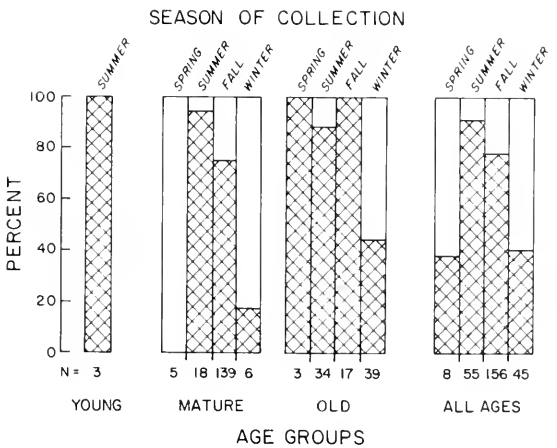
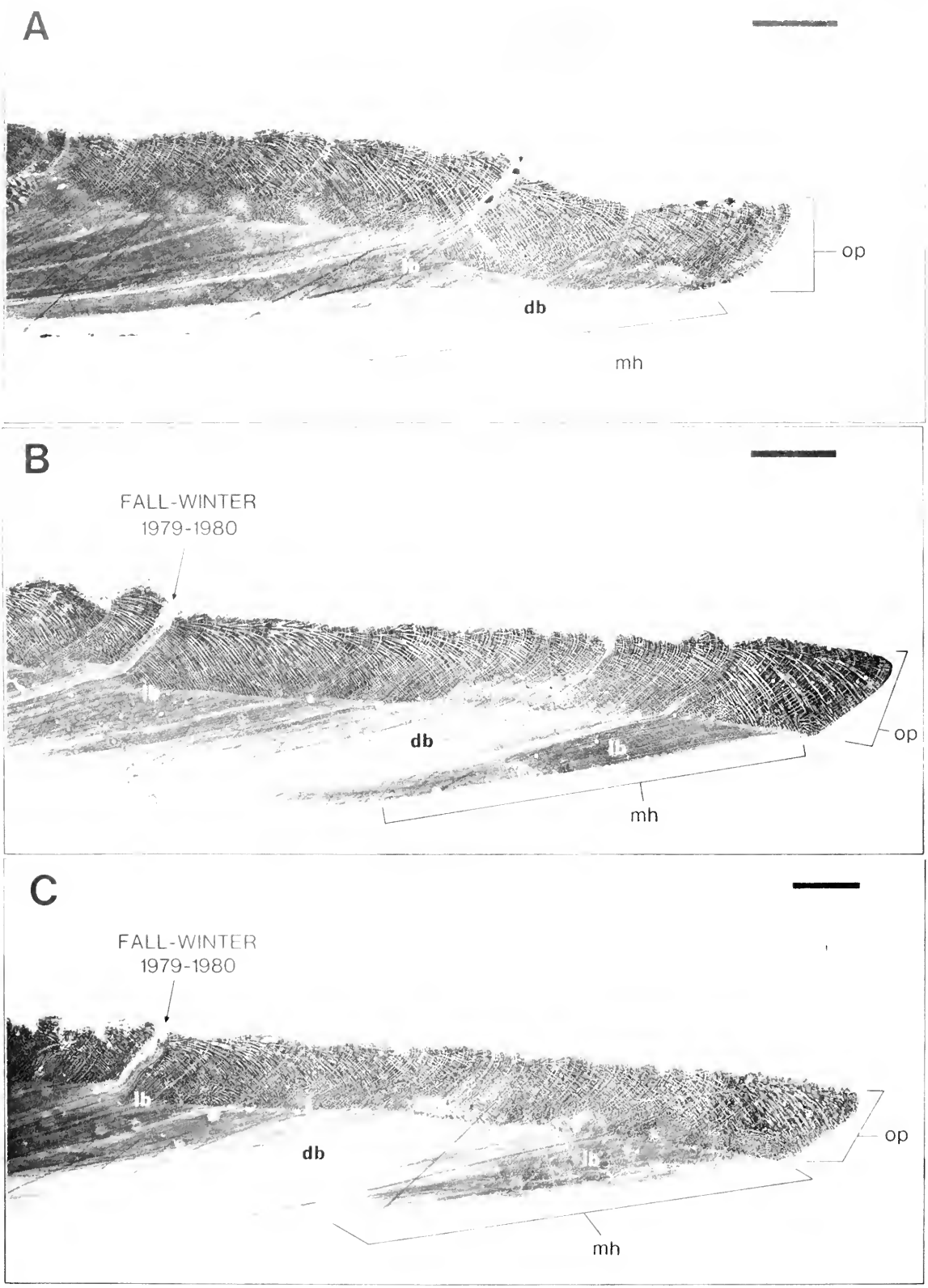


FIGURE 1.—Percent of young, mature, old, and all ages of long-term experimental and wild stock *Mercenaria mercenaria* with light (unshaded) or dark (shaded) bands at the shell margin in each season. Age groups: Young – under 3 yr, Mature – 3 to 8 yr, Old – over 8 yr (Kennish 1980).

Periodicity of Microgrowth Increment Formation

Experimental hard clams formed one microgrowth prismatic increment during each solar day of activity. Inactive periods, represented by growth cessation marks or thick organic lines in the prismatic layer, became longer and/or more frequent with increasing age and length of monitored growth periods. Thus, both factors (increasing age and length of monitored growth periods) tended to decrease the increment-to-day ratio. Three sets of increment counts were used to formulate these conclusions: 1) The number of increments from the growth disturbance of 30 May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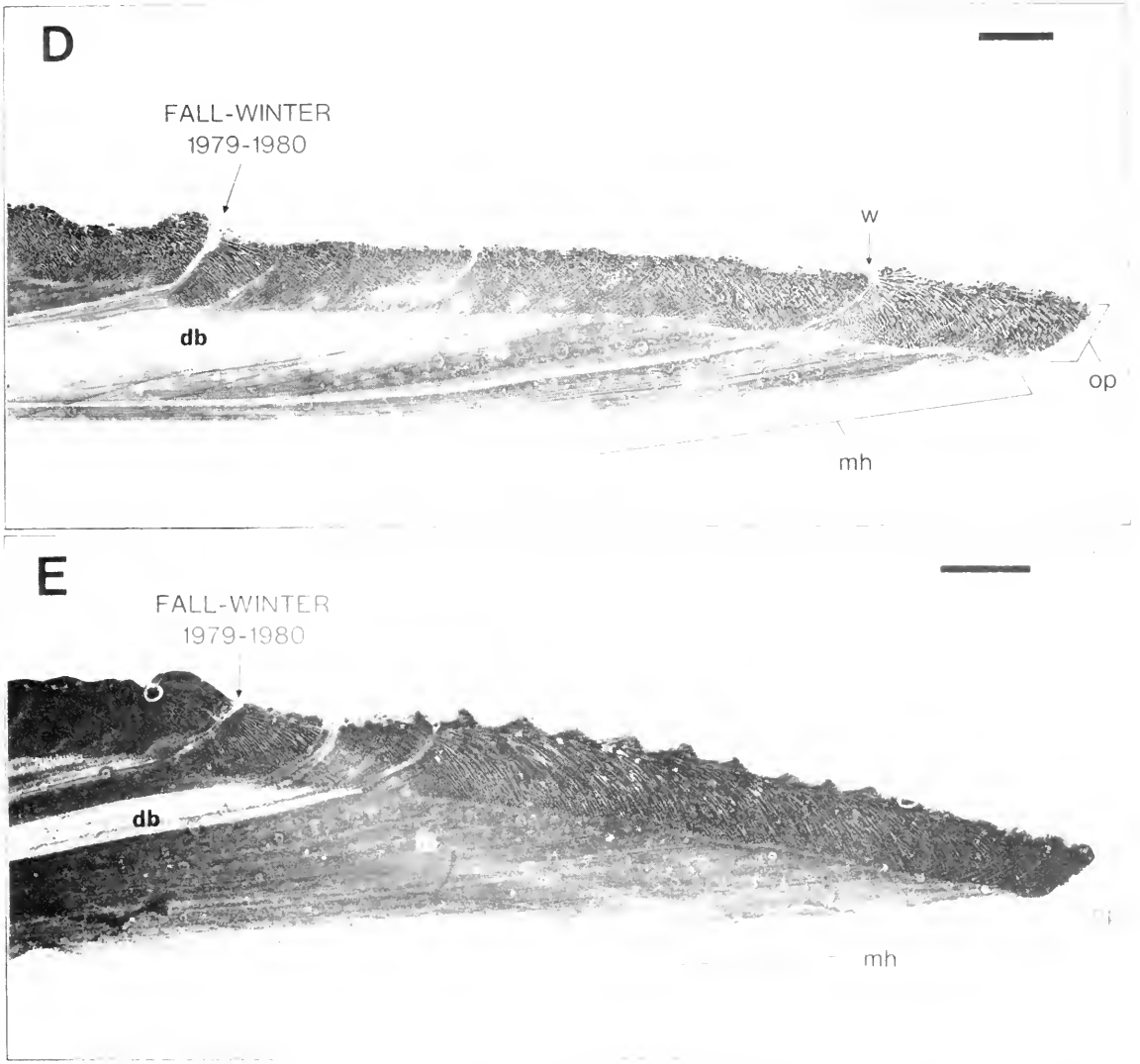

FIGURE 2.—Enlargements of acetate peels from five short-term experimental *Mercenaria mercenaria* showing shell growth from transplantation in October 1979 to each date of collection (shell margin). Growth disturbance due to transplantation is labelled fall-winter 1979-1980 in the outer prismatic layer (op) of each. Middle homogenous layer (mh) bands are labelled lb (light band) and db (dark band). Contrast in photographs is due to differences in transparency of portions of the peels. Light regions in photographs correspond to relatively opaque regions on peels, or those which appear dark in polished shell sections. Scale bars represent 1 mm and growth is to the right.

1980 to the shell margin in four collections of TI hard clams during summer 1980, 2) the number of increments from the growth disturbance caused by transplantation of short-term hard clams (from the Eastern Shore to the York River) on 16 October 1979 to the shell margin in hard clams collected from April 1980 (after growth had resumed) to June 1981, and 3) the number of increments between MDM formed 1 yr apart between 1969 and 1971 by hard clams in lot XI.

TI Series, From 30 May 1980

TI hard clams collected in summer 1980 had a strong tendency to form one increment each solar day (Table 6; Fig. 3). Regression of the number of increments formed on days since 30 May 1980 yielded a strong linear relationship ($F = 156.30$, $P < 0.001$) with a regression coefficient (b) not significantly different from 1.00 (Table 6). Consequently, TI hard clams tended to form one prismatic

TABLE 6.—Regression statistics for microgrowth increment counts on days in monitored growth periods of short-term experimental *Mercenaria mercenaria* a = Y-intercept, b = regression coefficient (slope); t_s = t-test statistic for H_0: $\beta = 1.00$ vs. H_1: $\beta \neq 1.00$; r = correlation coefficient.

Group	Collection period	N	a	b±95% C L[1]	t_s	r
TI	Summer 1980	12	−4 40	1 10±0.19	1 23 (P>0 20)	0 98
T and TI	Spring 1980 to summer 1981	58	−124 38	0.88±0.13	−1 80 (P>0 05)	0.88
T and TI	Spring to fall 1980	31	−197 48	1.14±0 29	0.99 (P>0.20)	0.87
T and TI	Winter 1980 to summer 1981	27	−48.60	0.74±0 52	−1.04 (P>0 20)	0 53

[1]C.L = confidence limits.

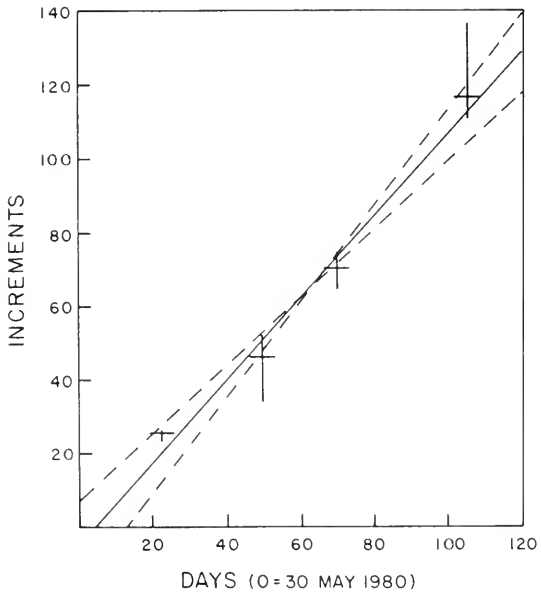

FIGURE 3.—Average (horizontal bar) and range (vertical bar) of the number of microgrowth increments formed by TI series hard clams, *Mercenaria mercenaria*, during summer 1980 after induced growth disturbance of 29-30 May 1980. Zero on abscissa equals 30 May 1980. Solid line = regression; dashed lines = ±95% confidence limits on regression coefficient (Table 6).

increment during each solar day for the 4 summer months.

T and TI Series, From 16 October 1979

T and TI hard clams collected from spring 1980 to summer 1981 also tended to form one increment for each solar day of activity. Regression analysis revealed a strong linear relationship between numbers of increments formed and days since 16 October 1979 ($F = 177.25, P < 0.001$; Table 6). Furthermore, the regression coefficient was not significantly different from 1.00 (Table 6). These statistics tend to obscure the fact that 85% of hard clams collected during or after winter 1980 had distinct winter growth cessation marks within the light band at the shell margin (as in Figure 2D). Growth cessations of varying durations should reduce regression (b) and correlation coefficients (r) in an analysis based on counts from hard clams collected during or after winter 1980 compared with one based on counts from hard clams collected from spring through fall 1980. Results from such analyses (Table 6; Fig. 4) revealed neither significant differences between the two regression coefficients ($F_s = 0.50, P > 0.25$) or significant differences of both from 1.00. However, con-

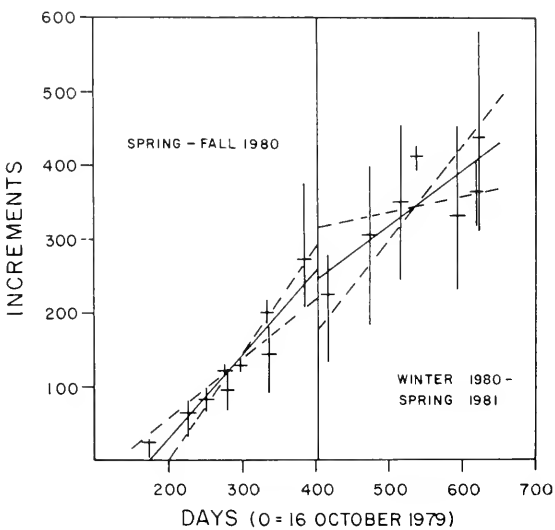

FIGURE 4.—Average and range (as in Figure 3) of the number of microgrowth increments formed by T and TI series hard clams, *Mercenaria mercenaria*, from fall 1979 to summer 1981 in hard clams collected after April 1980 to June 1981. Increments were counted from growth disturbance caused by transplantation in October 1979. Zero on abscissa equals 16 October 1979. Regression analyses based on 31 hard clams collected from spring to fall 1980 and 27 clams collected from winter 1980 to summer 1981. Solid and dashed lines as in Figure 3 (see also Table 6).

fidence limits on the regression coefficient from the winter 1980 to summer 1981 counts were almost twice as wide as from the spring to fall 1980 counts (Table 6). This was also reflected in the reduced, but significant correlation coefficient from the winter 1980 to summer 1981 counts compared with those from hard clams collected from spring to fall 1980 (Table 6). Despite the lack of significant statistical results, these data suggest that the ratio of increments to days was lower in hard clams collected during or after winter 1980 than in those collected from spring to fall 1980. This could have been due to growth cessations of varying durations in winter. However, growth cessations could also have occurred at anytime during the monitored growth period, and thus obscured the effects of winter on the number of increments in hard clams collected during or after it. Individual variability in numbers of days of growth was evident in the increasing range in increment counts from single collections with time. Chances of disturbances (such as storms, predation attempts, etc.) occurring in any season which could cause growth to cease in some hard clams would also increase with the length of monitored growth periods. Consequently, a one-to-one increment-to-day relationship only applied to short periods of monitored growth during favorable seasons, such as the TI hard clams discussed previously (Fig. 3). Prismatic microgrowth increments, however, each represented a solar day, despite the lack of one-to-one correspondence for long periods of monitored growth.

Lot XI, From 1969 to 1971

Percent agreement between increment counts and days between annually formed MDM decreased with increasing age of long-term experimental hard clams. Results of counts from lot XI hard clams age 3 to 10 in annual shell increments formed between 1969 and 1971 are shown in Figure 5. Results from other long-term experimental lots were similar. Consequently, experimental hard clams formed increments (were active) for fewer days each year with increasing age, indicating that growth cessations became more frequent, longer, or both.

Microgrowth Increment Widths, Seasonal Growth Rates

Average microgrowth increment widths associated with dark bands were generally smaller than those associated with light bands in all long-term and short-term experimental hard clams. The distribution of average increment widths formed between

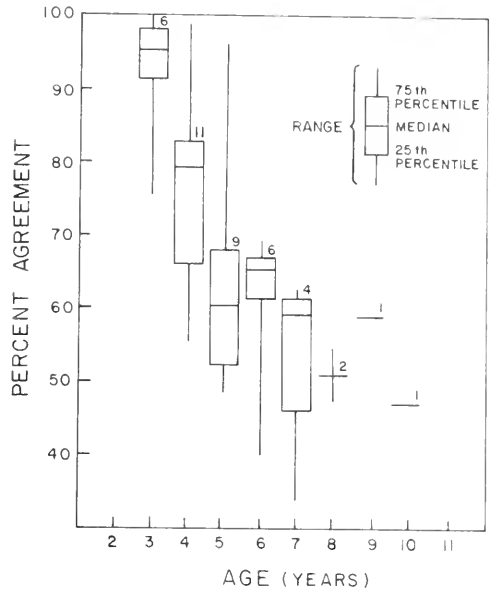

FIGURE 5.— Distribution of percent agreement (number of microgrowth increments divided by number of days between annual measurements (Richardson et al. 1979)) for each age of lot XI hard clams, *Mercenaria mercenaria*. Data from annual shell increments deposited from 1969 to 1971. Number of annual shell increments analyzed at each age is shown.

annually induced MDM in 1969-71 in lot XI hard clams (ages 3-10) are shown in Figure 6. Results from other experimental hard clams were similar. Since microgrowth increments were formed daily, these data indicate that growth rates tended to be slower in summer than in spring or fall of the same year. Median average summer growth rates (dark band) ranged between 21 and 33 μm/d, while those in spring and fall (light bands) ranged between 31 and 48 μm/d, respectively between 1969 and 1971 (Fig. 6). However, these figures represent only growth rates for days of growth and activity; there was a considerable number of inactive days in each annual shell increment (Fig. 5) which would make the actual seasonal average daily growth rate lower. There was also a large range in average increment width in any single band, and individuals in certain annual increments had average increment widths associated with dark bands which were greater than with either or both light bands. This occurred in only 17 of 181 bands analyzed in hard clams from both lots XI and II, or with a frequency of 9%.

Decreased growth rates associated with dark bands were probably due to summer water temperatures above the optimum for growth of hard clams (15°-25°C; Ansell 1968). York River water temperatures

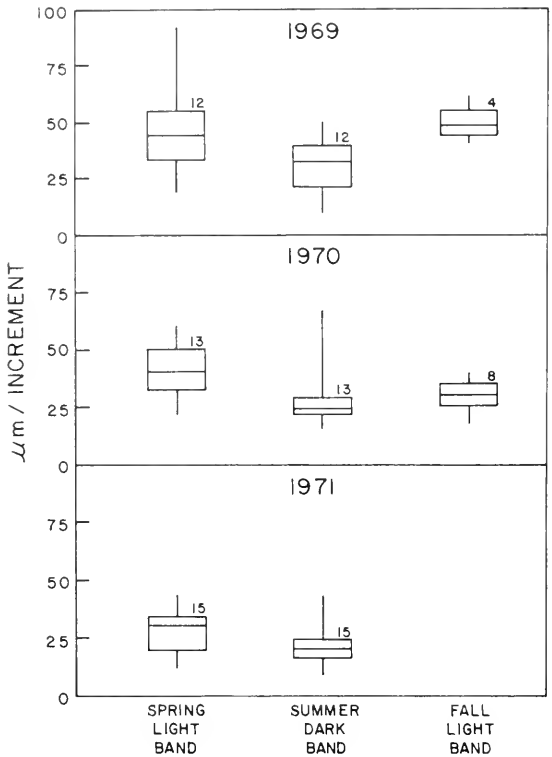

FIGURE 6.—Distribution of average microgrowth increment width (μm/inc) in light and dark bands formed from 1969 to 1971 by lot XI hard clams, *Mercenaria mercenaria*. Figures are drawn as in Figure 5. Increments were counted only between annual measurement disturbance marks in the number of hard clams listed with each spring light or summer dark band. The number of these which had formed light bands prior to measurement each fall in 1969 and 1970 are also shown.

(at 1 m depth) near the location of T and TI hard clams remained above 25°C from 22 June to 26 September 1980, which was approximately the period of dark band formation by all short-term experimental hard clams. For instance, microgrowth increment counts in hard clams collected on 8 August and 1 November 1980 (Fig. 2A, B) date the time of dark band initiation and completion as 29 June and 26 September 1980, respectively.

DISCUSSION

Dark bands in the middle homogenous layer of polished sections and on acetate peels of radial sections of *Mercenaria mercenaria* shells were formed each summer and early fall and were associated with slower growth rates (narrower microgrowth increments) than light bands. Consequently, hard clams from Chesapeake Bay may be aged on the basis of dark band counts in shell microstructure. Distinct winter growth cessation marks were not formed each year by each individual primarily because of a lack of light band formation in fall, especially by hard clams older than 8 yr. However, hard clams younger than 8 yr also did not form light bands consistently in fall which would separate winter growth cessation marks from summer dark bands. Consequently, dark bands were the only seasonal growth pattern in microstructure which was formed annually by each hard clam analyzed.

The relationships between bands in polished shell section and middle homogenous layer ultrastructure are unknown. According to a theory of growth line formation proposed by Lutz and Rhoads (1977), the ratio of organic matrix to shell carbonates could increase during extended periods of slow shell growth due to dissolution of carbonates in anaerobic (inactive) periods. This may cause shell deposited in summer to appear dark because of higher proportions of organic matrix. However, differences in average microgrowth increment width between light and dark bands in this study were only between 10 and 20 μm, which may be too small to cause such fundamental changes in shell appearance. Alternatively, differences in crystal size and/or orientation may also account for bands in the middle homogenous layer. Clark[7] hypothesized that translucent zones in thin section may result from slightly larger, and more uniformly oriented, crystals. This may result in light transmittance by translucent zones in thin section, and absorption by dark bands in polished shell section. However, it is not known why these areas also appear dark on acetate peels.

Latitudinal variation in seasonal microstructure of *Mercenaria mercenaria* shells is apparent from other studies (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Greene 1975; Kennish and Olsson 1975; Clark 1979). North of Chesapeake Bay (Massachusetts, Connecticut, New York, and New Jersey), distinct winter growth cessation marks were formed each year and the fastest growth during the year occurred most often in summer (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Greene 1975; Kennish and Olsson 1975). However, there was no discussion of association of wide or narrow microgrowth increments with bands in the middle homogenous layer. Seasonal shell microstructure of *M. mercenaria* in Georgia is very similar to that in lower Chesapeake Bay (Clark 1979). Translucent zones, or dark bands, were formed each summer

[7]G. R. Clark II, Department of Geology, Kansas State University, Manhattan, KS 66506, pers. commun. March 1982.

and early fall and were associated with narrower microgrowth increments than opaque zones, or light bands. *Mercenaria mercenaria* in Georgia, however, apparently grow throughout winter since no distinct winter growth cessation marks were observed (Clark 1979). Consequently, two aspects of seasonal shell microstructure appear to vary with latitude: 1) Formation of dark bands or translucent zones in summer and early fall is more common at lower latitudes, and 2) formation of distinct winter growth cessation marks is more common at higher latitudes. These trends are similar, at least in concept, to changes in sublayer crystal structure in the inner shell layer of *Geukensia demissa* which have been observed with latitude (Lutz 1977; Lutz and Rhoads 1978 (see footnote 5); Lutz and Castagna 1980). Latitudinal variation in the ultra- or microstructure of annual shell increments may preclude application of defined increments to all populations along its range.

Latitudinal variation in seasonal water temperature range may be the most important factor regulating seasonal microstructural growth patterns in *M. mercenaria* (Rhoads and Pannella 1970). In this study, it was found that dark band formation tended to occur when water temperatures exceeded 25°C, or the upper limit of the optimum range for shell growth (Ansell 1968). There is little evidence to support the contention that the optimum temperature range, 15°-25°C, changes with latitude in populations of *M. mercenaria* (Ansell 1968). Consequently, growth patterns within shell microstructure may reflect ambient seasonal cycles of water temperature (Lutz and Rhoads 1980).

The relationship between decreased microgrowth increment width (growth rate) as well as location of growth cessation marks with respect to elevated water temperatures has been well documented (Kennish and Olsson 1975; Kennish 1977). Furthermore, circadian formation of microgrowth increments by *M. mercenaria* has also been reported (Pannella and MacClintock 1968; Thompson 1975). However, Pannella and MacClintock (1968), Kennish and Olsson (1975), and Kennish (1980) stated that one increment was formed during each solar day regardless of season or age (up to 8 yr). Each annual shell increment would thus contain about 365 microgrowth increments, and age estimates (in years) could be obtained by dividing counts of all microgrowth increments formed by 365 (Kennish 1980). The results of this study, and that of Crabtree et al. (1979/1980) on daily increment formation by *Chione fluctifraga*, shed doubt on this method of age determination, since the percent agreement between increments and days in annual shell increments decreased with increasing age. Thus, dividing total microgrowth increment counts by 365 could underestimate age in years.

Decreasing number of days of growth each year with age, as well as individual variability in the number of days of growth in each age group, must be accounted for when shell microstructure of bivalves is used to monitor environmental change. Studies by Kennish and Olsson (1975), Pannella (1976), Kennish (1977), and Jones (1980) are testimony to the quality of information on environmental change stored in bivalve shell microstructure. However, individual variability among bivalves of the same age may require the use of large sample sizes to safely conclude that patterns observed in microstructure of recent or fossil shells were due to changes in environment and not artifacts of individual differences in shell growth.

ACKNOWLEDGMENTS

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SIZE, SEX RATIO, AND RECRUITMENT IN VARIOUS FISHERIES OF KING MACKEREL, *SCOMBEROMORUS CAVALLA*, IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT

Data from over 54,000 king mackerel, *Scomberomorus cavalla*, were analyzed to evaluate spatial and temporal variations in size and sex composition in seven areas of the southeastern United States. Data were obtained from the recreational hook-and-line fishery of coastal states from Texas to North Carolina and from commercial hook-and-line and gill net fisheries of south Florida. Of the three types of gear, recreational hook and line appeared to be the least selective and gill net the most selective for particular sizes of king mackerel.

Size composition in each area varied considerably among months; patterns of size change were discernible in some areas. Sizes of king mackerel varied significantly among areas and years. Catches from south and northwest Florida contained high proportions of small fish (<700 mm FL); those from Texas and North Carolina contained mostly medium-sized fish (700-900 mm FL). Mean lengths of king mackerel were larger in 1978 than in 1977 in all areas except northwest Florida. In northwest Florida, modal fork lengths were 749 mm in 1968-69, 649 mm in 1977, and 549 mm in 1978. The majority of the smallest fish (400-600 mm FL) were recruited to the fisheries in Florida, but the range and areas of abundance of king mackerel smaller than this are not known. For purposes of evaluating effects of minimum size regulations, the king mackerel population was divided into groups (the Florida winter, immature, spawning, and Louisiana groups).

Females dominated catches in all size groups and in all areas and years, except for south Florida in 1978. Annual, or ranges of annual, estimates of percentage female by area were as follows: Texas, 60.8-62.2%; Louisiana, 91.9-92.2%; northwest Florida, 57.1-75.1%; south Florida, 40.2-75.4%; and North Carolina, 75.8%. Females predominated in 31 of 38 sample groups at lengths <900 mm FL, and in all sample groups at lengths >899 mm FL.

The king mackerel, *Scomberomorus cavalla*, is one of the most important species in the coastal pelagic fisheries of the southeastern United States. Despite its high commercial and recreational value (Deuel and Clark 1968; Wise and Thompson 1977), many details pertaining to king mackerel catches and population structure are not available. Information needs include the following: 1) Seasonal size compositions by geographic area, 2) sizes and sex ratios of king mackerel caught throughout the southeastern United States, and 3) the number of groups supporting the fisheries. To meet these needs we 1) summarized data from previous analyses (Trent et al. 1981) on seasonal changes in size and sex compositions of king mackerel catches, 2) determined size and sex compositions in catches by capture gear, area, and year, and 3) separated the stock(s) into four groups for the purpose of evaluating minimum size regulations in the fisheries.

This undertaking is complicated by the widespread nature of the species and by the diversity of various fisheries harvesting it. King mackerel occur from the Gulf of Maine to Brazil and are common in the Caribbean and Gulf of Mexico (Randall 1968). The number of populations or stocks is unknown. The stock(s) fished off the continental United States are probably not the same as those fished in the Caribbean because, of over 1,100 tag returns from over 14,000 king mackerel tagged in the southeastern United States, not a single return came from the Caribbean.[4] In U.S. waters north of North Carolina, king mackerel is not a target species, either commercially or recreationally. The fish are highly migratory and the recreational fishing effort for them in any given area is directly related to their availability. Recreational fishing effort is exerted along the Atlantic and northern Gulf of Mexico coasts during the warmer

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months and along the south Florida and Louisiana coasts year-round, especially during the winter. In contrast to recreational fisheries, the commercial king mackerel fisheries are conducted almost completely in Florida. In 1976, for example, 96.5% of the king mackerel caught commercially along the east coast of the United States was landed in Florida, while almost 100% of the fish landed commercially in the Gulf of Mexico was caught off Florida's west coast (Manooch 1979).

STUDY AREA AND METHODS

King mackerel were sampled from commercial and recreational landings at seven locations (Fig. 1). King mackerel were caught by 1) recreational hook and line in each area, 2) commercial gill net off south Florida, and 3) commercial hook and line off Mississippi (snapper boats), south Florida, and North Carolina.

Baits used by recreational fishermen to catch king mackerel vary among areas and could influence the sizes of king mackerel that are caught. The baits differ in size, and large king mackerel consume larger food items than do small king mackerel (Saloman and Naughton[5]). The most frequently used baits and their comparative sizes by area are Texas — Atlantic cutlassfish, *Trichiurus lepturus* (large); Louisiana — sand seatrout, *Cynoscion arenarius* and Atlantic croaker, *Micropogonias undulatus* (large); northwest Florida — ballyhoo, *Hemiramphus brasiliensis* (small); Georgia, North Carolina, and South Carolina — strips of cut bait and live fish of several species (small to large).

King mackerel that were sampled from commercial snapper boats were caught incidentally during the snapper fishing. Standard bottom rigs with three to six hooks were baited with pieces of fish or squid. The king mackerel were caught in an area east of the mouth of the Mississippi River, where water depths ranged from 50 to 130 m.

Most king mackerel landed by commercial fishermen in south Florida are caught by runaround gill nets or hook and line (Beaumariage 1973; Austin et al. 1978; Manooch 1979). The nets are from 360 to 640 m long, about 22 m (200 meshes) deep, with a stretched mesh of 12.1 cm. The nets are fished in water depths as great as 21 m. In the commercial hook-and-line fishery, spoons or feathered jigs, sometimes with strips of mullet or squid, are trolled behind boats (Harris 1974).

Length and sex data on king mackerel were obtained by personnel of the Florida Department of Natural Resources and by personnel of the National Marine Fisheries Service. Data were summarized by number of fish in relation to sex, location, capture gear, and time (Tables 1, 2).

Length measurements were taken from uncut, gutted, or filleted fish. Fork Length (FL) was measured from the tip of the snout (mouth closed) to the fork of the tail to the nearest millimeter or 0.1 in. Measurements, in inches were later converted to

[5]Saloman, C. H., and S. P. Naughton. 1982. Food habits of king mackerel in the southeastern United States. Unpubl. manuscr., 28 p. Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA, Panama City, FL 32407.

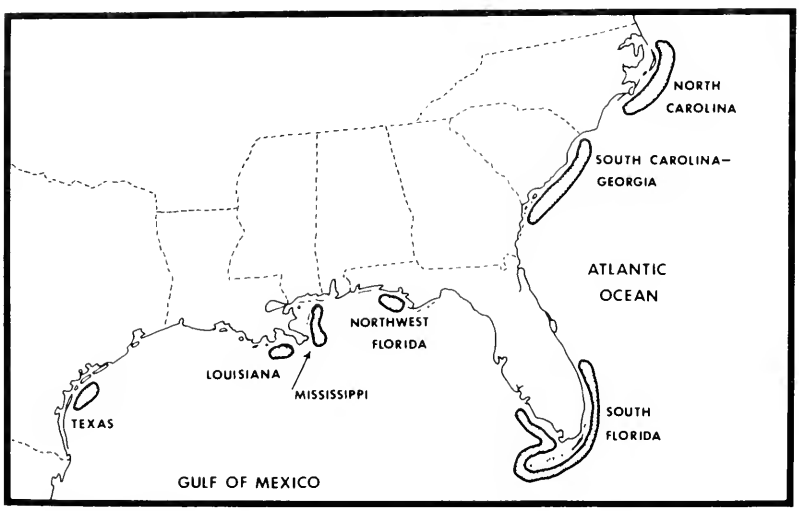

FIGURE 1.—Sampling locations in the southeastern United States.

TABLE 1.—Numbers of king mackerel by capture gear, year and month, and area (M = male, F = female, U = sex unknown). Data obtained by Florida Department of Natural Resources, St. Petersburg, Fla.

Year and month	Recreational hook and line		Commercial hook and line				Gill net		
	Northwest Florida		South Florida			North Carolina	South Florida		
	M	F	M	F	U	U	M	F	U
1968									
Jan.			135	316			361	473	
Feb.			182	457			792	816	
Mar.			283	667			460	578	
Apr.	22	36	28	19			5	13	
May	18	20	40	24					
June	17	55	26	33					
July	11	86							
Aug.	14	46	22	38					
Sept.	21	39	27	29					
Oct.	17	22	19	23	2				
Nov.				4			2	3	
Dec.			445	671					
1969									
Jan.			709	1,102					
Feb.			15	43					
Mar.			10	31			8	12	
Apr.	4	16					10	12	
May	17	15							
June	6	8							
July	1	32	26	34					
Aug.	5	24	11	19					
Sept.	3	27							
Oct.	1	8							
Nov.	12	18	14	44					
Dec.			6	9					
1975									
Jan.					534				
Feb.					1,343				
Mar.					117				
Apr.					35				
May					373				
June					121				
Aug.					203				
Oct.					3				
Dec.					244				
1976									
Jan.					304				
Feb.					1,796				313
Mar.					2,907				
Apr.					36				
May					1,226				
June					180				
Aug.					166				
Oct.					61				
Dec.					2,266				
1977									
Jan.					1,193				2,777
Feb.					4,106				1,062
Mar.									306
May					335				
June					246				
Aug.					227				
Dec.					708				
1978									
Jan.					2,475				
Feb.					1,107				
Mar.					2,931				
Apr.					1,305				
May					378				
June					20				
Sept.						72			
Oct.						36			
1979									
May						809			
Total	169	452	1,998	3,563	26,948	917	1,638	1,907	4,458

TABLE 2.—Numbers of king mackerel by capture gear, year and month, and area (M= male, F= female, U= sex unknown). Data obtained by the National Marine Fisheries Service, Panama City, Fla.

Year and month	Recreational hook and line																		Commercial hook and line			Commercial snapper hook and line		
	Texas			Louisiana			Mississippi		Northwest Florida			South Florida	South Carolina-Georgia			North Carolina			South Florida			Mississippi		
	M	F	U	M	F	U	M	F	M	F	U	U	M	F	U	M	F	U	M	F	U	M	F	U
1977																								
Feb.				1	24																			
May																		45						
June	5	18	20	2	16	40			9	26	6							28						40
July	17	21	106			32			49	352	48					2	4	11						
Aug.	9	9	251			19	1	7	4	255	59													
Sept.				8	59				260	673														
Oct				10	135	6			180	94	23													
Dec.				3	38																			
1978																								
Jan.				3	36																			
Feb.					8																			
Mar				4	64																			
Apr					3																			
May	23	99		1	4				1	5						13	41	4						
June	95	281	13	7	61		2	12	5	23						2	19	24				20	29	19
July	193	254	75	13	86	1			177	456	7					2	13	4				4	11	15
Aug	234	262	1	5	81				301	259			3		7	3	16	2				15	28	31
Sept					24	1			417	472			2	1	127	5	48	91	205	138	1	4	1	2
Oct				4	75				203	255	16		156	248	6	103	256	82						
Nov					34												10	6						
Dec.					7																			
1979																								
Jan.												371							209	346	12			
Feb.												482												
Mar												1,052							33	85				
Total	576	944	466	61	755	99	3	19	1,606	2,870	159	1,905	161	249	140	130	407	297	447	569	13	43	69	107

millimeters. Length data were grouped into 100 mm intervals and categorized by month, location, year, and gear type.

Seasonal differences in size were analyzed in great detail in an earlier version of this paper by examining length-frequency distributions by month within gear type, area, and year. This detailed evaluation (20 figures, 10 tables, and 7 appendix tables) is available upon request from the Florida Department of Natural Resources (footnote 3).

Chi-square tests were used to compare homogeneity of frequency distributions in relation to month and gear type and to compare observed sex ratios to a hypothetical 1:1 ratio (Simpson et al. 1960).

SEASONAL DIFFERENCES IN SIZE AND SEX RATIO

Within each area along the northern Gulf of Mexico, changes in mean and modal lengths between months of king mackerel were generally similar (Tables 3, 4; Fig. 2). Mean sizes along northwest Florida were high in spring and fall and low during July or August of each year, except in 1969. Mean sizes were also generally lowest during the warmer months in Louisiana and although the data were meager, seasonal changes in size in Texas appeared similar to those in northwest Florida.

In south Florida, seasonal size changes, as evidenced by commercial hook-and-line data, were only weakly discernible. During most years, mean lengths tended to be highest during warmer months. When monthly means from different years were averaged over 3-mo periods, the lengths were as follows: April-June, 808 mm; July-September, 816 mm; October-December, 769 mm; and January-March, 758 mm.

Seasonal size changes along the south Atlantic coast above Cape Canaveral, Fla., could not be defined with any certainty because of the paucity of data. In North Carolina, mean lengths of recreationally caught fish increased from May (682 mm) to June (735 mm) 1977, decreased from May (809 mm) to June (789 mm) 1978 and increased from September (844 mm) to October (856 mm) 1978. Fish caught by commercial hook and line also increased from September (804 mm) to October (836 mm) 1978 in North Carolina. In the South Carolina-Georgia area the recreationally caught fish decreased from September (895 mm) to October (811 mm) 1978.

Females dominated catches from all areas in most months and years (Tables 3, 4, 5). In Louisiana, annual estimates of percent females were 91.9 in 1977 and 92.9 in 1978. In other parts of the northern gulf and along North Carolina, South Carolina, and Georgia, the annual estimates of percent female

TABLE 3.—Mean length (mm, $\bar{x}$), modal length (mm, ML), and percent female (%F) of king mackerel samples by area, gear type, and month during 1968-69 and 1975-76.

Year and month	Recreational hook and line, Northwest Florida $\bar{x}$	ML	%F	Commercial hook and line, South Florida $\bar{x}$	ML	%F	Gill net, South Florida $\bar{x}$	ML	%F
1968									
Jan.				754	749	70.1	818	749	56.7
Feb.				746	749	71.5	757	749	50.7
Mar.				759	749	87.9	806	749	55.7
Apr	757	749	62.1	901	900	40.4			
May	729	749	52.6	832	849	38.1			
June	743	749	76.4	792	749	55.9			
July	660	549	88.7						
Aug	715	749	76.7	835	749	63.3			
Sept.	695	649	65.0	811	749	51.8			
Oct.	724	700	56.4	722	649	54.8			
Dec.				732	649	60.1			
1969									
Jan.				771	749	60.8			
Feb				802	749	74.1			
Mar.				777	749	75.6			
May	747	749	46.9						
July	798	849	97.0	842	849	56.7			
Aug.	595	549	82.8	850	849	63.3			
Sept.	703	749	90.0	900	849	75.9			
Nov	790	749	60.0						
1975									
Jan				780	749				
Feb.				732	749				
Mar				689	649				
Apr.				763	749				
May				774	749				
June				767	749				
Aug				782	749				
Dec.				704	749				
1976									
Jan.				735	749				
Feb				770	749		750	749	
Mar.				712	749				
Apr.				807	849				
May				800	749				
June				768	749				
Aug.				776	749				
Oct.				783	749				
Dec.				757	749				

ranged from 57.1 to 75.8. Only in south Florida did the sex ratio favor males; during 1978 the annual estimate based on commercial hook-and-line data was 40.2% females. Sex data were available from all seven areas in 1978; percent female ranged from 40.2 in south Florida to 92.9 in Louisiana (Table 5).

The degree of dominance by female king mackerel varied in relation to size of fish and type of capture gear (Table 5). Females were dominant in all size classes ≥900 mm FL and were dominant in 31 of 38 sample groups at lengths <900 mm FL.

COMPARISONS AMONG GEAR TYPES

An understanding of the variations in fishing techniques with a particular gear, and of the selective characteristics of each gear, is needed to interpret our data properly in making comparisons of size composition among years and geographic areas. The baits used by recreational fishermen in various areas

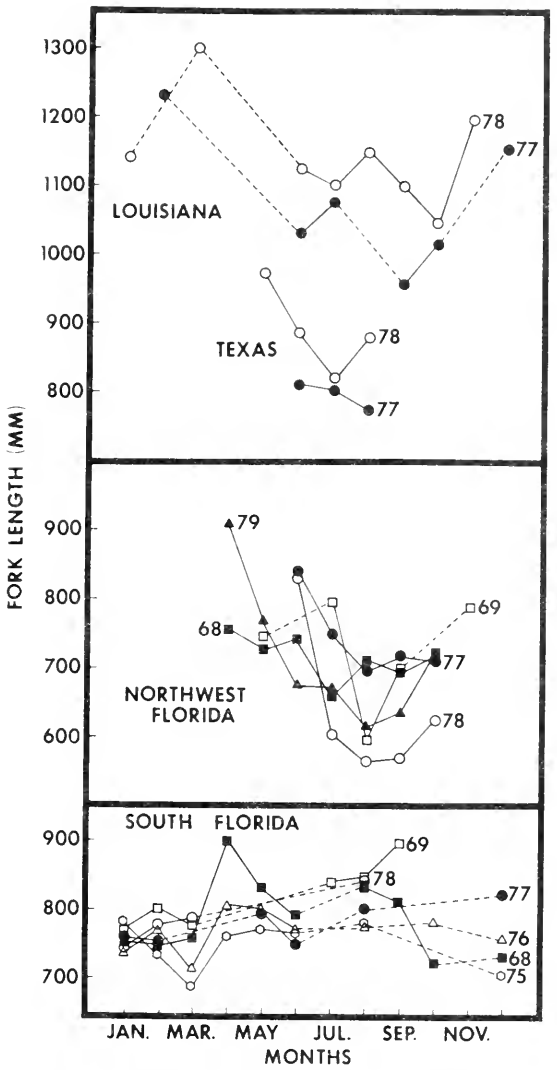

FIGURE 2.—Monthly mean fork lengths of king mackerel, *Scomberomorus cavalla*, caught by recreational hook and line by year and area.

are described above. Since data are not available for evaluating variations in recreational fishing techniques and their selectivity for particular sizes of fish, we assumed that the various baits and methods were not sufficiently selective to bias our analyses to this point. We did, however, have data to evaluate size selection among recreational hook and line, commercial hook and line, and gill nets.

Time, area, and sample size were used as criteria to select data for comparison. A minimum of 25 fish was required from the same geographic area during the same month from each of two compared gear types.

TABLE 4.—Mean length ($\bar{x}$), modal length (ML), and percent female (%F) of king mackerel samples by area, gear type, and month during 1977-79.

Year and month	Recreational hook and line																Commercial hook and line								Gill net	
	Texas			Louisiana			Northwest Florida			South Florida		South Carolina-Georgia			North Carolina			Mississippi			South Florida			North Carolina		South Florida	
	$\bar{x}$	ML	%F	$\bar{x}$	ML	%F	$\bar{x}$	ML	%F	$\bar{x}$	ML	$\bar{x}$	ML	%F	$\bar{x}$	ML	%F	$\bar{x}$	ML	%F	$\bar{x}$	ML	%F	$\bar{x}$	ML	$\bar{x}$	ML
1977																										
Jan.																				754	749				803	749
Feb				1,233	1,149	96 0														750	749				803	749
Mar																									903	749
Apr																									772	749
May															682	649				797	749					
June	812	849	78.3	1,032	1,049	88 9	844	849	74.3						735	749				751	749					
July	804	749	55 3	1,077	1,049		753	749	87 8																	
Aug	774	749	50.0				697	649	98 4											802	749					
Sept				958	949	88 1	720	649	72 1																	
Oct				1,016	949	93 1	713	749	34 3																	
Dec.				1,152	1,000	92 7														825	849					
1978																										
Jan.				1,141	1,149	92 3														742	749					
Feb																				779	749					
Mar				1,299	1,249	94 1														789	749					
Apr.																									772	749
May	973	949	81.1												809	849	75 9			842	849					
June	888	849	74 7	1,126	1,049	89 7	831	849	82 1						789	749	90.5	899	849	59 2							
July	821	849	56.8	1,104	1,049	86.9	606	549	72 0									962	849	73 3							
Aug	881	849	52 8	1,154	1,100	94 2	568	549	42 2									945	849	65.1							
Sept.				1,101	1,049	100 0	570	549	53 1			895		849	844	849	90 6							804	849		
Oct.				1,047	1,049	94 9	628	549	55 7			811	849	61 4	856	849	71 3							836	849		
Nov.				1,196	1,049	100 0																					
1979																										
Jan.										861	949									740	649	62 3				
Feb.										743	649															
Mar.										729	749									775	749	72.0				
Apr.							908	849																		
May							772	749																867	849		
June							679	649																			
July							675	649																			
Aug							619	649																			
Sept							639	649																			
Oct							725	649																			

TABLE 5.—Percentage composition of female king mackerel by area, type of gear, year, and size class. Ratios in parentheses were determined from samples of <10 fish.

Fork length interval (mm)	Texas		Louisiana		Mississippi	Northwest Florida				South Florida				South Carolina-Georgia	North Carolina
	Recreational hook and line		Recreational hook and line		Commercial snapper	Recreational hook and line				Commercial hook and line			Gill net	Recreational hook and line	Recreational hook and line
	1977	1978	1977	1978	1978	1968	1969	1977	1978	1968	1969	1978	1979	1978	1978
300- 499						(75.0)	(100.0)	(100.0)	33.3*	(100.0)	(100.0)		(100.0)		
500- 699	(57.1)	41.8	(100.0)		(0.0)	68.0*	70.7*	73.3*	57.0*	52.7	35.6*	(37.5)	58.2*	24.3*	57.8	61.9
700- 899	56.9	52.3	85.4*	80.0*	58.5	73.5*	72.2*	72.0*	72.7*	69.4*	65.0*	34.9*	63.4*	56.3*	54.6	68.2*
900-1,099	(100.0)	78.3*	90.2*	86.5*	61.0	85.0*	100.0*	88.6*	96.5*	78.5*	84.4*	67.9*	94.3*	70.7*	82.4*	94.0*
1,100-1,299		94.7*	98.1*	97.9*	100.0*	(100.0)	100.0*	(87.5)	100.0*	100.0*	93.3*	(100.0)	(100.0)	100.0*	100.0*	100.0*
1,300-1,499		(100.0)	100.0*	98.9*		(100.0)								(100.0)	(100.0)	
1,500-1,699			(100.0)	(100.0)												
300-1,699	60.8*	62.2*	91.9*	92.9*	63.5*	71.7*	75.1*	73.6*	57.1*	65.4*	61.8*	40.2*	64.0*	53.7*	61.5*	75.8*

*Significantly different (probability <0.05, chi-square test) from a 1:1 ratio.

All data meeting the above criteria were from fish caught off south Florida and North Carolina (Tables 1, 2) and are summarized in Table 6.

All comparisons of south Florida frequency distributions (recreational hook and line to commercial hook and line, and commercial hook and line to gill net) showed significant differences between size compostions; no significant differences were found in comparisons of compositions from North Carolina. The summary data (Table 6) from the south Florida samples showed the following: 1) Mean lengths were greater from gill nets than from commercial hook and line in 5 of 6 cases, 2) standard deviations about the mean were similar between gill nets and commercial hook and line, and 3) frequency distributions were slightly skewed to the right in 15 of 16 cases.

Although no significant differences were found between the size-frequency distributions of the recreational and commercial hook-and-line catches in North Carolina (Table 6), the summary data showed the mean size to be larger, and the standard deviation about the mean to be smaller, in the recreational catches.

The frequency distributions, from which data in Table 6 were computed, were converted to percent frequency and averaged within gear type and year. These distributions, summary statistics, and results of chi-square comparisons are shown in Figure 3 and Table 7. All comparisons between gear types were significantly different. Mean lengths and standard deviations were greater for the fish caught by gill nets than by commercial hook and line during 1968 and 1977; the opposite was true for 1976. Mean lengths of fish caught by recreational hook and line were greater than those caught by commercial hook and line in 1979 (south Florida) and by commercial hook and line 1978 (North Carolina).

The available data (above) were not adequate to evaluate selectivity and did not reflect the wide variations in mean and modal lengths that occurred among months in the catches. When individual monthly modes are viewed, we see that modal lengths varied from 649 to 849 mm FL in distributions from commercial hook and line but were always 749 mm FL in the gill net catches (Tables 3, 4). Modal lengths from recreational hook-and-line catches showed even more variation and ranged from 549 to 1,249 mm FL.

Although selectivity of the gears could not be properly quantified, we concluded, based on fluctuations (or lack of) in the modal lengths, that among the three gear types the gill net is the most selective and the recreational hook and line is the least selective toward sizes of king mackerel.

TABLE 6.—Monthly summary statistics (mean, standard deviation of mean, and skewness) of king mackerel length data used to compare size composition among gear and results of chi-square comparisons among length frequency distributions.

Area	Year and month	Recreational hook and line				Commercial hook and line				Gill net				Recreational vs. commercial hook and line		Commercial hook and line vs. gill net	
		N	$\bar{x}$	$s_{\bar{x}}$	Y_1	N	$\bar{x}$	$s_{\bar{x}}$	Y_1	N	$\bar{x}$	$s_{\bar{x}}$	Y_1	df	χ^2	df	χ^2
South Florida	1968																
	Jan.					451	754	3.7	1.4	834	819	3.7	1.0			5	149.5*
	Feb.					639	746	3.5	1.4	1,608	758	1.7	0.3			5	91.0*
	Mar.					950	759	2.8	0.6	1,038	807	3.2	0.7			6	124.1*
	1976																
	Feb.					1,796	771	2.5	0.8	313	751	3.0	0.1			5	136.6*
	1977																
	Jan.					1,194	755	2.2	0.1	2,777	804	2.0	0.7			6	246.8*
	Feb.					4,106	751	1.5	0.4	1,062	804	2.4	0.7			6	311.9*
	1979																
	Jan.	371	861	7.8	−0.3	567	742	4.7	0.5					6	211.3*		
	Mar.	1,052	729	4.9	0.3	118	775	7.9	0.1					6	54.0*		
North Carolina	1978																
	Sept.	144	844	10.1	−0.7	72	804	14.1	−0.5					5	6.9		
	Oct.	441	856	4.4	0.8	36	836	17.0	0.9					5	8.5		

*Probability ≤0.05

TABLE 7.—Annual summary statistics (mean, standard deviation of mean, and skewness) of king mackerel length data used to compare size composition among gear and results of chi-square comparisons among length frequency distributions.

Area	Year and month	Recreational hook and line				Commercial hook and line				Gill net				Recreational vs. commercial hook and line		Commercial hook and line vs. gill net	
		N	$\bar{x}$	$s_{\bar{x}}$	Y_1	N	$\bar{x}$	$s_{\bar{x}}$	Y_1	N	$\bar{x}$	$s_{\bar{x}}$	Y_1	df	χ^2	df	χ^2
South Florida	1968					2,032	752	4.9	1.1	3,480	794	6.0	1.0			5	11.3*
	1976					1,796	770	10.7	0.8	313	750	5.3	0.1			5	64.3*
	1977					5,300	752	6.1	0.3	3,839	803	6.6	0.7			6	15.3*
	1979	1,423	795	10.9	−0.1	685	757	7.1	0.2					6	24.0*		
North Carolina	1978	585	850	7.6	−0.3	108	769	8.2	0.1					6	33.0*		

*Probability ≤0.05.

SIZE COMPARISONS AMONG YEARS AND AREAS

The following categories were used to compare size compositions between years: 1) Northwest Florida, recreational hook and line: 1968, 1969, 1977, and 1978; 2) south Florida, commercial hook and line: 1968, 1969, 1977, and 1978; and 3) Texas, Louisiana, and North Carolina, recreational hook and line: 1977 and 1978. Monthly data were combined by summing frequencies within length intervals and plotted to yield figures of annual size composition for each category (Figs. 4, 5).

Size composition varied considerably in northwest Florida between 1968 and 1978 (Fig. 4). Modal lengths decreased from 749 mm in 1968 and 1969 to 649 mm in 1977 and 549 mm in 1978. The mean length was over 115 mm, smaller in 1978 than during any of the other three years. During 1978, few fish >700 mm FL were caught, but a large percentage of the fish during each of the other three years was >700 mm FL.

In south Florida, no large differences in size composition among years were apparent. Modal lengths in the commercial hook-and-line data remained constant among years, while mean lengths ranged between 752 and 778 mm. Percents of fish above 700 mm FL were high and did not vary greatly among the four years. Size composition could have varied considerably in the population, however, and may not have been reflected in the catches owing to gear selectivity.

In Texas, Louisiana, and North Carolina differences in size composition between 1977 and 1978 were opposite that observed in northwest Florida (Fig. 5). From 1977 to 1978, modal and mean lengths increased in Texas (749-849 and 785-872, respectively), Louisiana (949-1,049 and 1,050 - 1,145), and North Carolina (649-849 and 718-850).

Recreational hook-and-line data from 1977 and 1978 were used to compare size composition between the following areas: Texas, Louisiana, northwest Florida, and North Carolina (Fig. 5). South Florida data were compared also but were collected in January-March 1979. The comparisons produced the following results: 1) Texas and North Carolina size compositions were more similar than any other areas; 2) Louisiana catches were composed of much

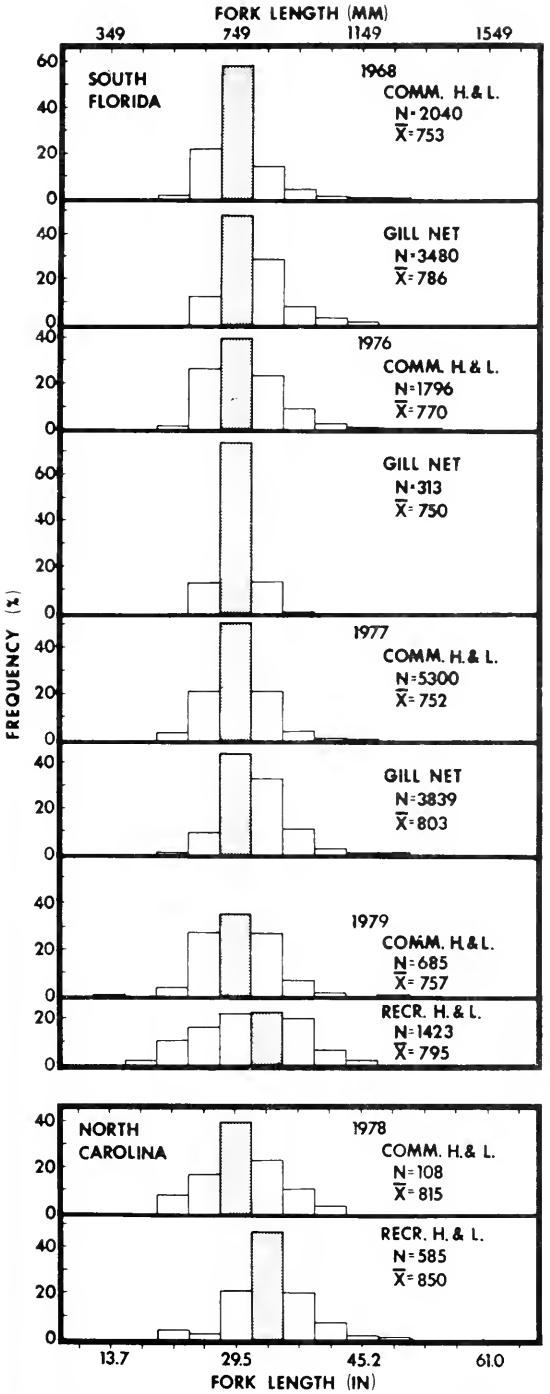

FIGURE 3.—Length-frequency distributions of king mackerel, *Scomberomorus cavalla*, by capture gear, area, and year.

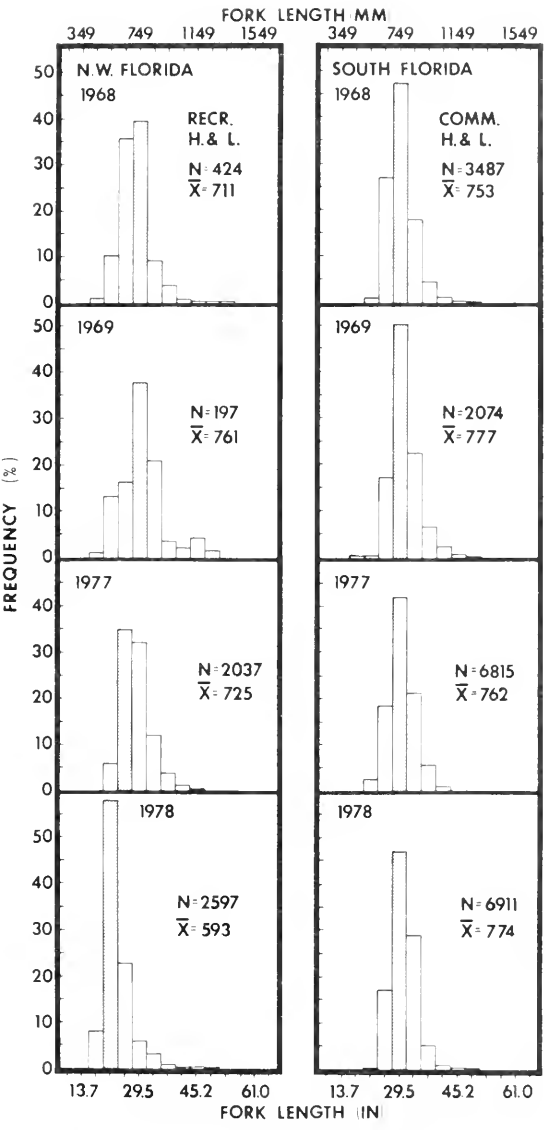

FIGURE 4.—Yearly length-frequency distributions of king mackerel, *Scomberomorus cavalla*, caught by recreational hook and line in northwest Florida and commercial hook and line in south Florida.

larger fish than were catches from any other area in either year; 3) northwest Florida catches, although similar to Texas and North Carolina catches in 1977, were composed of much smaller fish in 1978; 4) south Florida catches, like northwest Florida catches, contained fish in the 300-400 mm FL range as well as sizes representative of the Texas and North Carolina catches (fish in the 500-1,000 mm FL range).

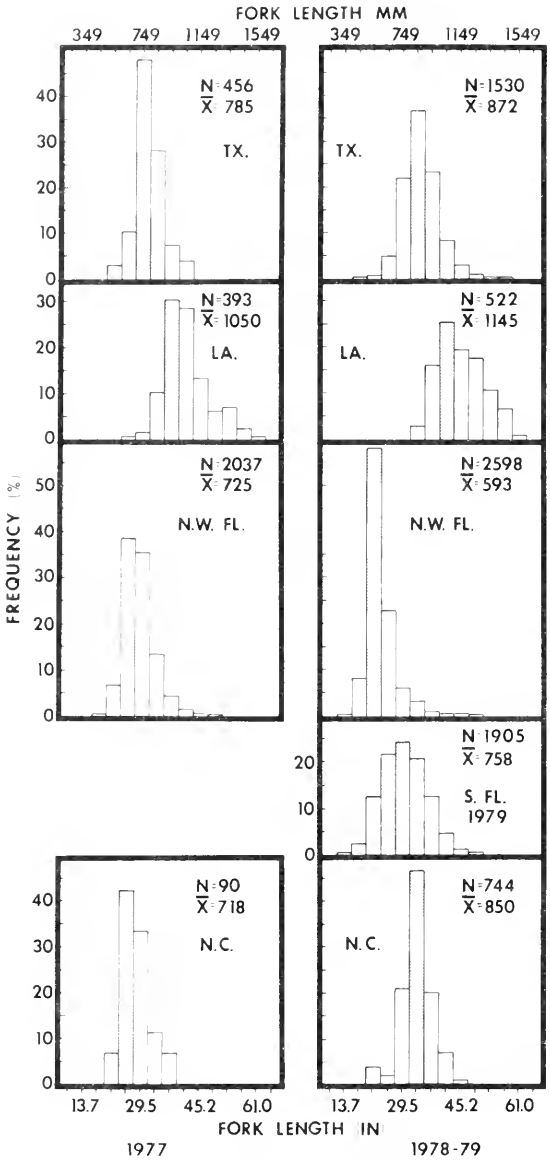

FIGURE 5.—Geographic variations in length-frequency distributions of king mackerel, *Scomberomorus cavalla*, caught by recreational hook and line during 1977-78 (and 1979 for south Florida).

SIZE AT RECRUITMENT AND EVALUATION OF MINIMUM SIZE LIMITS

Recruitment has been defined as 1) the addition of new fish to the vulnerable population by growth from among smaller categoreis (Ricker 1975; Royce 1972) and 2) a movement of fish onto the fishing grounds (Beverton and Holt 1957). For reasons discussed below, the latter definition appears most useful in evaluating recruitment of king mackerel.

King mackerel <400 mm (15.7 in) FL were reportedly not caught in appreciable numbers in any of the sampling areas in this study (Table 8). We suspect that small king mackerel did not occur in our collections for reasons related to fish distribution, gear selectivity, or both. Small king mackerel may occur offshore beyond the areas where recreational and commercial gill net fishermen normally fish for small coastal pelagic species such as bluefish, *Pomatomus saltatrix*, and Spanish mackerel, *Scomberomorus maculatus*, because few king mackerel are landed by these fishermen (Fable and Trent[6]). Whether small king mackerel intermingle to a great extent with large king mackerel offshore is unknown. Methods used by fishermen to catch king mackerel in the offshore areas (large hooks, large baits, and large mesh sizes) are selective towards fish >400 mm FL.

The size of king mackerel at recruitment into recreational fisheries varied among areas and among years within some areas (Table 8). In 1978, king mackerel were most available or susceptible to capture at lengths between 600 and 899 mm FL in all areas except Louisiana and northwest Florida. Most king mackerel from Louisiana were between 900 and 1,099 mm FL, while most from northwest Florida were between 500 and 599 mm FL. More king mackerel were reported at smaller sizes in Florida than in other areas.

King mackerel were fully vulnerable to the commercial hook-and-line and gill net fishermen at lengths between 700 and 799 mm FL during every year, except 1969 in gill nets (Table 8). In 1969, full recruitment to the gill net fishery occurred between 800 and 899 mm FL.

The management measure of adopting minimum size limits was considered by State and Federal agencies responsible for managing king mackerel. This measure would, however, drastically affect some areas because of the nonhomogeneous distribuion of the king mackerel stock(s). To illustrate, the data in Table 8 were used to estimate the percentage of king mackerel that would have been illegal to retain had particular minimum size limits been in effect. For example, a minimum size of 599 mm FL (23.6 in) would have had a great impact upon recreational fishermen in northwest Florida during 1978, because about 66% of the fish caught would have been below

[6]Fable, W. A., and L. Trent. 1982. The percentages of king mackerel and cero caught in the Spanish mackerel gill-net fishery. Unpubl. manuscr., 13 p. Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA, Panama City, FL 32407.

TABLE 8.—Percentage of king mackerel caught within fork length intervals (mm) by gear, area, and year.[1]

Area and year	Recreational hook and line							Commercial hook and line						Gill net				
	<400	400-499	500-599	600-699	700-799	800-899	>899	<499	500-599	600-699	700-799	800-899	>899	<599	600-699	700-799	800-899	>899
Texas																		
1977	0.0	0.0	2.8	10.1	48.0	28.0	10.9											
1978	0.0	0.1	0.4	4.7	22.1	36.8	35.9											
Louisiana																		
1977	0.0	0.0	0.0	0.5	1.5	10.1	87.9											
1978	0.0	0.0	0.0	0.0	0.0	2.9	97.1											
Northwest Florida																		
1968	0.0	0.9	10.1	35.6	39.4	9.0	5.0											
1969	0.0	1.0	13.2	16.2	37.6	20.8	11.2											
1977	0.1	0.1	6.6	38.5	35.2	13.3	5.9											
1978	0.1	8.1	58.2	22.8	6.1	3.1	1.7											
South Florida																		
1968								0.1	1.0	27.0	47.7	18.0	6.2	0.1	13.1	50.2	26.6	10.0
1969								0.0	0.3	17.2	50.3	22.5	9.7	0.0	0.5	30.9	38.1	21.5
1975								0.0	2.1	19.6	52.2	21.4	4.6					
1976								0.1	1.5	28.2	44.3	19.5	6.3	0.0	12.8	73.5	13.4	0.3
1977								0.0	2.8	20.2	46.2	23.4	7.4	0.1	10.7	41.4	30.4	17.4
1978								0.0	0.3	17.2	47.2	29.0	6.3	0.0	6.4	65.1	27.9	0.7
1979	0.3	2.2	12.4	21.6	24.4	20.7	18.2	0.1	5.0	30.5	33.6	23.1	7.5					
South Carolina-Georgia																		
1978	0.0	0.0	9.3	4.2	22.6	36.5	27.5											
North Carolina																		
1977	0.0	0.0	6.7	42.2	33.3	11.1	6.7											
1978	0.0	0.0	1.6	4.2	22.8	46.2	25.2	0.0	6.5	5.6	26.8	44.4	16.6					

[1]Percent of fish caught by commercial snapper fishermen from Mississippi by length group in 1978 were: <699 mm, 1.1; 700-799, 16.2; 800-899, 30.2; >899, 52.5.

the legal size. A minimum size of 699 mm FL (27.5 in) would have made significant portions (over 40%) of the 1977 recreational catch in northwest Florida and in North Carolina illegal. This minimum size of 699 mm FL would have made 17-36% of the commercial hook-and-line catch and 7-14% of the gill net catch illegal, depending on the year.

DISCUSSION

The seasonal distribution of adult king mackerel in the coastal zone of the southeastern United States can be inferred from catch data. These fish are caught in abundance along the south Atlantic coast (north Florida to North Carolina) in the spring and fall, along the northeast and northwest segments of the Gulf of Mexico in late spring, summer, and fall, and off the south Florida and Louisiana coasts year-round. Size and sex composition data indicate, however, that fish found in these areas and times do not belong to a homogeneous king mackerel population (assuming that we are dealing with only one) and should not be considered as such for management purposes. To evaluate the impact of proposed minimum size regulation and possibly to provide a framework for managing minimum size, we have partitioned the U.S. portion of the North American king mackerel population into four groups: 1) Florida winter group; 2) the immmature group; 3) the spawning group; and 4) Louisiana group. These groups are not known to be stocks or genetic groups, but rather they represent groups that can be identified in time, space, or sexual maturity states.

Florida Winter Group

This group occurs along the east and west coasts of the southern half of Florida, including the Florida Keys during colder months (December-March), and is thought to be sexually inactive during this period (Beaumariage 1973; Finucane et al.[7]). The group includes all sizes of king mackerel known to exist in the exploited populations. The abundance of medium-sized king mackerel each winter is well documented; several years of commercial hook-and-line and gill net data show that about 90% of the king mackerel landed by commercial fishermen in south Florida are between 600 and 899 mm FL. Large king mackerel (1,000-1,500 mm FL) caught by recreational fishermen from the south Florida area have been reported by Beardsley and Richards (1970). A 90-lb (about 1,800 mm FL) king mackerel was caught in south Florida in February 1976 (Anonymous 1976). The Florida winter group becomes reorganized, through movement and migration during spring, summer, and fall, into the more northerly immature and spawning groups.

The Immature Group

Members of this group include the small (300-600 mm FL) king mackerel from the Florida winter group

[7]Finucane, J. H., L. A. Collins, H. A. Brusher, and C. H. Saloman. 1983. Reproduction of king mackerel from the Gulf of Mexico and south Atlantic. Unpubl. manuscr., 15 p. Southeast Fish. Center Panama City Laboratory, National Marine Fisheries Service, NOAA, FL 32407.

and are, for the most part, sexually inactive (Beaumariage 1973, Finucane et al. footnote 7). Immature fish form a large proportion of the Florida winter catch but are proportionately less abundant along the North Carolina, South Carolina, and Texas coasts. For example, percent compositions of king mackerel between 300 and 600 mm FL in the recreational catches by area and year were as follows:

Location	*Year*	*%*
South Florida	1979	14.9
South Carolina-Georgia	1978	9.3
North Carolina	1977	6.7
	1978	1.6
Northwest Florida	1968	11.0
	1969	14.2
	1977	6.8
	1978	66.4
Texas	1977	2.8
	1978	0.5

King mackerel <600 mm FL were not observed from Louisiana. Members of the immature group are caught in abundance in areas other than south Florida only during summer months. They are proportionately abundant in the catches in July-August in northwest Florida, in August in Texas, and in September in North Carolina.

The Spawning Group

Members of this group include the sexually mature individuals (usually >600 mm FL) of the Florida winter groups and, during warmer months, are distributed throughout the coastal zone of the southeastern United States and along the northeast U.S. coast. In the Gulf of Mexico, most members of this group residing in south Florida during winter apparently migrate north earlier or faster than do members of the immature group (Trent et al. 1981). Early departure of the larger king mackerel is reflected, for example, in the recreational landings in south Florida during 1979; mean fork lengths decreased from 861 mm in January to 729 mm in March. King mackerel occurring in the early months of each fishing season in northwest Florida and Texas are usually the largest. Members of this group that migrate northward along the Atlantic coast in the spring did not reveal the same seasonal size pattern as did those in the Gulf of Mexico. The largest individuals did not arrive in North Carolina until June of each year and were preceded by smaller fish.

Louisiana Group

This group is characterized by large fish, most of which are female. Of all fish examined only 12.1% in 1977 and 2.9% in 1978 were <900 mm FL (about 12 lb) and 92.5% of all fish were females. Although king mackerel of both sexes were caught during all seasons, monthly estimates of the proportion of females were never <80%. The highest proportions of males occurred from May through September. Exceptionally large fish (>1,399 mm FL) were caught in highest proportions from November through March. Fish <800 mm FL were caught only during June, September, and October.

The range and migration patterns of the Louisiana group are not known. Most of the king mackerel observed from Louisiana were caught adjacent to oil rigs in water depths of 10-20 fathoms about 12-18 mi southeast of Grand Isle. This area is fished heavily by recreational fishermen, because it is within practical range of two ports (Grand Isle and Empire) that produce most of the fishing effort for king mackerel in Louisiana and because king mackerel fishing is known to be good in the area. The oil rigs, however, are numerous at depths from 10 to 50 fathoms from the Mississippi Delta (long. 89°30′) westward to areas off the Texas-Louisiana border (long. 93°50′), an east-west distance of about 250 mi. Members of the Louisiana group probably occur throughout the oil field but, evidently, do not participate in extensive north-south migrations as do smaller king mackerel. The presence of large king mackerel off the Louisiana coast in winter (Table 4) suggests that environmental factors are favorable for them there throughout the year. Munro (1943) stated that minimum temperatures of 20°C limit the distribution of members of the genus *Scomberomorus*. Large king mackerel were caught in abundance off the Louisiana coast during the winters of 1977 and 1978, two of the coldest winters on record (Ingham 1979). In 1978, surface water temperatures and their deviations from the 1948-67 mean (°C) in the one-degree square (long. 89°-90° and lat. 28°-29°) just south of the area where king mackerel were caught averaged 19.4°C (−1.3) in January, 18.7°C (−1.8) in February, and 18.6°C (−2.4) in March. Data collected during January-March 1976 indicated that bottom temperatures are about 1°-2°C higher than surface temperatures where depths are between 10 and 20 fathoms off Louisiana (Ragan et al. 1978); thus a habitat in which temperatures were 20°C or greater could have been available to king mackerel in 1978.

Atlantic croaker; longspine porgy, *Stenotomus ca-*

pirinus; silver seatrout, *Cynoscion nothus*; and other fish species acceptable as food by king mackerel are especially abundant during winter months in 10-30 fathom depths off Louisiana and east Texas (Moore et al. 1970). Food studies of large king mackerel from Louisiana indicate that sciaenids (seatrouts and Atlantic croaker) are the dominant species of prey during the winter and spring months (Saloman and Naughton footnote 5).

Sex Ratio

We could not explain why the sex ratio favored females. The ratios we observed may be real in that more females than males are produced at spawning or that mortality rates are higher for males than females at sizes (<400 mm FL) smaller than those we observed.

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THE ESTIMATION OF A CATCH LEVEL WHICH STABILIZES THE PARENTAL BIOMASS OF AN EXPLOITED FISH STOCK

J. MAJKOWSKI AND J. HAMPTON[1]

ABSTRACT

This paper addresses the problem of determining a catch level which stabilizes the parental biomass of a fish population at its present level. Initially, two methods are presented, both based on a simple catch equation and requiring estimates of recruitment, natural mortality, weights at age, proportions of sexually mature fish in each age class, and present parental biomass. Method I deals with a fishery assumed to have complete control over age composition of catches and requires age composition to be specified. Estimation of the catch age composition which results in the absolute maximum catch weight while holding parental biomass constant is also demonstrated. In method II no control over catch age composition is assumed; this composition is determined by catchability coefficients and the age structure of the population. Then, a simple modification of method II, method III, is presented for a fishery which has limited control over catch age composition through selective allocation of relative fishing effort among components of the fishery, the age composition of each component being different but not controllable by the fishery. This allows the determination of catches stabilizing the parental biomass for different allocations of relative fishing effort. Maximization of catch weight using methods I and III can be regarded as an improved yield per recruit analysis having the explicitly incorporated conditions of constant parental biomass and, as a consequence of other assumptions inherent in the methods, of constant recruitment. Consequences of incomplete compliance with assumptions inherent in these methods and their management implications are discussed. These methods are applied to southern bluefin tuna, *Thunnus maccoyii*, population and fishery data collected prior to 1981, and indicate that a total stabilizing catch of about 30,000 t per year is possible under the existing pattern of fishing.

Management of many commercial fisheries involves the determination of the maximum sustainable yield (MSY), (see reviews in Ricker 1975; Gulland 1977) and the imposition of restrictions which ensure that catches do not exceed this MSY. The estimation of MSY is usually made with the aid of production models which typically require historical catch per unit fishing effort data (Ricker 1975; Gulland 1977). Even if such data are available, assumptions underlying the use of these models are often violated or at least poorly complied with in real fisheries situations. Models taking account of the population age structure such as those reviewed by Getz (1979) are, in many cases, more appropriate for determining the MSY, but, in addition to estimates of natural mortality and growth rate, they also require information on the stock-recruitment relationship.

It is often the case that the stock-recruitment relationship for an exploited population is poorly known and the production models cannot be used for the reasons outlined. In this situation, a sensible management strategy is to stabilize the parental biomass at its present level which, through experience, is known to provide an adequate recruitment. As well as the assurance of reproductive success, the stabilization of parental biomass (and, as a consequence of the approach to be applied, of the entire age structure of the population) may be desired for completely different reasons, e.g., the preservation of a certain ecological equilibrium in a community of interacting species in which the exploited species is a member.

The objective of this paper is to demonstrate how a level of yearly catch that will stabilize the parental biomass of a population at its present level can be determined. This catch is hereafter referred to as the stabilizing catch. Initially, two methods developed for this purpose are presented. Method I deals with a fishery which has complete control over age composition of catches, while method II is relevant to a fishery having no such control. Method III, a simple modification of method II, is then presented for a fishery having limited control over catch age composition. It is assumed that this fishery can be divided into components, the catch age composition of each being different but not controllable by the fishery.

An estimation of stabilizing catch based on method I can be made for nearly any age composition of catches. This method allows also the determination of an age composition which results in the absolute maximum stabilizing-catch weight. If a fishery has

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limited control over age composition of catches, this maximum catch is usually not attainable. Method III allows the determination of stabilizing catches when relative fishing effort in one or more of the components of the fishery is changed. This enables the selection of a fishing strategy that is most suitable for achieving a management objective (e.g., the attainable maximum catch weight).

Maximization of catch weight using methods I and III can be regarded as an improved yield-per-recruit analysis. The advantage of this approach in comparison with the classical one (Beverton and Holt 1957) is the explicit incorporation of the condition of constant parental biomass and, as a consequence of other assumptions inherent in the methods, of constant recruitment. The condition of constant recruitment must be assumed in the classical analysis to make the interpretation of results practically useful. However, the difficulty in the classical approach is that the effect of changing the fishing strategy upon the recruitment level is not considered. As pointed out by Dunning et al. (1982), this may result in long-term yield losses if the reproductive potential of the population is reduced.

The three methods differ in their data requirements. Method I requires the relative catch age composition to be specified, while methods II and III can be used if estimates of age class-specific catchability coefficients (defined as the fraction of all fish in the age class caught using one unit of fishing effort) are available. These catchability coefficients in the case of method III have to be known for all components of the fishery being investigated. Also, the three methods require estimates of recruitment, natural mortality, weights at age, proportions of sexually mature fish in each age class, and present parental biomass.

Although few fisheries will exactly comply with all the assumptions underlying the use of these methods, fisheries scientists and managers, knowing the characteristics of their fisheries and the data available, should be able to decide which method best suits their particular cases. The consequences of incomplete compliance with the assumptions inherent in the methods and their management implications are discussed. The methods are illustrated by their application to southern bluefin tuna, *Thunnus maccoyii* (Castelnau), population and fishery data collected prior to 1981.

METHODS

Theoretical Background

A population satisfying the following assumptions is considered:

(a) Both recruitment to the fishable portion of the population and spawning are discrete events with respect to time and take place once per year at the same time each year.

(b) The magnitude of recruitment is dependent only upon the magnitude of parental biomass.

(c) Instantaneous rate of natural mortality may be dependent on age class only.

(d) Average weight of fish in the population at the time of spawning is a function of age only.

(e) Average weight of caught fish from any age class does not change from year to year.

If 1) these assumptions are satisfied, 2) both the magnitudes of yearly catches decomposed into age classes and their variability within a year do not change from year to year, and 3) a catch level is being maintained which ensures that the magnitude of parental biomass at spawning is constant, the population is in a regime referred to in this paper as a steady-state.

The question posed is what level of yearly catch would lead to the maintenance of parental biomass, P, at a specific level PS at the time of spawning over an infinite number of years. If a steady-state exists, only a single cohort need be considered to address this question.

The catch determination methods to be presented are based on the Pope (1972) catch equation:

$$C_i = No_i \exp(-0.5M_i) - Ne_i \exp(0.5M_i) \qquad (1)$$

where C_i is the yearly catch (in number) of fish from age class i (age class i is defined as a group of fish at age $i-1$ to i years), No_i and Ne_i are, respectively, the initial and final abundances of fish in age class i, i.e., at age $i-1$ and i years of age (in steady-state $Ne_i = No_{i+1}$), and M_i is the instantaneous rate of natural mortality for age class i. This equation was derived assuming that the entire yearly catch is taken in the middle of the year and M_i is constant during the year. It is a modification of the equation (Ricker 1975)

$$C_i = \frac{F_i}{Z_i} No_i(1 - \exp(-Z_i)) \qquad (2)$$

where Z_i and F_i are the yearly average rates of total and fishing mortalities, respectively, for age class i. Both equations are equally effective in the majority of cases, but the use of Equation (2) is complicated from the computational point of view (see discussions in Pope 1972; Ricker 1975). Therefore,

Equation (1) is used as the basis of the methods presented in this paper.

The assumptions associated with Equation (1) can be relaxed by using a time interval smaller than 1 yr. For example, if monthly periods were used, 12 equations could be formulated, each expressing the relationship between the monthly catch and the numbers of fish at the beginning and end of a month. In such a case, M_i and the fishing intensity could vary from month to month.

Method I (Complete Control Over Age Composition)

Here we consider a fishery which has complete control over the age composition of catches. The dynamics of a single cohort are described in such a case by the system of equations:

$$Cf_i = No_i \exp(-0.5M_i) - No_{i+1} \exp(0.5M_i) \quad i = r, \ldots n \tag{3}$$

where C is the total yearly catch in number, f_i is the fraction of the total catch belonging to age class i ($f_i = C_i/C$), and r and n, respectively, denote the youngest and oldest age classes numerously represented in the fishable portion of the population. The abundances of age classes should satisfy the condition:

$$\sum_{i=r}^{n+1} \alpha_i No_i Ws_i = PS \tag{4}$$

where α_i is the fraction of sexually mature fish in the ith age class and Ws_i is the average weight of a sexually mature fish belonging to age class i at the time of spawning.

The system of $n - r + 2$ algebraic Equations (3) and (4) is solvable for C and No_i's if the values of PS, No_r, f_i, M_i, α_i, and Ws_i ($i = r, \ldots, n$) are known. Meaningful solutions are restricted by the conditions

$$C \geq 0$$

and

$$No_i \geq 0 \quad i = r + 1, \ldots, n + 1. \tag{5}$$

Because of these conditions a meaningful solution may not exist for a given set of input values. In such a case, a change in fishing strategy (and also, therefore, in the f_i values) may resolve the problem. The stabilizing total catch, CB, can be found from the formula:

$$CB = \sum_{i=r}^{n} Cf_i \overline{W}_i \tag{6}$$

where $\overline{W}_i$ is the average weight of a fish from the ith age class.

If the basic management objective is to maintain the parental biomass at its present level, only the coefficients f_i may be subject to manipulation. According to their definition, they have to satisfy the following conditions:

$$f_i \geq 0 \quad i = r, \ldots, n$$

and

$$\sum_{i=r}^{n} f_i = 1 \tag{7}$$

but their individual values can be selected freely to the extent determined by the nature of Equations (3), (4), and (5). If alternative fishing strategies defined by different values of f_i are feasible, it is of interest to know 1) which of these are possible under the basic management objective of stabilizing the parental biomass and 2) what catches and age structures of the population are associated with these strategies. These questions can be easily addressed by solving the system of Equations (3) and (4).

It may be desirable to select such a fishing strategy which, in addition to maintaining the parental biomass at its present level, would yield the absolute maximum weight of yearly catch. This strategy could be determined by finding the set of f_i coefficients which maximizes CB. The problem is readily solvable with the aid of linear programming methods using Equation (6) as an objective function (treating Cf_i as a single variable C_i, thus making the problem linear) constrained by Equations (3), (4), and (5).

Method II (No Control Over Age Composition)

Here we consider a fishery which may be age selective, but that selectivity is beyond the fishermen's control. This being the case, changes in the age composition of catches can only be caused by alterations in the age composition of the population.

In this case, C_i can be expressed as

$$C_i = q_i E No_i \exp(-0.5M_i) \quad i = r, \ldots, n \tag{8}$$

where q_i is the catchability coefficient for age class i and E is an index of effective fishing effort. Substituting for C_i in Equation (1) we obtain

$$q_i E No_i \exp(-0.5M_i) = No_i \exp(-0.5M_i) - No_{i+1} \exp(0.5M_i) \quad i = r, \ldots, n. \tag{9}$$

If the values of No_r, PS, q_i, α_i, and Ws_i ($i = r, \ldots, n$) are known, the system of $n - r + 2$ algebraic Equations (9) and (4) can be solved with respect to E and No_i ($i = r+1, \ldots, n+1$). Note that this equation system can be reduced to an $n - r + 1$ th order polynomial equation and solved for E using a standard computer routine which finds the zeroes of a function. The values of No_i can then be found by substitution. Meaningful solutions for E are constrained by the conditions

$$E \geq 0$$

and

$$No_i \geq 0 \quad i = r+1, \ldots, n+1. \tag{10}$$

Knowing E and No_i's, the C_i values can be determined on the basis of Equation (8).

Method III (Limited Control Over Age Composition)

If a fishery can be divided into components, each of which is characterized by a unique set of q_i values, some control over the age composition of the total catch can be exercised by varying the relative amount of fishing effort expended in these components. In such a case, it is appropriate to replace q_iE in Equation (9) with $\sum_{j=1}^{K} q_{ij} E_j$ where j denotes one of k components of the fishery. The system of Equations (4) and (9) (modified) may then have a number of solutions (i.e., sets of E_j's and No_i's), but only the management strategies defined by nonnegative solutions will be possible for implementation. Determination of the meaningful solutions and the associated catches will be helpful for fisheries managers in selecting a fishing strategy that is most suitable for achieving their objectives (e.g., the attainable maximum yearly catch weight).

VALIDITY OF ASSUMPTIONS AND MANAGEMENT IMPLICATIONS

Assumption (a) limits the number of species for which the methods can be applied. It is not satisfied for most tropical species (see review in Saila and Roedel 1980), but does hold well for many temperate species (see reviews in Gulland 1969, 1977; Ricker 1975).

The magnitude of recruitment to most fish stocks is affected to some degree by environmental variation; therefore, assumption (b) will rarely be strictly satisfied. However, as long as the environmentally induced variation in recruitment is random and not large, results derived on the basis of the methods should provide a good indication of the stabilizing catch level.

Assumptions (c) to (e) are standard for most fisheries analyses (see reviews in Gulland 1969; Ricker 1975) although their validity is not always obvious. If both the age structure of the population and the environment are stable, assumptions (c) to (e) will likely be satisfied. The assessment of compliance with assumption (c) is extremely difficult. Simple methods used for estimating M (Gulland 1969, 1977; Ricker 1975) are usually unsuitable for testing this assumption. More complex methods are available (e.g., Majkowski 1981), but these have considerable data requirements and are frequently impractical. Assumptions (d) and (e) can usually be tested, especially if a technique of direct age determination is available for the species under consideration.

A management policy defined by the values of C and f_i's (satisfying Equations (3) and (4)) or E and q_i's or E_j's and q_{ij}'s (satisfying Equations (4) and (9)) can be effective immediately if the age structure of the population at the beginning of the first year of policy implementation is identical to that defined by the calculated values of No_i's (corresponding to the values of C and f_i's, E and q_i's or E_j's and q_{ij}'s). This will rarely be the case because of historical variation in catches. As a consequence, the parental biomass during an initial period of harvesting CB may fall below or increase above the specified level. As long as this has no effect upon recruitment, the population age structure will approach that defined by the calculated No_i's over the life span of the species.

The accuracy of the input parameters is implicitly assumed. Uncertainty in the management recommendations (i.e., in the value of CB) due to inaccuracies (caused by estimation errors and/or natural variability) in estimates of the input parameters for the procedures is generally difficult to predict, but can be examined for each specific application of the procedures using a sensitivity analysis technique (see reviews in Majkowski et al. 1981a; Majkowski 1982, in press; Majkowski and Hampton 1983).

EXAMPLE

Application of the methods described is demonstrated by using southern bluefin tuna population and fishery data collected prior to 1981.[2] This

[2]This analysis has since been updated (Hampton et al. in press).

species is highly migratory and spawns in waters off the south coast of Java. Juveniles migrate to waters off the coast of Australia, passing Western and South Australia and New South Wales. The general direction of their movement within the 200 mi Australian Fishing Zone (AFZ) is from west to east; however, some fish also move in the reverse direction. Schools of juveniles within the AFZ support the most important and valuable Australian finfish fishery. The fishing methods used are pole and line, purse seining, and, to a small extent, trolling. Southern bluefin tuna passing Australia gradually leave the nearshore fishing areas and become available to the Japanese longline fishery.

The parental biomass of this population, presently (i.e., in 1980) equal to about one-third of the preexploitation level, has been continuously and significantly reduced over the period of exploitation (Murphy and Majkowski 1981). Recruitment to the fishable portion of the stock has been quite stable over the same period, although reliable recruitment estimates are available only to 1976. Due to the absence of accurate information on the southern bluefin tuna stock-recruitment relationship and the lag in evaluation of the recruitment level, a conservative approach to fisheries management is most appropriate at this stage. Therefore, it is recognized by scientists of Australia, Japan, and New Zealand, the countries involved in the southern bluefin tuna fishery, that the present level of parental biomass should not be reduced further. This scenario provided the impetus for this paper.

Determination of Input Parameters

The input values required for the application of method I, their symbols, descriptions, and reference sources are presented in Table 1. The values of No_r and PS were estimated by cohort analysis while the f_i values were derived from the 1980 catch-at-age data. The catchability coefficients (calculated by using No_i's from cohort analysis), required for the application of methods II and III, are presented in Table 2.

Results

Results from several applications of methods I and II are presented in Table 3. Values of CB calculated on the basis of method I using the catch age composition specified in Table 1 and calculated on the basis of method II using the global catchability coefficients (see Table 2) are almost identical (30,012 and 29,013 t, respectively). The associated age structures of both population and catch produced by the two methods are also very similar (Table 4).

Estimates of CB derived using method I are dependent on the specified values of f_i. CB is maximized at 52,690 t/yr under the condition that only age classes 10 and 11 are fished. This fishing strategy requires catches of 123,100 fish from age class 10 and 688,100 fish from age class 11. The result is obtained using a linear programming computer program from the Numerical Algorithm Group Library, utilizing the contracted simplex method (McMillan 1970).

Within method II it is possible to examine the effect of various fishing regimes on CB simply by varying the values of q_i. Examples are presented in Table 3. The catchability coefficients used in these examples reflect the operation of 1) single components of the southern bluefin tuna fishery (i.e., the Australian fisheries off the coasts of Western Australia, South Australia, or New South Wales, or the Japanese fishery), or 2) the entire fishery with the exclusion of a selected component. The range of CB's estimated in this way was 12,523-44,695 t. These extreme values of CB corresponded to the lone operation of the Western Australian and Japanese fisheries, respectively.

Method III allows calculations of various combinations of stabilizing catches by the components of the global fishery. Examples of possible catch combinations are given in Table 5. These catch values are generated by specifying combinations of E's associated with the Western Australian, South Australian, and New South Wales fisheries, then calculating the Japanese fishing effort index and all related catches which would enable the stabilization of parental biomass. These results show that, as the fishing efforts of the Western Australian, South Australian, and New South Wales components increase, the Japanese and global stabilizing catches decrease. The minimum and maximum CB values generated by using method III are equivalent to the values in Table 3, relating to the lone operation of the Western Australian and Japanese fisheries, respectively.

Sensitivity Analysis

The sensitivity analysis technique used is referred to as ordinary sensitivity analysis (Majkowski and Bramall 1980; Majkowski and Waiwood 1981; Majkowski 1982, in press). The procedure consists in individually perturbing input parameters by various relative amounts and observing the resultant changes in CB.

The results of ordinary sensitivity analyses of the CB estimates of 30,012 and 29,013 t derived by using methods I and II, are presented in Tables 6 and 7, re-

TABLE 1.—Input parameter values for southern bluefin tuna necessary for the evaluation of CB using method I.

Parameter	Symbol	Value	Source of Information
Youngest exploited age class	r	2	Majkowski et al. (1981b)
Oldest exploited age class	n	20	Shingu (1978)
Proportion of fish belonging to age class which is sexually mature	α_i		Shingu (1978)
	i = 2-8	0	
	i = 9-20	1	
Abundance of fish about to enter age class r	No_r	5,258,422	J. Hampton (unpubl. data)
Yearly average rate of natural mortality	M	0.2	Hayashi et al. (1972)
Existing parental biomass (kg)	PS	167,371,601	J. Hampton (unpubl. data)
Fraction of the total 1980 catch (in number) belonging to age-class i (1980 calendar year)	f_i		J. Hampton (unpubl. data)
	i = 2	0.085321	
	3	0.411359	
	4	0.221376	
	5	0.053785	
	6	0.041523	
	7	0.022783	
	8	0.027565	
	9	0.031522	
	10	0.043063	
	11	0.034070	
	12	0.015556	
	13	0.007112	
	14	0.003083	
	15	0.001021	
	16	0.000505	
	17	0.000175	
	18	0.000096	
	19	0.000046	
	20	0.000037	
Weight (kg) at the beginning of the year for a fish belonging to age class i	Ws_i		Robins (1963) Kirkwood (1983)
	i = 9	47.11	
	10	55.07	
	11	62.53	
	12	69.42	
	13	75.68	
	14	81.31	
	15	86.34	
	16	90.80	
	17	94.72	
	18	98.17	
	19	101.17	
	20	103.79	
Weight (kg) at the middle of the year for a fish belonging to age class i	$\overline{W}_i$		Robins (1963) Kirkwood (1983)
	i = 2	1.81	
	3	5.55	
	4	11.19	
	5	18.26	
	6	26.22	
	7	34.58	
	8	42.99	
	9	51.14	
	10	58.87	
	11	66.05	
	12	72.62	
	13	78.57	
	14	83.90	
	15	88.64	
	16	92.82	
	17	96.50	
	18	99.72	
	19	102.53	
	20	104.97	

TABLE 2.—The catchability coefficients characterizing the global southern bluefin tuna fishery and its major components, the Australian fisheries off the coasts of Western Australia (WA), South Australia (SA), and New South Wales (NSW), and the Japanese fishery.

Age class	Fishery				
	Global	WA	SA	NSW	Japanese
2	0.0404	0.0259	0.0145	—	—
3	0.2608	0.1139	0.1430	0.0036	0.0003
4	0.1906	0.0148	0.1509	0.0170	0.0078
5	0.0609	0.0002	0.0167	0.0235	0.0206
6	0.0649	—	0.0066	0.0231	0.0352
7	0.0490	—	0.0005	0.0063	0.0422
8	0.0896	—	—	0.0074	0.0822
9	0.1057	—	—	0.0015	0.1042
10	0.1506	—	—	0.0002	0.1504
11	0.1827	—	—	—	0.1827
12	0.1413	—	—	—	0.1413
13	0.0964	—	—	—	0.0964
14	0.0654	—	—	—	0.0654
15	0.0421	—	—	—	0.0421
16	0.0224	—	—	—	0.0223
17	0.0063	—	—	—	0.0063
18	0.0050	—	—	—	0.0050
19	0.0024	—	—	—	0.0024
20	0.0023	—	—	—	0.0023

TABLE 3.—Estimates of CB and fishing effort index associated with various fishing strategies. WA = Western Australia, SA = South Australia, NSW = New South Wales, n.a. = not available.

Method	Specification of f_i's or q_i's	CB (t)	Effort index
I	f_i's from Table 1	30,012	n.a.
	f_i's corresponding to the "absolute" maximum catch weight	52,690	n.a.
II	Global q_i's	29,013	0.798
	WA q_i's	12,523	4.842
	SA q_i's	17,212	2.495
	NSW q_i's	29,314	10.968
	Japanese q_i's	44,695	1.606
	WA q_i's subtracted from global q_i's	32,479	0.928
	SA q_i's subtracted from global q_i's	35,256	1.136
	NSW q_i's subtracted from global q_i's	29,015	0.856
	Japanese q_i's subtracted from global q_i's	16,773	1.501

TABLE 4.—The estimated age composition of the southern bluefin tuna population and its catches (C_i) associated with the fishing strategies determined by the f_i values from Table 1 and the q_i values for the global fishery from Table 2.

Age class	Fishing strategy defined by			
	f_i values		q_i values	
	No_i	C_i	No_i	C_i
2	5,258,422	146,536	5,258,422	153,436
3	4,172,641	706,495	4,166,397	784,576
4	2,777,006	380,206	2,701,244	371,679
5	1,929,596	92,374	1,875,282	82,522
6	1,496,236	71,314	1,460,682	68,482
7	1,160,487	39,129	1,133,941	40,158
8	914,721	47,342	892,056	57,695
9	706,073	54,138	678,149	51,767
10	529,098	73,959	508,381	55,268
11	366,268	58,514	366,218	48,305
12	246,929	26,717	256,126	26,123
13	177,994	12,215	186,061	12,948
14	134,677	5,295	140,618	6,637
15	105,473	1,754	109,123	3,319
16	84,767	867	86,339	1,393
17	68,617	301	69,428	317
18	55,907	165	56,555	205
19	45,623	79	46,118	81
20	37,282	64	37,685	63

spectively. Several facts are evident from these results:

1) Both estimates of CB are most sensitive to perturbations of M_i and N_r.

2) Approximately linear relationships exist between CB and No_r, M_i, PS, and W_i (but not Ws_i) in the case of both CB estimates.

3) Perturbing all q_i values (method II) by the same percentage has no effect on CB, but does produce changed values of E.

4) Method II appears slightly more robust than method I in that CB (Method II) is less sensitive to changes in No_r, M_i, PS, and Ws_i than CB (Method I).

The results of sensitivity analysis presented in Tables 6 and 7 reflect the sensitivity of the CB estimates to changes in the individual input parameters. In the case of southern bluefin tuna, the input parameter estimates are related and this complicated the interpretation of the results. The effect of such interrelationships upon the CB estimates is illustrated by examining the dependence of No_r and PS upon M_i. These three parameters are probably subject to the greatest estimation error.

In the presented example, No_r and PS are estimated on the basis of cohort analysis for which M_i is an input parameter. Therefore, both No_r and PS values are dependent on the M_i estimate in which a relative error of up to $\pm 50\%$ may have existed. Table 8 shows the effects of perturbations in M_i, and the consequent changes in No_r and PS, upon the CB estimates of 30,012 and 29,013 t. Here, the percentage changes in CB in both cases are much smaller than the corresponding changes brought about by perturbations in M_i only (Tables 6, 7). This mostly results from the fact that No_r estimated on the basis of cohort analysis is a strongly increasing function of M_i and the effects of No_r and M_i on the CB estimates are antagonistic. Therefore, if No_r is estimated from cohort analysis, the results of both methods are considerably less sensitive to perturbations in M_i than in the case when No_r and M_i are independently estimated. If, however, M_i and No_r for southern bluefin tuna are independently estimated, a high degree of accuracy is necessary to confidently evaluate CB. Note that the degree of sensitivity of a CB estimate to changes in M_i is dependent also on the age composition of CB. For example, the sensitivity of the CB estimate of 52,690 t (age classes 10 and 11 only are fished), derived by using method I, to changes in M_i is much higher than that of 30,012 t (age classes 2-20 are fished). More extensive sensitivity examinations are beyond the scope of this

TABLE 5.—Possible combinations of stabilizing catches (in tonnes) in the four component fisheries when fishing effort index is specified for Western Australia (WA), South Australia (SA), and New South Wales (NSW) and calculated for Japan.

WA		SA		NSW		Japan		Total
Effort	Catch	Effort	Catch	Effort	Catch	Effort	Catch	catch
0.5	1,546	0.5	4,321	0.5	1,504	1.33	30,307	37,678
0.5	1,546	0.5	4,310	1.0	2,958	1.26	28,253	37,067
0.5	1,545	0.5	4,298	1.5	4,363	1.19	26,250	36,456
0.5	1,517	1.0	8,062	0.5	1,282	1.16	23,115	33,976
0.5	1,516	1.0	8,041	1.0	2,519	1.09	21,346	33,422
0.5	1,515	1.0	8,020	1.5	3,714	1.02	19,620	32,869
0.5	1,487	1.5	11,255	0.5	1,079	0.97	16,845	30,666
0.5	1,487	1.5	11,225	1.0	2,121	0.90	15,337	30,170
0.5	1,486	1.5	11,195	1.5	3,125	0.83	13,868	29,674
1.0	3,025	0.5	4,084	0.5	1,382	1.30	27,317	35,808
1.0	3,024	0.5	4,073	1.0	2,717	1.23	25,425	35,239
1.0	3,023	0.5	4,063	1.5	4,007	1.16	23,580	34,673
1.0	2,966	1.0	7,604	0.5	1,170	1.12	20,597	32,337
1.0	2,965	1.0	7,584	1.0	2,300	1.05	18,977	31,826
1.0	2,964	1.0	7,563	1.5	3,390	0.98	17,399	31,316
1.0	2,909	1.5	10,589	0.5	978	0.93	14,782	29,258
1.0	2,907	1.5	10,560	1.0	1,921	0.86	13,413	28,801
1.0	2,906	1.5	10,532	1.5	2,830	0.79	12,079	28,347
1.5	4,437	0.5	3,853	0.5	1,263	1.26	24,475	34,028
1.5	4,435	0.5	3,842	1.0	2,484	1.19	22,740	33,501
1.5	4,434	0.5	3,832	1.5	3,663	1.12	21,049	32,978
1.5	4,350	1.0	7,156	0.5	1,062	1.09	18,218	30,786
1.5	4,349	1.0	7,136	1.0	2,087	1.01	16,745	30,317
1.5	4,347	1.0	7,117	1.5	3,076	0.94	15,309	29,849
1.5	4,265	1.5	9,938	0.5	880	0.90	12,851	27,934
1.5	4,263	1.5	9,911	1.0	1,729	0.82	11,617	27,520
1.5	4,262	1.5	9,885	1.5	2,546	0.75	10,414	27,107

TABLE 6.—Results of ordinary sensitivity analysis of the CB estimate of 30,012 t derived by using method I.

Parameter perturbed	Perturbation magnitude			
	−25%	−1%	+1%	+25%
[2]M_t	[1]+52.3	+2.1	−2.1	−53.5
No_r	−39.9	−1.6	+1.6	+39.9
[3]f_t	+24.8	+1.0	−1.4	−36.7
[2]W_t	−25.0	−1.0	+1.0	+25.0
[2]Ws_t	−29.9	−0.6	−0.6	+12.0
PS	+14.9	+0.6	−0.6	−14.9

[1]All values in this table represent relative changes (expressed in percentages) in CB

[2]All values (i.e., for t = 2-20) are simultaneously perturbed by the same percentage indiated in the first row

[3]The f_t values for t = 2-6 are simultaneously perturbed by the percentage indicated in the first row, and all reamining f_t values (i.e., for t = 7-10) are changed by a percentage such that $\sum_{t=2}^{20} f_t$ is equal to one

TABLE 7.—Results of ordinary sensitivity analysis of the CB estimate of 29,013 t derived by using method II.

Parameter perturbed	Perturbation magnitude			
	−25%	−1%	+1%	+25%
[2]M_t	[1]+45.0	+1.9	−1.9	−50.8
No_r	−35.9	−1.4	+1.4	+33.4
[2]W_t	+25.0	+1.0	+1.0	+25.0
[2]Ws_t	−15.9	−1.2	−0.4	+ 6.3
PS	+ 8.1	+0.4	−0.4	−10.5
[2]q_t	0.0	0.0	0.0	0.0

[1]All values in this table represent relative changes (expressed in percentages) in CB

[2]All values (i.e., for t = 2-20) are simultaneously perturbed by the same percentage indiated in the first row

TABLE 8.—Effects of perturbations in M_t's (t = 2,...,20) and consequent perturbations in No_r and PS upon the CB estimates of 30,012 and 29,013 t derived by using methods I and II, respectively.

Method	Perturbation magnitude					
	−50%	−25%	−1%	+1%	+25%	+50%
I	[1]+1.5	+1.9	+0.1	−0.1	−5.1	−14.5
II	+14.8	+7.3	+0.3	−0.3	−8.0	−17.8

[1]All values in this table represent relative changes (expressed in percentages) in CB

paper. These examples are presented to illustrate the use of the sensitivity analysis technique in the case of the CB estimation rather than to make a final judgment of the validity of the CB estimates presented. The knowledge, lacking in the case of southern bluefin tuna, of probability distributions of all input parameters would allow the application of stochastic sensitivity analysis (Majkowski and Waiwood 1981; Majkowski et al. 1981a; Majkowski 1982, 1983; Majkowski and Hampton 1983, in press) and assist in making such a judgment.

CONCLUDING REMARKS

The methods presented are mathematically very simple. The system of equations associated with method I is linear with respect to the CB and No_t variables. Therefore, the estimate of CB related to a specified set of f_t coefficients can be obtained an-

alytically. The determination of the age composition which results in the absolute maximum stabilizing catch weight requires a standard computer program from a linear programming package. The system of equations associated with methods II and III cannot be solved analytically; a computer program which finds the zeros of a function has to be used.

Data requirements for the methods are not extensive. They are usually available from an established and well-documented fishery. Data required for method I may be more easily obtained than those for methods II or III. This is the major advantage of method I.

Assumptions associated with methods II and III are more realistic for most fisheries than those related to method I. Therefore, if the data for methods II and III are available, these methods will be superior in the majority of cases. However, the example presented clearly indicates that methods I and II, at least for southern bluefin tuna, provide nearly identical results if the present age specific pattern of fishing is considered.

The example also suggests that the methods, at least in the case examined, are relatively robust with respect to uncertainties in the input parameters. This is a very important consideration because many population and fisheries parameters are frequently poorly known.

Because of their deterministic nature and the assumptions involved, none of the methods will be completely realistic in their description of the fishery and population. However, they should provide managers with a valuable tool for gaining an impression of the level of sustainable catch and for assessing the relative merits of harvesting alternatives.

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ASPECTS OF REPRODUCTION OF THE BLUE MUSSEL, *MYTILUS EDULIS* (PELECYPODA: MYTILIDAE) IN LONG ISLAND SOUND

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ABSTRACT

A population of *Mytilus edulis* in Long Island Sound, Fairfield, Conn., was studied for 2 years to determine the sequence of gametogenic development of gonadal tissue and the frequency and duration of spawning under natural conditions. This population spawned annually in May-June. "Dribble spawning" occurred during the winter months of 1982. Sexes were distinguishable in all size classes studied, except those individuals in an "inactive" condition (stage 0). A low incidence of simultaneous hermaphroditism suggests that *M. edulis* is a stable gonochoric species. There was no evidence of protandry. Sex ratios of *M. edulis* 26.0-72.1 mm shell length did not differ significantly from 1:1. Photomicrographs of the gametogenic cycles of both male and female mussels are included.

The edible blue mussel, *Mytilus edulis*, is a widely distributed species, common to littoral and shallow sublittoral habitats in boreal and temperate waters of both Northern and Southern Hemispheres. The literature on the reproduction of *M. edulis* is extensive, probably because of the species' ubiquity in nature, as well as its commercial value (see Bayne 1976). Most of the studies have been done on European populations of *M. edulis*, which, in general, are characterized by extended spawning seasons with gamete release possible throughout the year (Lebour 1938; Lubet 1957; Havinga 1964; Andreu 1968; Jensen and Sakshaug 1970).

Limited information on North American populations suggests that although spawning can occur throughout the year (Moore and Reish 1969), the majority of the populations have a well-defined breeding season. On the basis of a 6-mo study (April-September) of the larval settlement period of *M. edulis*, Loosanoff and Engle (1944) concluded that the spawning period for blue mussels in Long Island Sound is May-August. Similarly, Hrs-Brenko (1971), after a 5-mo study (March-July) involving the examination of gonadal tissue, concluded that the spawning season of blue mussel in the southwestern part of Long Island Sound occurred with a single release of gametes during May and June. Since neither study followed the reproductive cycle for an entire year, however, it is difficult to draw conclusions about the annual spawing cycle of blue mussels in this locale.

In the most complete study to date in the Long Island Sound region, Newell et al. (1982) concluded that *M. edulis* from Stony Brook, Long Island, (southeastern shore of Long Island Sound) spawn in the spring, while they noted that a population at the same latitude on the southern shore of Long Island spawns 3 mo later. Clearly, it is difficult to make generalizations about the spawning behavior of this species.

In an attempt to more clearly define the breeding habits of *M. edulis* in Long Island Sound, the results of a 2-yr study to determine 1) the age of maturation and annual gametogenic development in a natural population and 2) the frequency of spawning of blue mussels along the southwestern shore of Long Island Sound are presented in this paper.

MATERIAL AND METHODS

Monthly collections of *M. edulis* were made from the mouth of Southport Harbor in Fairfield, Conn., (lat. 41°08'N, long. 73°17'W) from September 1980 to January 1982 and March 1982 to August 1982 (Fig. 1). In February 1982, two sampling collections were made, one in the beginning of the month and the other at the end. Sample sizes varied from 18 to 25 mussels, 26.0-72.1 mm shell length. A total of 534 mussels were examined and used in the analysis of the reproductive cycle.

In the laboratory, *M. edulis* samples were numbered, their maximum length (±0.1 mm) measured, and their gonad color noted. A section of the mantle with gonad was removed and fixed in 10% buffered

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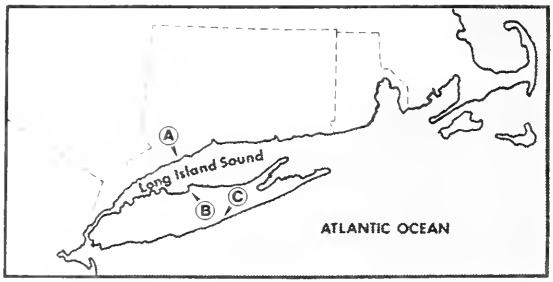


FIGURE 1.—Map showing locations of the Fairfield, Conn., study site (A) and the Stony Brook and Shinnecock, N.Y., study sites (B and C, respectively) (Newell et al. 1982).

Formalin[2]. This procedure was carried out during the first 4 mo of study. During the remainder of the study, sections of the mantle tissue and the visceral mass gonadal tissue were removed, since a closely related mussel of the family Mytilidae, *Geukensia demissa*, was shown to contain one type of sex cell in the mantle and the other in the visceral mass (Brousseau 1982). The *M. edulis* tissues were then prepared histologically for examination according to the method described by Brousseau (1978). A microscopic examination was made of the mantle and visceral mass gonadal tissues before assigning each individual to the appropriate category of gonadal condition as described by Chipperfield (1953). The results were based on the developmental condition of the mantle tissue in all individuals examined.

Mean oocyte diameter was determined for a representative sample of ripe females, selected at random from each of the reported spawning periods. Twenty oocytes per individual were measured using an ocular micrometer. Only those oocytes which were spherical in shape and ready for release were selected for measurement.

The reproductive condition of the mussels was measured by stereology, a procedure adopted by Bayne et al. (1978) and Newell et al. (1982). This method is based on a procedure referred to as point-counting volumetry, which is accomplished by superimposing a regular point lattice on the tissue section and counting the points which lie on transections of the sex cells (Weibel et al. 1966). The proportion of gonadal tissue that is comprised of follicles containing developing or ripe gametes is reported as the "gamete volume fraction" (GVF). For any individual mussel, the GVF can vary between zero, for a reproductively inactive mussel, and one, for a mussel showing maximal reproductive development. The monthly mean GVF represents the mean of 10 estimates of the GVF from each mussel sampled. The number of mussels included in the estimate varied from 18 to 25. These proportions were then arcsine transformed, and the variance for each monthly GVF was calculated.

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

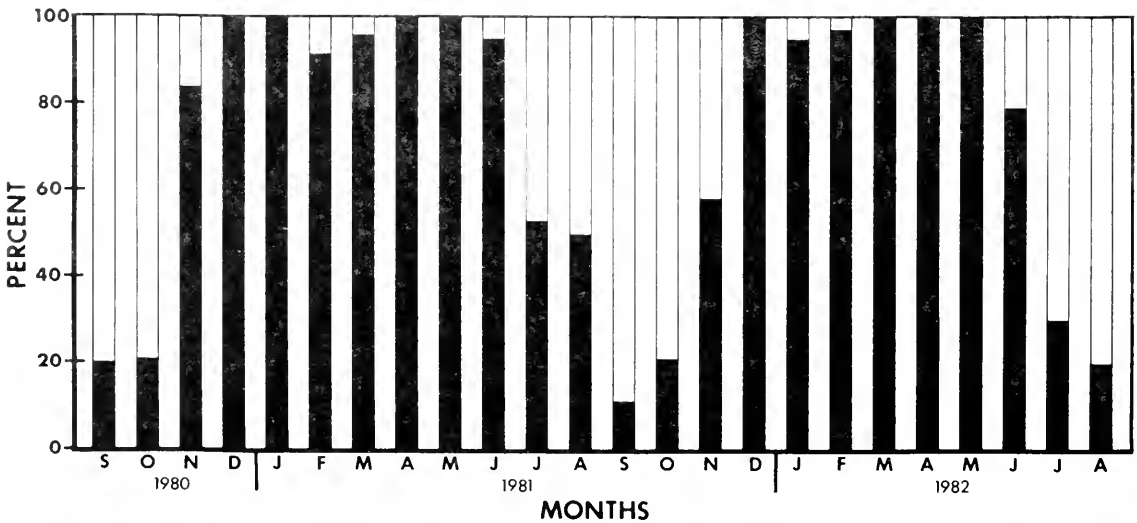


FIGURE 2.—Proportion of *Mytilus edulis* population with active or inactive gonads during 1980-82. Open portions of each represent inactive gonads (indifferent, no gametogenesis, or spent); solid portions represent active gonads (developing, ripe gametes, or partially spawned). Observations on males and females are combined.

RESULTS

Reproductive Cycle

Reproductively active individuals were encountered throughout the 2-yr study period with the largest numbers occurring in December 1980; January, April, May, and December 1981; and March, April, and May 1982 (Fig. 2). In September 1980, gametogenesis had begun in both sexes. Ripe mussels were observed in the February samples and by mid-April about 96% were gravid (Fig. 3). Spawning began in May and continued through the summer with most of the gametes released in June.

A similar spawning pattern was observed in 1981-82, except that gametogenesis began 1 mo later, and individuals with ripe gametes appeared in December. Presence of a sizable number of ripe individuals in the population during winter months suggests that the spawning period in 1981-82 was earlier and less defined than in the previous year. Although completely spent individuals were not present in any of the samples until June 1982, the presence of partially spawned mussels indicates that during the second year of this study, "dribble spawning" may have occurred during the winter and early spring. Although no direct information is available on the environmental factors, such as temperature and food availability, it seems reasonable to assume that annual variation in one or a combination of such factors was responsible for this difference in the timing of gametogenic events.

The GVF values for male and female *M. edulis* from this population are given in Figure 4. During both

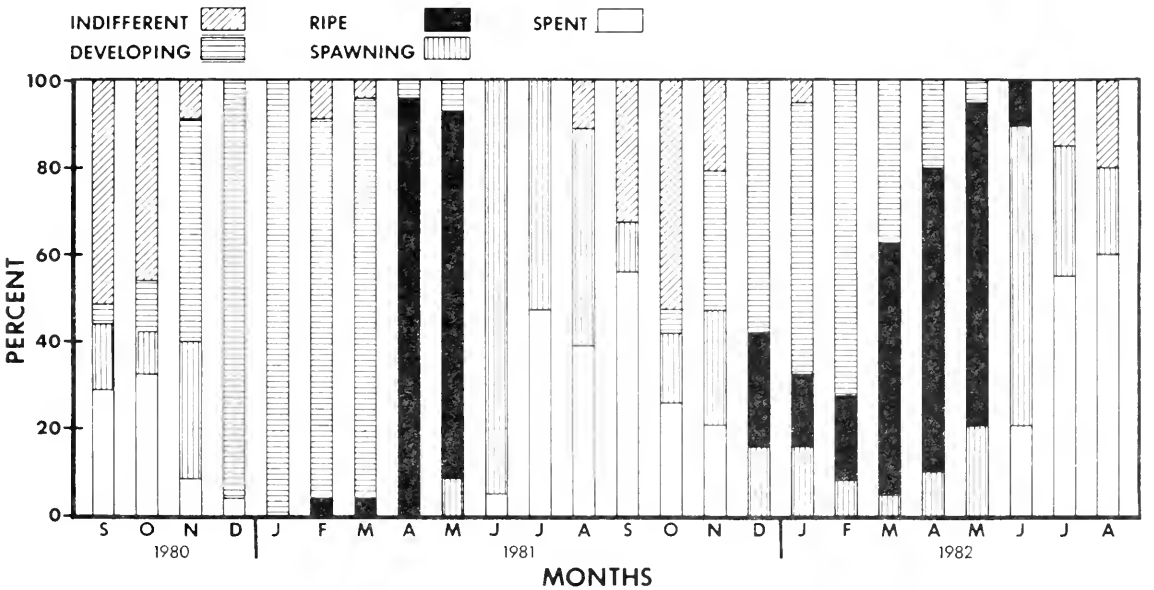


FIGURE 3.—Proportions of *Mytilus edulis* with gonads in each developmental phase during 1980-82. Values for males and females are combined.

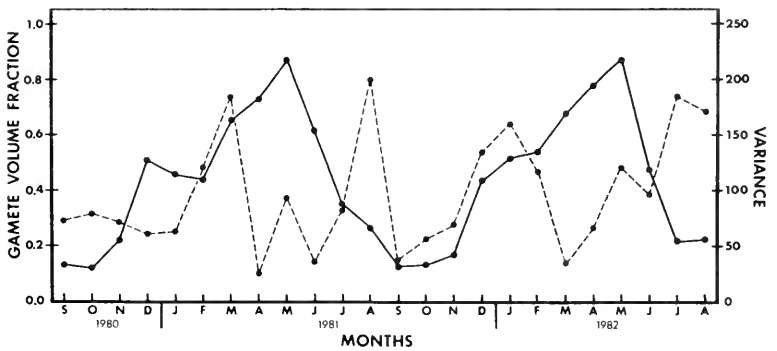


FIGURE 4.—Mean gamete volume fractions (solid line) and variance (dotted line) for *Mytilus edulis*. Values for males and females are combined.

years of the study, the pattern of the GVF values and the maximum GVF attained were similar. The postspawning minimum GVF occurred in October 1980 and in September 1981. Increasing GVF values in November of both years were due to the onset of gamatogenesis. Peak GVF values of 0.87 were observed in May of both years.

Variance in GVF during each sampling period provides a measure of the intrapopulation synchrony of the reproductive cycle. The larger the variance, the greater the variability in the gametogenic condition of individuals during that sampling period. In general, the mussels were most closely synchronized (i.e., lowest variance) during the spring months, when

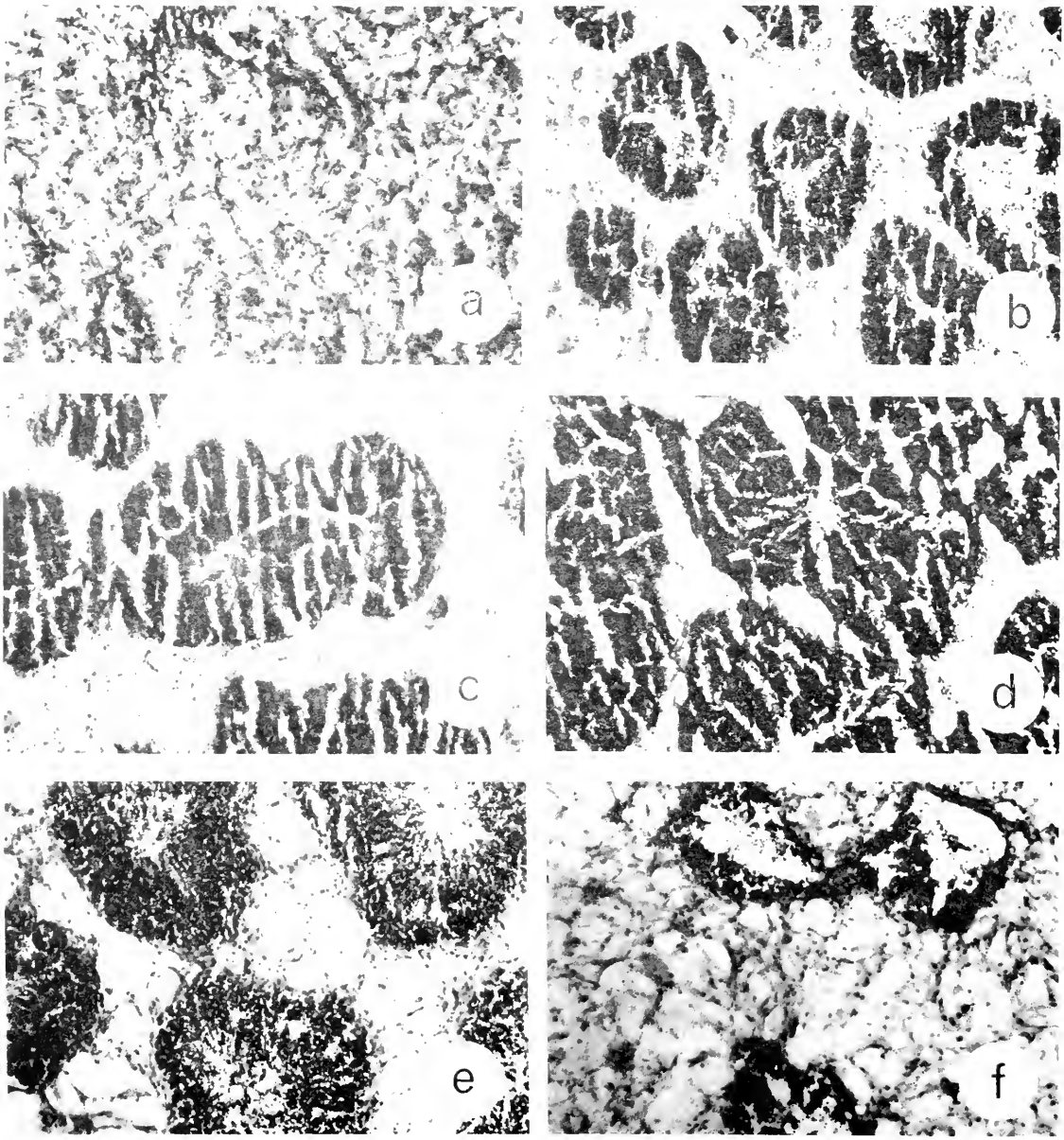
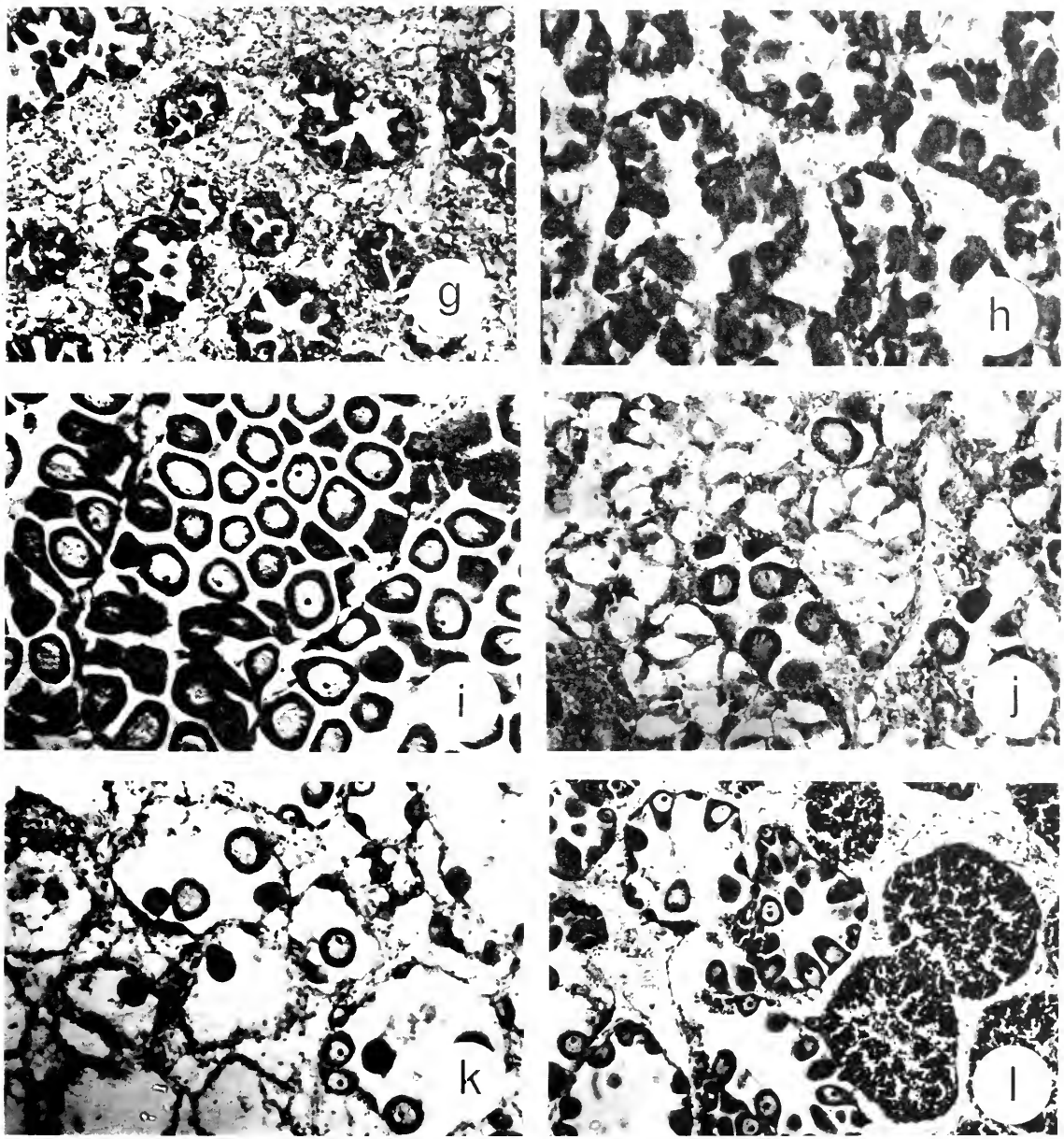


FIGURE 5.—Photomicrographs of the gonadal stages of male and female *Mytilus edulis* at 125× magnification. a) Inactive male or female (stage 0), 9 September 1980, b) early-developing male (stage I), 25 January 1981, c) late-developing male (stage II), 17 March 1981, d) ripe male (stage III), 15 April 1981, e) spawning male, 22 June 1982, f) recently spent male, 15 July 1981, g) early-developing female (stage I), 22

most mussels were in a ripe condition (stage III) (Fig. 3). As spawning proceeded, the variance increased, indicating that the mussels did not all release gametes at the same time. A second peak in the variance, however, occurred during February and March 1981 and December and January 1982. This apparent synchrony was probably due to an extended spawning period, especially during 1982. During that period, mussels were reported in various reproductive states (gametogenic, gravid, and spawning).

Photomicrographs of representative male and female stages in the spring and summer peaks of the annual cycle are shown in Figure 5. Stages are assigned according to the "index of bivalve gonad



December 1981, h) late-developing female (stage II), 17 March 1981, i) ripe female (stage III), 4 May 1982, j) spawning female, 5 October 1981, k) recently spent female, 22 June 1982, l) hermaphrodite, 22 January 1982.

maturity" procedure, first used by Chipperfield (1953). One problem with such a subjective approach is that it does not recognize intermediate stages of development. However, the stereology technique described above is also subject to criticism, since different gametogenic stages may have similar GVF values, as is the case with *M. edulis* (Fig. 6). It is only when the two methods are used together that a meaningful description of the gametogenic development of an animal can be constructed.

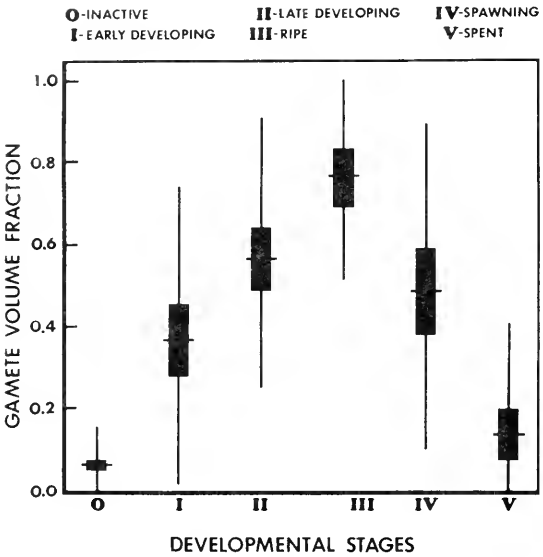


FIGURE 6.—Mean values of gamete volume fraction for each developmental stage of *Mytilus edulis*. Values for males and females are combined.

Sex Ratios and Gonad Color

Oocyte diameter of ripe females at the time of spawning was 0.065-0.070 mm. It is possible to determine the sex of mussels from the gonad color once the animal has reached stage III. At this time, the female gonad (mantle) is a definite apricot hue, while the male gonad is cream or yellow. During the other developmental stages, however, gonad color does not serve as a reliable indicator of the animal's sex.

In the population studied, the proportion of females in all size classes ($N = 235$) did not differ significantly from one-half. Male and female gonads were distinguishable in all size-classes studied (>26 mm). Although no protandry was observed, there was evidence of a simultaneous hermaphroditism in some individuals. One mussel contained both male and female gametes in the mantle, and 7 of 360 mussels (2%) contained one type of sex cell in the mantle and the other in the visceral mass. Trematode sporocysts (species undetermined) were found in the digestive gland and gonadal tissue of eight individuals collected from June to November.

DISCUSSION

Mytilus edulis is dioecious, the sexes of which are distinguishable either by examining the sex products or from inspection of gravid individuals. Female *M. edulis* are characterized by a bright orange to apricot gonad, whereas the males have a cream-colored gonad. This is due to the accumulation of carotenoids in the gonads at maturation (Campbell 1969). Few species of bivalves can be sexed in this manner. The low incidence of hermaphroditism exhibited by this species suggests *M. edulis* possesses stable gonochorism, a condition characterized by the presence of some hermaphrodites in a normally gonochoristic species.

Gonad examinations indicate that *M. edulis* from Fairfield, Conn., spawn once annually during May and June; however, the presence of ripe and partially spawned mussels during the winter months in 1982 (January and February) suggests that the major reproductive effort in the spring may have been preceded by a less synchronous release of gametes. It is interesting to note that Newell et al. (1982), in their study of two *M. edulis* populations on Long Island, reported that the one from Stony Brook exhibited one spring spawning peak, whereas the Shinnecock population spawned 3 mo later and over a more prolonged period. The spawning pattern of the Fairfield population is more similar to that observed for the mussels from Stony Brook than that of the Shinnecock population. This is not surprising; although all three populations are located at approximately the same latitude, only the Stony Brook and Fairfield populations are in Long Island Sound (Fig. 1). This finding, therefore, reinforces the interpretation by Newell et al. (1982) that latitudinal effects on the reproductive cycle of *M. edulis* are secondary to effects of habitat-specific differences in the time and duration of maximum food availability.

As more information on bivalves is gathered, it becomes clear that the traditional view of a single, fixed pattern of spawning for a population is inadequate. Instead, a certain degree of flexibility is possible, depending on variation in environmental factors. This flexibility can be manifested either as geographic variation among populations or as annual variation within a population. Existence of the former is well documented (see Bayne 1976; Sastry

1979); reproductive cycles of spatially separated populations differ. Annual variation is more difficult to document since establishing that this type of variation exists requires long-term, descriptive studies which are often laborious to carry out. Nevertheless, some information is beginning to emerge.

The dribble spawning which occurred during the winter of 1982 in the Fairfield mussels suggests such annual variation does exist in the *M. edulis*. Data on European populations also indicate that this species shows a remarkable ability to vary its spawning cycle in response to annual fluctuations in exogenous conditions (Bayne 1976). Similarly, data for other shallow water species, such as *Mya arenaria* (Brousseau 1978) and *Petricola pholadiformis* (Brousseau 1981), point to the existence of year-to-year variability within populations

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SEASONAL VARIATION IN SURVIVAL OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, ESTIMATED FROM THE AGE DISTRIBUTION OF JUVENILES

RICHARD D. METHOT, JR.[1]

ABSTRACT

Juvenile northern anchovy, *Engraulis mordax*, collected during autumn of 1978 and 1979 were aged using daily increments in their otoliths. Neither year class was dominated by individuals born during some short period, but March and April had the highest frequency of births in each year. Monthly ichythoplankton surveys indicated that significant spawning occurred from January through May of each year and peaked in early March. Comparison of the temporal distribution of birth dates with larval abundance indicated that larval survival was similar in the first half of each spawning season and greater during April to May of the 1978 spawning season than the same period in 1979. This difference in seasonal pattern of survival was nearly sufficient to account for the observed greater recruitment in 1978 and is consistent with the hypothesis that offshore transport of larvae influences recruitment.

One goal of fish population dynamics is to understand the processes responsible for annual variation in recruitment. The variation can be more than an order of magnitude and is poorly correlated with abundance of spawners (Cushing and Harris 1973). The concept of a critical period during the early larval stage (Hjort 1926; Marr 1956; May 1974) has structured much of the research. Recent work has focused on the importance of temporal and spatial coincidence of first feeding larvae and concentrations of prey (Beyer and Laurence 1981; Lasker 1978; Vlymen 1977). However, transport of larvae away from juvenile nursery areas can influence recruitment (Nelson et al. 1977; Parrish et al. 1981) and the role of predation is unknown.

Seasonal variation in factors that cause annual variation in recruitment probably influences the average timing of spawning. Support for this hypothesis comes from the latitudinal correlation between duration of the spawning season and the plankton bloom (Wyatt 1980). More direct evidence is found within the North Sea where the short spawning season of each herring population bears a fixed phase relation to the mean date of the local plankton bloom (Cushing 1975). The timing of the most favorable environmental conditions may not be predictable in each year. The match-mismatch hypothesis (Cushing 1975) suggests that variation in the relative timing of spawning and the seasonal plankton bloom contributes to variation in recruitment.

Collection of sufficient years of data to test any recruitment hypothesis is difficult. However, a testable corollary of Cushing's hypothesis is that, in any year, larvae born during favorable environmental periods constitute most of the year class. The age distribution of juveniles—the survivors of the larval stage—is a function of the seasonal distribution of spawning and seasonal changes in larval survival. To test the match-mismatch hypothesis, the birth dates of juvenile northern anchovy, *Engraulis mordax*, were determined from daily increments in otoliths (Brothers et al. 1976; Methot and Kramer 1979; Pannella 1971) and compared with the seasonal distribution of spawning determined from ichthyoplankton surveys conducted during the 1978 and 1979 spawning seasons.

METHODS

Larval Abundance

The seasonal distributions of the northern anchovy larval abundance were estimated from ichthyoplankton surveys (Kramer et al. 1972) on the sampling grid (Fig. 1) of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Seven surveys were conducted between December 1977 and August 1978 and four surveys between January 1979 and May 1979. Only larvae from 2.6 mm (live standard length at hatch) to 5.1 mm (few days after yolk absorption and onset of feeding) were used in the analysis.

Each cruise's larval census was the summed abun-

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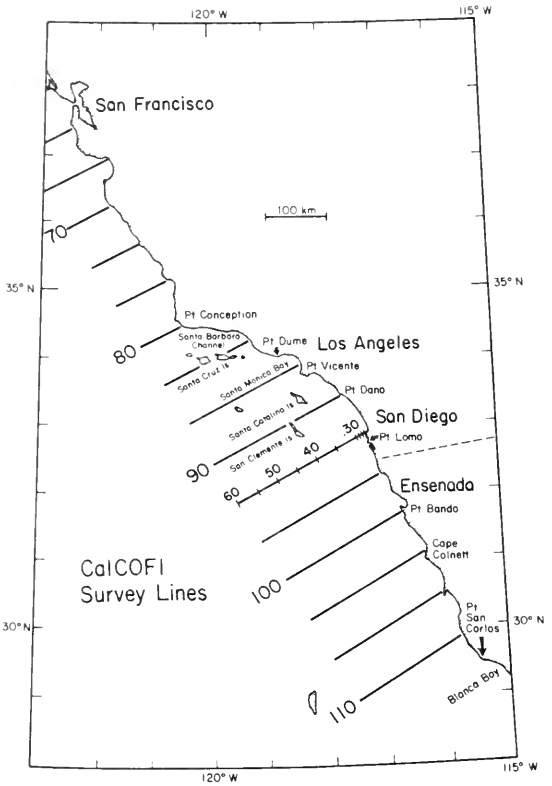

FIGURE 1.—Geographic region inhabited by the central population of northern anchovy. Ichthyoplankton samples were collected along CalCOFI survey lines. Location of stations is indicated only on line 93.3. Samples of juvenile anchovy were collected along the mainland coast. In 1978 these samples were obtained from the bait fishery from Pt. Conception to the United States-Mexico border. In 1979 samples were collected with a midwater trawl from Pt. Conception to Blanca Bay.

dance along CalCOFI lines 60-110. The catch at each station was adjusted for volume of water filtered and weighted by the distance to adjacent stations along the line. Abundances along unsampled lines were estimated from abundance in adjacent lines and cruises. A more complete description and further analyses of these data are in Hewitt and Methot (1982).

The mean and variance of date of larval catch were calculated for each cruise. Each station's contribution to these statistics was weighted by the distance to adjacent stations and by the catch of larvae. The effective duration of each cruise was considered to be ±2 standard deviations of catch date.

Juvenile Northern Anchovy Samples

During the period 28 October-14 December 1978, 30 samples of northern anchovy were collected from bait receivers at sport fishing docks from San Diego to Pt. Conception, Calif. A total of 1,101 fish were measured, but sample size varied from 11 to 86 fish so each fish's contribution to the overall size distribution was weighted by the inverse of sample size. From 15 of the 30 samples, 141 fish were aged using daily increments in otoliths.

During 1-19 November 1979, specimens were obtained from samples taken with a 15 m midwater trawl on a survey conducted by the California Department of Fish and Game (CFG) to investigate the abundance of juvenile northern anchovy (Mais 1980). Trawls were taken parallel to the coast between the 30 and 90 m isobaths at 7.4 km coastwise intervals between Blanca Bay, Baja California, and Pt. Conception, Calif. Past trawl surveys indicate that the juveniles are concentrated into the nearshore zone (Mais 1974). A total of 2,356 fish were measured from the 93 positive trawls; sample size typically was 25 fish per trawl. In addition, 10 of the 25 fish per trawl were aged by CFG personnel using annual growth marks in otoliths (Collins and Spratt 1969). Juveniles are defined here as those fish with no otolith annuli. The fraction of fish with no annuli in each 5 mm size interval was calculated (Table 1). From 8 of the 93 samples, 129 fish were aged using daily increments in otoliths.

Size distributions were calculated in each of three alongshore regions: North of Pt. Dume (north), San Diego to Pt. Dume (central), and south of San Diego (south). These regions were selected on the basis of the distribution of samples in 1978 and minima in the

TABLE 1.—Frequency of northern anchovy with and without otolith annuli. Specimens were collected by trawl during November 1979 (Mais 1980). Results are stratified by region and 5 mm size interval.

Size interval (mm)		North of Pt. Dume		San Diego-Pt. Dume		South of San Diego	
	N annuli:	0	>0	0	>0	0	>0
50						1	
55				4		9	
60		1		7		3	
65		0		12		6	
70		2		11		18	
75		3		28		59	
80		8		23		50	
85		6		13		41	
90		12		8		41	
95		4		4	1	26	26
100		5		5	6	3	71
105		3	5	4	23	2	73
110		2	19	1	66	2	45
115		1	33	1	33		18
120			17		21		3
125			22		8		1
130			7		6		
135			5		5		
140			1				
145			4				

alongshore distribution of juveniles in 1979 (Methot 1981). The regional breakdown was necessary because the overlap in size between juveniles and older fish varied latitudinally (Table 1). Although data in Table 1 are entirely from 1979, they were used to calculate juvenile size distributions from overall size distributions in both 1978 and 1979. In 1978 few adults were collected and no comparable samples were obtained from south of San Diego.[2]

Otolith Preparation

Thawed specimens were measured to the nearest 1.0 mm standard length. Sagittae (largest otoliths) were removed, cleaned in distilled water, dried, and mounted on a microscope slide with a clear methacrylate-based mounting medium. Otoliths of northern anchovy larger than about 40 mm are too thick to transmit sufficient light for viewing the increments. Material was removed from the otolith's medial surface by applying 5-10% HCl to selected regions for about 10 s at a time. Immersion oil, petroleum jelly, or mounting medium were used to mask the outer edge of the otolith and regions already sufficiently thin. The selectively etched surface develops high relief but a thin layer of immersion oil renders this relief nonrefractory and permits examination of the otolith. After most increments became visible, the mounting medium was softened with 80% ethanol, and the otolith was turned over and remounted. Etching of the lateral surface continued until all increments were visible within, but not necessarily at the surface of, the remaining material.

The otoliths in 1978 were prepared by embedding in polyester casting resin and grinding sagittal sections on 400 and 600 grit wet sandpaper. Selective etching was faster and more successful than grinding.

Age Determination

Specimens used for this study also were used to back calculate juvenile growth and a direct count of all increments in an otolith was rarely made. Instead, age was determined from numerical integration of otolith growth (increment width). Increments were measured with a video camera mounted on a compound microscope, an electronic device which positioned a cursor in the video image, and a microcomputer interfaced to the device. All measurements were made along the longest radius of the otolith (towards the posterior margin). The observer positioned the cursor at the outer edge of an increment and keyed in the number of increments between that point and the previous point while the computer recorded the radius to that increment. Increment width usually did not change rapidly so 2-10 increments of similar size were entered together. Data from different regions along the longest radius were recorded at various stages of the etching process.

Data from both otoliths and several replicate transects per otolith were combined in the calculation of age. Mean increment width was calculated at all points along the longest radius. Etching errors occasionally produced a region in which increments could not be seen. When this occurred, increment width was interpolated from mean increment width in adjacent intervals by a linear interpolation of increment width on radius. Age was calculated from numerical evaluation of the following expression:

$$\sum_{i=1}^{n} \frac{r_i - r_{i-1}}{G(r_i)}$$

where the following definitions and boundary conditions apply:

r_i = set of all radial distances where increment width changed perceptibly
$G(r_i)$ = average increment width between r_{i-1} and r_i
r_0 = otolith radius at onset of increment formation (6.5 μm)
r_n = maximum otolith radius
$G(r_1)$ = typical initial increment width (0.8 μm per increment)
$G(r_n)$ = $G(r_{n-1})$ if $G(r_n)$ not measurable.

The result converges exactly to the count of increments if each individual increment is measured once. The age estimate was accepted if $<20\%$ of the age was from interpolated increments. About 3% of the fish were rejected by this criterion. The mean percentage of interpolated increments for the accepted fish was 4.7% and the median was 2.5%. Usually an independent age estimate could be made from each otolith. When fish were stratified into 50-d age intervals, the coefficient of variation of age between otoliths within fish averaged 4.6% in 1978 and 3.5% in 1979. Thus, the 95% confidence interval for a 250-d-old fish was ± 14 d.

[2]Two samples from the Ensenada commercial fishery were provided by G. Broadhead (Living Marine Resources, San Diego). The fish had a similar size/birth-date relation to fish from the bait fishery in the U.S. coastal waters. Because the commercial fishery is biased against small fish, the size distribution of juveniles in Mexico could not be estimated.

The birth dates calculated in this study are actually dates of onset of increment formation. The northern anchovy larvae deposit the first increment at about the end of yolk absorption, the fifth day after hatching at 16°C (Brothers et al. 1976). This is close to the mean age of larvae used to estimate larval abundances so no constant was added to the juveniles' ages when calculating birth dates.

The fish in the present study usually had 150-400 increments but the daily deposition of increments in northern anchovy otoliths has been confirmed only to 100 d in the laboratory (Brothers et al. 1976). The accuracy of my interpretation of daily increments in juveniles was tested by comparing birth-date distributions calculated from early samples with distributions calculated from late samples. The distributions should be indistinguishable if the samples were of the same cohort and mortality during the period was not age selective. In addition to the December 1978 samples used in this study, samples were collected at San Diego in September 1978 and February 1979 (Table 2). The three birth-date distributions were compared by the Smirnov test for differences in cumulative probabilities (Conover 1971, p. 309). The September and December distributions were very similar (maximum difference = 0.105, $P < 0.2$) and the February distribution was also not significantly different from September's (0.243, $P < 0.02$). This test is sensitive to aging errors of the same magnitude as the precision of the ages. If ages of February's fish had been overestimated by 15 d (one-half of fish in each month shifted to the following month) the difference between September and February would have increased to 0.376, $P < 0.1$. A 1-mo error in aging the February juveniles would have made the September 1978 to February 1979 comparison highly significant ($P < 0.01$). I conclude that any bias in aging must be less than about 15 d.

TABLE 2.—Birth-date frequency of juvenile northern anchovy collected at San Diego between September 1978 and February 1979.

		Sept.-Oct. 1978	Dec. 1978	Feb. 1979
	N samples:	2	2	1
	N fish:	28	19	15
	Length (mm):			
	mean	77.8	76.4	82.1
Month	SD	5.5	6.5	5.9
Jan.		0	2	1
Feb.		3	1	1
Mar.		15	9	4
Apr.		10	6	7
May		0	1	2

Birth-Date Distribution

The selected specimens produce a biased estimate of the juvenile birth-date distribution because they were selected to span a wide size range for an analysis of seasonal patterns of juvenile growth (Methot 1981). A less biased estimate of the birth-date distribution was obtained from the size-frequency distribution of a large sample of juveniles and a size/birth-date nomograph (Fridriksson 1934; Kimura 1977). In each year's nomograph, birth-date frequencies (by month) were calculated for fish in each 10 mm size interval. All samples within each year were combined in that year's nomograph.

RESULTS

Larval Abundance

The temporal distributions of northern anchovy larvae differed between the two years (Table 3). The maximum abundance occurred in February-March of each year but the peak was greater in 1978. Larvae were much more abundant during May 1979 than during May 1978. The average larva in 1979 was in water 1°C colder than the average larva in 1978 and was further offshore (Table 3). Larval production per 30-d date interval was calculated by numerical integration of the area under the dashed lines in Figures 2 and 3. Total larval production during January-May 1979 was 2.1% greater than during the same period in 1978.

Size and Birth-Date Distributions

In 1978 and 1979 northern anchovy juveniles, collected north of Pt. Dume, were typically larger (Table 4) and had been born earlier (Table 5) than juveniles collected to the south. The size/birth-date nomograms (Table 6) applied to the juvenile size distributions produced birth-date distributions (Table 7) with peaks in March-April for southern fish and

TABLE 3.—Abundance of northern anchovy larvae. Value in parentheses is the fraction of the abundance that was interpolated. *N* samples exclude offshore samples with no larvae. Date, distance offshore, and temperature at 10 m were weighted by larval catch at each station.

Date	*N* samples	Abundance	Distance (km)	Temp. (°C)
1977-78				
Dec. 15	42	448 (0.08)	119	16.3
Jan. 18	70	558 (0.00)	65	15.5
Feb. 25	87	2,367 (0.00)	65	14.9
Apr. 9	74	686 (0.00)	41	15.8
May 26	64	143 (0.00)	44	15.2
June 30	48	26 (0.00)	72	16.1
Aug. 13	20	26 (0.00)	22	18.1
1979				
Jan. 18	33	448 (0.45)	111	14.0
Mar. 2	71	1,524 (0.00)	65	13.9
Apr. 14	34	1,392 (0.40)	113	14.5
May 10	54	653 (0.00)	54	14.8

TABLE 4.—Size distributions of juvenile northern anchovy calculated from size distributions of all fish and size-specific juvenile fraction (Table 1). The percentage of the population composed of juveniles was also calculated (% juveniles). Area is the surface area (square nautical miles) nearshore of the 50 fathom isobath and excludes the shallow area around islands that was not sampled.

		1978		1979		
		north	central	north	central	south
	Area:	476	484	476	484	1,905
	N samples	9	21	26	41	66
Size	*N* fish:	429	724	460	757	1,333
(mm)	% juveniles:	82 0	98 8	28 0	40.8	54 4
40-49		0.0	0.3	0.0	0 0	0 3
50-59		0.0	1.9	0 0	2 9	2.8
60-69		3 3	17.1	3 1	17 8	3 9
70-79		18.3	45.4	10 1	31.7	27.3
80-89		26.9	27.3	22 5	26.9	41.0
90-99		34.3	7.7	31.8	11.3	22.5
100-109		16 7	0.3	24 8	8.4	1.8
110-119		0.5	0.0	7.7	1 0	0.6

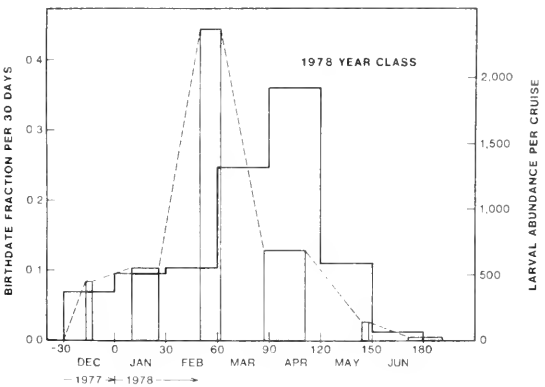

FIGURE 2.—Comparison of the seasonal distributions of northern anchovy larval abundance and birth dates of the 1978 year class. The width of the stippled bars is the effective duration of the ichthyoplankton survey (±2 standard deviations of the sample date where each sample is weighted by its catch of northern anchovy larvae). The dashed line was used to interpolate larval abundance per 30-d period. The open histogram indicates the fraction of juvenile's birth dates occurring per 30 d.

TABLE 5.—Frequency of observed birth dates of juvenile northern anchovy stratified by year and region and summarized by 10-d date interval.

Date interval		1978 north	1978 central	1979 north	1979 central	1979 south
	<−30	3	0	7	1	2
Dec	−30	2	0	0	0	0
	−20	2	0	2	0	0
	−10	6	0	2	1	0
Jan	0	1	0	4	1	0
	10	5	2	5	0	0
	20	3	1	3	0	1
Feb.	30	1	4	3	0	0
	40	1	0	1	1	0
	50	6	0	2	3	1
Mar	60	2	9	0	2	4
	70	0	9	7	7	5
	80	1	6	3	7	5
Apr.	90	2	12	2	7	7
	100	0	14	0	1	0
	110	1	16	0	0	0
May	120	0	10	2	1	1
	130	0	7	2	0	0
	140	0	7	0	0	0
June	150	0	2	2	0	0
	160	0	2	1	0	0
	170	0	0	1	1	0
July	>180	0	4	3	13	2

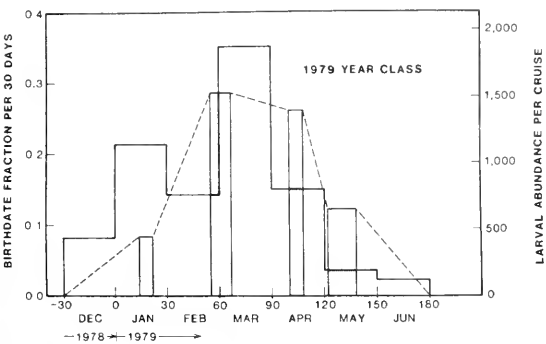

FIGURE 3.—Comparison of the seasonal distributions of northern anchovy larval abundance and birth dates of the 1979 year class. See Figure 2 for explanation.

December-January for northern fish. The calculated birth-date distributions were similar to the observed birth-date occurrences in the two regions in 1978; the calculated differed from the observed in 1979 because selection of specimens was highly nonrandom in 1979. A substantial fraction of 90-110 mm fish in 1979 were assigned to birth dates before December 1978. Because these fish had no otolith annulus they are considered part of the 1979 year class.[3]

[3]Among the 95-105 mm anchovy examined in 1979, all those with an annulus (1978 year class) had 400-510 daily increments so had been born during summer of 1978. Among the similar-sized fish without an otolith annulus, some had been born in December 1978 and some as early as late summer 1978. This observation indicates the occasional ambiguity of assigning year classes when some spawning occurs throughout the year.

TABLE 6.—Size/birth-date nomograms stratified by 10 mm size interval and 30-d date interval (labeled by approximate month).

Size interval (mm)	Birth month								
	<Dec.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	>June
				1977-78					
40								1	2
50							4	2	1
60			1	0	2	14	10	0	1
70				2	7	20	5	1	
80			4	4	15	10			
90	2	5	4	4	3	1			
100	1	5	3	2					
				1978-79					
30									4
40									6
50								1	6
60					3	0	4	3	2
70				2	19	9	1	1	
80	1	2	7	6	17	8	1		
90	7	3	6	2	1				
100	2	0	1	1					

TABLE 7.—Birth-date distributions calculated from size/birth-date nomograms (Table 6) and regional juvenile size distributions (Table 4). Distributions are presented as %/30-d date intervals (labelled as approximate months). Combined birth-date distribution is mean of regional distributions with weighting factors proportional to nearshore shallow area (Table 4). Mortality correction factor accounts for the greater duration that the early born fish are exposed to juvenile mortality (see text). After multiplying the combined distributions by the mortality correction factors, the distributions are presented only for those months with larval abundance data.

	<Dec.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	>June	Weight factor
Regional distributions:										
1978										
central	0.8	2 1	5.5	7 6	23.7	41 9	15.4	2.0	1.0	83.4
north	5 2	16 8	15 3	14 7	21.5	21 8	4.1	0.5	0.1	16.6
1979										
south	10 5	5.5	14 5	10.5	34.9	15.5	3.1	2.2	3.3	66.5
central	9 5	3 1	10 4	9 3	34 7	14 0	7 6	5.9	5.5	16.9
north	28.5	6 1	21 9	15 4	17.0	7 6	1.9	1.1	0.5	16.6
Combined distributions										
1978	1 5	4.6	7 1	8.8	23.4	38 5	13 5	1.7	0.9	
1979	13 3	5.2	15.0	11.1	32.0	13 8	3.7	2.7	3 2	
Mortality correction factors										
		2.09	1 85	1 64	1.45	1.28	1 13	1.0		
Combined distributions corrected for juvenile mortality:										
1978		7.0	9 6	10 4	24 7	35 9	11.1	1 3		
1979		8 5	21 8	14 2	36.3	13.9	3.2	2.1		
1979			24 4	15 9	40.6	15 5	3.6			

Combining the regional results to produce an overall juvenile birth-date distribution is problematic, especially in 1978 when no samples were collected south of San Diego. Each region's weighting factor should be proportional to the abundance of juveniles in the region. Because local abundance of a pelagic schooling fish is measured crudely by a trawl survey, the areas of the primary juvenile habitat (Table 4) were used as weighting factors. The north region has only 16.6% of the total area nearshore of the 90 m (50 fathom) isobath, so contributes little to the total. Although the north region contributed nearly 50% of the total area from which samples were obtained in 1978 (Table 4), I assume that the unsampled fish from Baja California had birth dates similar to those of San Diego-Pt. Dume fish so I use 16.6% for the north's weighting factor in 1978. The combined birth-date distributions are in Table 7.

Correction for Juvenile Mortality

The birth-date distributions for the northern anchovy presented above represent the birth dates of those fish which survived until November. A monthly cohort's contribution to the birth-date distribution of its year class is a function of the spawning rate during that month, the mortality rates experienced by that cohort, and the age of that cohort when sampled. Northern anchovy juveniles which had been born during January are expected to be less abundant in November than juveniles born in May because the older juveniles experienced mortality as juveniles for

a longer period. A correction for this difference in age is necessary before differences between the seasonal distribution of larval abundance and the resultant distribution of juvenile birth dates can be interpreted as differences in larval survival. Few juveniles collected in November were <5-mo-old so the relative abundance of older juveniles need only be adjusted by the inverse of survival from age 5 mo to age at capture. Age-specific survival rate was assumed to increase from 64% per month at age 3 mo to 88% at 10 mo (calculated from preliminary estimates of juvenile mortality rates in Smith 1981). If one assumes no seasonality in juvenile survival, the resultant birth-date distributions are as if all the monthly cohorts had been sampled at the same age rather than at variable ages in November. Because most juveniles were between 6 and 10 mo old, corrected birth-date distributions are similar to the uncorrected distributions (Table 7).

Relative Larval Survival

The juveniles' birth-date distributions, corrected for juvenile mortality, and the seasonal distributions of larval production for the northern anchovy are presented in Figures 2 and 3. The ratio of monthly birth-date frequency to monthly larval production is an index of larval survival relative to survival from other months in the same spawning season. Survival tended to increase within the 1978 season and decrease within the 1979 season (Fig. 4). In both years the only anomalies to the trends were low relative survival of larvae born in February.

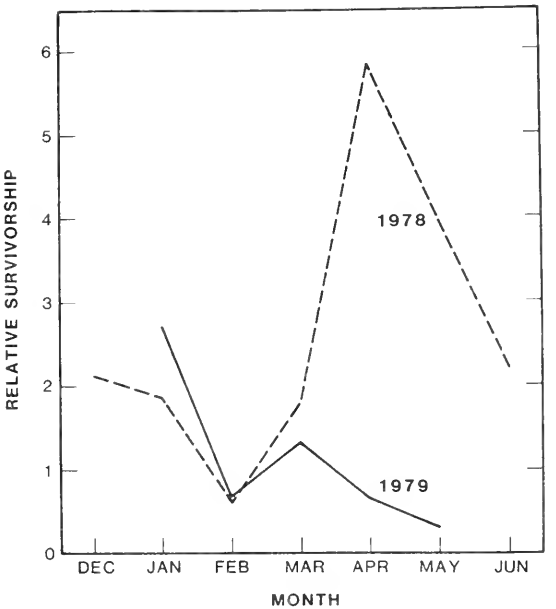

FIGURE 4.—Relative survivorship is the ratio of the fraction of northern anchovy juvenile's birth dates to the fraction of annual larval production per 30 d. To enable comparison between years the relative survivorship for 1978 has been scaled by the ratio of recruitment (2.0) and the ratio of annual larval production (0.98) between the 2 years.

DISCUSSION

This study has documented seasonal changes in survivorship of larval northern anchovy. Both the magnitude and the timing of changes are important. The magnitude of the seasonal changes determines whether annual variation in recruitment could be caused by short seasonal events. The timing of the changes in survival relative to environmental events elucidates the linkage between oceanographic conditions and recruitment.

Temporal Patterns in Larval Survival

To evaluate the importance of seasonal changes in larval survival of the northern anchovy requires estimates of annual variation in recruitment. The age composition of the central population of northern anchovy is monitored through the fishery and trawl surveys. Mais (1981a) analyzed the age composition of the commercial fishery in southern California and suggested the following ranking of recent year classes: 1974 weak, 1975 weak, 1976 mediocre-strong, 1977 weak, and 1978 very strong. During the 1978-79 fishing season the 1978 year class of the northern anchovy contributed 65% of the southern California catch and in the following season the 1979 year class contributed 35% (Mais 1981a). In the spring 1979 trawl survey the 1978 year class contributed 62% and in spring 1980 the 1979 year class contributed 35% (Mais 1980, 1981b). Thus the fishery and the survey indicate that the 1978 year class was about twice as large as the 1979 year class.

This difference in recruitment cannot be explained by the abundance of young northern anchovy larvae. Northern anchovy larval production in 1979 was 2.1% greater than in 1978. Thus the larger 1978 year class resulted from higher survival because larval abundance was less in 1978 than in 1979.

The critical question is whether the recruitment variation described above requires more annual variation in larval survival than is caused by the seasonal changes described in this study. I evaluated this question by scaling the northern anchovy larval abundance estimates (Figs. 2, 3) with the ratio of lar-

val abundance between the 2 years (0.979), and the monthly fractions of juvenile birth dates (Table 7) were scaled by the ratio of recruitments (2.0). The ratio, (scaled birth date fraction)/(scaled larval abundance fraction), estimates relative survival of a month's spawn (Fig. 4). Because of the scaling, these ratios can be compared both between and within years. Survival of winter spawn in 1979 was similar to survival of winter spawn in 1978, but survival was much greater in April-May 1978 than April-May 1979. Thus, the larger 1978 year class was not necessarily the result of greater survival throughout the spawning season. The increase in survival during the last 2 major months of the 1978 spawning season was sufficient to cause a large increase in recruitment.

Detection of Changes in Survival

Detection of a match between spawning and favorable environmental conditions of the northern anchovy seems more likely than detection of an event which results in poor survival. If a short-duration favorable environmental period results in a doubling of year class abundance, then more than half of the year class would have been born during that period. Such a concentration of birth dates could have been, but was not, detected in 1978 and 1979. A particular match apparently was not necessary for these two year classes. Conversely, a short-duration unfavorable environmental period that destroys all northern anchovy larvae born during the period may cause only a small reduction in year class abundance and a short gap in the birth-date distribution that would be difficult to detect with small sample sizes.

The effect of other environmental events will be more difficult to detect. Long-duration events or events that affect larvae of a wide age range will have little effect on the birth-date distribution. Secondly, environmental events which do not extend over the geographic range of spawning may not be detected even though they have important local effects.

Spatial Pattern

This study was designed to study temporal changes in frequency of juvenile birth dates but a strong spatial pattern also was detected. Northern anchovy juveniles collected north of Pt. Dume were larger than southern juveniles because of earlier birth dates. Hewitt and Methot (1982) showed that spawning contracted towards the San Diego area as the 1978 and 1979 spawning seasons progressed. This trend would contribute to an earlier mean birth date for northern fish, if currents and eddies did not substantially redistribute the larvae. In addition, if juveniles routinely move northward along the coast, early born fish will be further north by November. There are no data on the distribution of late larvae with which to investigate the cause of latitudinal pattern in juvenile birth dates. Geographic pattern in birth date will contribute to geographic pattern in size at age of adults.

Relation to Environmental Conditions

Two oceanographic factors, stability of the upper water column (Lasker 1978) and offshore transport (Parrish et al. 1981), have been suggested as factors in recruitment of northern anchovy. These factors should have had different effects on recruitment in 1978 and 1979.

Lasker (1975, 1978) suggested that northern anchovy larvae are likely to encounter adequate prey concentrations only when the upper water column is stable and prey are aggregated into layers. Of particular importance is the inshore chlorophyll maximum layer which may be composed of dinoflagellates suitable as prey for first feeding larvae. These layers are homogenized as storms or upwelling events destroy the stratification of the upper tens of meters of the water column. The winter of 1977-1978 was particularly stormy (Lasker 1981) and the isothermal surface layer was as deep as 50 m until stratification was restored in March. This hypothesis correctly predicts lower larval survival in winter 1978 than in spring 1978, but incorrectly predicts a poor year class in 1978.

Any hypothesis concerning the availability of prey will predict increasing survival through the major spawning season (December to June). Zooplankton biomass increases to its seasonal maximum in June (Smith and Lasker 1978). Stratification (differences between temperature at 10 and 30 m) increases so the prey of larval fish probably are increasingly aggregated into layers. Day length increases so that larvae can feed longer per day (Hunter 1972). A measurable response of northern anchovy larvae to the above factors is an increase in growth rate from 0.43 mm/d in January to 0.55 mm/d in June (Methot 1981) despite trivial changes in mean temperature (Table 3). If food availability is important to larval survival then survival should consistently increase through the spawning season.

The second major hypothesis concerns offshore transport and coastal upwelling caused by the predominantly northwest winds (Parrish et al. 1981).

Northern anchovy larvae which are transported offshore may experience higher larval mortality rates, and the survivors may be unable to return to the inshore juvenile nursery areas. Monthly indices of upwelling (Bakun 1973) at lat. 30° and 33°N, relative to long-term monthly means, were exceptionally low during January-March 1978 (downwelling occurred) and remained below normal through May 1978 (McLain and Ingraham 1980). Seckel et al. (1978) suggested that these conditions entrained larvae close to shore and correctly predicted an abundant 1978 year class. However, the results obtained here suggest that larval survival was higher during late spring 1978 than during the winter when downwelling occurred.

Upwelling was as low in December 1978 and January 1979 as in winter 1978, but the storms were less severe in 1979. Later in 1979, upwelling was near normal. The increased upwelling in 1979 relative to 1978 may have been responsible for the greater offshore displacement of northern anchovy larvae in 1979 (Table 4). The transport hypothesis correctly predicts a poorer year class in 1979 relative to 1978 and decreasing larval survival through the 1979 spawning season.

This brief examination of environmental data does not completely account for the patterns of recruitment of the northern anchovy in 1978 and 1979. Indices of offshore transport seem more important than indices of food availability, but the seasonal pattern of survival in 1978 could not be explained by transport. It is simplistic to assume that only one factor is involved in recruitment and that the effect of this factor is linear. One plausible scenario is that the winter storms of 1978 caused high mortality of early larvae, but the low upwelling throughout the year permitted high entrainment of late larvae and resulted in the good year class. It is also possible that the extremely low upwelling during winter 1978 did not have a proportionally greater effect than the low upwelling of spring 1978. Relatively low upwelling late in the spawning season may be important because absolute upwelling and transport typically increase through the spring (Smith and Lasker 1978). The spawning season may be timed to avoid low food availability in winter and high transport in late spring.

Other evidence indicates that survival of early northern anchovy larvae was nearly constant during the 1978 and 1979 spawning seasons. Hewitt and Methot (1982) inferred larval mortality from the slopes of the larval age-frequency distributions and found no significant seasonal changes. This evidence is consistent with the hypothesis that the significant change in survival which caused the difference in recruitment occurred after the early larval stage. Adverse larval drift would not necessarily cause increased mortality during the age interval examined by Hewitt and Methot but may affect the fraction of the surviving larvae which are entrained in the range of the juvenile habitat.

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GROWTH, MORTALITY, AND AGE/SIZE STRUCTURE OF THE FISHERIES FOR TILEFISH, *LOPHOLATILUS CHAMAELONTICEPS*, IN THE MIDDLE ATLANTIC-SOUTHERN NEW ENGLAND REGION

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ABSTRACT

Otoliths of tilefish taken in 1978 from the Middle Atlantic Bight and Southern New England region were used to determine length at age and growth rates. Marginal increment analysis revealed that annuli were formed once each year between March and May, and modes in the length-frequency histogram for small tilefish (<31 cm FL) in March-May agreed with back-calculated lengths at ages 1-3. Tilefish (sexes combined) grew about 10 cm FL per year for the first 4 years, and beyond that age males grew more rapidly than females. Maximum size of females was 95 cm FL and of males 112 cm FL, and maximum ages were 35 and 26 years, respectively. Von Bertalanffy growth formulae for both sexes were found to be significantly different with Hoetelling's T^2. Sex ratios at age generally were not significantly different from 1:1, and skewed sex ratios at length were attributed to differential growth rates. No significant differences were found between males and females in the regressions of both whole and eviscerated weights on length.

Length-frequency histograms of tilefish from the longline fishery in 1974-80 showed truncation of the size structure accompanied by a decrease in the size at full recruitment in more recent years. In 1974, 71% were >70 cm FL, while in 1980 these larger fish made up about 19% of the catch. Length frequencies from three fisheries in 1978 had a similar modal size (51-55 cm FL), but some differences in size structure. The recreational and longline fisheries caught larger fish (37 and 53%, respectively, between 56 and 75 cm FL) than the foreign trawl fishery (17% at 56-75 cm FL and 51% at 26-50 cm FL). The differences in length frequencies were reflected in the age structures of the three fisheries, with the foreign trawls exploiting 3-7 year olds (91% of the catch), recreational anglers 4-9 year olds (98%), and longline 4-9 year olds (90%).

The catch curve for the longline fishery was concave, probably the result of increased fishing pressure in recent years. Estimates of the instantaneous rate of total mortality were 0.46 for the more linear portion of the longline catch curve and 0.60 for the catch curve from the foreign trawl fishery.

Tilefish, *Lopholatilus chamaeleonticeps*, are large [to about 120 cm FL (fork length) and 30 kg], demersal branchiostegids found along the outer continental shelf in 80-540 m from Nova Scotia to Surinam (Dooley 1978; Markle et al. 1980). In the Middle Atlantic Bight and Southern New England waters they have usually been found in temperatures of 9°-14°C and depths of 100-240 m.[4] After a brief period as pelagic larvae (Fahay and Berrien 1981; Berrien in press), tilefish settle to the bottom. Both juvenile and adult tilefish ranging in size from 10 or 20 cm FL to >1 m FL have been observed occupying vertical burrows (Able et al. 1982), horizontal excavations in submarine canyon walls called "pueblo villages" (Cooper and Uzmann 1977; Warme et al. 1978), and scour depressions around boulders (Valentine et al. 1980). Tilefish excavations appear to be local centers of abundance for several species of crustaceans and fish; thus through their burrowing activity, tilefish may have considerable impact on outer continental shelf communities (Able et al. 1982).

Commercial exploitation of Middle Atlantic-Southern New England tilefish began in 1915, and landings have been made in nearly all years since that time. Annual landings from this unit stock (Katz et al. 1983) have fluctuated from a peak of 4,500 metric tons (t) landed in 10 mo in 1916 to <1 t reported for several years since then. Commercial landings have risen during the 1970's, due to the development of a longline fishery currently centered in New Jersey and New York. Landings in 1977-80 (2,061, 3,412, 3,840, and 3,575 t, respectively) have exceeded all years except 1916 for which information is available (Freeman and Turner footnote 4; U.S. Department of

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[4]Freeman, B. L., and S. C. Turner. 1977. Biological and fisheries data on tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean. Tech. Ser. Rep. 5, 41 p. Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

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Commerce 1980a-c; Christensen[5]), and the tilefish fishery has been the most valuable finfish fishery in New Jersey during 1978-80 and New York in 1979-80 (U.S. Department of Commerce 1980a-c; Grimes et al. 1981; Christensen footnote 5). Small fisheries which exploit another stock of tilefish (Katz et al. 1983) exist off South Carolina (Creel 1981; Christensen footnote 5), southeastern Florida, and in the Gulf of Mexico (Grimes et al. 1980)

Despite the economic and ecological importance of tilefish, little is known about its life history or the impact of fishing on the Middle Atlantic-Southern New England population (Freeman and Turner footnote 4; Grimes et al. 1980). The purpose of this paper is to present age, growth, and mortality information on tilefish from that region, to compare size and age structure of the catch of some of the recently active tilefish fisheries, and to examine changes in the size structure of longline catches during 1974-80.

MATERIALS AND METHODS

Samples of tilefish from the Middle Atlantic-Southern New England region were obtained from domestic longline and recreational fisheries, National Marine Fisheries Service (NMFS) trawl surveys, and the foreign trawl fishery. Sample information included the nature of the sample (random or nonrandom), capture method, location, and date. Length (FL in cm) was recorded for individual fish and often sex and weight (whole and/or eviscerated) were noted as well. It was often impossible to determine the sex of some small tilefish by macroscopic examination of the gonads so that three sex classifications—male, female, and unknown—were used. No males were identified <50 cm FL, and most of the fish of unknown sex were <55 cm FL, though some were as large as 71 cm FL.

After preliminary examination of scales and sections of sagittal otoliths and third dorsal rays, otoliths were selected as primary aging structure. Up to five sections (0.15-0.35 mm thick) were taken from the center of each otolith in the dorsoventral plane using a diamond blade saw. Sections were examined with a dissecting microscope at 10× with reflected light and a dark background. The transition from the translucent (hyaline) to opaque tissues was most pronounced, and was defined as the edge of an annulus. It was usually impossible to follow annuli around an entire section of a tilefish otolith, so that, when the number of rings was in doubt, rings were counted on each side of the sulcus acusticus (Fig. 1). We made measurements to each annulus and to the otolith edge in the medioventral region of the section which passed through or closest to the center of the otolith. We used a filar micrometer and recorded distances in ocular micrometer units (one unit = 0.082 mm). Because tilefish otoliths grow allometrically in the medioventral region, measurements were made from the core of the otolith to the furthest point from the core on each annulus and on the edge of the section (Fig. 1B). Hayashi (1976a) made similar measurements, though in a different plane, on the whole otoliths of the red tilefish, *Branchiostegus japonicus japonicus*.

All otoliths of *Lopholatilus chamaeleonticeps* were read once, and one-third were reexamined. All of the first 120 otoliths were read twice. Close agreement between first and second readings occurred in a subsample of 50 from the next 150 otoliths; therefore, routine second readings were discontinued for fish with <10 annuli. Otoliths with 10 or more annuli were assigned an age only after agreement was reached between several counts; when agreement was not achieved, the median number of annuli from at least five counts was used.

Empirical lengths at age were used in constructing an age-length key; however, a few fish did not form annuli by the end of the usual period of annulus formation. To reduce bias which would result from assigning such fish to a younger age, we adopted the following rule: Any fish captured in the 3 mo after the end of the usual annulus formation period with hyaline tissue at the edge of the otolith and a marginal increment at least half as large as the increase in size of the otolith in the previous full year was assigned an age corresponding to its number of rings plus one.

Least-squares linear regression was used to describe the otolith size (OS): fork length (FL) relationship and the length:weight relationships. The final regression lines were converted to functional regression equations (Ricker 1973). We added a factor to the OS:FL equation which compensated for variation in otolith size at a given fork length. The distance to each annulus was adjusted by the ratio of the average otolith size for fish of the fork length in question to the observed otolith size for that fish (Bagenal and Tesch 1978). The resulting equation was used to compute back-calculated lengths.

Analysis of covariance (ANCOVA) was used to compare slopes of regression lines between sexes, and analysis of variance (ANOVA) was used for comparison of mean marginal increments, mean growth increments, and mean lengths at age. The SAS

[5]D. J. Christensen, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun., 1982.

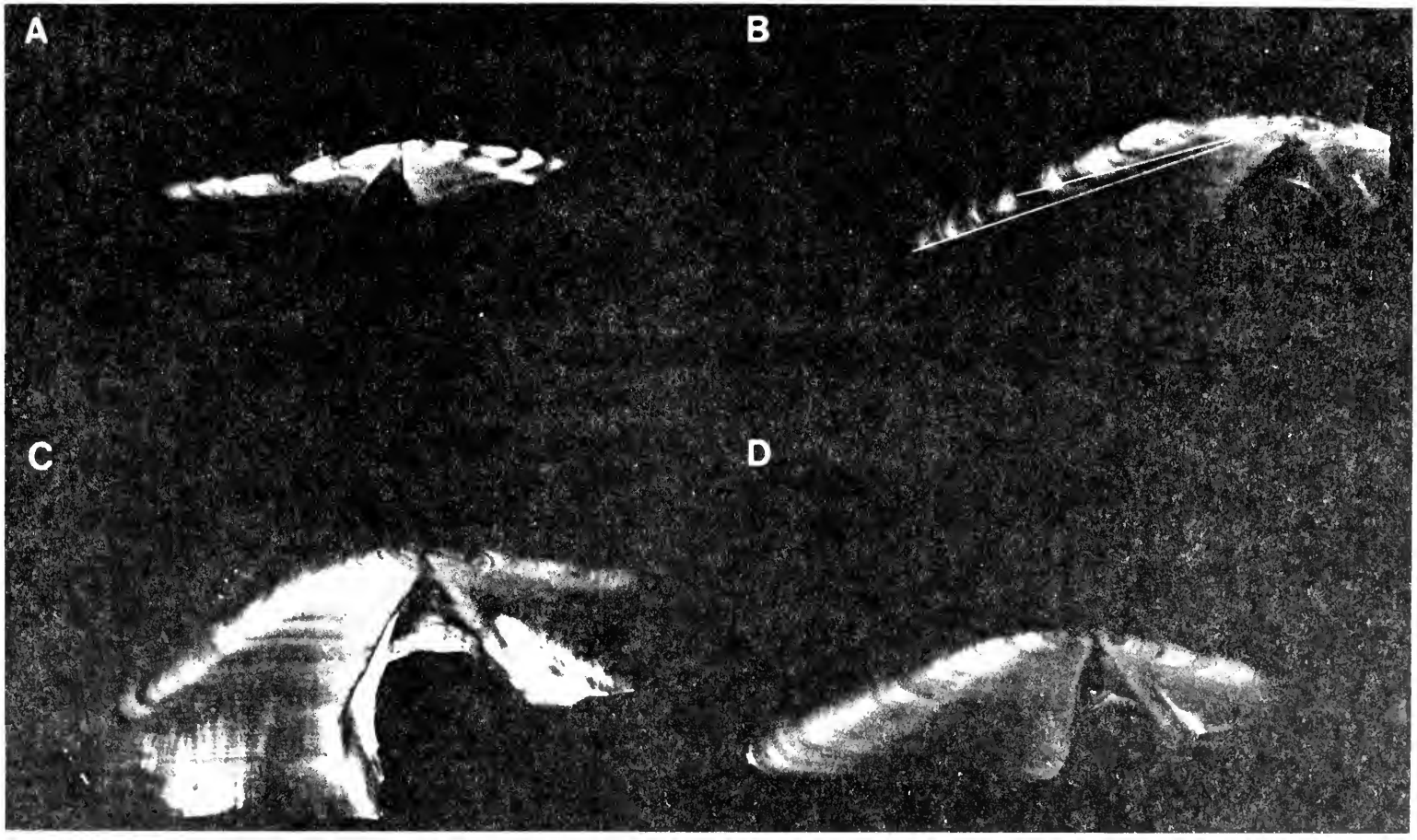

FIGURE 1.—Four sections of tilefish otoliths. The mediodorsal region is on the right in A and on the left in B, C, and D. The medial edge is the lower edge of each section, and the sulcus acusticus is the notch seen in the middle of the medial face. A) Section of an otolith from a 3-yr old tilefish of 33 cm FL and of unknown sex. B) An otolith section from an 8-yr old male tilefish of 77 cm FL. White lines indicate lines used to measure from the core to the edge of the first and fifth annuli and to the edge of the otolith. C) An otolith section from an 89 cm FL female tilefish aged 30 yr showing the aberrent otolith growth pattern with tissue only being deposited on the medial edge. D) Section of an otolith from an 89 cm FL male aged 8 yr.

general linear model (Helwig and Council 1979) was used for these analyses, and the partial sums of squares (Type IV) were used as test criteria.

The von Bertalanffy growth formula was fit to the data from each fish with SAS nonlinear regression, using Marquardt's method (Helwig and Council 1979). This provided repeat observations of length at each age, allowing us to estimate variance about the regression line and to compare curves with Hoetelling's T^2 (Morrison 1976; Bernard 1981).

We divided the fishing grounds into two areas, Hudson Canyon and Southern New England (Fig. 2), to consider differences in the length frequency of tilefish. A weighting procedure was used in calculating length frequencies to eliminate bias introduced by excessively large samples collected during a season. Equal weight was given to each large sample ($n > 50$) from an area in a year and season, and seasonal longline landings (Christensen footnote 5) were used to weight the seasonal length frequencies when computing the annual length frequency. If a year and area had <200 observations, no weighting was used in calculating the length frequencies.

The total instantaneous mortality rates (Z) were calculated through least-squares regression of the natural log of the number in an age group on age.

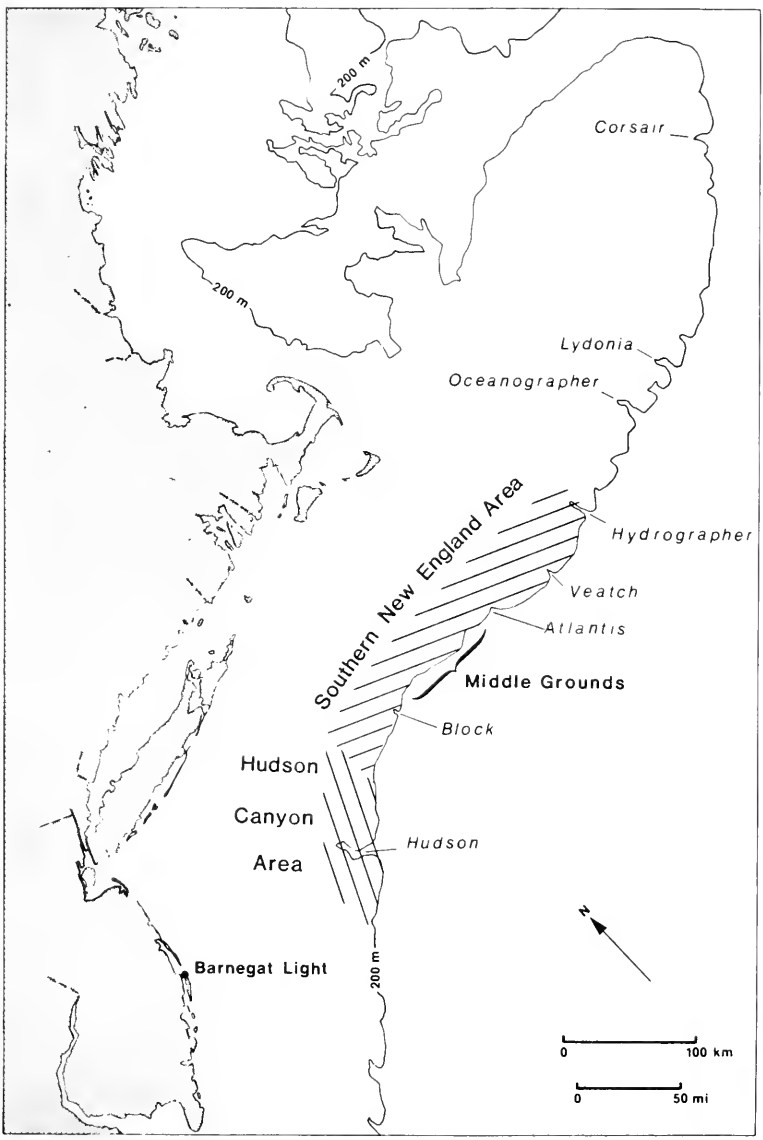

FIGURE 2.—Map of the continental shelf from New Jersey to Maine showing some of the major submarine canyons from the Middle Atlantic Bight to Georges Bank. Two primary fishing areas are labeled, Hudson Canyon (long. 71°55'-72°42'W) and southern New England (long. 67°00'-71°54'W).

RESULTS

Otoliths were collected from 755 tilefish in 1978. Ninety percent of the sections (682) were readable and used for age and growth studies. Of these, 305 were females, 233 were males, and 144 were of unknown sex. Changes in growth pattern of the otolith of some of the largest fish presented problems for analysis of growth rates. Thirteen fish (11 females and 2 males) of 84-108 cm FL stopped depositing tissue on the ventral side of the otolith but continued to grow on the medial face (Fig. 1C). Fish with this aberrant otolith growth pattern were not included in marginal increment analysis or in estimation of the OS:FL relationship. However, measurements were made to annuli formed before the otolith growth change.

Validation

Mean marginal increments in ocular micrometer units were lowest in June and increased to a maximum in January and February (Fig. 3). ANOVA indicated highly significant differences between monthly means ($P < 0.01$). We concluded that annuli were formed once and only once each year, and most fish completed annulus formation by 1 June. Younger tilefish apparently formed annuli later than

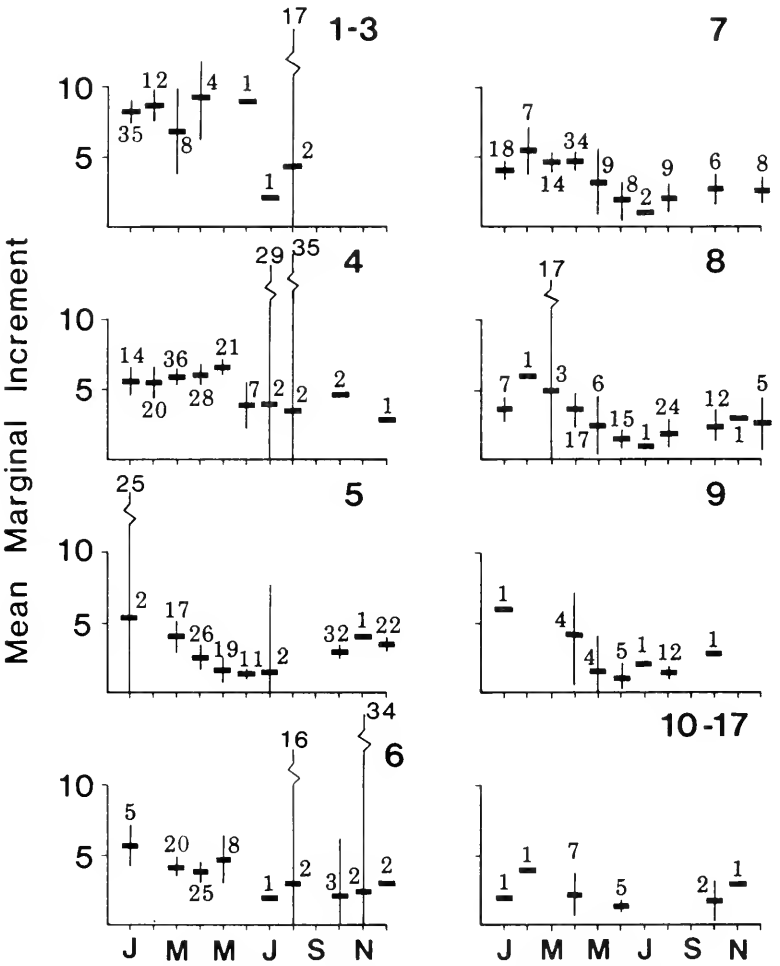

FIGURE 3.—Mean marginal increment in ocular micrometer units by month for eight age groups of tilefish, based on number of annuli formed. Number of annuli is in the upper right corner of each graph, the horizontal bar is the mean, the number just above or below the mean is the sample size, and the vertical line is the 95% confidence interval. Some confidence intervals exceed the size of the graph with their smallest values <0 and their largest values given above the end of the interval.

older tilefish; the mean marginal increment for fish with 1-3 and 4 bands did not decline until late in spring, while the mean marginal increment of older fish usually began to decline in March (Fig. 3). Eleven fish apparently had not formed annuli by 1 June. They had hyaline edges and marginal increments equal to 50-120% of the increase in their otolith size in the previous year. Four of these fish (one female and three of unknown sex) had formed 3 or 4 annuli, six were females with 7-9 annuli, and one was a male with 6 annuli.

Otolith size increased with fish size and thus provided added evidence for the validity of using the otoliths for aging tilefish. A log-log regression model fit the data best. ANCOVA showed no significant differences in slope or elevation between males and females ($P > 0.05$) in the 50-73 cm FL range for which there were nearly equal numbers of each sex. Therefore, one least-squares regression line was derived for all fish ($r^2 = 0.90, n = 663$) and converted to a functional regression equation [ln (FL) = $-0.4369 + 1.1112$ ln (OS)].

Seasonal length-frequency analysis of small tilefish (2-30 cm FL) taken over several years (Fig. 4) showed modes near the time of annulus formation that agreed closely with the back-calculated lengths (Table 1). These histograms were compiled from our data, other published data (Bigelow and Schroeder 1953; Fahay and Berrien 1981), and unpublished data (Fahay and Berrien[6]). In the winter and spring, three distinct modes occurred at 6-11, 17-21, and 27-30 cm FL which approximated the mean back-calculated lengths (see below) at ages 1, 2, and 3 yr, respectively. Tilefish spawn from at least May into October (Freeman and Turner footnote 4; Idelberger et al. 1981; Fahay and Berrien 1981), and the smallest fish observed were in the fall. The progressive increase in size of the smallest fish from the fall through the summer, and the progressive increase of other modes, also indicated that these modes represented age groups.

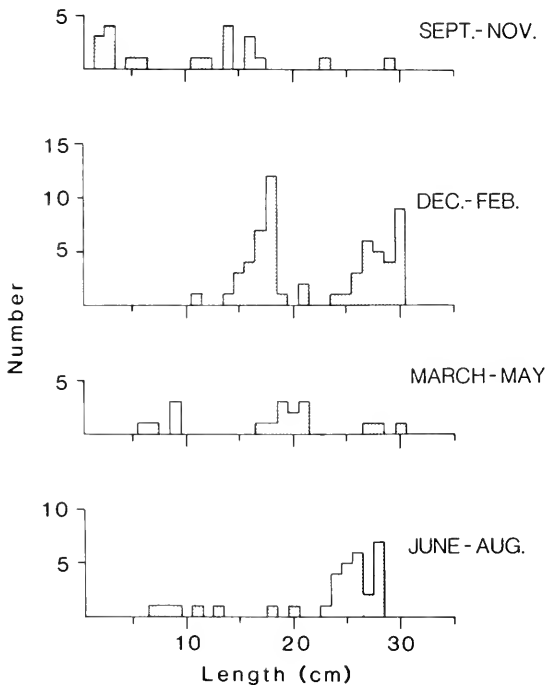

FIGURE 4.—Length frequency of small tilefish sampled by various researchers (see text) in 3-mo intervals.

Progressive increase of modes in the longline length frequencies for 1977-79 (Fig. 5) also suggested that age data were valid. In 1977 a mode existed at 41-45 cm FL; in 1978 there was a more pronounced mode at 51-55 cm FL; and in 1979 there was one at 56-60 cm FL. The sizes of these fish in 1977-79 compared well with mean empirical lengths at ages 4-6 of fish we aged (see below).

Longevity and Length at Age

Length-at-age data suggested that males grow faster than females, but females live longer. On average, tilefish (sexes combined) grew about 10 cm FL/yr for the first 4 yr and thereafter growth slowed, especially for the females (Table 1). After age 3, mean back-calculated lengths of males were larger than those of females. At age 4, males and females averaged 43 and 41 cm FL, respectively, and by the ninth year males averaged 74 cm FL while females averaged 64 cm FL. The oldest fish was a 35-yr-old female of 89 cm FL, and the largest female was 95 cm FL at 32 yr. The largest male was 112 cm FL at 20 yr old, and the oldest male was 96 cm FL at 26 yr.

Back-calculated growth increments for males and females were significantly different in years 3-16 (ANOVA: $P < 0.05$). For years 17-25, they were either not significantly different ($P > 0.10$) or not comparable because of small sample sizes. Statistical analyses were not performed on data involving back-calculated lengths at age 1, because the OS:FL conversion formula was fit to fish >16 cm FL so back-calculations below that size (including nearly all back-calculated lengths at age 1) may have been inaccurate. Males achieved significantly more growth than females in all years (3-16) except the third (Dun-

[6]M. P. Fahay and P. L. Berrien, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun., 1982.

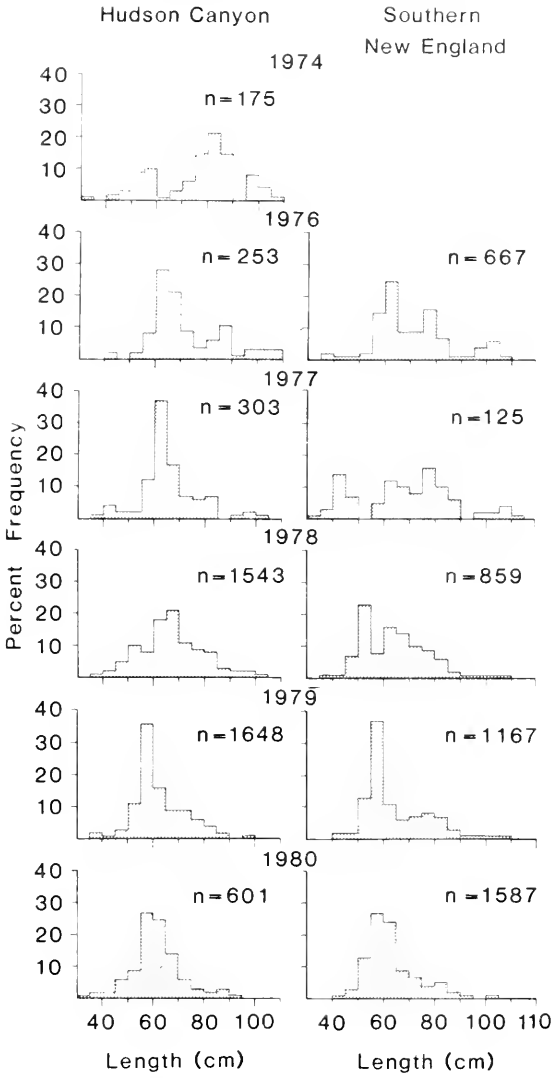

FIGURE 5.—Length frequency of tilefish caught by longline in the Hudson Canyon and Southern New England areas, 1974-80. If there were 200 or more observations in a year and area, the data were weighted equally by trips within a season and by percentage of annual landings made in each season; no weighting was used if there were <200 observations in a year and area. n = sample size.

can's multiple range test: $P = 0.05$), and these differences exceeded 1 cm FL after the fifth year (Fig. 6). Fish of unknown sex grew more slowly than females through their fifth year (significantly slower at ages 3-4, Duncan's test: $P = 0.05$), and they always grew more slowly than males (significantly so for ages 3-5, Duncan's test: $P = 0.05$).

ANOVA and Duncan's multiple range test on last back-calculated lengths for fish caught in different locations and by different fishing gears showed no significant differences between areas ($P > 0.05$) and indications of gear selection for only some ages. Sex was included as an effect in the ANOVA to account for differential growth rates. Foreign trawl and longline caught fish were equal or nearly equal (within 1 cm) in size at ages 3, 4, 6, and 7, when their average lengths were 29, 41, 53, and 63 cm FL, respectively. Recreationally caught fish were significantly larger at age 4 (Duncan's test: $P = 0.05$) when they averaged 46 cm FL and at age 5 when all gears were significantly different (ANOVA: $P < 0.01$ and Duncan's test: $P = 0.05$) with the recreational catch averaging 51 cm FL, the longline catch being intermediate in size (49 cm FL), and the foreign trawl-caught fish being smallest (46 cm FL). The recreational catch at age 7 was significantly smaller (Duncan's test: $P = 0.05$) than the catch by the other gears (63 cm FL). In all other years, differences in size were not significant.

Growth Models

Growth models (von Bertalanffy 1938) for males and females were found to be significantly different with Hoetelling's T^2 ($P < 0.01$). Curves were fit using last back-calculated length at age, except for the 13 fish with aberrant otolith growth patterns for which empirical length was used. Females had a much smaller L_∞ (90 cm FL) and a larger K (0.153) than males ($L_\infty = 111$ cm FL and $K = 0.130$). To describe growth of the entire population, a von Bertalanffy curve was also fit for all tilefish (Fig. 7).

Ricker's (1975) population growth statistic (G)

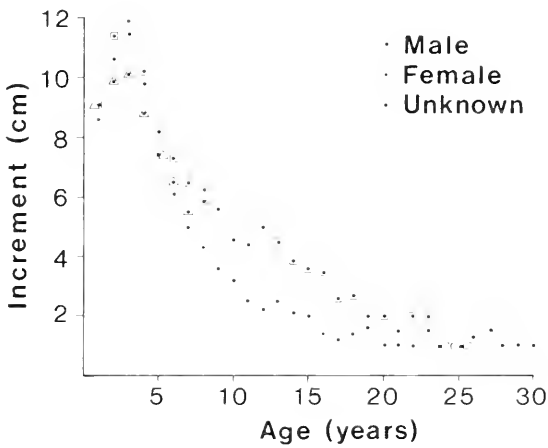

FIGURE 6.—Annual growth increment of tilefish by age and sex. Data for the first year may be inaccurate, because the back-calculation formula was fit to tilefish that were at least 1 yr old. The mean of each increment is shown by the point (·).

calculated for each sex reflected the length-at-age data with similar values for both sexes through age 4 and faster growth rates for males of age 5 and older (Table 1).

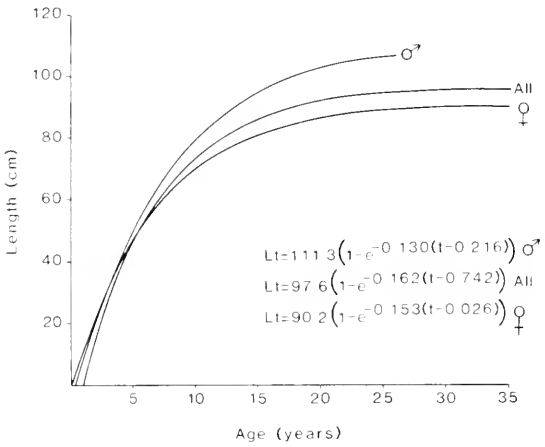

FIGURE 7.—von Bertalanffy growth formulae for male, female, and combined tilefish.

Length and Weight Relationships

The length:weight regressions for both whole and eviscerated weights were not significantly different between males and females. Log-tansformed regressions were most appropriate. The data were examined with ANCOVA between 50 and 95 cm FL where there were about equal numbers of observations for each sex. Differences between slopes for males and females were more nearly significant for the whole weight regressions than the eviscerated weight regressions (ANCOVA, $P = 0.08$ and 0.26, respectively). Final regressions were therefore computed for all tilefish combined and converted to Ricker's (1973) functional regression equations. These were

$$\ln (\text{wt}) = -5.32 + 3.26 \ln (\text{FL})$$

and

TABLE 1.—Mean back-calculated fork length (cm) at age[1], empirical length at age, annual increment, and population growth rate (exponential) for female, male, and all tilefish combined in 1978.

	Age																	
	1[2]	2[2]	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Female																		
Mean back-calculated length	9	19	31	41	48	54	59	62	64	67	70	72	73	75	77	78	79	80
Mean empirical length	—	—	38	47	52	58	64	65	66	68	—	90	—	—	84	77	—	84
Mean Increment	9	11	11	10	7	6	5	4	4	3	3	2	2	2	2	1	1	1
Population growth rate (× 10^{-2})	261	153	91	55	39	30	17	10	16	12	10	6	8	7	3	5	6	7
n	—	—	14	47	61	40	65	52	11	1	—	1	—	—	1	1	—	1
Male																		
Mean back-calculated length	9	21	32	43	51	58	64	70	74	77	79	83	87	91	94	97	99	101
Mean empirical length	—	—	40	50	53	60	71	74	79	86	89	93	—	—	99	102	104	—
Mean Increment	9	11	12	10	8	7	6	6	6	5	4	5	4	4	4	4	3	3
Population growth rate (× 10^{-2})	264	150	90	55	43	37	25	22	11	8	18	16	14	12	10	6	5	6
n	—	—	4	51	55	17	44	41	23	5	1	1	—	—	5	1	1	—
Combined																		
Mean back-calculated length	9	20	31	41	49	55	62	66	71	73	75	78	81	84	87	86	89	88
Mean empirical length	18	25	37	48	52	58	67	69	75	83	89	92	—	—	97	90	104	84
Mean Increment	9	11	11	10	8	7	6	5	5	4	4	4	4	3	3	2	2	2
Population growth rate (× 10^{-2})	258	149	92	56	42	35	24	22	11	7	14	13	12	10	−2	11	−4	6
n	7	5	60	131	135	67	112	95	34	6	1	2	—	—	6	2	1	1

	Age																
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Female																	
Mean back-calculated length	82	83	83	84	85	86	87	89	90	91	92	90					
Mean empirical length	82	—	—	—	—	—	—	—	—	—	92	89	91	89	95	—	88
Mean Increment	2	1	2	1	2	1	1	1	2	1	1	1	—	—	—	—	—
Population growth rate (× 10^{-2})	4	1	4	6	4	4	5	6	4	4	−7	—	—	—	—	—	—
n	1	—	—	—	—	—	—	—	—	—	1	1	1	3	1	—	2
Male																	
Mean back-calculated length	103	105	101	103	105	106	107	—									
Mean empirical length	96	109	—	108	—	—	108	96									
Mean Increment	2	2	1	2	2	1	1	—									
Population growth rate (× 10^{-2})	6	−12	6	6	3	3	—	—									
n	2	2	—	1	—	—	1	1									
Combined																	
Mean back-calculated length	90	91	86	88	89	90	91	89	90	91	92	90	—	—	—	—	—
Mean empirical length	91	109	—	108	—	—	108	96	—	—	92	89	91	89	95	—	88
Mean Increment	2	1	1	1	2	1	1	1	2	1	1	1	—	—	—	—	—
Population growth rate (× 10^{-2})	5	−17	5	6	4	4	−10	6	4	4	7	—	—	—	—	—	—
n	3	2	—	1	—	—	1	1	—	—	1	1	1	3	1	—	2

[1]Because of apparent otolith growth patterns; back-calculations were not possible for females above age 30 or males above age 25
[2]Back-calculated lengths of <18 cm FL may be inaccurate because no otoliths from fish <18 cm FL were used to fit the otolith size fork length regression line

$$\ln(\text{eviscerated wt}) = -5.18 + 3.21 \ln(\text{FL}).$$

Overall, whole weights were 7% greater than eviscerated weights. However, this percentage increased from about 5% for 40-54 cm FL females to 14% for 90-94 cm females, while it increased only from 5% for males of 50-54 cm FL to 8% for males of 90 cm FL or more.

Size Structure

Randomly collected length measurements from longline, recreational, and foreign trawl fisheries showed differences in sizes of tilefish exploited. All three fisheries had similar modal sizes, but the majority of the foreign trawl catch was smaller than the modal size, while the majority of the longline and recreational catches exceeded the modal size (Fig. 8). Size structure was available for the longline and recreational landings in 1977 and for all three fisheries in 1978. Because sample sizes were often small, no weighting was used in preparing length-frequency histograms and all fishing areas were combined. In 1977 the longline and recreational fisheries had one mode at 61-65 cm FL, and similar size distributions (65-70% of the fish between 56 and 75 cm FL, Fig. 8). In 1978 there was a mode for all three fisheries at 51-55 cm FL. Foreign trawl catches were most distinct; the majority of the catch was below the modal size (51% from 26 to 50 cm FL), and only 17% was in the 56-75 cm FL interval. The longline and recreational catches were similar in that most of the catch exceeded the modal size, but the longline landings had a second mode (61-70 cm FL) while the recreational catch did not. Fifty-three percent of the longline catch was in the 56-75 cm FL interval, and 37% of the recreational catch was in that size range.

Size structure in the longline fishery became truncated between 1974 and 1980. In some years, the size structure differed between the two fishing areas (Fig. 5). The earliest length-frequency histogram (1974) for the Hudson Canyon area showed what Grimes et al. (1980) considered to be a relatively unexploited population, and the first histogram for the Southern New England fishing area (1976) showed smaller modal sizes than the 1974 data for the Hudson Canyon. In 1974, 71% of the tilefish from the Hudson Canyon area were >70 cm FL. In 1976, 43% of the fish from the Hudson Canyon area and 46% from the Southern New England area were >70 cm FL. These percentages declined in 1978 to 36 and 30%, respectively, and in 1980 to 16 and 21%, respectively.

Size at complete recruitment to the longline fishery (occurring just above the modal size in the length-

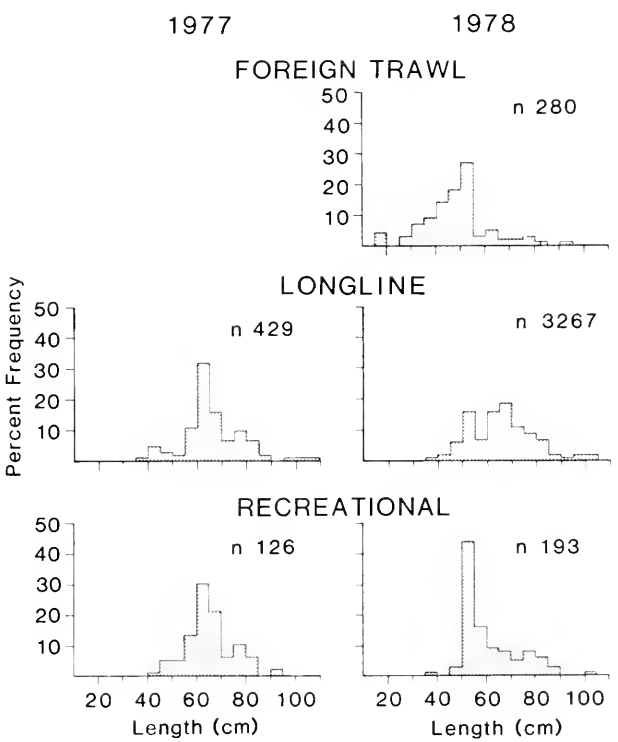

FIGURE 8.—Length frequencies of tilefish caught during 1977 and 1978 in all fishing areas by recreational and longline fishermen and foreign fishing vessel trawls. n = sample size.

frequency data) decreased in 1974 to 1980. The 1974 data indicated that complete recruitment occurred after 81-85 cm. By 1976 the peak frequency occurred at 61-65 cm, and this continued to be the case in 1977 and nearly so in 1978 in the Hudson Canyon area. In the Southern New England area, the lowest modal size occurred during 1978 at 51-55 cm FL. In succeeding years the modal size was generally 56-60 cm FL for both areas.

Strong modes at successively larger sizes in consecutive years were apparent in the longline length-frequency data, suggesting the presence of strong year classes and variable recruitment. The presence of such modes in both fishing areas indicated that they were not simply a result of discovering new concentrations of tilefish as the fishery expanded. Particularly noticeable was a mode at 41-45 cm FL in 1977, 50-55 cm FL in 1978, and 56-60 cm FL in 1979. These sizes were similar to our empirical lengths at age in 1978 of 4-, 5-, and 6-yr-old fish suggesting that these modes represented the 1973 year class.

Age Structure and Mortality

Age composition of the longline, recreational, and foreign trawl fisheries was quite different in 1978. Longline landings were dominated by 7 and 8 yr olds which represented 24 and 25% of the catch, respectively, and 90% of the catch were 4-9 yr olds (Fig. 9). The recreational catch was comprised mainly of 5 yr olds (32%), and 98% of the catch were 4-9 yr olds. Four-yr-old tilefish accounted for 33% of the foreign trawl catches; 72% of the catches were 3-5 yr olds, and 91% were 3-7 yr olds. Age at full recruitment was clearly different for each fishery—age 9 for longline, 6 for recreational, and 5 for the foreign trawl. The differences in length frequencies of longline catches in the Hudson Canyon and Southern New England areas resulted in higher percentages of 7 yr olds in the former area and more 4-6 yr olds in the latter.

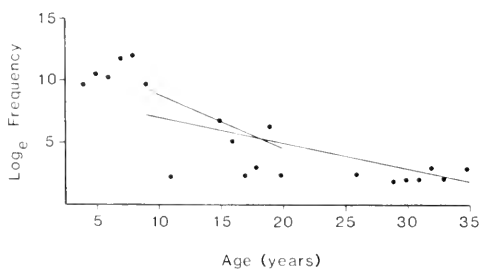

FIGURE 9.—Catch curve for tilefish caught by longline during 1978 in the Middle Atlantic-Southern New England region. Regression lines from data for fish age 9-20 yr and 9-35 yr are shown.

Total mortality rates (Z) computed for the longline and foreign trawl fisheries were found to be similar. ANCOVA revealed no significant differences between sex-specific catch curves in total mortality rates in the 1978 longline fishery ($P > 0.05$), thus Z was computed for all tilefish combined. The number at age in the longline fishery (Fig. 9) was typical of both fisheries in that there were numerous fish at the younger ages (<10 yr) and few fish between 10 and 35 yr. This resulted in a concave catch curve indicating either a lower rate of mortality for the oldest fish, or that those fish had not been subjected to fishing pressure for their entire lives, or both. The total mortality estimate from the longline data was 0.17 ($r^2 = 0.416$) for all ages; however, the effect of the curvilinearity in the catch curve was considered significant, and a more representative age range was selected. The instantaneous rate of total mortality was reestimated to be 0.46 for ages 9-20 from the longline fishery (the number at age 11 was considered an outlier and not included, $r^2 = 0.52$). The rate of total mortality for the foreign trawl fishery was estimated to be 0.60 for ages 5-8 ($r^2 = 0.84$).

DISCUSSION

Growth

All branchiostegids studied to date exhibit differences in growth rates between sexes with the females growing more slowly than males. *Lopholatilus chamaeleonticeps*, the largest and longest lived branchiostegid, shows the most pronounced difference in this regard with males reaching 105-115 cm FL in 20-26 yr and females ranging from 85 to 95 cm FL in 29-35 yr. Hayashi (1976b) reported that the average male *Branchiostegus japonicus japonicus* from the East China Sea was 32 cm TL (reported as body length) at 8 yr while females averaged only 29 cm TL at 8 yr. Ross (1978) demonstrated similar, though proportionally less pronounced, differences for *Caulolatilus microps* from North Carolina and South Carolina. Differences in mean back-calculated length at age between the sexes during the oldest ages were on the order of 15-20% of the average male's length for *L. chamaeleonticeps* (this study), 10-12% for *B. japonicus japonicus* (Hayashi 1976b), and from −1 to 5% for *C. microps* (Ross 1978).

The divergence of growth rates in branchiostegids is correlated with sexual maturation of females. Pronounced differences in growth between the sexes in *L. chamaeleonticeps* was evident at 5 yr (Fig. 6) when the average female was slightly smaller (51 cm empirical FL) than the observed size of maturation (52-57 cm

FL) based on visual staging of gonads (Idelberger et al. 1981). Both sexes of *B. japonicus japonicus* and *C. microps* exhibited similar prematurational growth rates, and the rates diverged in association with the maturation of females (Ross and Huntsman 1982). The divergence of growth rates of the sexes simultaneous with female maturation presumably reflects earlier and higher energetic costs of reproduction for females. The relatively slow growth of the *L. chamaeleonticeps* of unknown sex suggests that they may be among the smaller members of their year class, and their more rapid growth than females at ages 6-8 suggests that at least the older ones may be males.

Differential growth rates of males and females should lead to skewed sex ratios at size as Wenner (1972) had demonstrated. Idelberger et al.[7] have shown that in 1978-80 the sex ratio of tilefish >55 cm FL was disparate (Table 2). Fewer males than females occurred between 56 and 65 cm FL (38-42% males), males predominated between 71 and 85 cm FL (64-84% males), nearly equal numbers of each sex occurred in the 86-95 cm FL range (50-58% males), and only males were above 95 cm FL. Dooley (1978) suggested that the skewed sex ratios of tilefish might have been caused by either protogynous sex reversal or differential growth. Idelberger et al. (footnote 7) have examined histological sections of tilefish gonads and reported that adult tilefish do not undergo sex reversal. Additionally we tested sex ratio at age (for ages 4-10 and all ages above 10 combined) and found significant deviations from 1:1 only at age 7 (log-likelihood test: $G = 5.32$, $P < 0.05$). We concluded that differential growth rates probably caused the skewed sex ratios at length. We believe that more rapid growth of males out of the 56-65 cm FL range causes the initial, smaller percentages of males. The greater numbers of males in the 71-85 cm FL range is a result of their younger age and thus shorter exposure to mortality. The males in this size range were 9-12 yr olds, while the females were 12-23 yr olds. Continued rapid growth of males through the 86-95 cm FL interval (only males age 13-15 yr fall within the range) and the much slower growth of females, in conjuction with their greater longevity, result in an accumulation of old females between 86 and 95 cm FL (50-58% males). Ross (1978) also hypothesized that differential growth rates, not protogynous sex reversal among adults, caused skewed sex ratios in *Caulolatilus microps*. Clearly, mortality rates influence sex ratio at length in *L. chamaeleonticeps* and, if mortality is increased by fishing, the proportion of females in the larger size intervals will decrease.

[7]Idelberger, C. F., C. B. Grimes, and K. W. Able, Rutgers University, New Brunswick, NJ 08903, unpubl. data, 1982.

TABLE 2.—Percentage of male tilefish > 50 cm FL in 1978-80 (from Idelberger et al. text footnote 7) and results of log-likelihood tests of the hypothesis that sex ratio did not differ from 1:1 (G).

Length (cm)	n	% males	G
51-55	268	54	1.976
56-60	140	38	8.844*
61-65	166	42	3.779
66-70	180	46	0.940
71-75	117	64	8.865*
76-80	116	84	55.745*
81-85	80	71	14.028*
86-90	24	58	0.376
91-95	10	50	0.100
96-100	6	100	—
101-105	3	100	—
106-110	1	100	—
Total	989	48	Pooled 0.369

*$P < 0.01$.

Size Structure and Mortality

The prominence and progression of strong modes through the length-frequency data from the longline fishery indicate that strong year classes were present and recruitment of tilefish has varied. Evidence of weak year classes may be seen in the relatively low frequencies of 61-65 cm FL fish in 1974 and of 56-60 cm FL fish in 1978, especially in the Southern New England area (Fig. 5). Such fluctuations in year-class strength will cause variations in population size and thus create problems in estimating allowable catches.

The truncation in size structure of longline catches, which Grimes et al. (1980) attributed to the effect of fishing, has continued. The proportion of fish >70 cm FL declined from 71% in 1974 to 16-21% in 1980 (Fig. 5). This was accompanied by an increase in the longline fleet size from about five vessels in 1974 (Grimes et al. 1980) to about 30 vessels in 1980 and increased effort per vessel at least through 1980[8].

The difference in size structure of the foreign trawl and the longline catches (Fig. 8) shows that longlines select for larger fish. In addition, the reduction in size at full recruitment in the longline landings since 1974 suggests that when larger tilefish are present, smaller ones are either less vulnerable to the gear or they are avoided by the fishermen. If this is true, longline length frequencies show higher relative frequencies of large fish than actually exist in the population, which would lead to an underestimation of mortality rates.

[8]Grimes, C. B., K. W. Able, and S. C. Turner, Rutgers University, New Brunswick, NJ 08903, unpubl. data, 1982.

The estimate for instantaneous total mortality rate (0.17) from the longline fishery in 1978 using all fully recruited ages was undoubtedly too low. Estimates of 0.46-0.60 derived from more linear portions of the longline catch curve and the foreign trawl catch curve, respectively, are considered by us to more realistic. The difference between the two estimates may be due to a variety of factors, including variation in year-class strength, gear selection, and increased mortality rates. The longline estimate may be low if the selectivity for larger sized tilefish noted above applies to fully recruited age groups as well. The foreign trawl estimate may be high because the strong 1973 year class was the first fully recruited year class in 1978, and trawls appear to be biased towards smaller tilefish. Alternately, the estimate of total mortality rate from 5 to 8 yr olds from the foreign trawl fishery may more accurately represent recently increased mortality rates than the estimate from 9 to 20 yr olds taken in the longline fishery, because catch curve estimates of Z reflect the history of mortality rates over the lifetime of the year classes sampled (Ricker 1975; Csirke and Caddy 1983). More information on the age structure in different years and for the older members of the tilefish population (>10 yr) is needed to improve the estimates of mortality rate. While our results showed no significant differences in mortality rates in 1978, the older ages of the females suggest that they may have a lower mortality rate than males. The question of sexual differences in mortality should be addressed in greater detail.

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A MARK-RECAPTURE TEST OF ANNUAL PERIODICITY OF INTERNAL GROWTH BAND DEPOSITION IN SHELLS OF HARD CLAMS, *MERCENARIA MERCENARIA*, FROM A POPULATION ALONG THE SOUTHEASTERN UNITED STATES

C. H. Peterson, P. B. Duncan, H. C. Summerson, and G. W. Safrit, Jr.[1]

ABSTRACT

Individually marked and measured *Mercenaria mercenaria* were placed at natural depths in the sediments inside field enclosures of three types in an estuary near Cape Lookout, N.C., in June 1978. Subsets of hard clams were collected and sacrificed on October 1979, May 1980, October 1980, and October 1981. Sectioning one valve of each experimental clam along the axis of greatest growth revealed growth discontinuities (both in texture and coloration) in the middle and outer shell layers. These growth bands were deposited annually during the summer-early fall season. Enclosure type (microhabitat variation) did not alter the regular annual pattern of band deposition; 93% of the experimental clams in October collections (115 of 123) exhibited the predicted number of added growth bands in the increment of shell growth that had been deposited since initial marking. Examination of presumed daily lines on acetate peels and thin sections suggested that the annual band corresponds to a period of relatively slow growth. Only a few (≃6.7%) of the *M. mercenaria* recruits in spring samples failed to exhibit an identifiable growth band from their first summer-fall period. A comparison of the size-frequency distribution at first band on older clams to the size distributions of new recruits in September-October and in April-May revealed that the first growth band on a new *M. mercenaria* recruit is usually deposited soon after September-October during the clam's first fall. Thus, southeastern *M. mercenaria* near Cape Lookout can be aged by counting internal growth bands but, unlike northern populations, exhibit slow growth and annual band deposition during summer-early fall rather than in winter.

Application of the aging technique to a January-February 1980 collection of *M. mercenaria* from Core Sound, N.C., revealed a high proportion of older clams (up to 32 years of age) and a mean age of >9 years. Growth rates, inferred from the relationship between size and estimated age, were high; on average a legally harvestable size (4.46 cm in length) is reached by 1½ years. The age-frequency distribution from this collection revealed lower recruitment success of the 1977, 1978, and 1979 year classes than of previous year classes. This partial year-class failure corresponds with the period of fourfold increase in commercial harvest of *M. mercenaria* in North Carolina and suggests that further studies should test for a spawner-recruit relationship among hard clams.

The depositional regularity of macro- and microstructural features in bivalve mollusc shells has been exploited as a chronometer by scientists in several disciplines (reviewed succinctly by Jones 1980). Deposition patterns in bivalve shells have proved useful to 1) paleontologists and environmental biologists in reconstructing the local history of environmental change (Pannella and MacClintock 1968; Clark 1974; Rosenberg and Runcorn 1975; Pannella 1976; Rhoads and Lutz 1980), 2) archaeologists in dating the seasons of prehistoric site occupation (Coutts 1970; Koike 1973), and 3) population biologists and fisheries managers in constructing quantitative life history and growth schedules for the bivalves themselves (Rhoads and Pannella 1970; Kennish and Olsson 1975; Jones et al. 1978; Kennish 1980). Biologists and managers should probably make more use of the historical records preserved in bivalve shells to estimate survivorship curves by assessing age at death and growth curves by measuring growth increments between successive chronological markers because these integrative methods are more efficient than all rigorous alternative methods, which require measurements over at least a year's time. Concern over the paucity of controlled tests of the regular periodicity of repeating shell features (Clark 1974; Gould 1979; Jones 1981) may be partly responsible for the cautious use of shell information by invertebrate population biologists.

The hard clam, *Mercenaria mercenaria* (L.), has been used frequently by paleontologists, archaeologists, and population biologists as a subject for shell macro- and microstructural analysis (Barker 1964; Pannella and MacClintock 1968; Rhoads and

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Pannella 1970; Crenshaw 1972; Kennish and Olsson 1975; Gordon and Carriker 1978; Kennish 1980). Most published analyses of shell deposition patterns which are directed towards estimating life history parameters and growth rates in *M. mercenaria* have been conducted on northern populations (but see Clark 1979; Clark and Lutz 1982). Like many other marine bivalves (e.g., *Pecten maximus* in Mason 1957; *Scrobicularia plana* in Green 1957; and *Macoma baltica* in Segerstrale 1960), *M. mercenaria* from New Jersey (Kennish 1980) to Massachusetts (Pannella and MacClintock 1968) deposits a winter band of slow-growth increments that can serve as an annual marker. Because hard clams in southeastern populations show a pattern of nearly constant monthly growth year-round (Ansell 1968), we questioned whether *M. mercenaria* in the southeast would deposit a clear annual marker in its shell. Here we report on mark-recapture tests of whether *M. mercenaria* from the vicinity of Cape Lookout, N.C., deposits any regularly periodic feature in its shell that could be used to age the individual clams. A rigorous experimental test of the aging technique is of vital importance to the wide spectrum of scientists who would like to utilize internal shell markers to age *M. mercenaria* but cannot with confidence until test data displace the doubts justifiably expressed by Gould (1979) and Jones (1981). We also apply our results to a southeastern population of hard clams to demonstrate estimation of age-frequency distribution and to draw inferences about population dynamics and growth.

MATERIALS AND METHODS

Tests of Aging Methodology

1-Year Class and Older

A mark-recapture study was designed to test whether *Mercenaria mercenaria* in the vicinity of Cape Lookout deposits any distinct annual marker in its seasonal pattern of shell growth. On 21-22 June 1978, we placed 28 individually marked and measured *M. mercenaria* into each of six 1 m^2 field enclosures. This density is within the range occurring naturally in this area but about four times the average observed in a nearby Bogue Sound seagrass bed (Peterson 1982). We employed a wide range of initial sizes from 1.8 to 10.2 cm in length and kept size-frequency distribution similar in each enclosure. Marking was achieved by applying color-coded dots of Mark-Tex Corp.[2] paints to the external shell surface of each clam. Three perpendicular linear dimensions (length along the longest anteroposterior axis, height, and width) were measured to the nearest 0.1 mm on each clam using vernier calipers. On four subsequent occasions (17 October 1979; 22 May 1980; 8 October 1980; 9 October 1981), 5 to 11 (usually 7) clams were removed from each enclosure and killed by steaming in the laboratory to provide shells with varying, but known, histories of terminal (marginal) growth for macro- and microstructural analyses.

Field enclosures were located in muddy-sand sediments at a low-tide water depth of ≈0.5 m within a protected embayment inside Middle Marsh in Back Sound, N.C. (Fig. 1). Nelson (1979) and Homziak et al. (1982) have described this site. Water temperature in Back Sound is seasonally variable; monthly means at nearby Beaufort, N.C., vary from 4° to 29°C (Sutherland and Karlson 1977). Salinities remain high year-round, ordinarily above 32‰ but with lower values recorded after heavy rainstorms (unpublished data for nearby Bogue Sound, by H. J. Porter, University of North Carolina). All six enclosures were located in an unvegetated area within an eelgrass, *Zostera marina*, bed and were protected on the north, east, and west by emergent salt marshes (*Spartina alterniflora*) and on the south by a sandbar which was exposed on spring low tides.

Enclosures were constructed from 4.2 m long by 13 cm high strips of 6 mm Dupont Vexar mesh, folded to form a 1 m^2 square, and forced vertically 10 cm into the sediments. To anchor the enclosures, 0.6 m long steel reinforcing rods were also pushed into the sediments and were attached with nylon cable ties to the Vexar mesh at each corner and at halfway points along each side. The belowground mesh inhibited *M. mercenaria* migration, while the aboveground mesh served to identify the boundaries of the plots and thereby aided recovery of the marked clams. To induce locally differing sets of environmental conditions, we added 1 m^2 tops made of 6 mm Vexar mesh to two enclosures and partial tops made of two parallel 0.25 m^2 Vexar strips to two other enclosures. All complete and partial tops were fastened to the enclosure walls with nylon cable ties at 5 cm intervals and supported above the sediment surface with wooden dowels implanted inside each enclosure. Thus, our complete design consisted of replicate clams inside two replicate enclosures of each of three different caging treatments.

Before introducing the experimental *M. mercenaria* into the field plots, we removed all large resident *M.*

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

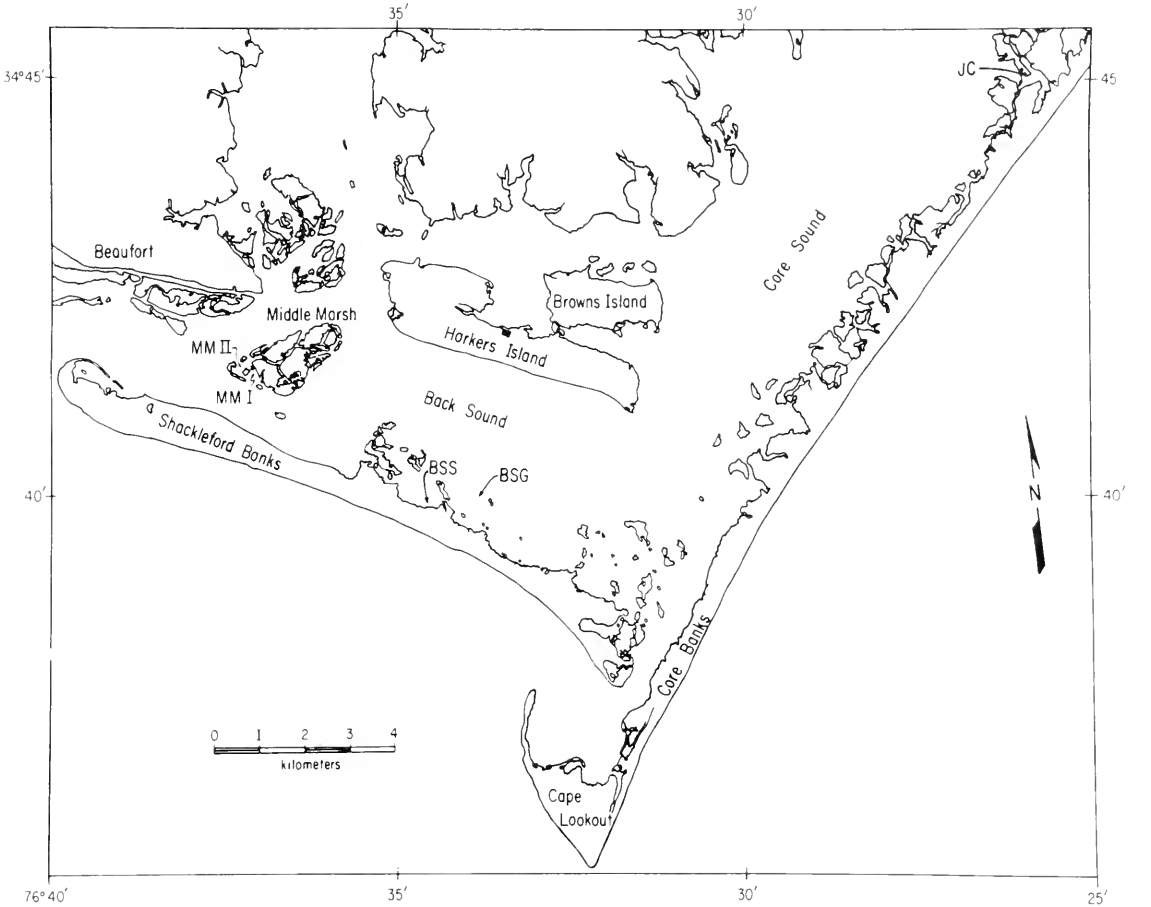

FIGURE 1.—Geographic relationships among study and collection sites in the Cape Lookout vicinity of North Carolina: MM I—the site of the mark-recapture experiment in a seagrass, *Zostera marina*, meadow at Middle Marsh and of the fixed 1 m² enclosures sieved seasonally for new recruits; MM II—the other site of fixed 1 m² enclosures sieved seasonally for new recruits on a muddy-sand flat near the west end of Middle Marsh; JC—the Johnson Creek collection site in Core Sound; BSS and BSG—the sand flat and the seagrass sites (respectively) in Back Sound from which 0-year class *Mercenaria mercenaria* were collected in February-April 1980 for estimation of the proportion without an annual band.

mercenaria by systematically plowing with fingers to a 10 cm depth followed by in situ sieving with 6 mm mesh to that same depth. This process permitted establishment of constant *M. mercenaria* density across all treatments and all replicates. The same procedure was also used to recover all marked clams from each plot on 20 September 1978 and on 21 April 1979. On those dates, each marked clam was remeasured and returned within 1 h to its assigned plot. On both those dates and on all four dates when clams were sacrificed for shell analyses, tops and partial tops were removed and replaced with new mesh to prevent extensive fouling. On the first two dates (17 October 1979 and 22 May 1980) when clams were sacrificed and returned to the laboratory for shell analyses, all clams were again excavated by this same sampling procedure and remeasured. Those not sacrificed were returned to their assigned plots within 1 h. On the two subsequent sampling occasions, no remeasuring occurred and a preset number of clams was removed from each field plot without excavating the others.

In the laboratory, we used calipers and a fine, felt-tipped pen to locate and mark on the outer shell surface of each clam its size at each measurement date (including size at introduction). A low-speed Buehler Isomet saw with a diamond blade was used to cut the marked valves from umbo to the ventral margin along the axis of greatest growth (Pannella and MacClintock 1968; Rhoads and Pannella 1970). This cut revealed the cross-sectional growth surface, which was then sanded with increasingly fine-grained grit and polished with alumina powder on a polishing wheel. We examined macroscopically the polished

cross section of each clam to determine whether any repeating feature, like the winter growth bands of northern *M. mercenaria* (Pannella and MacClintock 1968; Kennish 1980), served as an annual chronometer. By comparing the inked lines marking size at introduction and size at known dates of measurement on the outer shell surface to the polished cross section, each of three independent observers recorded 1) an estimate of the number of growth bands deposited on each clam since introduction and 2) the season of band deposition. For a subset of experimental clams, acetate peels were prepared by the standard procedures (Rhoads and Lutz 1980) and examined under a Wild M11 microscope equipped with ocular micrometers 1) to ascertain if annual markers were more or less evident than in macroscopic view and 2) to utilize presumed daily growth lines to estimate the exact period of annual band deposition and to determine by measuring the daily increments whether the annual band represented a period of relatively slow or rapid growth

0-Year Class

Because our mark-recapture test of the aging technique did not include any clams in the 0-year class (which was unavailable in June) and because the first annual band might easily be overlooked, we designed an independent test of our ability to recognize the very first annual band in *M. mercenaria*. From February to April 1980, we collected all *M. mercenaria* from 432 samples that were taken by hydraulic suction dredge (described below) from 0.25 m^2 sampling frames to a depth of 15 cm and passed through a 3 mm mesh. This sampling process collected all clams >0.5 cm long with high efficiency and without size selectivity (see Appendix). Equal numbers of samples were taken from a shallow, subtidal eelgrass meadow and from nearby unvegetated sandy bottom at similar depths (≃1.0 m) along the Shackleford Bank edge of Back Sound, about 8 km northwest of Cape Lookout (Fig. 1). All *M. mercenaria* were brought to the laboratory, killed by steaming, measured with calipers, and sectioned to expose growth bands. Here we compared the total numbers of clams which lacked any growth band with the numbers with a single band. Recruits sampled in February-April lacked a growth band if 1) we failed to recognize the initial annual band or 2) the recruits settled too late in the season to be branded with that season's band. Under the assumption that the winter dredge sampling faithfully collected all surviving recruits from the previous year's recruitment season, the ratio of clams with zero bands to those with zero or one band represented an estimate of the frequency of clams in each year class whose age is underestimated by 1 yr.

We devised one further test of the accuracy of identification of the initial annual band in *M. mercenaria* collected from the Cape Lookout vicinity of North Carolina and of the assumption that by late winter (February-April) *M. mercenaria* recruits had grown sufficiently to be efficiently collected in our hydraulic dredge sampling. In June 1978, we installed at Middle Marsh 36 1 m^2 field enclosures of the identical design described above and used in the topless treatment for the mark-recapture test of the aging methodology. All enclosures were located in shallow subtidal areas (≃0.5 m deep at low tide): 17 on a muddy-sand flat in a protected embayment at the western end of Middle Marsh and 19 in the *Zostera marina* meadow adjacent to the site used for the mark-recapture experiment (Fig. 1). After installation, all *M. mercenaria* >7 mm were removed from each plot by twice systematically sieving the top 10 cm through a 6 mm mesh. Marked *M. mercenaria* individuals were returned to these plots at densities varying from 0 to 28 per m^2 as a part of another experiment not reported here. The plots were resampled in September 1978, April 1979, October 1979, and May 1980. At each sampling, any unmarked *M. mercenaria* were collected by sieving, measured, and removed. Because most of these were new recruits, these data provided an indication of the size-frequency distributions of 0-year class *M. mercenaria* for both early fall and spring seasons in the Cape Lookout region of North Carolina. In April 1979, additional 1 m^2 enclosures were added at both sites, such that total areas sampled in October 1979 and May 1980 were 27 m^2 at the western Middle Marsh site and 29 m^2 at the *Z. marina* meadow site. We compared the seasonal size-frequency distributions of these new recruits with the distribution of size (length) at first band in a field collection of all age classes of clams (methods described below) made from nearby Johnson Creek in Core Sound, N.C. (Fig. 1). This comparison provides a further test of the accuracy of our recognition of the initial annual band of North Carolina *M. mercenaria*.

Application of Aging Technique to a Field Population

We collected *M. mercenaria* on two occasions from Johnson Creek to provide samples on which to apply our aging technique. Johnson Creek is a tidal creek on eastern Core Sound ≈18 km northeast of Cape Lookout (Fig. 1). Bottom type was soft, muddy sand.

The sampling site was in shallow subtidal waters just outside the area legally open to "clam kicking," a form of mechanical clam harvesting practiced by local commercial clammers. Our sampling site contained no bottom ruts or other disturbance features commonly left by mechanical clam harvesters.

On 16 January 1980, we collected 73 clams using a hydraulic suction dredge to sample haphazardly chosen locations within Johnson Creek. On 15 February 1980, another 51 clams were collected by excavating haphazardly located 0.25 m^2 sampling frames either using the hydraulic dredge (24 samples) or hand digging and sieving through 3 mm mesh (10 samples).

The hydraulic dredge consisted of a 3 hp gasoline engine attached to a pump which generated a water flow of ≈5 l/s through a 0.8 cm diameter metal tube. The tube penetrated at an angle into the side of a 12.7 cm diameter pipe. When water was forced into the pipe, suction was created at one end. To collect hard clams, the suction end of the pipe was swept slowly and systematically across the bottom such that it vacuumed up the top 15 cm of sediments and their living contents. All of this material was deposited into a 3 mm mesh nylon bag to permit sorting of clams from sediments and debris. This technique was nearly 100% efficient and was not size selective for *M. mercenaria* >5 mm long (tests given in Appendix).

All *M. mercenaria* collected from Johnson Creek were returned to the laboratory live, held overnight at 4°C, killed by steaming, and measured. One valve from each clam was then sectioned and aged by the techniques that we had tested earlier. From these measurements of length and estimates of age, we estimated the size (length)-frequency distribution, age-frequency distribution, and growth rate of *M. mercenaria* in the Johnson Creek area of Core Sound.

RESULTS

Tests of Aging Methodology

1-Year Class and Older

In total we recovered, sectioned, and analyzed marginal shell growth in 152 individual *M. mercenaria*, all initially planted on 21-22 June 1978. These clams were retrieved in approximately equal numbers on each of four dates from each of the three caging treatments (Fig 2). Macroscopic inspection of polished and sectioned shells revealed repeating features that could conceivably serve as annual markers. These features (analogous to those described by Jones (1980) for other species) appeared as bands in the outer and middle layers (following the terminology of Pannella and MacClintock 1968) that differed in appearance from the surrounding shell structure (Fig. 3). Bands near the umbo tended to be lighter in color and more translucent in appearance than the surrounding shell matrix, whereas bands toward the shell margin tended to be darker than the surrounding shell matrix and were usually purple in color. The first band deposited (nearest the umbo) differed consistently from all subsequent bands. It appeared more diffuse and was often united with the second band in the middle shell layer without an obvious termination at the shell surface. Although all bands extended to the external shell surface and were present in the outer layer, they did not always retain the coloration and textural distinctions outside of the middle shell layer. Attempts to relate surface growth breaks to the presence and absence of internal bands failed on most clams. The outer shell surface contained many more lines suggesting growth changes or interruptions, thus making an unambiguous matching with internal bands impossible.

Figure 2 presents the numbers of bands counted in the marginal growth increment of each hard clam retrieved from our field plots as a function of caging treatment and time of retrieval. For 91% of all clams, three independent observers counted an identical number of growth bands. In the rare cases of disagreement (listed by date on the legend to Figure 2), the majority vote was plotted. All 152 clams without exception showed a growth band having just begun at the time of initial planting (21-22 June 1978). For Figure 2 we chose to count that band and all successive ones. The numbers of bands added did not differ as a function of caging treatment on any of the four retrieval dates (Fig. 2). Thus, although our caging treatments may have altered the hydrodynamic regime and thereby the local growth environment for the test clams, the aging technique was consistent. This result extends the scope and generality of our test of whether growth bands are predictably repeating annual markers in a southeastern population of *M. mercenaria*.

At each retrieval date, there was little variance among clams in the number of bands added since planting (Fig. 2). In the October 1979 collection, 38 of 39 clams had deposited exactly 2 additional bands; in the October 1980 collection, 35 of 38 clams had deposited 3 additional growth bands; and in the October 1981 collection, 42 of 46 clams had 4 additional growth bands. This represents a 93% level

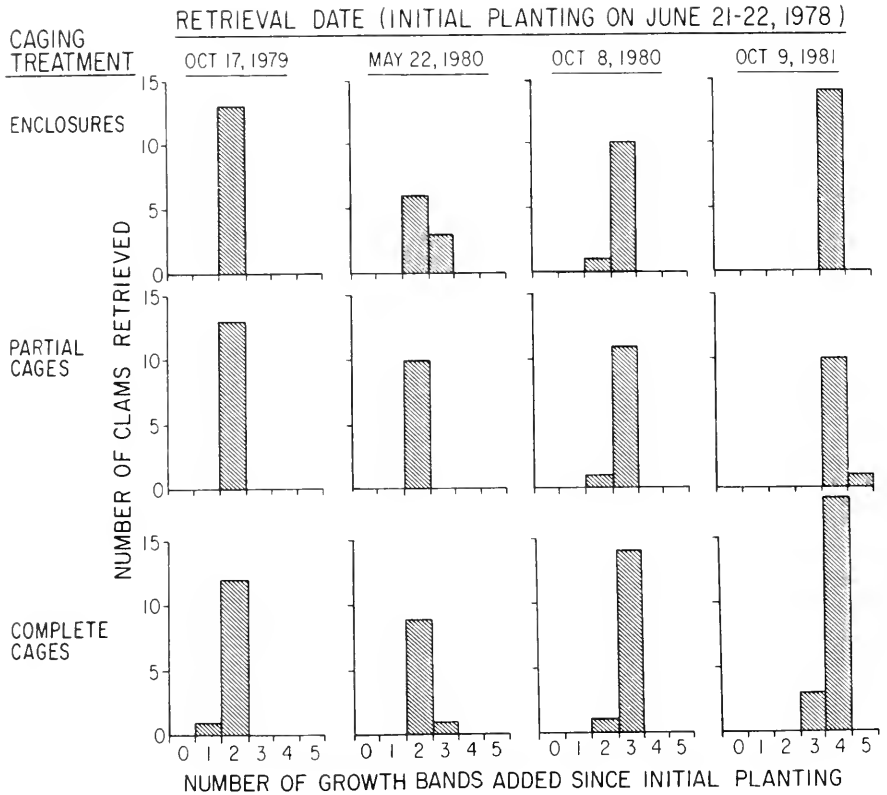

FIGURE 2.—The number of growth bands added per hard clam in the increments of marginal shell growth that occurred since planting in the field on 21-22 June 1978. Numbers of bands added were determined for each clam by majority vote of three independent observers, although disagreements in counts were rare (only 2 for October 1979, 4 for May 1980, 3 for October 1980, and 4 for October 1981). All counts include an annual growth band that had just begun to appear in all clams at the initiation of the experiment (21-22 June 1978). Each histogram represents the pooled results from duplicate 1 m^2 field plots for each caging treatment.

of agreement among clams collected on all October dates. In the May 1980 collection, 25 of 29 clams showed 2 additional growth bands. Although this represents a slightly higher level of disagreement among replicate clams, an examination of the seasonal pattern of line deposition helps explain this discrepancy. From the temporal data presented in Figure 2, the band appears to be laid down annually and predictably sometime during May to October. Each year's band was evident (although not necessarily completed) in virtually all clams collected on the three October dates. Furthermore, the initiation of the band was evident in June 1978 for all 152 clams. Thus, the somewhat higher variance in estimated numbers of growth bands added among replicate clams retrieved in May 1980 may be a consequence of variable dates of band initiation. All four clams that deviated from the mode of 2 in the May 1980 collection had a third band just beginning at the terminal margin of the shell, suggesting that late May was the approximate time of initiation of band deposition in 1980.

In June 1980, we counted annual bands to estimate the age of each of the 152 experimental clams at the time of their introduction into field enclosures. Figure 4 shows the initial age-frequency distribution 1) for all those clams that laid down an additional number of growth bands equal to that predicted by the number of additional summer seasons and 2) for all those clams for which additional age was either inaccurately or inconsistently estimated by the three age readers. Clams in this mark-recapture experiment ranged in initial age from 1 to 10. Because some clams planted as 10-yr-olds were not retrieved until October 1981, we actually examined line deposition in clams up to 13 yr of age. The two size-frequency distributions do not differ significantly ($P > 0.05$ in χ^2 tests of independence), implying that aging mistakes did not vary as a function of absolute age.

Microscopic examinations of acetate peels made

FIGURE 3.—A photographic illustration of a representative sectioned clam shell from each of the four collection dates (A-D; dates given in Figure 2 legend) in the mark-recapture test of whether *Mercenaria mercenaria* from Cape Lookout, N.C., deposits annual growth bands. Lines drawn on the outer surface of each clam shell represent the sizes at each measuring date: 21-22 June 1978, 20 September 1978, 21 April 1979, 17 October 1979, and 22 May 1980. Clam A lacks surface lines for the last two dates because it was collected on 17 October 1979, whereas clam B, collected on 22 May 1980, lacks the last surface line. The annual bands are visible as dark bands in the middle and outer layers in the cross-sectional cuts through each shell.

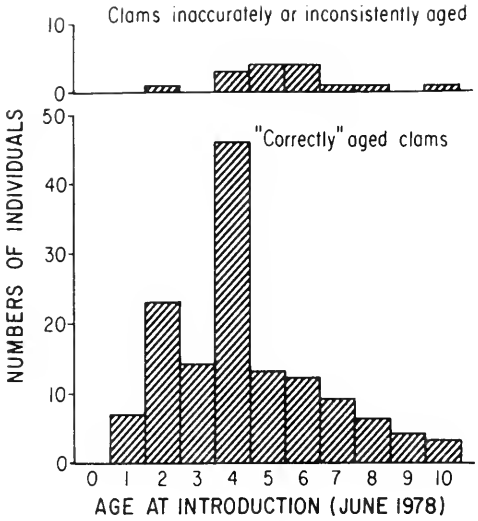

FIGURE 4.—The frequency distribution of age at introduction in June 1978 of all clams used in the mark-recapture test of whether growth bands are annual in *Mercenaria mercenaria* from Cape Lookout, N.C. Two age distributions are presented: The bottom distribution includes all 137 clams possessing marginal growth that was correctly aged without disagreement among three independent examiners and the top distribution includes all 15 clams with either incorrectly aged marginal growth or with disagreement among age readers. The two distributions do not differ significantly at $\alpha = 0.05$ in a χ^2 test of independence, pooling adjacent age classes where necessary to maintain expectations above unity.

from the sections of 20 of the October 1980 and October 1981 clams did not reveal any additional repeating patterns in the shell deposition of *M. mercenaria* that might be used as annual markers. Furthermore, the growth band that was so evident in macroscopic view of the polished section did not retain its coloration and textural distinctions on the acetate peels and was thus not as obvious. Numerous finer growth breaks found in acetate peels were not evident in macroscopic view. Some resembled disturbance checks (Kennish and Olsson 1975; Kennish 1980), occurring only in the outer layer and, in macroscopic view, appearing with slight brown discolorations incorporated into the shell matrix.

Many of these possible disturbance checks appeared to be associated with the excavation and measuring of the clams. To document this association, we examined closely the polished sections of 23 clams retrieved in October 1981 and drawn approximately equally from the three caging treatments. On the outer surface of each shell, we marked the position of the shell margin (the size) at each of the known measurement dates. Because each clam in this sample (except two that were missed during one sampling) was excavated and measured on five occasions, 113 ($5 \times 23 - 2$) disturbance lines would be expected from sampling, if the sampling process suffices to produce disturbance checks in the shell matrix. Of these 113 positions on the shells, 96 contained clear disturbance checks in the outer shell layer. Only 35 additional disturbance checks were evident in these shells during the period June 1978 to October 1981, and 29 of those coincided with the initiation of deposition of the annual band. The six remaining disturbance checks were not associated with our handling or with annual band deposition, but their presence is not surprising given that natural disturbance breaks have been reported for *M. mercenaria* elsewhere (Kennish and Olsson 1975; Kennish 1980).

Disturbance checks deposited at most times of measuring provided several specific chronological markers. We used these markers together with presumed daily growth lines to estimate the exact period of annual band deposition and relative growth rates within and outside of the period of annual band deposition. Because we had no good test of the daily nature of the presumed daily lines, we chose to carry out these estimates only for shell growth increments where we had an approximately year-long period of growth bracketed by measurement growth checks and containing the expected number (± 20) of "daily" lines.

We examined six growth periods, one on each of four clams and two on a fifth individual, which met our criteria (Table 1). These clams exhibited great variability in date of annual band initiation (June-October) and termination (September-January). However, the period of annual band deposition consistently included summer or fall. Average daily growth rate during the period of annual band deposi-

TABLE 1.—The period of Annual band deposition and the average daily growth[1] of hard clams during and outside the period of annual band deposition, as estimated by using daily growth lines on acetate peels or on thin sections. The six intervals examined (all but the first two on separate clams) were bracketed by disturbance checks in the outer shell layer that served as known chronological markers and contained a number of daily lines equal to the number of days (± 20) between the known dates.

Time interval examined	Period of annual band deposition	Average daily growth during band deposition (μ)	Average daily growth outside period of band deposition (μ)
6/21/78-4/10/79	6/21/78-1/4/79	4.6	4.8
4/10/79-5/22/80	10/17/79-11/10/79	2.4	3.8
10/17/79-10/8/80	8/5/80-10/8/80[2]	1.8	2.9
6/21/78-4/10/79	6/21/78-9/28/78	2.3	2.4
9/25/78-10/17/79	7/3/79-10/17/79	1.7	3.3
9/25/78-10/17/79	7/12/79-10/17/79	1.1	2.4

[1]Growth was measured by calibrated ocular micrometer in the center of the shell cross section along the axis of growth but converted geometrically to corresponding lengths.

[2]The annual band was still being deposited on 10/8/80, whereas for all other intervals examined these dates mark actual initiation and termination dates for band deposition.

tion was consistently lower than when the band was not being deposited. The magnitude of the ratio of these two different growth rates varied considerably from 1.01 to 3.27. The major reason for this variability was probably the logarithmic nature of growth in *M. mercenaria*. All clams chosen for this analysis of daily lines were young (1-3 yr old at introduction in June 1978) and within a size range (3-6 cm long) where the rate of decline in absolute growth rate with increasing size is substantial. Consequently, in those clams where the annual band fell at the end of the time period that was analyzed, the inherent logarithmic growth pattern enhanced the apparent difference in growth rate in- and outside of the period of annual band deposition. Conversely, when the annual band fell at the beginning of the time period analyzed, the relative difference in growth rate was masked by the inherent general pattern of slowing of growth with increased size. Despite this dependence on the band's position within the growth interval analyzed, it is clear that the period of annual band deposition represents a time of relatively slow growth.

0-Year Class

In the 432 0.25 m^2 samples taken in February-April 1980 from Back Sound, we collected 546 *M. mercenaria*. Only 9 individuals (all <1.25 cm long) lacked evidence of a growth band, whereas 126 contained a single annual band. (The other 411 clams contained more than one band.) Assuming that virtually all clams in the 0-year class had grown sufficiently by winter (February-April) to be efficiently captured in our sampling process (this assumption is tested below), then the fraction 9/135 (6.7%) estimates the frequency of error made in assuming that all clams in the 0-year class are branded with their first identifiable growth band in their first fall season. This result implies that we underestimate the age of a relatively

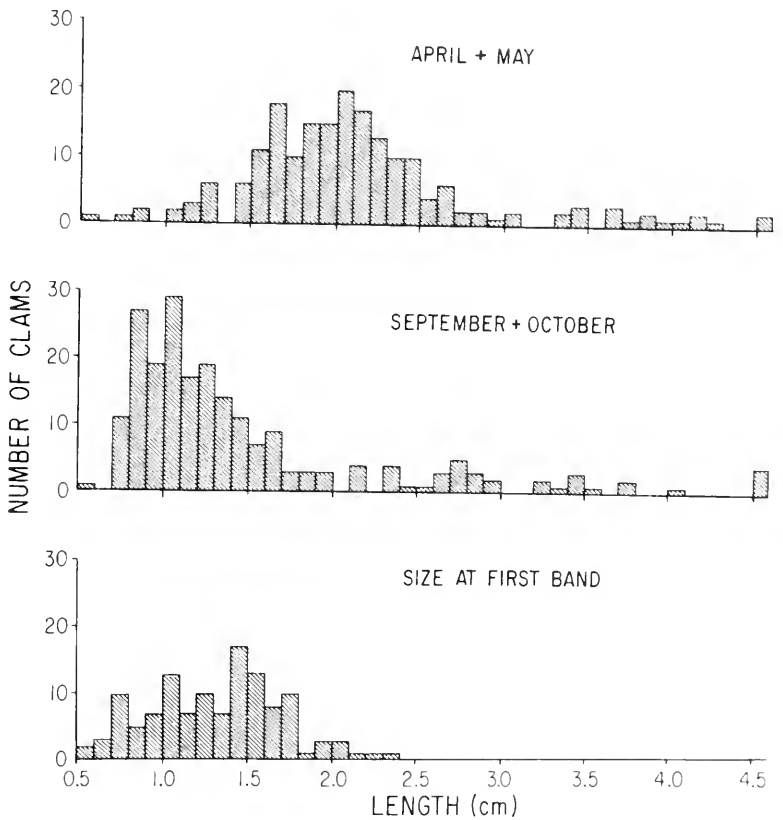

FIGURE 5.—The size (length)-frequency distributions of all unmarked *Mercenaria mercenaria* recruits collected and removed at two seasons (fall and spring) from fixed 1 m^2 enclosures in Middle Marsh, as compared with the distribution of size (length) at first band for all clams collected in January-February 1980 from Johnson Creek, Core Sound, N.C. See text for details on methods.

small percentage of *M. mercenaria* in the Cape Lookout region by using the technique of counting internal growth bands.

Figure 5 presents the size-frequency distributions of all unmarked *M. mercenaria* collected from the fixed 1 m^2 plots in Middle Marsh in both falls (pooled) and both springs (pooled) along with the size (length)-frequency distribution at first band for all *M. mercenaria* collected in our samples from nearby Johnson Creek. Because *M. mercenaria* > 0.7 cm long could not easily invade our fixed 6 mm mesh enclosures, virtually all unmarked clams collected in the sampling enclosures are recruits. Recruitment occurs during the summer months in North Carolina (Chestnut 1952; Ansell 1968). Consequently, the fall size-frequency distribution (Fig. 5) represents the fall sizes of the 0-year class, truncated at 0.7 cm because smaller clams are not efficiently retained on our 6 mm sampling mesh and extended to larger size classes by inclusion of some recruits from previous year classes that were missing during sampling. The spring size-frequency distribution (Fig. 5) contains those 0-year class recruits that were missed and, therefore, not removed during the previous fall's sampling or that settled late (after September-October) plus some larger recruits from other year classes that were missed in previous years' sampling.

The spring size-frequency distribution given in Figure 5 is biased towards smaller size classes, relative to the natural spring distribution of 0-year class *M. mercenaria* near Cape Lookout, because the previous fall's sampling already removed the larger sizes preferentially. Despite this bias, the sizes at which the first annual band was deposited in the Johnson Creek clams resemble the fall size-frequency distribution of 0-year class recruits much more closely than the spring size-frequency distribution (Fig. 5). This helps confirm the accuracy of our recognition of the initial growth band in *M. mercenaria* from Cape Lookout. A comparison of the fall size-frequency distribution of 0-year class clams and the distribution of size at first band (Fig. 5) also suggests that the first annual band may be deposited somewhat later in the season (perhaps October-November) than the subsequent bands (June-October in our earlier mark-recapture data).

The size-frequency distribution of unmarked clams in spring (Fig. 5) demonstrates that virtually all new recruits in this system have grown sufficiently large to have been efficiently sampled in our late winter dredge sampling of Back Sound. Dredge sampling efficiently captures clams down to 0.5 cm long (see Appendix), and Figure 5 demonstrates that even in this spring size-frequency distribution, which is biased towards the smaller size classes, a very small proportion of the 0-year class in the Cape Lookout region is ± 1.0 cm long.

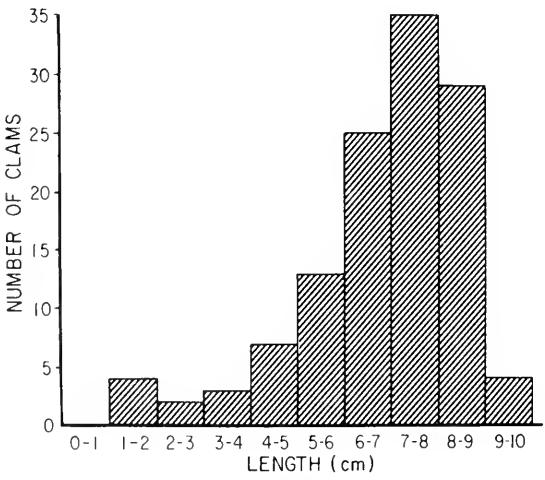

FIGURE 6.—Size (length)-frequency distribution for all 124 *Mercenaria mercenaria* collected during 2 d (16 January and 15 February 1980) of sampling from Johnson Creek in Core Sound, N.C.

Application of Aging Technique to a Field Population

Because the size (length)-frequency distributions of *M. mercenaria* collected on the two sampling dates did not differ significantly ($0.10 < P < 0.20$ in a χ^2 contingency test), we pooled all samples to form estimates of the size- and age-frequency distributions of *M. mercenaria* at Johnson Creek in January-February 1980. Average clam density from

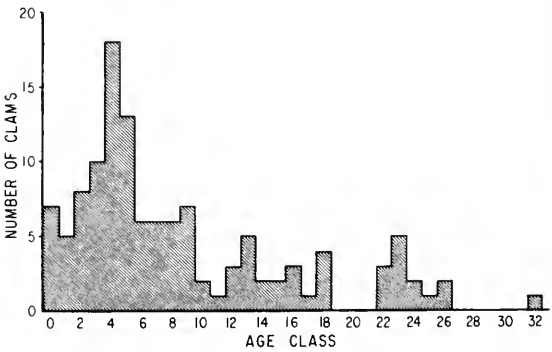

FIGURE 7.—The distribution of 124 clams collected in January-February 1980 at Johnson Creek, Core Sound, N.C., into age classes. Age class was estimated for each clam by counting the number of annual growth bands and subtracting one (assuming that each new recruit laid down its first annual band in its first fall). Average age class is 8.59 and, assuming that settlement occurred in July-August, average age is 9.09 yr.

the 34 quantitative samples was 1.59 ± 1.28 (SE) per 0.25 m². The size-frequency distribution of all 124 clams collected (Fig. 6) was dominated by relatively large clams in the 6-9 cm range. Figure 7 presents the distribution of these same 124 clams among age classes. This figure was constructed by counting the number of annual growth bands on each clam and subtracting one, under the assumption (tested earlier) that new recruits lay down their first annual growth band during their first fall. Because the January-February sample occurred about ½ yr after settlement (assuming an average settlement time of July), the ages of clams in years are estimated by their year class plus one-half. Average age of the clams collected at Johnson Creek was 8.59 + 0.50 or just over 9 yr old. The oldest clam in the sample was estimated to be 32 yr old (Fig. 7). This age distribution (Fig. 7) reveals that each of the three most recent year classes (1977-78-79) at Johnson Creek contributed less to the total sample than each of the three previous year classes (1974-75-76).

In Figure 8, the shell length of each clam collected is plotted against its total number of annual bands (= age + ½). This graph illustrates the generally logarithmic form of growth and provides an estimate of age-specific growth of *M. mercenaria* in the Johnson Creek area of Core Sound. The best fitted logarithmic growth curve through all points is

$$\text{length (in cm)} = 3.176 + 1.819 \ln (\text{no. of annual bands})$$
$$r^2 = 0.673, P < 0.001.$$

On the graph, we plot the minimum length at which hard clams can be legally harvested in North Carolina. This size was calculated by converting the minimum legal width of 25.4 mm to length by the regression equation

$$\text{length (in mm)} = -1.73 + 1.83 \text{ width (in mm)}$$

derived from fitting all 124 Johnson Creek clams ($r^2 = 0.97$; $P < 0.001$). Figure 8 implies that most clams at Johnson Creek reach legal size by age 1½, sometime during their second winter. This graph also reveals how extremely variable a clam's size is for any given age older than about 4½ yr. For instance, a clam 75 mm long can be anywhere from age 4½ to at least age 25½. For clams older than 4½ yr of age, size is a very poor predictor of age ($r^2 = 0.07, n = 75, 0.02 < P < 0.05$ in a linear regression).

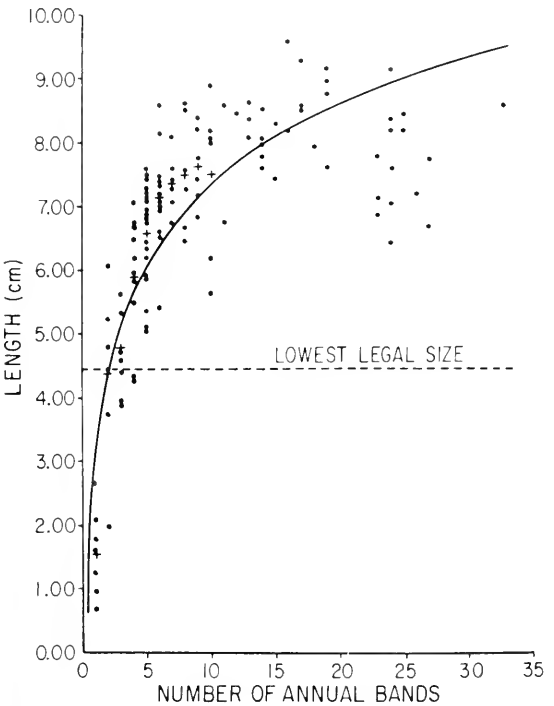

FIGURE 8.—The relationship between number of annual bands (= age in years + one-half for clams collected in January-February) and length for all 124 clams collected in January-February 1980 from the Johnson Creek site in Core Sound, N.C. Also indicated on the graph is the minimum legal size for harvest in North Carolina. + indicates mean sizes in each age class up to the 10th. The growth line drawn in is the best fitted ($r^2 = 0.673$; $P < 0.001$) logarithmic curve [length (cm) = 3.176 + 1.819 ln (no. of annual bands)].

DISCUSSION

The results of mark-recapture (Fig. 2) demonstrate that the individuals of at least one population of hard clams along the southeastern coast of the United States can be accurately aged by counting macroscopic annual growth bands in sectioned shells. The population that we examined exhibited little ambiguity in what constituted an annual band and little variation among individual clams. These results held true across a wide range of clam ages (1-13 yr) and the aging errors made were not a function of clam age (Fig. 4). Attempts to alter local environment by adding mesh cages of two differing structures also failed to alter the clear pattern of annual band deposition. Nevertheless, because growth rate declines with age (Fig. 8), annual bands came at closer intervals in older clams and were somewhat difficult to resolve in *M. mercenaria* older than about 19 yr of age. An examination of all small *M. mercenaria* collected in February-April 1980 from a location in Back Sound revealed that only a small percentage (6.7%) of the 0-year class lacked an annual band. Since settlement had almost certainly

occurred before the onset of winter (Chestnut 1952; see also data in Figure 5), this implies that for a small percentage of *M. mercenaria* age was underestimated by 1 yr. This is not a large bias in view of *M. mercenaria*'s life span (Fig. 7), but may cause misinterpretation in studies where distinguishing small differences is important.

Prior to our mark-recapture results and recent observations by Clark and Lutz (1982), most scientists suspected that this aging technique, so successful for northern populations of *M. mercenaria* (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Kennish and Olsson 1975), could not be used for hard clams in the southeastern United States because *M. mercenaria* there lacked the winter period of slow, almost negligible, growth that is associated with annual band deposition in northern populations (Ansell 1968). Our analysis of presumed daily growth increments along with sectioning evidence in Clark and Lutz (1982) implies that southeastern *M. mercenaria* also deposit the annual band during a period of slow growth, but that this period usually occurs from about June to October. The results of our mark-recapture study confirm that annual band deposition in 1-year class and older clams occurs sometime in that same period (Fig. 2). This season of annual band deposition corresponds both with maximum seasonal water temperature (Sutherland and Karlson 1977) and with the spawning season for *M. mercenaria* in the Cape Lookout region of North Carolina (Porter 1964). Because water temperature serves as the usual proximate cause of spawning in marine bivalves, separation of these two factors is difficult. The deposition of an initial band in clams only a few months old (Fig. 5) does not permit rejection of the spawning hypothesis because this initial band differed in appearance from all subsequent annual bands and seemed to occur later in the fall season (Fig. 5), implying that this first band is of a different nature from all subsequent ones. Jones (1980) also demonstrated that both *Spisula solidissima* and *Artica islandica* deposit annual bands at times of spawning, analogous to our results for *M. mercenaria*. Regardless of the mechanism, results of our mark-recapture experiments dispel the justifiable doubts expressed by several scientists concerning the interpretation of shell growth lines (Clark 1974; Gould 1979; Jones 1981) and permit paleontologists, archaeologists, and environmental biologists to interpret banding patterns in shells of *M. mercenaria* from the southeastern coast of North America and to apply this biological chronometer to a wide spectrum of problems.

Application of this aging technique to a population of *M. mercenaria* in Johnson Creek off Core Sound revealed a surprisingly large frequency of older clams and a high average age (>9 yr old). In comparison, Kennish (1980) demonstrated almost 100% mortality of *M. mercenaria* in Barnegat Bay, N.J., by age 9. A relatively low rate of commercial fishing mortality in North Carolina prior to 1977 may contribute to this difference in population parameters. Figure 9 presents clam landing data illustrating the recent increase in hard clam harvest in North Carolina. This recent intense harvest is perhaps made possible by the sudden utilization of the accumulation of several years' reproduction, whereas northern populations of *M. mercenaria* may have been subjected to continuous high fishing intensity for a long period and therefore exhibit age-frequency distributions that are shifted towards the younger age classes. Alternatively, the differences in age distributions between areas could be the consequence of natural differences in factors affecting hard clam life histories.

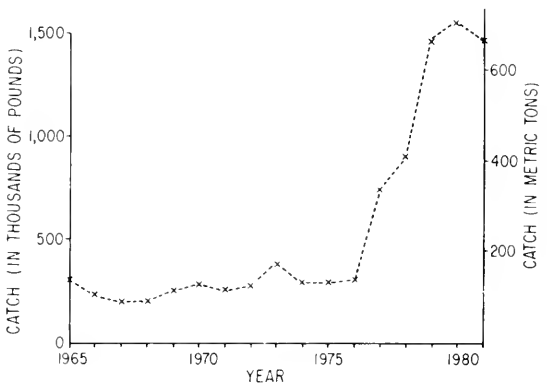

FIGURE 9.—Annual hard clam, *Mercenaria mercenaria*, catch by commercial clammers in North Carolina from 1965 to 1981, as estimated by the North Carolina Division of Marine Fisheries.

The growth rate exhibited by *M. mercenaria* from Johnson Creek (Fig. 8) is higher than that demonstrated by Chestnut (1952) for a sand-bottom area of Bogue Sound, and higher than many (but not all) of the growth rates recorded from other areas (Ansell 1968). In particular, our age-size plot (Fig. 8) implies that the average *M. mercenaria* in Johnson Creek reaches the legal minimum size for harvest (4.46 cm long) by age 1½, whereas Chestnut's (1952) data implied that it usually required 3 yr for North Carolina hard clams to enter the catchable population. Clearly there is a large degree of individual variation in growth rate and size at any given age (Fig. 8). Nevertheless, this new estimate of average time to

marketable size at Johnson Creek is quite important to managers of the commercially harvested and valuable *M. mercenaria* resource in North Carolina. For instance, although gametes produced by a 1-yr-old clam, even of this size, may be viable (Porter 1964; pers. commun.[3]), the mass of gametes produced is almost negligible when compared with larger individuals (Peterson 1983).

Although the general shape of the estimated *M. mercenaria* growth curve (Fig. 8) is logarithmic, as expected, the variance in the relationship is substantial. Among all clams older than 4½ yr of age collected from Johnson Creek, age explained only 7% of the variance in size. Consequently, aging of Johnson Creek *M. mercenaria* by inference from size-class frequency would fail. Only in a population dominated by young clams in the fast growing sizes could North Carolina *M. mercenaria* be adequately aged by size information. Thus, the utilization of growth band analysis is an important key to inference on population parameters in North Carolina *M. mercenaria*. Unfortunately, the annual bands are not unambiguously evident on the outer shell surface, where disturbance checks and other growth breaks appear (as reported for other species such as *S. solidissima* (Jones et al. 1978)), so that shell sectioning is necessary for accurate aging.

If recruitment success (reproductive effort times subsequent larval and early postlarval survivorship) were to remain constant across years, frequencies of age classes would decline progressively with age at a rate corresponding to the age-specific mortality function. Yet, the age-frequency distribution for Johnson Creek *M. mercenaria* in January-February 1980 (Fig. 7) is characterized by lower numbers in each of the three most recent year classes (1977-78-79) than in the three previous year classes (1974-75-76). Tests of sampling efficiency (Appendix) and data on the seasonal progression in the size distributions of 0-year class recruits (Fig. 5) demonstrate that the "gap" in *M. mercenaria*'s age distribution (Fig. 7) is not caused by a sampling artifact. The relatively low numbers in the 1977-78-79 year classes are a consequence of reduced reproductive success, relative to at least the three previous years, either because of reduced reproductive effort or increased mortality of larvae and early postlarvae. Although we have no unequivocal way of distinguishing between these two explanations, the close match between the increase in North Carolina's commercial harvest of *M. mercenaria* (Fig. 9) and the 3-yr decline in recruitment success suggests that future studies should investigate the possibility that a recent reduction in the spawning population of *M. mercenaria* in North Carolina through increased harvest (mostly from Core Sound) has had an impact on reproductive effort and recruitment success. The persistent uncertainty among invertebrate population biologists about the strength and nature of spawner-recruit relationships remains the single biggest barrier to effective management of invertebrate fisheries.

[3]H. J. Porter, Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557, pers. commun. July 1982.

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APPENDIX

Two tests were performed to estimate the efficiency and size selectivity of our hydraulic dredge sampling. First, two sets of quantitative samples were taken at Johnson Creek by placing a circular 0.25 m^2 sampling frame at haphazard locations and then excavating it to a depth of 15 cm. For one set of 24 samples, we used the hydraulic dredge, while we excavated the other set of 10 samples by hand. In each case, the contents of the top 15 cm were passed through a 3 mm mesh sieve. By comparing the average hard clam densities and size-frequency distributions in these two sets of samples, we have one test of whether the efficiency and size selectivity of samples from the hydraulic dredge differ significantly from analogous hand-collected samples, all collected in the actual field site.

As a second test of the size selectivity and as a quantitative estimate of sampling efficiency, 22 marked *Mercenaria mercenaria* were placed at natural living depths within an otherwise undisturbed bottom inside our 0.25 m^2 sampling frame. The lengths of these clams ranged from 0.89 to 9.53 cm, with 5 in the 0-2 cm range, 3 in the 2-4 cm range, 3 in the 4-6 cm range, 7 in the 6-8 cm range, and 4 in the 8-10 cm range. We then used the hydraulic dredge to sample this 0.25 m^2 area within the frame in the usual fashion to a 15 cm depth. This trial was repeated five times, moving the frame to a new location each time and recording the numbers and sizes of all clams recovered.

Average density of hard clams did not differ significantly (at $\alpha = 0.05$ in a Student's t-test) between the dredged and hand-collected samples from Johnson Creek (Appendix Table 1). Furthermore, the size-frequency distributions (Appendix Table 1) were nearly identical and did not differ significantly (at $\alpha = 0.05$ in a χ^2 contingency test). These results imply that the two techniques did not differ in efficiency or size selectivity. *Mercenaria mercenaria* as small as 0.5 cm long were collected by both techniques. In the five trials to estimate the numerical efficiency of the dredging technique, only one clam was missed (5.84 cm long). Thus, the capture efficiency exceeded 99% and did not vary significantly with clam size within the range of clams used (0.89-9.53 cm). This result implies that we did not collect a biased size (or age) distribution of hard clams in our field sampling.

APPENDIX TABLE 1.—A comparison of the relative efficiency and size selectivity of hydraulic dredge and hand sampling of hard clams in Johnson Creek, Core Sound, N.C. Also given are results of quantitative estimates of capture efficiency as a function of clam size for the hydraulic dredge technique.

a) Johnson Creek sampling results

Statistics	Sampling technique: Hand excavation	Sampling technique: Hydraulic dredge
Number of samples (0.25 m^2)	10	24
Average hard clam density (±1 SD)[1]	1.70 (±1.70)	1.54 (±1.02)
Size frequency distribution[2]		
0.5-2 cm	12%	16%
2-4 cm	6%	5%
4-6 cm	24%	19%
6-8 cm	41%	32%
8-10 cm	18%	27%

b) Results of five trials to estimate capture efficiency

Size class (cm)	Numbers present	Numbers collected by dredge	Sampling efficiency (%)
0.5-2	25	25	100
2-4	15	15	100
4-6	15	14	93
6-8	35	35	100
8-10	20	20	100
Total	110	109	99

[1] Difference not significant at $\alpha = 0.05$ in t-test
[2] Difference not significant at $\alpha = 0.05$ in χ^2 test

EARLY DEVELOPMENT OF THE LONGHORN SCULPIN, *MYOXOCEPHALUS OCTODECEMSPINOSUS*[1]

WILLIAM A. WALSH AND WILLIAM A. LUND, JR.[2]

ABSTRACT

Illustrations and descriptions of the early development of longhorn sculpin, *Myoxocephalus octodecemspinosus*, reared in the laboratory included six symmetrical cleavages, cell multiplication, blastula formation, gastrulation, eight embryonic and six larval stages, and a juvenile stage. Development at 5° C began with initial cleavage at 8 hours, proceeded to gastrulation at 132 hours, early embryogenesis at 168 hours, and hatching between 36 and 65 days, with maximum activity between 41 and 48 days. Absorption of the yolk sac was completed about 10 days after hatching, metamorphosis to the juvenile stage occurred at about 55 days, and adult pigmentation developed between 65 and 104 days.

Characters useful for the identification of longhorn sculpin eggs included egg color, egg capsule diameter, width of the perivitelline space, and appearance of the chorion. Identification of longhorn sculpin larvae and juveniles was possible utilizing size, pigmentation, meristics, and cephalic spination.

Comparison of reared longhorn sculpin larvae with descriptions of larvae collected in the Gulf of Maine and Canadian waters revealed some differences in pigmentation, development of anal and dorsal fins, and duration of retention of the embryonic finfold.

Longhorn sculpin, *Myoxocephalus octodecemspinosus*, is a common inhabitant of the coastal waters of the northwest Atlantic; it occurs north to the Gulf of St. Lawrence and is common around Prince Edward Island, the Scotian shelf (Leim and Scott 1966), and south regularly to New Jersey (Bigelow and Schroeder 1953). It is found from very shallow water out to at least 50 fathoms (Huntsman 1922; Vladykov and McKenzie 1935).

In Block Island Sound, R.I., longhorn sculpins move inshore to spawn from November through February, and maximum spawning occurs from mid-December to mid-January (Morrow 1951). They deposit demersal egg masses of various colors (Morrow 1951; Bigelow and Schroeder 1953; Leim and Scott 1966).

Little is known about the early life history of this species. Chenoweth (1973) believed that three species of *Myoxocephalus* utilize the estuaries near Boothbay Harbor, Maine, as primary spawning and nursery areas because larval longhorn sculpins, shorthorn sculpins, *M. scorpius*, and grubbies, *M. aenaeus*, are abundant in the upper reaches of estuaries in late winter and early spring. Herman (1963) reported that *Myoxocephalus* spp., which are the predominant larvae in January and March ichthyoplankton collections in Narragansett Bay, R.I., are mostly longhorns. Khan (1971) stated that longhorn sculpin larvae are common in the Gulf of St. Lawrence and the Gulf of Maine in late winter and early spring. Pearcy and Richards (1962) and Wheatland (1956) believed that *M. aenaeus* larvae are predominant in the Mystic River, Conn., estuary and Long Island Sound and that longhorn sculpin larvae are rare or absent.

Little detailed information on the early development of *M. octodecemspinosus* is published. Morrow (1951) described gametogenesis and ripe ovarian eggs and stated that longhorn sculpins mature in their third year, at about 24 cm TL (total length), and an average female produces about 8,000 eggs annually. Khan (1971) provided illustrations and descriptions of longhorn sculpin larvae from ichthyoplankton collections. This paper presents a complete description of the early development of *M. octodecemspinosus*.

MATERIALS AND METHODS

Ripe longhorn sculpins were obtained during December 1980 and maintained at ambient temperature in continuous-flow aquaria. Eggs were artificially fertilized on seven occasions in 20 cm glass fingerbowls containing about 1,000 ml of filtered seawater. Eggs were kept in 20 cm fingerbowls and 4,000 ml glass beakers in either a temperature-controlled water bath at $5.0° \pm 0.5°$ C or at ambient temperature in a bath of running seawater. Water in the closed system was initially changed two or three times weekly, but was changed daily after the presence of bacterial contamination was detected in some containers.

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Samples were preserved in 5% neutral Formalin[1]. Eggs were cleared over glycerin according to the method of Galat (1972). All developmental rates are at 5° C. Larvae were fed wild plankton which were obtained with a #20 mesh net, and after a month brine shrimp nauplii were added to the diet.

Drawings and descriptions are from all series. All drawings were done with the aid of a camera lucida.

RESULTS AND DISCUSSION

The egg of the longhorn sculpin was spherical and adhesive. The chorion was leathery and translucent. Egg color was variable but consistent within a single female. Eggs were green, red, and reddish brown. Morrow (1951) reported variable coloration of longhorn eggs. Lund and Marcy (1975), Bigelow and Schroeder (1953), and Westin (1968) described various egg colors of *M. aenaeus*, *M. scorpius*, and *M. quadricornis*, respectively. Egg color remained constant throughout development. Subsequent statements refer to morphological changes.

Unfertilized, water-hardened eggs: These eggs of longhorn sculpins were spherical with a mean diameter of 2.21 mm and a range of 2.1-2.3 mm. Mean yolk diameter was 2.10 mm (range 2.0-2.2 mm). The number of oil droplets was variable; some eggs had several small droplets scattered throughout the yolk, whereas others had only two or more large droplets. Perivitelline space was less than one-tenth of the egg capsule radius. Surface of the yolk capsule was slightly irregular. Chorion was colorless, translucent, and leathery (Fig. 1A).

Two-cell stage: Initial cleavage was meroblastic and was first observed at 8.0 h. Most eggs had cleaved by 8.5 h. Blastomeres were about equal in size and slightly elevated. Egg capsules had a mean diameter of 2.18 mm (range 2.1-2.3 mm). Yolk capsule had a mean diameter of 2.06 mm (range 1.9-2.1 mm). The number of oil droplets was variable. Perivitelline space was about one-tenth of the radius of the egg capsule. Yolk surface was slightly corrugated (Fig. 1B).

Four-cell stage: Second cleavage was perpen-

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

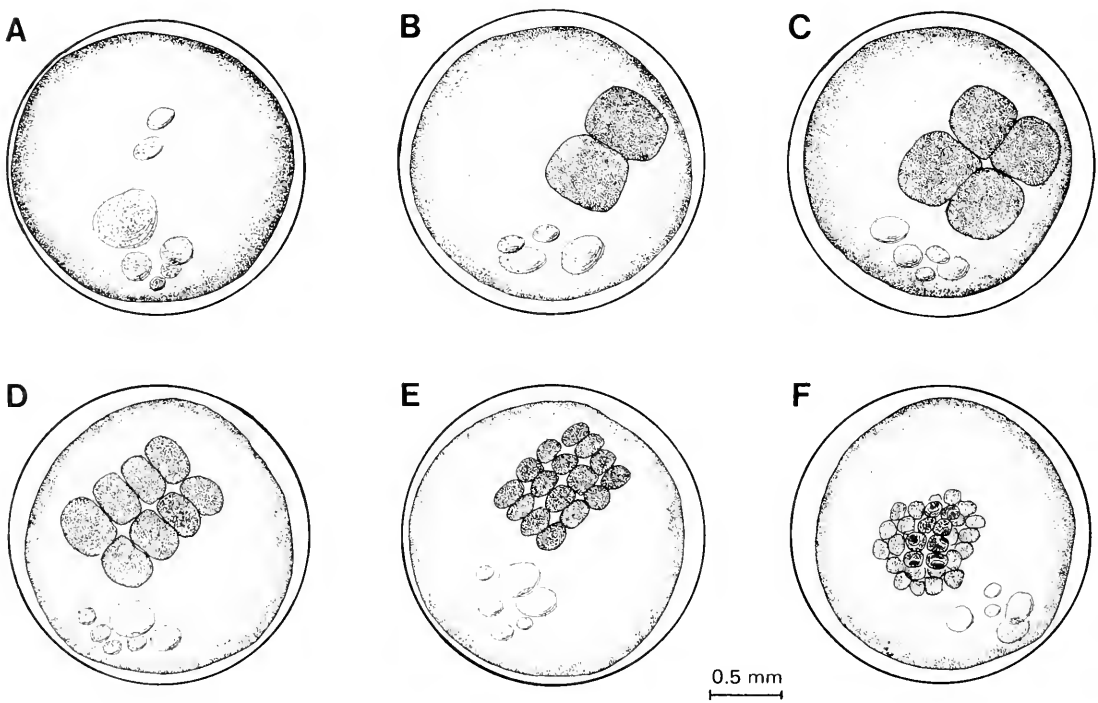

FIGURE 1.—Early development of the eggs of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A) unfertilized water-hardened egg, 2.21 mm; B) fertilized egg, 2.19 mm, 2-cell stage (8.5 h); C) 4-cell stage, 2.15 mm (10.5 h); D) 8-cell stage, 2.22 mm (14.0 h); E) 16-cell stage, 2.15 mm (20.0 h); F) 32-cell stage, 2.21 mm (24 h); scale = 0.5 mm. Measurements refer to mean egg capsule diameters.

dicular to the first. Four blastomeres were about equal in size. This stage was first observed at 10.0 h; most eggs had reached this stage by 10.5 h (Fig. 1C).

Eight-cell stage: Third cleavage was vertical. Blastomeres were about equal in size. First observation of eggs at this stage was at 12.0 h, and all observed eggs had reached this stage by 14.0 h (Fig. 1D).

Sixteen-cell stage: Another vertical cleavage resulted in 16 cells in a single layer. In some eggs, the shape of the cells and the lines of cleavage appeared irregular. This stage was first observed at 18.0 h and all eggs were in this stage by 20.0 h (Fig. 1E).

Thirty-two-cell stage: A horizontal cleavage produced a central double layer of cells, with peripheral cells in a single layer. Cells were irregular in shape. This cleavage was first noted at 23.0 h; all observed specimens had attained this stage by 24.0 h (Fig. 1F).

Sixty-four-cell to multicell stage: Eggs classified as this stage were first seen at 27.0 h. By 52 h, all eggs were considered to be at this stage. The blastodisc became raised, but did not yet begin moving over the yolk. This long stage was characterized by continued increase of cell number and decrease of cell size (Fig. 2A, B).

Blastula stage: This stage was initially observed at 86.0 h, and all observed eggs had reached this stage by 110.0 h. Blastoderm began to expand over the yolk. Periblast was visible at the periphery of the blastoderm. Blastocoel was flattened out over the yolk (Fig. 2C).

Gastrula stage: Epiboly proceeded. Germ ring was first noted at 132.0 h (5.5 d). Embryonic shield was most easily viewed on the horizon of the egg (Fig. 2D).

Early embryogenesis: Eggs with clearly discernible embryos were first observed at 168.0 h (7.0 d). Blastopore was reduced to a small opening. Oil droplets were aggregated near the opening. Neural groove was apparent and extended less than one-half way around the yolk. From a dorsal view, rudiments of the optic vesicles were visible (Fig. 2E).

At 196.0 h (7.75 d), closure of the blastopore was first seen. Optic vesicles were larger, and visible to direct view. Slight cephalic swelling was apparent. Oil droplets were coalescing (Fig. 2F).

Middle embryogenesis: Differentiation of the main divisions of the brain had begun by 250.0 h (10.4 d). Cephalic and caudal swelling were present. Optic cup and lens of the eye were best seen in dorsal view; the

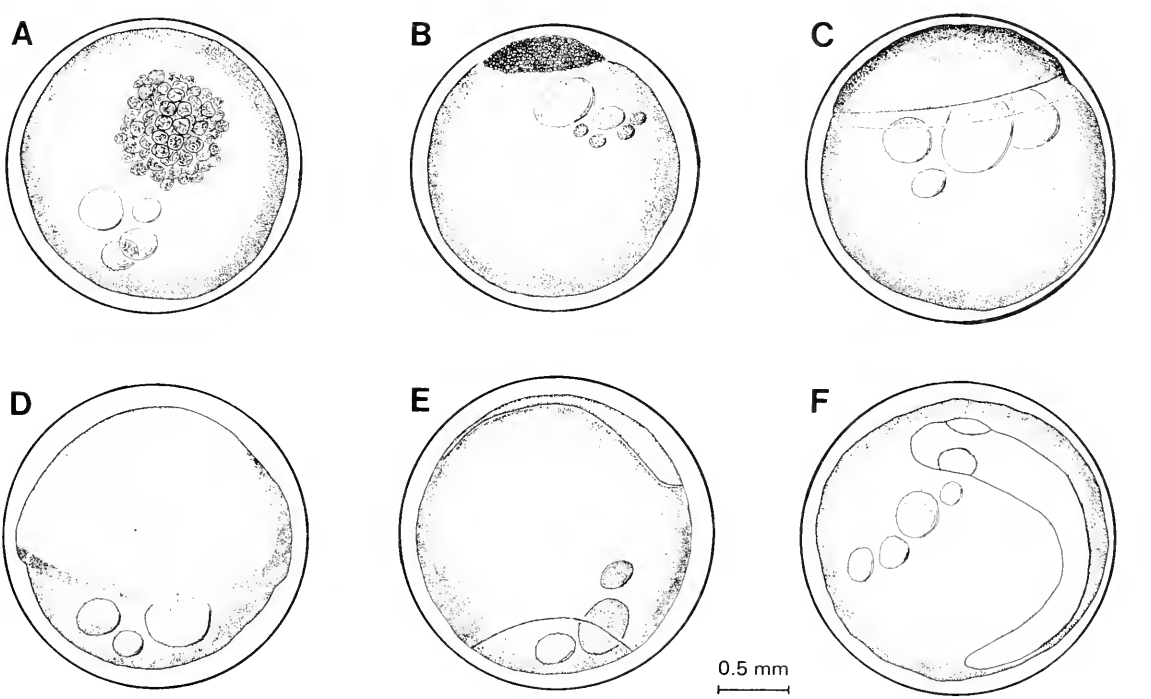

FIGURE 2.—Development of the eggs of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A) 64-cell stage, 2.19 mm (27 h); B) multicell stage, 2.19 mm (52 h); C) blastula stage, 2.22 mm (86 h); D) gastrula stage, 2.15 mm (132 h); E-F) early embryonic stages, 2.19 mm (168 and 186 h); scale = 0.5 mm. Measurements refer to mean egg capsule diameters.

lens was not bulging out of the cup. In most specimens, one or two large oil droplets were near the cephalic region. Embryos extended slightly more than one-half way around the yolk (Fig. 3A).

At 302.0 h (12.6 d), the divisions of the brain were more clearly differentiated. The mid- and hindbrains had increased in size. Lens of the eye protruded from the optic cup. Otic vesicles, Kupffer's vesicle, pectoral buds, and notochord were present. Toward the caudal end of the embryo, clearly distinguishable somites were first observed and ranged in number from 12 to 14. The embryo reached about two-thirds way around the yolk (Fig. 3B).

Embryos in the tail-free stage were first noted at 424 h (17.7 d). Kupffer's vesicle was deeper. The olfactory placode was visible. Somites had increased in number to 16 or 17. The embryos stretched about three-fourths way around the yolk (Fig. 3C).

Late embryogenesis: Darkly pigmented eyes were first visible at 472.0 h (19.7 d). All observed embryos had dark eyes and a pulsating heart by 520.0 h (21.7 d). Lens of the eye was large. Head was large and rather flattened. Brain ventricles were apparent in dorsal view. Otoliths were present. The rudiment of the lower jaw was visible. Pectoral fins were spread over the yolk sac. Finfold was apparent. Tip of the tail was curved around past the mouth. There were about 25 somites. Most specimens had a single large oil globule located beneath the head (Fig. 3D, E).

Embryo movement within the eggs was first observed at 545.0 h (22.7 d). The tail passed well over the hindbrain on the lateral flexion. The lower jaw became more developed, but the mouth was not yet open. Opercular margin was well defined. The anal vent was visible. The circulatory system became functional along the length of the tail; this was first noted at 800.0 h (33.3 d), and all observed embryos had noticeable circulation by 825.0 h (34.4 d).

Prehatching stage: Embryos in this stage were characterized by silvered eyes and by the onset of pigmentation of the body. Most embryos were in this stage at about 850.0 h (35.4 d). Contracted melanophores densely covered the dorsal surface of the yolk sac. A few large stellate melanophores were present behind the head. Evenly spaced melanophores were present from near the vent along the ventral line of the tail. Yolk sac was much reduced in size. Tail was wrapped about 1½ times around the

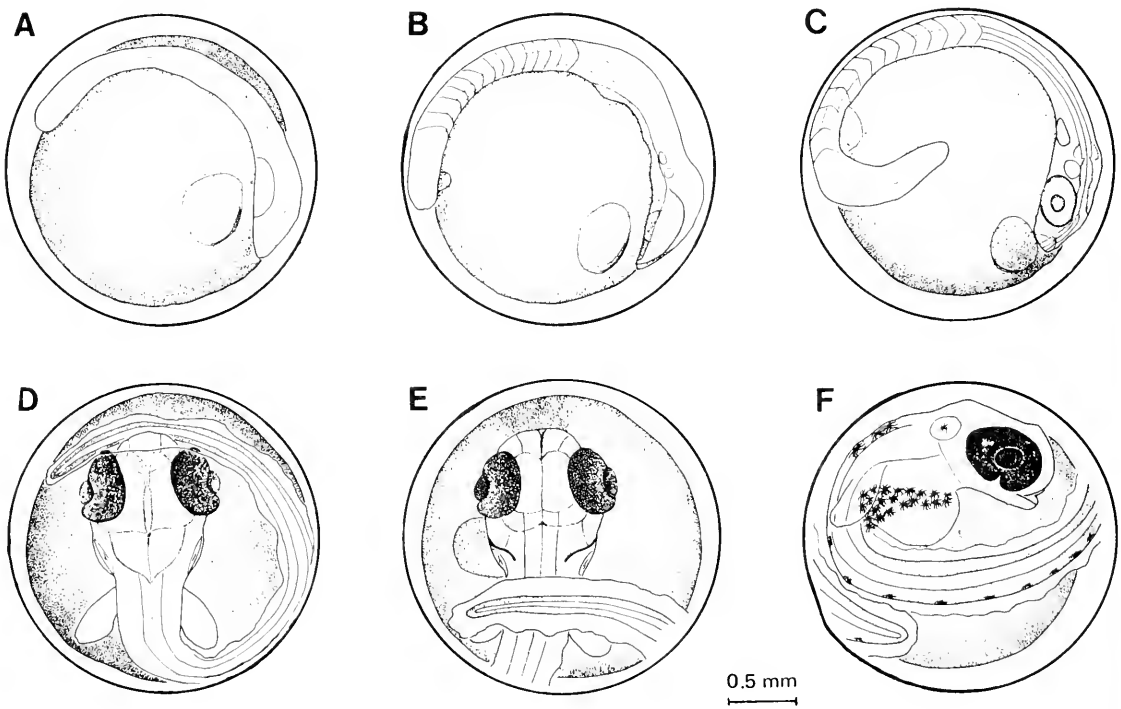

FIGURE 3.—Later development of the eggs of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A-C) middle embryonic stages, 2.16 mm (250-424 h); D-E) late embryonic stages, 2.16 mm (578-780 h); F) prehatch stage, 2.18 mm (880 h); scale = 0.5 mm. Measurements refer to mean egg capsule diameters.

yolk sac. Pectoral fins were larger and were first seen to make intermittent fluttering motions. Mouth was open. Embryos exhibited considerable movement within the eggs, including complete rotations (Fig. 3F).

Hatching of eggs occurred between 36 and 65 d after fertilization. Newly hatched longhorn sculpin prolarvae ranged from 6.2 to 7.8 mm TL (mean 6.8 mm) and 6.0 to 7.2 mm SL (mean 6.4 mm). Yolk sac averaged 1.2 mm (range 1.1-1.3 mm). Oil droplet was 0.4 mm (range 0.3-0.5 mm) and transparent. Eye was darkly pigmented, and choroid fissure was apparent. Bulging of the lens could best be seen from the dorsal view. Mouth was wide open in some specimens, but did not yet appear well developed. A pair of olfactory buds flanked a deep pit located on the midline anterior to the eyes. Auditory vesicles were large and could be seen to protrude when viewed from above. A few stellate chromatophores were present above and behind the auditory vesicles. Some specimens had a single large stellate melanophore at the anterior end of the yolk sac near the oil globule. Dorsal surface of the yolk sac was densely covered by contracted chromatophores. A series of spots were present along the ventral line of the tail and ranged in number from 18 to 28. Larvae had 37 or 38 myomeres. Anus was situated just anterior to the ventral origin of the finfold. Dorsal finfold originated posterior to the auditory vesicles and had a smooth margin; its caudal portion was lunate. Pectoral fins had broad bases and were approximately as deep as they were wide (Fig. 4A).

Absorption of the yolk sac was completed about 10 d after hatching. Postlarvae averaged 7.7 mm TL (range 7.1-8.3 mm). Although reduced in size, a remnant of the oil globule was present. The mouth was well developed. In most specimens, a pair of small head spines and 3 or 4 preopercular spines were visible. A pair of nostrils flanked the nasal pit. The eyes retained the fissure. Most specimens had a single large stellate chromatophore above and posterior to the uppermost cheek spine. The other major change in pigmentation was the approach of dense contracted chromatophores toward the anus. Pectoral fins increased in size and were deeper than wide. Larvae had 37 or 38 myomeres. Stomach and liver were visible. Finfold was smooth and continuous (Fig. 4B).

Absorption of the oil globule was completed at about 15-20d, when larvae averaged 8.7 mm TL (range 8.3-9.1 mm). Larvae at this stage exhibited large stellate melanophores scattered over the top of the head, and on the midline above and between the nostrils. Several stellate chromatophores were present on the isthmus. Additional stellate melanophores developed almost down to the anus, beyond the extent of the contracted chromatophores. Several contracted chromatophores were posterior and parallel to the cleithrum. Margins of the pectorals were ragged in appearance. In most specimens, incipient rays of the caudal fin became visible. Four preopercular spines were present on each cheek. One pair of spines was well developed on the crown of the head above the auditory vesicles. Nostrils appeared slightly larger. Fissure of the eye remained visible. Ventral spots on the tail ranged in number from 16 to 24. Finfold was smooth and continuous (Fig. 4C).

Among larvae which were 25-30 d old, the head was more densely pigmented, including the presence of some contracted chromatophores on the crown and a few stellate chromatophores within the auditory vesicles. Pigmentation was also increasing posterior to the auditory vesicles. There were four spines along the operculum and one pair of spines on the crown of the head. Fissure of the eye was difficult to see. Caudal rays were more clearly visible. Pectoral fins appeared more thick and fleshy at their bases, where 1-3 stellate chromatophores were located. Some specimens had incipient pectoral rays. Pelvic buds were present. The margin of the finfold was slightly ragged (Fig. 4D).

The onset of development of dorsal and anal fins was observed at 33-40 d, when larvae were about 9.0 mm TL. Some larvae at this stage had an anlage of the dorsal fin, whereas the larger specimens possessed the rudiments of 9 dorsal spines, 6 dorsal rays, and 13 anal rays. Pectoral fins had 15 or 16 rays, and the stellate chromatophores at the anterior margin of the fin had increased in number from 7 to 10. Caudal fin had 9-12 rays, and the hypurals were present. Pelvic fins appeared slightly larger. The crown of the head was densely pigmented with stellate and contracted melanophores. Dark vertical bars were located posterior to the auditory vesicles. Four spines were present on each cheek and two pairs of spines were present on the crown. The nostrils were beginning to constrict. The notochord was not yet flexed (Fig. 5A).

Forty-eight day larvae measured about 10.5 mm TL. They exhibited a first dorsal fin with 9 spines, and a second dorsal with 14 rays. The first dorsal was lower than the second, the two were continuous, and the finfold remained complete in the region of the caudal peduncle. Anal fin had 14 rays. Caudal fin had 13 or 14 rays, and urostyle pointed dorsally. Pelvic fins were somewhat larger, but the rays were not yet visible. Pectoral fins were large and fanlike; these had 17 or 18 rays and the bases of the fins were well pigmented. The pigmentations of the crown of the

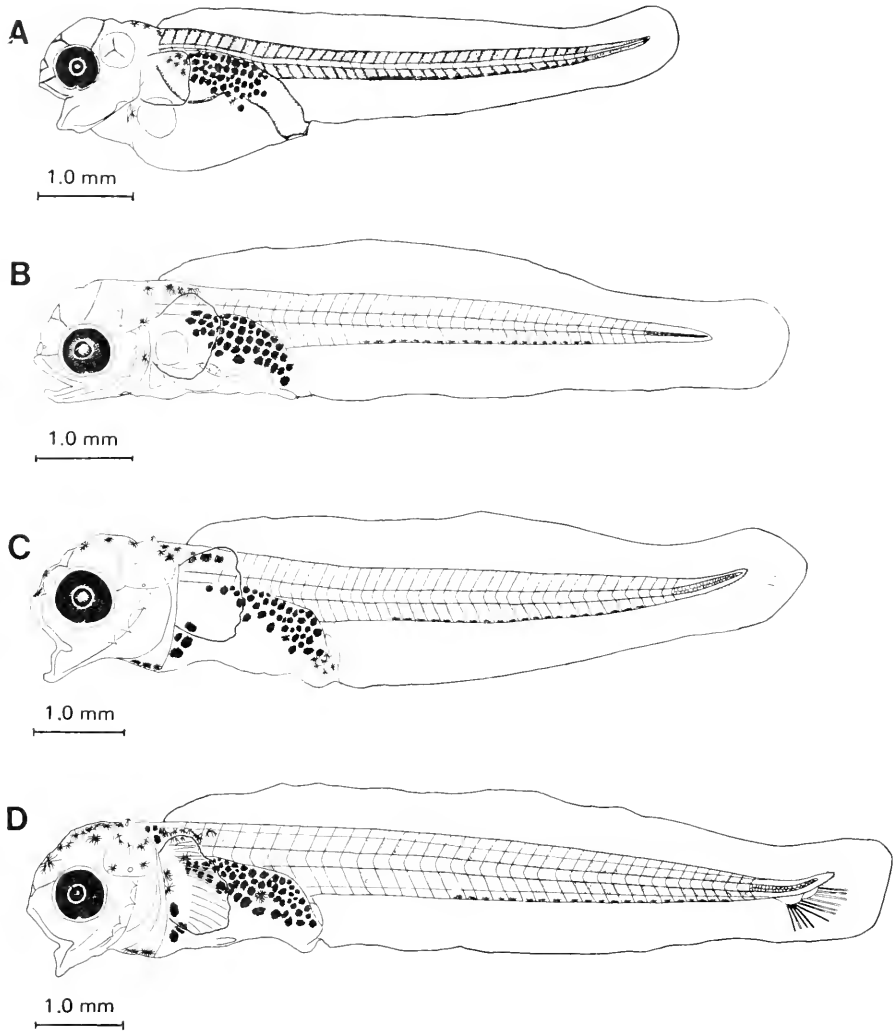

FIGURE 4.—Prolarval and early postlarval stages of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A) newly hatched prolarva 6.8 mm TL, scale = 1 mm; B) postlarva 7.7 mm TL (10 d old), scale = 1 mm; C) postlarva 8.7 mm TL (20 d old), scale = 1 mm; D) postlarva 8.8 mm TL (30 d old), scale = 1 mm. Measurements refer to mean total length of larvae.

head and the dorsal aspect of the gut region were so dense as to produce an almost uniformly dark appearance. About 25 spots were along the ventral line of the tail, including some beyond the point of flexion. There were four preopercular spines on each side, and two pairs of head spines. The nostrils were almost completely constricted (Fig. 5B).

Longhorn sculpins metamorphosed from the larval stage at 51-58 d, when they were about 12.0 mm TL. A small remnant at the caudal peduncle and incomplete separation of the two dorsals were the only relics of the embryonic finfold. There were nine spines in the first dorsal. This fin was shorter than the second dorsal and approximately equal in height; fish at this stage did not yet exhibit the higher first dorsal characteristic of adults. Second dorsal fin had 14 or 15 rays. Anal fin had 14 rays. Pelvic fin had three rays. Pectoral fins had 17 or 18 rays and extended beyond the origin of the second dorsal. Five spines were now on each cheek, and the uppermost had begun growing strongly, signalling the development of the long cheek spine characteristic of adults. Two pairs of head spines were fusing and appeared as a single large flesh-covered structure. There was one pair of

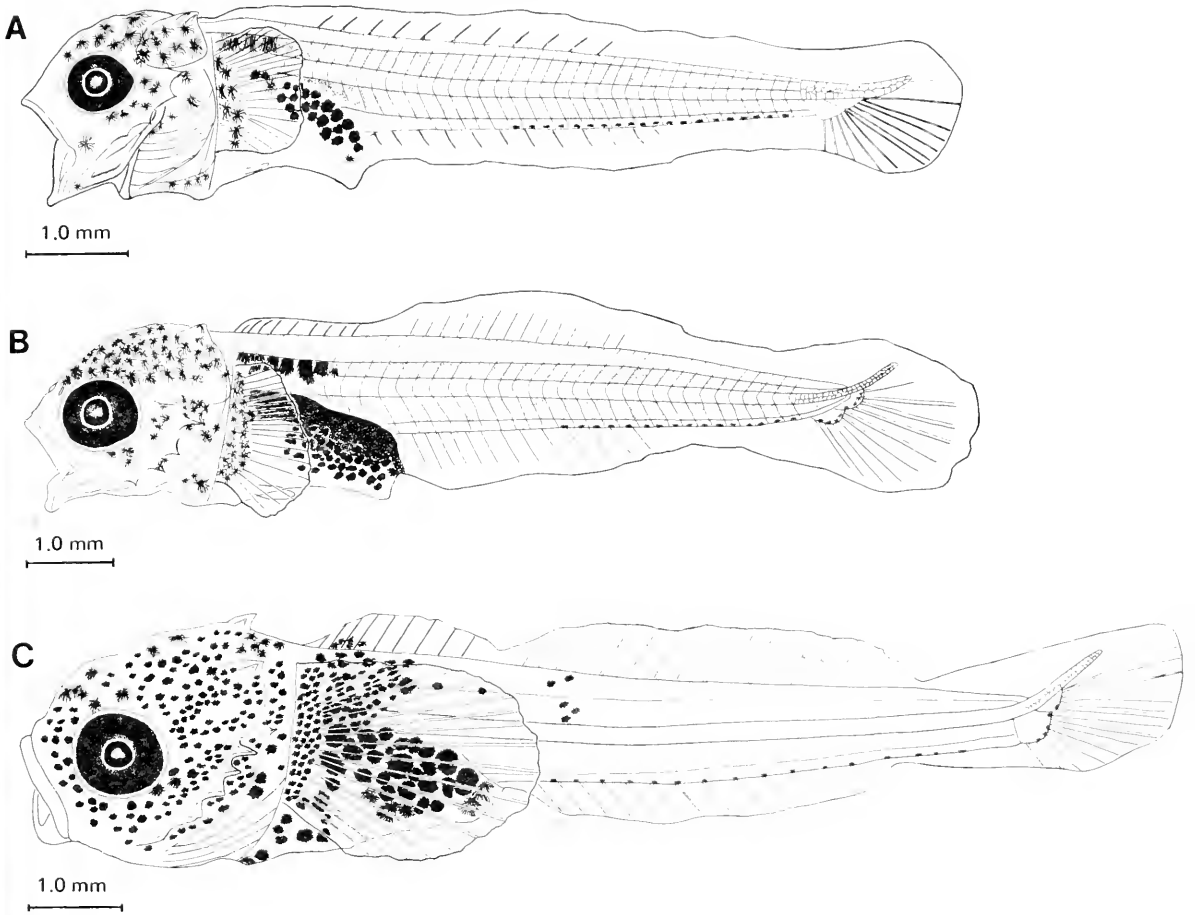

FIGURE 5.—Later postlarval and young stages of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A) late postlarva, 9.0 mm TL (40 d old), scale = 1 mm; B) postlarva prior to transformation to young, 10.5 mm TL (48 d old), scale = 1 mm; C) transformed young, 13.0 mm TL (65 d old), scale = 1 mm. Measurements refer to mean total length of larvae and young.

shoulder spines. Two pairs of nostrils resulted from the completed constriction. The gills had four arches and six branchiostegal rays on each side.

The earliest indication of the onset of development of adult pigmentation was apparent at about 65 d, in juveniles of about 13.0 mm TL. Dark spots were present at the base of the first dorsal and on the body beneath both dorsals. Melanophores beneath the first dorsal covered the vertical bars which had previously been visible posterior to the auditory region. The other noticeable change in the pigmentation relative to the previous stages was contraction of chromatophores located along the operculum, pectoral fin bases, and isthmus; these now had the appearance of dense, dark spots rather than large, stellate melanophores (Fig. 5C).

Juvenile fish of 92-104 d exhibited the characteristic four crossbar marks of adults. These fish averaged 16.7 mm TL (range 15.2-17.7 mm). Another change in pigmentation was the presence of a line of spots extending from the first crossbar down to and surrounding the anal vent. Many of the melanophores of the head and body were reduced in size, so that the basic coloration resulted from the presence of many densely crowded, small melanophores, rather than the large melanophores characteristic of earlier stages. Pigmentation increased at the base of both dorsals and was observed on the anal and caudal fin membranes in a 104-d specimen. A pair of well-developed ridges ran longitudinally along the crown of the head. Supraorbital spines and large head spines were located along the ridges. There were four cheek spines on each side, the uppermost being the largest and the two lowest being quite small. There

were two pairs of shoulder spines, the lower spine having emerged close above the upper margin of the pectoral fin. There was a single pair of small nasal spines. The fins had all acquired the characteristic adult shapes, including the high profile of the first dorsal. The pelvics had acquired a single spine in addition to the three rays; all other fins had the same meristic characteristics as the preceding stage. There were no longer any visible remnants of the embryonic finfold.

Descriptions of longhorn sculpin larvae from the Gulf of Maine and Canadian waters (Khan 1971) were somewhat different. Khan found that early larvae had ventral pigmentation near the anus and absorbed the oil globule prior to yolk-sac absorption, whereas ventral pigmentation along the intestine was absent and yolk-sac absorption was completed prior to oil globule absorption among larvae reared in this study. He found that anal and dorsal fins developed consecutively, whereas in this study these fins developed concomitantly. Finally, he found that juvenile longhorn sculpins retained remnants of the finfold at a larger size (ca. 15 mm) than occurred here (ca. 13 mm).

Development of eggs and larvae of *M. octodecemspinosus* was very similar to *M. aenaeus*, as described by Lund and Marcy (1975). Grubbies reared at mean temperatures between 4.6°-6.0°C underwent the stages of fertilization, cleavage, cell multiplication, gastrulation, embryogenesis, hatching, and larval development to the juvenile stage at rates which differed very little from the longhorn sculpin larvae of this experiment. Eggs of the two species were distinguishable as grubby eggs had a mean diameter of 1.58 mm and a transparent chorion (Lund and Marcy 1975), while longhorn sculpin eggs had a mean diameter of 2.19 mm and a translucent chorion. The larvae of the two species can be distinguished by size, pigmentation, and meristics.

Behavior of longhorn sculpins as observed in aquaria underwent marked changes during development. Immediately after hatching, the larvae swam toward the surface, sometimes making random turns, after which they sank to the bottom where they remained quiescent for variable periods. The longest observed continuous posthatch swim was almost 5 min, whereas other larvae swam for only a few seconds before sinking. This resting behavior was characteristic of prolarvae. Ennis (1970) reported similar behavior of newly hatched *M. scorpius* larvae.

Activity of the larvae increased considerably as absorption of the yolk sac neared completion. The larvae foraged actively near the surface. Postlarvae did rest on the bottom intermittently, but did so to a lesser extent than prolarvae. Lund and Marcy (1975) described intermittent resting of *M. aenaeus* postlarvae, particularly after a strike at prey.

The assumption of benthic behavior was considered to signify metamorphosis from the larval stage. After taking to the bottom, juvenile fish made sudden darting movements in search of prey or when disturbed, and they maintained this behavior throughout the juvenile period when the adult pigmentation was developing.

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FISH AND SHRIMP MIGRATIONS IN THE NORTHERN GULF OF MEXICO ANALYZED USING STABLE C, N, AND S ISOTOPE RATIOS[1]

BRIAN FRY[2]

ABSTRACT

Natural stable isotope tags were used in the northern Gulf of Mexico to interpret migrations of five commercial fish and shrimp species: *Leiostomus xanthurus*, *Micropogonias undulatus*, *Penaeus aztecus*, *P. duorarum*, and *P. setiferus*. Along the south Texas and Florida coasts, isotopic analyses showed that seagrass meadows and possibly other shallow estuarine habitats are important feeding grounds for shrimp that are later caught in offshore fisheries. Thus stable carbon, nitrogen, and sulfur values of juvenile shrimp in grassflats coincided with isotopic values of small shrimp collected offshore. These values were −11 to −14‰ for $\delta^{13}C$, and +6 to +8‰ for both $\delta^{15}N$ and $\delta^{34}S$. In contrast to these south Texas and Florida results, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values showed a second pattern off the Louisiana and north Texas coasts. This difference was most pronounced in the $\delta^{13}C$ values which ranged from −17 to −24‰ instead of −11 to −14‰. Because isotopic values were similar in *Spartina* marshes and open bays along this northern coast, no conclusions could be reached about the relative importance of *Spartina* marshes as inshore feeding grounds.

During feeding and growth offshore, eventual convergence about offshore isotopic values should result for the migratory species studied. However, striking differences in convergence patterns were evident for the five species, ranging from close convergence at small, subadult sizes (*P. aztecus* and *P. duorarum*) to nonconvergence among adults (*L. xanthurus*). These differences point to contrasts in the basic life history patterns of migration (especially the juvenile vs. adult size at which offshore migration occurs), and, for one species, showed that isotopic methods can trace yearly variations in these patterns.

Migrating animals constitute one form of export from estuaries to offshore waters. Most of the commercial species in the offshore Gulf of Mexico are estuarine dependent, migrating offshore after a juvenile growth phase in coastal bays (Lindall and Saloman 1977). Through their sheer numbers, estuarine dependent animals constitute an important part of benthic communities in the Gulf of Mexico (Hildebrand 1954; Moore et al. 1970). They also constitute an energy subsidy to the many offshore animals that consume them.

In this paper, I examine stable C, N, and S isotope distributions in five estuarine dependent species from the northern Gulf of Mexico. These species are brown shrimp, *Penaeus aztecus*; pink shrimp, *P. duorarum*; white shrimp, *P. setiferus*; spot, *Leiostomus xanthurus*; and Atlantic croaker, *Micropogonias undulatus*. Previous work on fish (Fry and Parker 1979) and shrimp (Fry 1981a) has shown that offshore animals have very constant isotopic values within an approximate 0.6-2.0‰ range. Against this rather uniform isotopic background, recent migrants from estuaries are often identifiable via their deviant isotopic values. These deviant values arise from consumption of foods that are isotopically more diverse in estuaries than offshore (e.g., McConnaughey and McRoy 1979a, b).

For animals migrating from estuaries, offshore feeding should lead to eventual convergence upon offshore isotopic values. Laboratory experiments and model calculations show that this convergence should be essentially complete to within ±1‰ following a fourfold increase in weight for rapidly growing animals (Fry and Arnold 1982). While this rapid convergence is primarily due to simple growth, metabolic turnover should also lead to eventual convergence upon offshore values for adult migrants that are not actively gaining weight. These considerations have two consequences for an offshore sampling program directed at studying patterns of recruitment from estuaries: 1) Animals recruiting as adults will retain isotopic traces of their estuarine past for relatively long times; and 2) recruiting juveniles, in contrast, rapidly lose their estuarine isotopic values and hence must be sampled soon after offshore migration.

This study of estuarine dependent species had two objectives. The first was to use offshore catches to infer important estuarine feeding grounds utilized prior to offshore migration. Collections were made during several seasons and years in three different

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regions of the northern Gulf of Mexico to find consistent isotopic patterns among animals recruiting to offshore areas. These patterns ultimately distinguish estuarine habitats in which animals feed prior to offshore migration. Secondly, isotopic data were used to study the importance of estuarine foods to the five species during their adult lives. By examining the rapidity of isotopic convergence upon offshore values it was possible to distinguish species that utilize estuarine foods well into adulthood.

Methods

Animals were collected with a 10.2 m otter trawl during October 1978, 1979, and 1980, along 10 offshore transects in the northern Gulf of Mexico (Fig. 1A). Additional May collections were made off the Texas coast along transects 1 and 2 (Fig. 1A) in 1980. Trawling stations were located at various depths along these transects. Station depths ranged from 5 m near the beach to 150 m on the continental shelf; the majority of trawl tows were taken at depths of 5-50 m. A bar seine was used to collect juvenile shrimp from marshes and shallow bays of the Barataria Bay region of Louisiana (Fig. 2).

In all offshore collections, animals were frozen and white muscle tissue dissected from abdomens (shrimp) or areas above the lateral line (fish). For some Barataria Bay collections, whole shrimp were used as samples rather than muscle tissue. Whole shrimp and stomach content samples were acid-treated to remove carbonates prior to isotopic analysis.

For all penaeid shrimp, total length (tip of rostrum

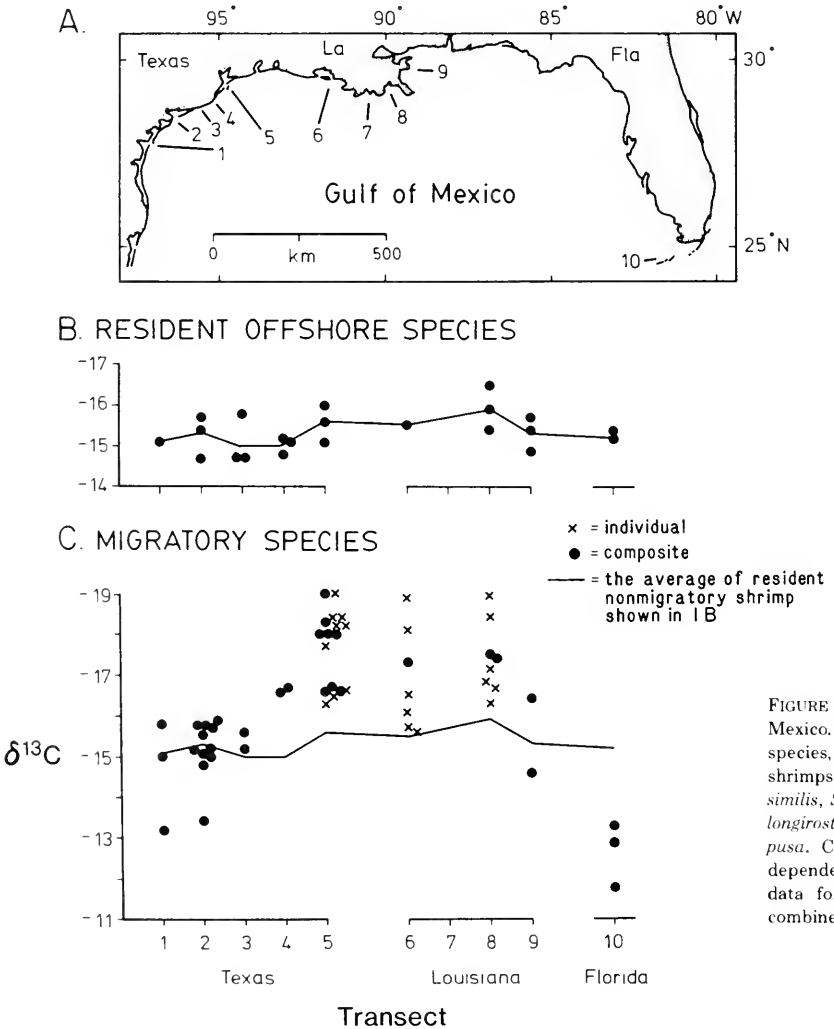

FIGURE 1.—A, Collection areas in the Gulf of Mexico. B, $\delta^{13}C$ values of offshore resident species, October 1978; species included the shrimps *Sicyonia dorsalis*, *Trachypenaeus similis*, *Solenocera vioscai*, and *Parapenaeus longirostris*, and the stomatopod *Squilla empusa*. C, $\delta^{13}C$ values of migratory, estuarine-dependent penaeid shrimp, October 1978; data for brown, pink, and white shrimp combined.

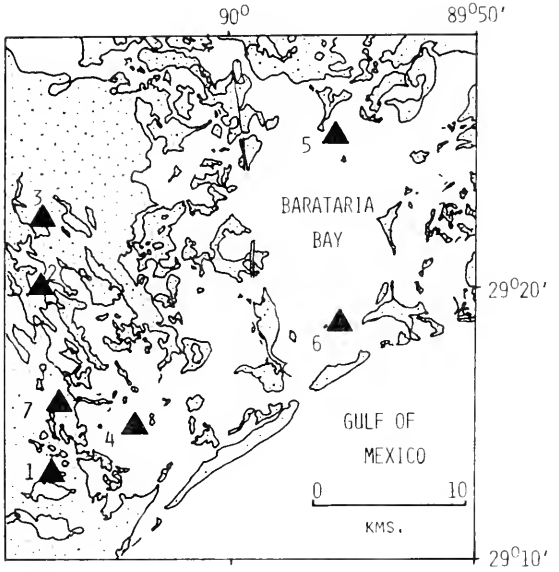

FIGURE 2.—Sampling locations in the Barataria Bay complex of Louisiana. This area is located landward of transect 8 (Fig. 1A). 1 = Airplane Lake; 2 = Bay Rambo; 3 = Round Lake; 4 = Caminada Bay; 5 = St. Mary's Point; 6 = Independence Island; 7 = Bayou Garci.

to tip of the telson) and weights (when possible) were taken. Shrimp were often pooled by size categories in which individuals typically did not differ by more than 10 mm in length. Weights were obtained in three ways: 1) Directly on a laboratory balance to the nearest 0.1 g, 2) when seas were calm, estimated to within ±15% with a pan balance, or 3) estimated from length using the length-weight regressions of Fontaine and Neal (1971) for combined sexes.

Fish were measured for total length to the nearest millimeter, and, if not weighed directly in the laboratory, their weights were estimated by using Dawson's (1965) length-weight regressions.

In the laboratory, tissue samples were rinsed in freshwater, dried, and powdered. Gas samples for mass spectrometry were prepared from powdered tissues as follows: 1) For carbon, 3-8 mg subsamples were combusted in sealed Pyrex[3] tubes at 590°C using CuO as an oxidant (Sofer 1980); 2) for nitrogen, 10-20 mg subsamples were mixed with a CuO/Cu mixture in quartz tubes and combusted at 900°C for ½ h (Macko 1981); 3) for sulfur, 0.5-1 g subsamples were combusted in a Parr bomb, the resulting sulfate precipitated with barium, and SO_2 subsequently generated by thermally decomposing $BaSO_4$ in a sealed quartz tube (Fry et al. 1982). Following combustion, all sealed tubes were broken under vacuum, and gases purified and transferred using liquid N_2 and dry ice/acetone mixtures. Gases were analyzed for their stable isotope contents using a dual inlet, isotope ratio mass spectrometer (VG-Micromass, Model 620E). Results are reported in δ notation where $\delta X = [R_{sample}/R_{standard}) - 1] \times 10^3$, $R = {}^{13}C/{}^{12}C$, ${}^{15}N/{}^{14}N$, or ${}^{34}S/{}^{32}S$, and $X = {}^{13}C$, ${}^{15}N$, or ${}^{34}S$. Values reported in this paper are given relative to PDB carbonate, air, and Canyon Diable troilite standards for C, N, and S, respectively. Mass spectrometric corrections were applied for oxygen contributions in both carbon and sulfur measurements (Craig 1957; Nakai and Jensen 1964). Replicate determinations showed that measurements were generally precise to within ±0.3‰ for $\delta^{13}C$, ±0.2‰ for $\delta^{15}N$ and ±0.5‰ for $\delta^{34}S$.

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

RESULTS

Regional Patterns

Throughout the northern Gulf of Mexico, benthic shrimp and stomatopod species that reside offshore have $\delta^{13}C$ values that usually range between −14.5 and −17.5‰ (Fry 1981a, b). Figure 1B shows this broad geographic similarity for one set of collections obtained in October 1978; isotopic values among 21 composite samples showed only a 1.8‰ range, from −14.7 to −16.5‰. In contrast to this relatively uniform distribution of $\delta^{13}C$ values, isotopic values for migratory, estuarine dependent shrimp showed regional patterns (Fig. 1C). The $\delta^{13}C$ values for migratory shrimp averaged less negative than offshore values along the south Texas and south Florida coasts; along the Louisiana and north Texas coasts, in contrast, isotopic values were more negative than the offshore values (Fig. 1C). The transition between the south vs. north Texas regions occurred at transect 4, approximately opposite Freeport, Tex. (Fig. 1C).

Further sampling showed that these less vs. more negative regional divisions were consistently present over the 3 yr of study (Figs. 3-5). The regional patterns held true not only for shrimp but also for two estuarine dependent fish species, spot and croaker (Figs. 3F, 5E, 5F).

While striking regional patterns among estuarine dependent animals were discernable in the carbon isotope results, this was not true of the nitrogen and sulfur results. Figure 6 shows that for both N and S, isotopic values of estuarine dependent shrimp

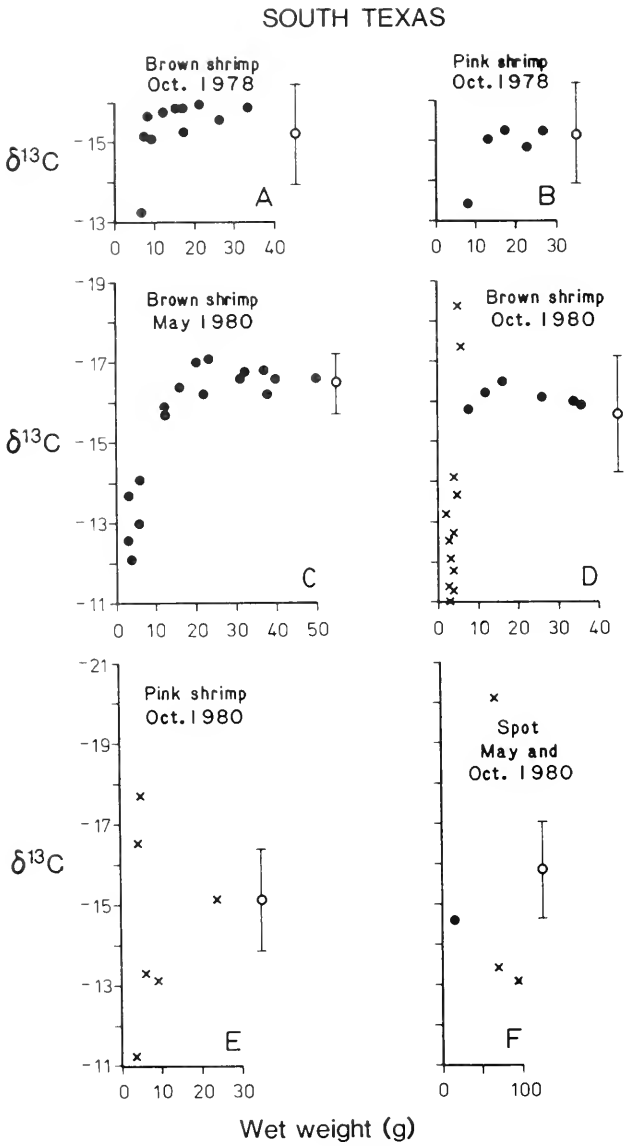

FIGURE 3.—$\delta^{13}C$ variation with size for collections made along the south Texas coast (transects 1-4, Fig. 1A). Symbol to the right of each figure indicates 1) mean (○) of 5-15 composite samples of benthic shrimps and stomatopods that reside offshore, and 2) confidence limits (vertical bar) beyond which single samples differ from the offshore mean at the 95% confidence level (Sokal and Rohlf 1981). x = individual; ● = composite sample.

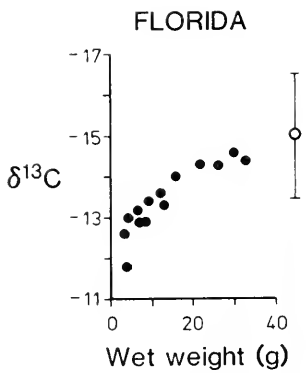

FIGURE 4.—$\delta^{13}C$ variation of pink shrimp with size for the October 1978, 1979, and 1980 collections in the Tortugas fishing area, Florida (transect 10, Fig. 1A). Symbols as in Figure 3.

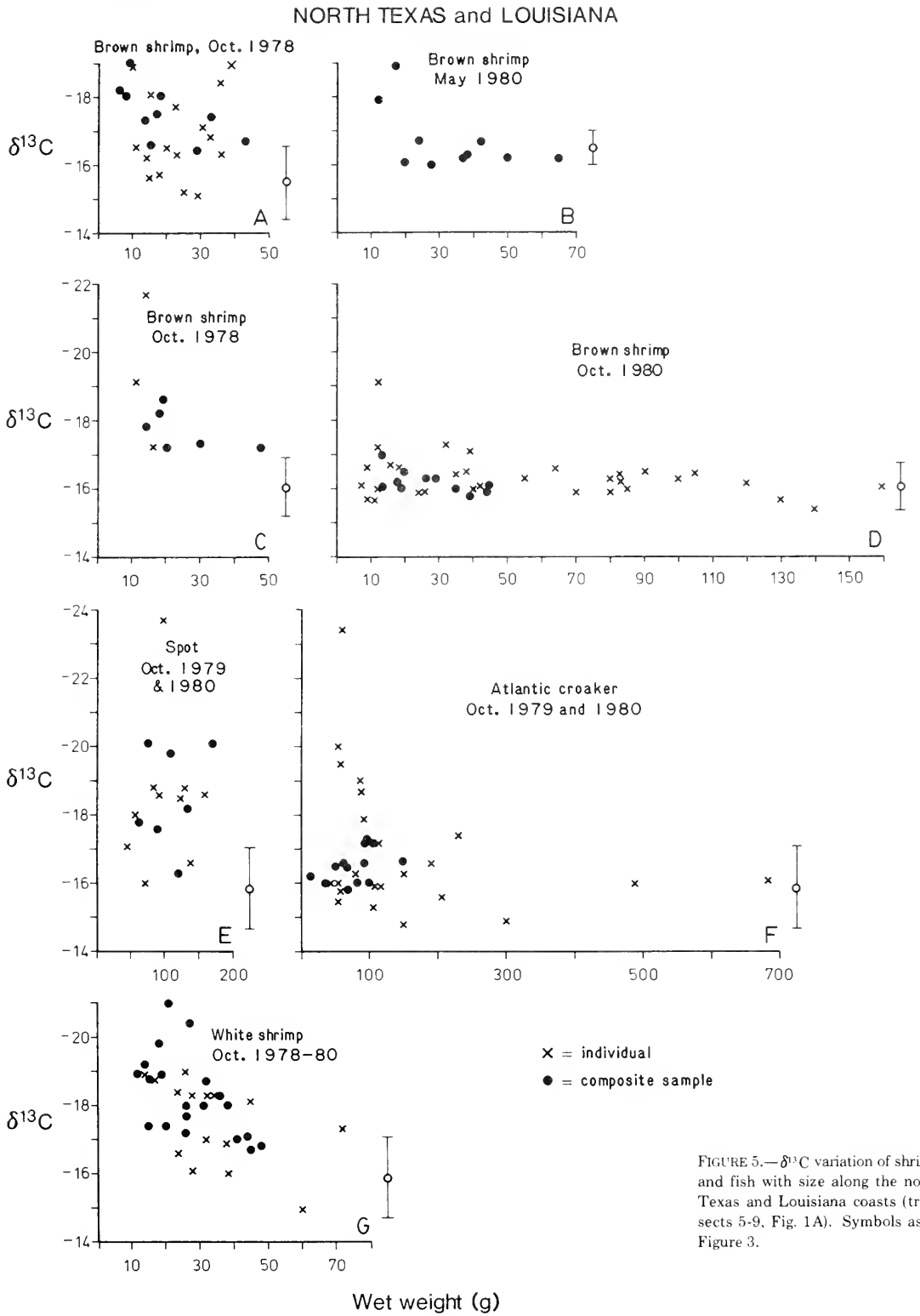

FIGURE 5.—$\delta^{13}C$ variation of shrimp and fish with size along the north Texas and Louisiana coasts (transects 5-9, Fig. 1A). Symbols as in Figure 3.

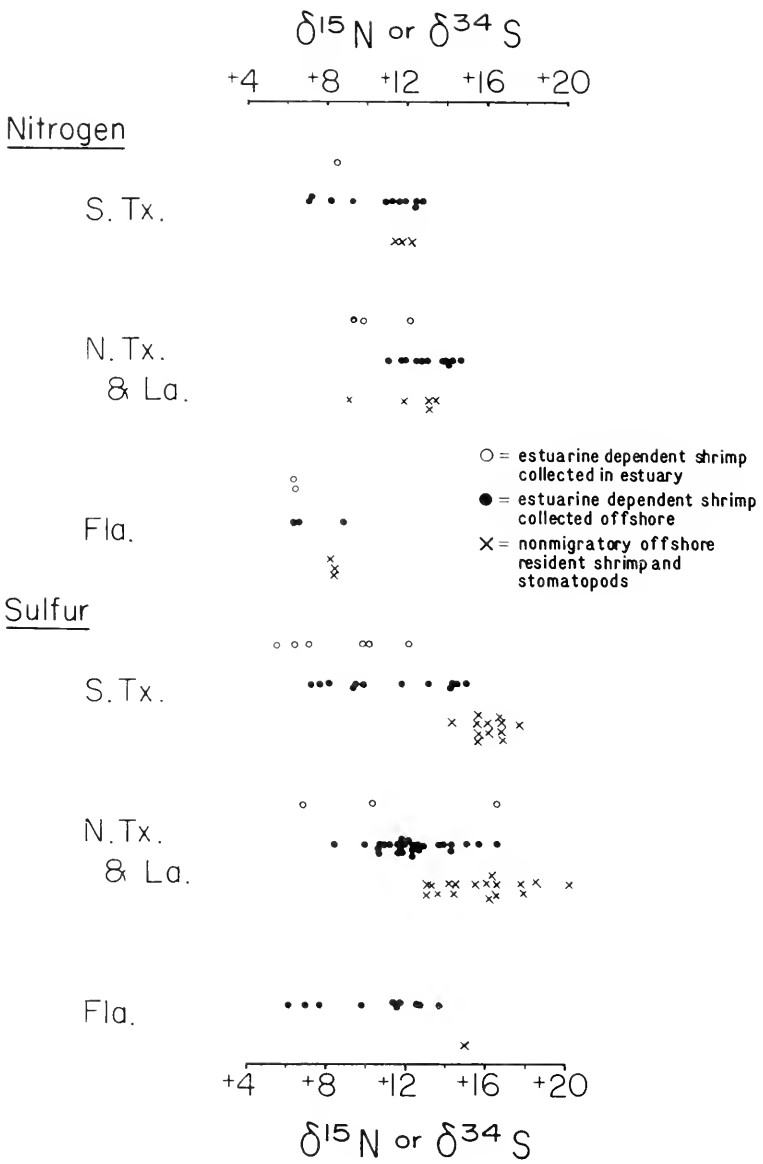

FIGURE 6.—Regional δ^{15}N and δ^{34}S values of benthic shrimp and stomatopods. Most samples are composites. Estuarine collections were made in seagrass meadows in south Texas and Florida, but in both open bays and *Spartina* marshes along the Louisiana and north Texas coasts.

averaged less than values of offshore residents in all three regions of the Gulf. The only striking regional difference in these two smaller data sets was not among the estuarine dependent animals but in the δ^{15}N data for offshore resident species. Residents collected in offshore Florida waters averaged +8.3‰, significantly less ($P < 0.05$) than the +11.8 and +12.2‰ means of the western Gulf. While mean offshore values may thus vary by region, the regional uniformities in δ^{15}N and δ^{34}S values of estuarine dependent species did not suggest striking regional differences in the isotopic compositions of estuarine foods.

Estuarine Sampling

To clarify the regional patterns observed in the δ^{13}C data and also to establish δ^{15}N and δ^{34}S values of

some estuarine animals prior to their offshore migrations, a limited number of estuarine samples was analyzed. The causes of the more negative $\delta^{13}C$ values observed among estuarine dependent animals off the Louisiana coast were investigated in estuarine collections from the Barataria Bay region (Table 1). With the exception of two brown shrimp collections from Caminada Bay ($\delta^{13}C = -13.9$ to -15.1‰), shrimp values fell between -16.6 and -22.0‰ and did not differ significantly between the *Spartina* and open bay habitats sampled (Table 1). The -16.6 to -22.0‰ estuarine range is in good accord with the -17 to -21.8‰ range observed off Louisiana among small recruiting shrimp (Fig. 5A-D, G).

For $\delta^{15}N$ and $\delta^{34}S$, a few samples were analyzed from seagrass meadows in Texas and Florida and from both *Spartina* marshes and open bays in Louisiana (Fig. 6). Low $+5.6$ to $+8.4$‰ $\delta^{15}N$ and $\delta^{34}S$ values were frequently observed among shrimp from seagrass meadows (Fig. 6); animals recruiting off south Texas and Florida initially possessed values in this range (Fig. 7A, B). Sampling in Louisiana marshes and open bays yielded scattered results for both $\delta^{15}N$ and $\delta^{34}S$ (Fig. 6) but showed that values of $+10$‰ or lower are not confined to seagrass meadows.

Isotopic Convergence

During offshore feeding and growth, the isotopic values of estuarine dependent animals should gradually converge upon average offshore values. In fact, four patterns of convergence and nonconvergence were evident, when isotopic values were plotted against animal weight. Most commonly, a close and rapid convergence toward the mean value of resident, offshore species was observed for C, N, and S (e.g., Figure 7B). Less frequently, convergence occurred, but the end-value reached by larger migratory animals was significantly different than the mean value for offshore residents (Fig. 5C; Fig. 7A, $\delta^{34}S$ data). Nonconvergence, a third pattern, was most evident in the $\delta^{13}C$ data for spot (Figs. 3F, 5E). Finally, a mixed pattern of very gradual convergence with a few deviant large individuals was indicated in two cases (Fig 5A, G).

TABLE 1.—$\delta^{13}C$ Values of estuarine shrimp from the Barataria Bay region of Louisiana, 1980. BS = brown shrimp; WS = white shrimp; GS = grass shrimp.

Location,[1] collection date, and sample size		Mean dry weight (g)	Total length (range in mm)	$\delta^{13}C$		
				Whole shrimp	Muscle	Stomach contents
Open bays						
Caminada Bay						
8 April	10 BS	0 04	19-24	−15 1	—	—
15 April	20 BS	0.07	23-33	−13 9	—	—
Independence Island						
29 July	6 WS	—	72-107	—	−19 5	—
29 July	1 WS	—	130	—	−19.9	—
29 July	35 seabob[2]	—	50-70	—	−16.6	—
1 October	9 BS	1 2	74-90	—	−19.5	−20.5
1 October	25 WS	0 8	70-107	—	−17.5	−20.0
St. Mary's Point						
1 April	6 WS	2.2	69-102	−19.0	—	−20.7
8 April	20 GS	0.065	22-26	−19.5	—	−21.0
Spartina marshes						
Airplane Lake						
25 March	20 BS	0.04	19-30	−17.8	—	—
25 March	5 BS	0.7	47-62	−17.6	—	—
8 April	20 BS	0.08	24-33	−19.6	—	—
8 April	6 BS	0.8	45-67	−17.8	—	−19.3
15 April	20 BS	0.14	24-42	−17.8, [3] −17.5	—	[4] −25.5
1 October	40 WS	0.4	60-70	—	−17.0	—
1 October	3 BS	0.7	63-86	—	−18.4	—
Bayou Garci						
25 March	11 BS	0.55	36-54	−18.3	—	—
Bay Rambo						
18 March	20 GS	0.045	17-21	−18.3	—	—
8 April	20 GS	0.06	21-23	−19.8	—	−21.1
18 April	20 BS	0.05	21-30	−17.2	—	—
18 April	7 BS	0.9	52-73	−18.3	—	−19.3
Round Lake						
3 March	9 BS	0.22	28-42	−22.0	—	—
1 April	15 GS	0.05	14-23	−20.4	—	—
15 April	20 BS	0.03	18-23	−20.9	—	−25.2
15 April	2 BS, 5 WS	0.9	57-75	−21.3	—	—

[1] Locations are shown in Figure 2.
[2] *Xiphopenaeus kroyeri*.
[3] Replicate samples, 20 brown shrimp each.
[4] Hindgut, rather than stomach (proventriculus) sample.

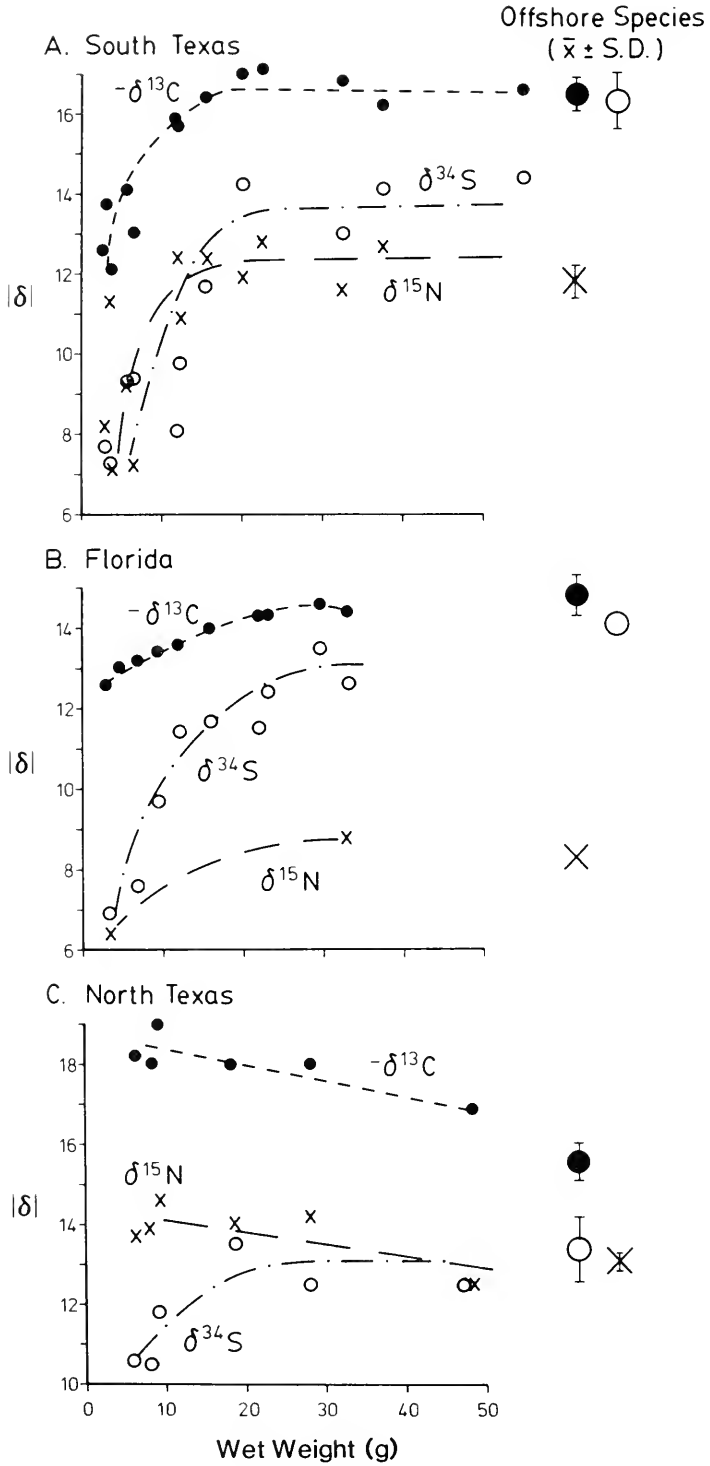

FIGURE 7.—Isotopic variations with size for migratory penaeid shrimp in three regions of northern Gulf of Mexico. All samples are composites of 5-25 individuals. Enlarged symbols at the right of each figure give the mean and standard deviation for samples of co-collected offshore resident shrimp. A, Brown shrimp, May 1980, transect 1 (Fig. 1A). B, Pink shrimp, October 1980, transect 10 (Fig. 1A). (Symbols for $\delta^{34}S$ and $\delta^{15}N$ of offshore residents lack error bars because only one species was available for analysis). C, Brown (smallest four samples) and white (largest two samples) shrimp, October 1978, transect 5 (Fig. 1A).

When these patterns are examined by species, several consistencies and contrasts are noteworthy. Rapid convergence was characteristic for pink shrimp (Figs. 3B, E, 4, 7B) and usually for brown shrimp (Figs. 3A, C, D, 5B, C, D, 7A), although one brown shrimp collection showed only a gradual convergence (Fig. 5A). With this exception, convergence was complete by subadult, 20 g sizes. In contrast to pink and brown shrimp, white shrimp exhibited only gradual convergence that was incomplete well beyond 20 g sizes (Fig 5G). The two fish species also showed contrasts in their convergence patterns. With the exception of six 50-100 g individuals collected off Barataria Bay in October 1980, Atlantic croaker in all size categories exhibited near-offshore values (Fig. 5F). Spot of all sizes, however, showed widely variable $\delta^{13}C$ values both off south Texas (Fig. 3F) and north Texas plus Louisiana (Fig. 5E).

$\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ Correlations

If two diets differ simultaneously in their C, N, and S isotopic compositions, and animals switch from one diet to the other, isotopic shifts occurring on the new diet should be parallel and therefore correlated for all three isotopes. In general, correlations between C, N, and S data followed this prediction and were good for the three examples examined (Fig. 7; Table 2). While C and N appeared consistently correlated (Table 2), correlations for S vs. N or C in the smaller set of north Texas samples (N = 6 vs. 10-12 in the other regions) were much weaker (Table 2).

TABLE 2.—Correlation coefficients (r) for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ data of Figure 7.

Region	$\delta^{13}C$ vs $\delta^{15}N$	$\delta^{13}C$ vs. $\delta^{34}S$	$\delta^{15}N$ vs $\delta^{34}S$
South Texas	0.90*	0.81*	0.69**
North Texas	0.93*	0.31 N.S	0.36 N.S.
Florida	—	0.94*	—

*$P < 0.01$.
**$P < 0.05$.
N.S = not significant.

DISCUSSION

The two most striking results of this study were 1) a strong regional division in the carbon isotopic composition of estuarine dependent species (Fig. 1) and 2) marked contrasts in the rate at which carbon isotopic values of these species converged on offshore values (Figs. 3, 4, and 5). The comparative C, N, and S data also allow preliminary observations on isotopic fractionations occurring in food webs of the Gulf of Mexico.

Regional Patterns in $\delta^{13}C$

The striking regional patterns found in $\delta^{13}C$ values of estuarine dependent shrimp closely parallel regional $\delta^{13}C$ patterns previously documented in nearshore sediments. These sediments have $\delta^{13}C$ values averaging less negative than deeper offshore sediments along the Florida and south Texas coasts (Plucker 1970; Calder 1971[4]; Fry et al. 1977; Behrens et al. 1980), but more negative than offshore sediments along the north-central Gulf coast (Sackett and Thompson 1963; Shultz and Calder 1976; Hedges and Parker 1976; Gearing et al. 1977). Similar less vs. more negative regional patterns were also evident in the $\delta^{13}C$ data for estuarine dependent animal species (Figs. 1, 3, 4, 5). For sediments, the regional variations have been ascribed to average $\delta^{13}C$ differences of the carbon that nearshore sediments receive from rivers and estuaries. In the former two regions, abundant ^{13}C-enriched seagrasses and macroalgae ($\delta^{13}C \cong -10$ to -15‰) grow or are exported offshore, while near the large rivers of the north-central Gulf coast, -27‰ terrestrial matter is carried offshore (Plucker 1970; Calder footnote 3; Shultz and Calder 1976). Interestingly, the isotopic transition between the north-central Gulf vs. the south Texas region occurs at about the same place for both sediments and shrimp—approximately offshore of Freeport, Tex. (Fig. 1, transect 4; Gearing et al. 1977).

While regional patterns are thus very consistent, their origin along the north-central Gulf coast is somewhat puzzling. Extensive stands of -13‰ *Spartina* marshes replace seagrasses as sources of ^{13}C-enriched carbon along this coast (Chabrech 1972; Diener 1975), yet this replacement is not sufficient to maintain the ^{13}C-enrichments (less negative $\delta^{13}C$ values) observed along the Florida and south Texas coasts (Fig. 1C). Sampling small juvenile shrimp within *Spartina* marshes showed that even in areas where *Spartina* influences should be strongest, shrimp $\delta^{13}C$ values were substantially more negative than *Spartina* values and ranged from -17 to -22‰ (Table 1). Similar discrepancies between -13‰ *Spartina* values and more negative values for C in animals, sediments, and water-borne particulates in marshes have also been found in previous studies (Haines 1976a, b, 1977; Spiker and Schemel 1979; Hackney and Haines 1980), and Peterson et al. (1980) have discussed one possible explanation for these discrepancies.

[4]Calder, J. A. 1971. Carbon isotope ratios of shelf sediments. Paper presented at the 1971 Annual Fall Meeting of the American Geophysical Union, San Francisco, Calif.

Regional results from Florida and south Texas more clearly show the importance of feeding on ^{13}C-enriched foods prior to offshore migration (Figs. 3, 4). Such foods are found in shallow areas such as seagrass meadows and some shoreline algal mats (Fry 1981b) rather than in deeper open bays (Fry 1981a). The isotopic data thus point to the importance of these shallower habitats as feeding grounds for spot, pink shrimp, and brown shrimp prior to their offshore migrations. The N and S isotopic results shown in Figure 7A and B are consistent with this conclusion, as the +6 to +8‰ values found among small migratory shrimp were also found in shrimp from seagrass meadows (Fig. 6). Additionally, this conclusion agrees well with previous studies that have documented high abundances of these three species in grassflats (e.g., Hutton et al. 1956; Hellier 1962; Hoese and Jones 1963; Kobylinski and Sheridan 1979; Orth and Heck 1980).

In summary, isotopic values found among small migrants in all three offshore regions closely mirrored isotopic values found in local estuaries. The sharp division in $\delta^{13}C$ values occurring opposite Freeport, Tex. (Fig. 1A, transect 4), suggests little migratory interchange between offshore regions, at least for smaller sized shrimp. Future sampling near transect 4 and in other areas where two isotopically contrasting regions interface could be useful in tracing the movements of shrimp and fish after their offshore migrations. This should be easiest for animals that migrate offshore as adults and show only a slow convergence upon offshore values.

Convergence

To understand the four patterns of isotopic convergence and nonconvergence that were observed, it is useful to consider two extreme cases. In the first, animals migrate offshore as small juveniles and remain permanently offshore during growth to adult sizes. This leads to the pattern of early isotopic convergence that was most often observed (e.g., Figure 7A). Alternately, animals may mature in estuaries, migrating offshore as large adults. When sampled offshore, animals of this kind will show very little convergence upon offshore values, for most of their tissues have been formed from estuarine foods. Results for spot most clearly conformed to this pattern (Figs. 3F, 5E).

Gradations exist between these extreme cases. For example, if some species have mixtures of small juvenile and large adult migrants, the result may be a gradual convergence such as that observed for white shrimp (Fig. 5G). Such mixed cases could also result 1) if animals do not stay permanently offshore but freely move between estuarine and offshore regions, or 2) if animals stay offshore but consume small migrants or detrital foods that come from estuaries.

The isotopic results thus lead to some predictions about the migratory life histories of these species—predictions that can be checked against previous findings of mark-recapture and trawl studies. The five species studied can be divided into two groups on the basis of migration patterns and offshore location as adults. Trawling studies of both pink and brown shrimp show that they move offshore as small juveniles and continue to move into deeper waters as they mature (Iverson et al. 1960; van Lopik et al. 1979[5]). The other three species—white shrimp, croaker, and spot—are more coastal, with the center of their offshore ranges at <10 m depths (Chittenden and McEachran 1976). For these latter three species, several reports exist documenting 1) occasional or frequent reentry into estuaries from the offshore Gulf of Mexico (Simmons and Hoese 1958; White and Chittenden 1977; van Lopik et al. footnote 4), and 2) delayed migration until adult sizes are reached in estuaries (e.g., Gunter 1950; Suttkus 1955; Hellier 1962; van Lopik et al. footnote 4).

In general, the isotopic patterns of convergence closely conformed to what was expected from these previous life history studies. Pink shrimp and most brown shrimp collections showed close convergence to offshore values by the 20 g size in good accord with observations that these shrimp leave estuaries at an average size <6 g (Copeland 1965; Trent 1967; Parker 1970; Ford and St. Amant 1971). The less marked convergence observed among spot, white shrimp, and, to some extent, Atlantic croaker, suggests that these species continue to rely on estuarine foods throughout their adult lives, and is consistent with their closer association with estuarine areas.

Two aspects of the isotopic data deserve special mention. First, while most of the isotopic data gathered are consistent with early migration of brown shrimp as young juveniles, this was not always true. Collections of brown shrimp made off the Louisiana and north Texas coasts in October 1978, showed only a gradual convergence (Fig. 6A) similar to that observed for white shrimp (Fig. 6G). While the causes of this one exceptional set of results are not clear, it appears that some variability can exist in migration patterns.

[5]Van Lopik, J. R., K. H. Drummond, and R. E. Condrey. 1979. Draft environmental impact statement and fishery management plan for the shrimp fishery of the Gulf of Mexico, United States waters. Gulf of Mexico Fishery Management Council.

Secondly, it is interesting to carefully contrast the isotopic data for spot and Atlantic croaker collected along the Louisiana and north Texas coasts (Fig. 5E, F). Although the migratory biology of these two species is generally held to be quite similar (e.g., Parker 1971), the isotopic results show clear differences. Of the two patterns, that of the Atlantic croaker conforms closest to findings of trawl studies which show that most animals leave estuaries as juveniles <25 g during late spring and early summer migrations (Nelson 1969; Parker 1971; Kobylinski and Sheridan 1979). The October collections of this study should thus primarily reflect summer growth offshore, and show the general isotopic convergence that was observed in the Atlantic croaker data. The six individuals with deviant $\delta^{13}C$ values that were collected off Barataria Bay in October 1980 could represent the much smaller pool of individuals that continues to reside in bays until early winter weather triggers their exodus (Gunter 1950; Suttkus 1955). It is striking that this latter class of adult migrants seems to represent a much larger fraction of the population for spot than Atlantic croaker (compare Figure 5E and F).

While further study in other seasons is required to confirm these differences between Atlantic croaker and spot, these data point out both strengths and weaknesses of this isotopic approach to studying migrations. This approach is weakest for tracing the movements of small individuals because these animals rapidly lose their estuarine isotopic tag during offshore growth. The approach is much stronger when applied to adult migrants that only gradually lose their estuarine isotopic tag during metabolic turnover offshore. Trawling methods are probably superior for studying movements of small juveniles that cannot easily avoid nets, but for larger adults that can, isotopic methods of following movements may lead to a clearer understanding of seasonal and year-to-year variations.

C, N, and S Food Web Fractionations

Table 3 summarizes C, N, and S isotopic values observed in the Gulf of Mexico and other offshore ecosystems. Relative to phytoplankton at the base of the food web, some fractionations or changes in isotopic compositions are evident at higher trophic levels for C and N isotopes. Mean δ values increase for both C and N isotopes in these food webs (Table 3). Such cumulative fractionations have been attributed to preferential respiration of $^{12}CO_2$ in the case of C isotopes (McConnaughey and McRoy 1979a) and to excretion of ^{14}N-enriched compounds in the case of nitrogen (Wada 1979).

TABLE 3.—Stable isotope values for seawater and offshore marine biota.[1]

Measurement	Seawater	Phytoplankton	Marine animals			References[2]
			Zooplankton	Fish	Benthic invertebrates	
$\delta^{13}C$	+1	−18 to −24	−19 to −22	−15 to −19	−14 to −19	1, 2, 3, 4, 11
$\delta^{15}N$	+1	−2 to 0 and 7 5 to 8.5	8 to 9.5	9 9 to 20.5	8 to 13 3	5, 6, 11
$\delta^{34}S$	+20	[3]17 to 20.3	18.1	16 to 19	12 9 to 20	7, 8, 9, 10, 11

[1]Whenever possible, values cited are those from the Gulf of Mexico or other temperate and tropical waters.
[2]References: 1 = Fry 1981b; 2 = Fry and Parker 1979; 3 = Gormly and Sackett 1977; 4 = Sackett and Moore 1966; 5 = Macko 1981; 6 = Miyake and Wada 1976; 7 = Hartmann and Nielsen 1969; 8 = Mekhtiyeva et al. 1976; 9 = Kaplan et al. 1963; 10 = Rees et al. 1978; 11 = this study.
[3]Values for macroalgae.

For S isotopes, marine algae typically show a small 0-4‰ fractionation relative to seawater sulfate and thus closely reflect its +20‰ isotopic composition (Table 3). Previous studies show that marine animals closely reflect the isotopic composition of their +17 to +20‰ algal foods and seldom have values lower than +16‰ (Kaplan et al. 1963; Mekhtiyeva et al. 1976).

In this study, the majority of resident offshore shrimp and stomatopod samples had somewhat lower +13 to +17‰ values (Fig. 6). This apparent discrepancy may reflect an undersampling of soft-bottom benthic fauna in previous studies. Recent work in estuarine marshes has shown that sulfur with low $\delta^{34}S$ values can enter rooted plants from sediments, resulting in plant tissues with $\delta^{34}S$ values lower than +5‰ (Carlson and Forrest 1982; Fry et al. 1982). Consumption of low $\delta^{34}S$ benthic bacteria or plants seems responsible for the low +6 to +8‰ values found in many estuarine and offshore samples of pink and brown shrimp (Figs. 6, 7A, B). Among offshore resident shrimp, the lowest $\delta^{34}S$ values were observed in Louisiana waters (Fig. 6), offshore of Barataria Bay (Fig. 1, transect 8). The occurrence of low $\delta^{34}S$ values in this area may have as their cause

low $\delta^{34}S$ benthic bacterial foods, rather than cumulative food web fractionations. The various means by which benthic algae and bacteria take up low $\delta^{34}S$ sulfur from sediments is the subject of current investigations.

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GEOGRAPHIC AND HISTORIC VARIATIONS IN GROWTH OF WEAKFISH, *CYNOSCION REGALIS*, IN THE MIDDLE ATLANTIC BIGHT

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ABSTRACT

The growth of weakfish, *Cynoscion regalis*, throughout the Middle Atlantic Bight was examined. Six geographic subdivisions were initially established for growth comparisons. Covariate analysis of the total length-scale size relationship revealed three distinct regions. Back-calculated lengths at age were compared using analysis of variance and showed significant differences between regions ($P < 0.001$) and between sexes ($P < 0.05$). Mean lengths at age of northern weakfish were greater than southern fish and females were larger than males after age 6. Maximum mean lengths at age were also greater in the north, 81 cm at age 11, and became progressively smaller towards the south, declining to 42 cm at age 4 in the southernmost region. The growth variations may result from varying allocations of energy to somatic growth according to environmental and migratory requirements. Growth differences resulting from the availability of food items in each habitat are also examined.

Mean and maximum lengths at age have changed over the past 50 years, with current growth greater than in 1929 or 1952. A possible relationship exists between fluctuating population sizes and historic growth variations. The current age/size structure of weakfish fisheries in Delaware Bay is discussed.

Weakfish, *Cynoscion regalis*, has been an important fishery resource within the Middle Atlantic Bight since the 19th century (Hildebrand and Schroeder 1928). In 1945, a record 41.4 million pounds of weakfish were landed by commercial interests (Wilk 1981) and, more recently, a recreational fishery has accounted for an increasing percentage of the total catch (Wilk 1981). Unfortunately, the abundance of weakfish has not always kept pace with the demand. Commercial landings totaled 27.6 million pounds in 1947 but declined thereafter, and by 1967 only 3.1 million pounds were caught. Recent landings have increased, reaching 28.7 million pounds in 1979 (Wilk 1981).

Weakfish availability to fisheries also fluctuates seasonally due to the migratory nature of the species. In April or May, weakfish migrate into estuaries to spawn (Hildebrand and Schroeder 1928) and are subjected to an inshore fishery. The migratory route is reversed in the fall, with the fish moving to warmer offshore waters (Nesbit 1954). During winter months, an offshore fishery for weakfish operates in the Virginia-North Carolina region (Pearson 1932; Jess Hawkins[3]).

Despite the importance of weakfish as a commercial resource, relatively little is known about the species migrations or population structure and dynamics. Previous age and growth investigations (Eigenmann 1901; Taylor 1916; Welsh and Breder 1923; Nesbit 1954; Perlmutter et al. 1956; Daiber 1957; Massmann 1963; Merriner 1973) have generally been localized studies done prior to or during the period of population decline. Following a reduction in population size, as occurred during the 1950's and 1960's, individual growth rates could theoretically be altered (Beverton and Holt 1957). Geographic variations in growth have also been suggested in previous studies, but were never examined for a single time-series of data (Perlmutter et al. 1956; Merriner 1973). This study was undertaken to assess current growth information, examine the variation throughout the Middle Atlantic Bight, and describe any long-term changes in growth that may have occurred.

METHODS AND MATERIALS

Sample Collection

Samples were collected by the National Marine Fisheries Service (NMFS) groundfish survey from 1979 to 1981. All weakfish were captured between Cape Fear, N.C., and Cape Cod, Mass., in depths between 5 and 200 m. Fish were collected with a #41 Yankee trawl in the spring and a #36 Yankee trawl in

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the summer and fall (Grosslein 1969). Supplemental samples were collected from May 1980 to June 1981 from commercial pound net operations in Gardiner's Bay, N.Y., and Sandy Hook Bay, N.J., and from a trawl fishery in Delaware Bay.

Weakfish from NMFS and Gardiner's Bay catches were randomly sampled and total length (TL) to the nearest millimeter (nearest centimeter for NMFS samples), sex, and maturity stage were recorded. Scales were removed from an area midway between the center of the second dorsal fin and lateral line (Perlmutter et al. 1956) on 25-30 fish per haul. Weakfish from Sandy Hook and Delaware Bays were sampled by random selection of 50-lb boxes in each size category available from the catch. Biological data and scales were collected from the subsample. Whole and gutted weights to the nearest gram were recorded for fish collected in Sandy Hook and Delaware Bays. Length-frequency data for the Delaware Bay fishery were collected by random sampling weakfish during off-loading operations in Cape May, N.J.

Aging Methods

Impressions of nonregenerated scales were prepared on laminated polyethylene plastic and examined with a standard microfiche reader at a magnification of 32 times. Annuli were identified as the area of cutting over circuli occurring in the proximal as well as the lateral fields of the scale (Taylor 1916; Perlmutter et al. 1956). Scale measurements were made from the focus to each annulus in the lateral field and recorded directly onto ruled cards. The data were subsequently stored in an IBM[4] 370 computer.

Data Analysis

To examine variations in growth, we subdivided the sampling range into geographic areas in regions and estimated growth by area. The designated regions were I, Delaware Bay to North; II, Chesapeake Bay; and III, Cape Hatteras. Six areas were established based on locations of reported spawning grounds (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Daiber 1957; Thomas 1971; Merriner 1976). The designated areas were 1) Cape Cod, Mass., to Block Island, R.I.; 2) Block Island to Fire Island, N.Y., which encompassed Gardiner and Peconic Bays; 3) Fire Island to Great Bay, N.J.; 4) Great Bay to Ocean City, Md., which includes Delaware Bay; 5) Ocean City to Virginia Beach, Va., which includes Chesapeake Bay; and 6) Virginia Beach to Cape Fear, N.C. (Fig. 1).

Back-calculated lengths at age of individual fish were calculated from scale annulus measurements using a fish TL-scale size regression equation. Individual scale measurements were adjusted according to average scale size for each fish length to reduce the variance in scale size created by scale samples not being removed from exactly the same location on each fish (Ricker 1975). Von Bertalanffy growth curves were fit to mean back-calculated lengths at age (weighted by n) using a nonlinear regression program available in the Statistical Analysis System (Helwig and Council 1979). High correlations between L_∞ and K invalidated univariate

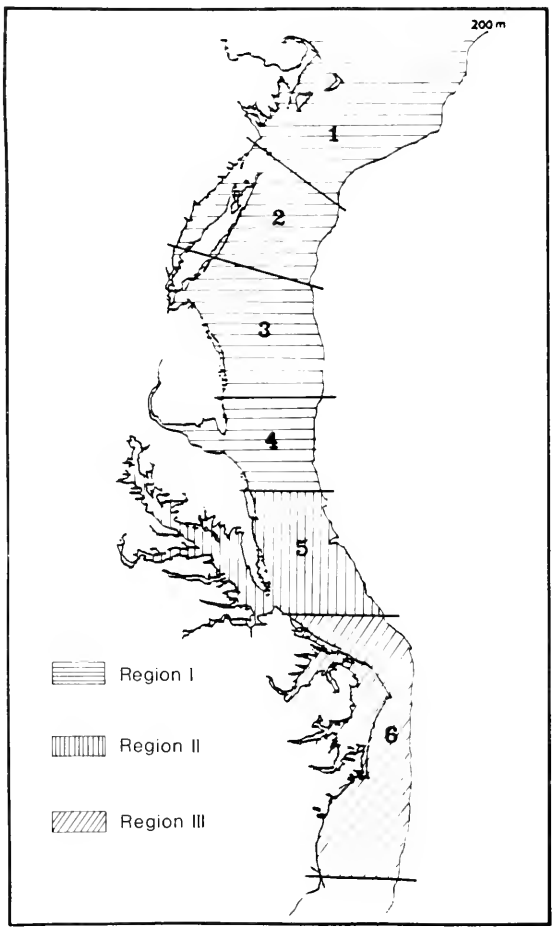

FIGURE 1.—Map of Middle Atlantic region showing stratification into three regions (I-III) and six sampling areas (1 - Cape Cod, Mass., to Block Island, R.I.; 2 - Block Island to Fire Island, N.Y.; 3 - Fire Island to Great Bay, N.J.; 4 - Great Bay to Ocean City, Md.; 5 - Ocean City to Virginia Beach, Va.).

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

statistical comparisons of growth curves; therefore, we compared von Bertalanffy curves following Bernard (1981). This method incorporates a Hotelling T^2 test to compare matrices of parameter estimates, variances, and correlation coefficients.

RESULTS

We made age determinations and annulus measurements on scales from 1,240 weakfish, 647 males and 593 females, ranging in size from 50 to 910 mm TL. The validity of growth rings on weakfish scales has been previously established by Taylor (1916) and Perlmutter et al. (1956). Our data show that annulus formation occurred from April to June, the point at which mean marginal increments approached minimum values (Fig. 2), which corroborates the earlier findings of annuli validity.

The relationship between fish TL (cm) and scale size (SS) per area (see Methods) was best described by a logarithmic equation. The six equations were

Area 1 $\ln TL = -1.620 + 1.054 \ln SS$
$r^2 = 0.874 \quad n = 23$

Area 2 $\ln TL = -1.830 + 1.117 \ln SS$
$r^2 = 0.956 \quad n = 132$

Area 3 $\ln TL = 0.622 + 1.073 \ln SS$
$r^2 = 0.958 \quad n = 171$

Area 4 $\ln TL = -2.145 + 1.178 \ln SS$
$r^2 = 0.879 \quad n = 524$

Area 5 $\ln TL = -1.174 + 0.971 \ln SS$
$r^2 = 0.857 \quad n = 190$

Area 6 $\ln TL = -0.327 + 0.785 \ln SS$
$r^2 = 0.639 \quad n = 200.$

The logarithmic transformation was justified following examination of the residual values (Draper and Smith 1966).

Body length-scale size regressions were compared between the six geographical areas to determine which equations should be used in back-calculating lengths at age. The equivalence of TL-SS equations between areas, sexes, and interactions was tested using analysis of covariance. Significant differences ($P < 0.001$) were found in TL-SS equations between areas but not between sexes or interaction effects. Adjacent areas with similar slopes were combined into a single region. Area 1 was excluded from the analysis because of a small sample size, and the range of lengths in other areas was truncated to include equal sizes. The differences between areas were evident when the slopes of the six equations were examined (Fig. 3). Areas 2, 3, and 4 were statistically similar ($P > 0.329$) and were therefore pooled into one region (Region I). Area 1 was included in the final pooled data for Region I, as the inclusion did not

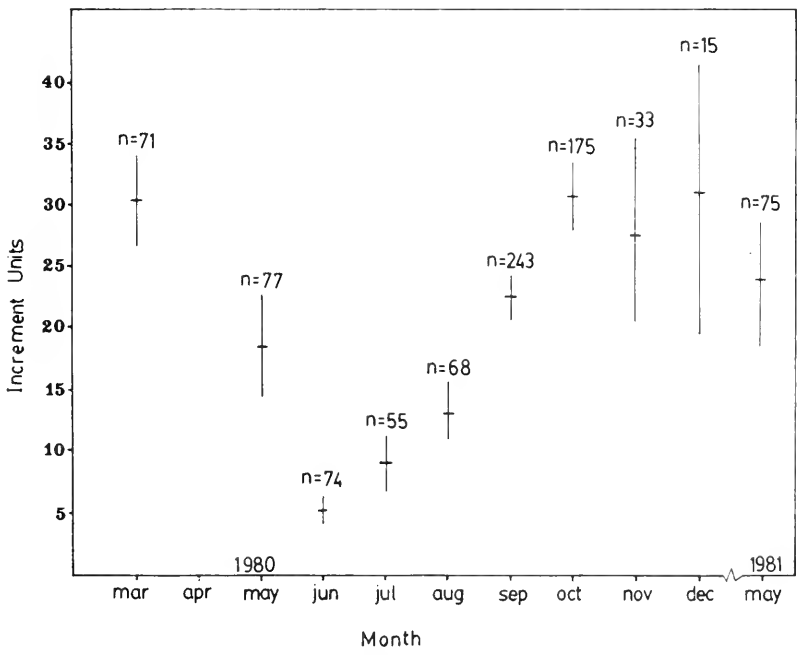

FIGURE 2.—Mean marginal scale increments ±95% confidence intervals of weakfish, *Cynoscion regalis*, in the Middle Atlantic Bight for all ages combined. Sample size given for each month.

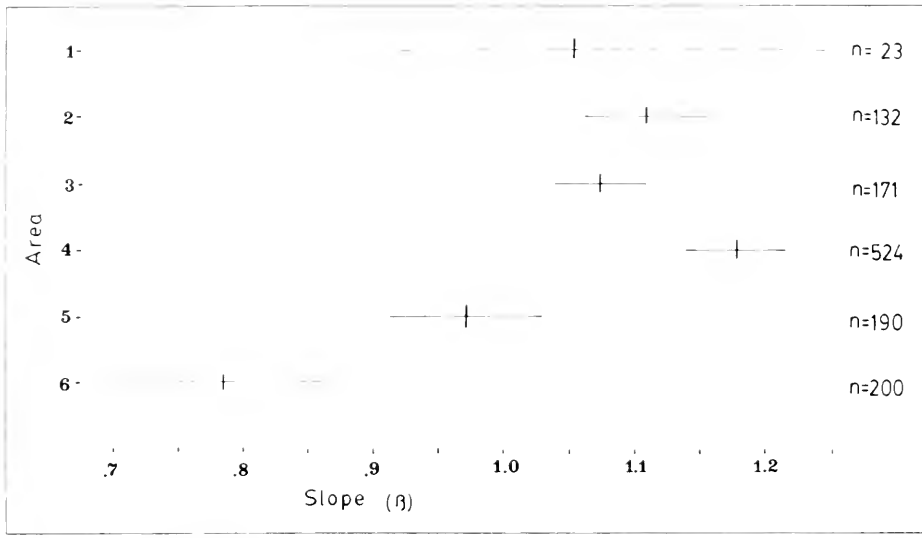

FIGURE 3.—Slopes ±95% confidence intervals for body length (cm)—scale size regression equations of weakfish, *Cynoscion regalis*, for each area.

significantly alter the regression. Area 5 and Area 6 were each significantly different ($P < 0.001$) from other equations and were thus considered separate regions. The three regional equations determined from this analysis were

Region I (areas 1-4): $\ln TL = 1.948 + 1.139 \ln SS$, $r^2 = 0.883$, $n = 850$

Region II (area 5): $\ln TL = -1.179 + 0.974 \ln SS$, $r^2 = 0.835$, $n = 190$

Region III (area 6): $\ln TL = -0.329 + 0.786 \ln SS$, $r^2 = 0.639$, $n = 200$.

Maximum age differed substantially between regions but not between sexes. The greatest ages occurred in Region I where both sexes attained age 11. Females in Region II did not exceed age 6 while maximum age for males was age 5. In samples from Region III, the oldest age for both sexes was 4 yr.

Using the above regional equations we back-calculated lengths at age and tabulated mean lengths by sex, age group, and region (Table 1). Mean lengths for successive age groups were examined for evidence of differential survivorship, i.e., Lee's phenomena, using analysis of variance. Although a few older groups had larger size at age 1, there was no significant increase in size of the first year ($P < 0.05$).

An analysis of variance (ANOVA) of back-calculated lengths at age revealed significant differences between regions for ages 1-4 ($P < 0.05$). The regions responsible for the differences were determined by Duncan's new multiple range test (Table 2). Region III fish were significantly larger ($P < 0.001$) at age 1, 22 cm, compared with 20 cm for Regions I and II. By age 2, the mean length for Region I was largest, 32 cm, and significantly different from Regions II and III at 29 and 28 cm, respectively. The difference between Regions II and III was not significant. Greatest size differences existed for mean calculated lengths at age 3, between Regions I and III at 47 and 35 cm, respectively. Calculated mean length at age 4 was significantly greater in Region II than Region I ($P < 0.05$), while lengths at ages 5 and 6 were not significantly different between regions.

Lengths at age were greater for females in all regions and the differences increased with age. These differences did not become statistically significant until age 6, except for 2-yr-olds in Region III where females were 3 cm larger ($P < 0.05$). Region I had significant differences between sexes ($P < 0.05$) for ages 6-11, except at age 9. Lengths at age 6 were 68 cm for females ($n = 53$) and 66 cm for males ($n = 39$); the comparison at age 11 was 81 cm for females ($n = 3$) and 70 cm for males ($n = 1$). No significant interactions were found between sexes and regions. Based on this analysis, length at age data were pooled for sexes in Regions II and III but separated for Region I in the subsequent fitting of growth curves.

In all three regions, the greatest growth in length

TABLE 1.—Mean back-calculated lengths at age of weakfish, *Cynoscion regalis*, by sex and region with the grand mean weighted by *n*.

Age	*N*	BCL1	BCL2	BCL3	BCL4	BCL5	BCL6	BCL7	BCL8	BCL9	BCL10	BCL11
Region I: Female												
1	57	21										
2	74	19	29									
3	97	20	33	48								
4	33	21	33	49	59							
5	18	21	34	51	60	66						
6	14	21	36	48	60	65	68					
7	13	22	35	49	60	66	70	70				
8	11	24	33	46	57	64	69	73	75			
9	6	21	30	38	49	57	63	66	69	71		
10	6	22	31	42	52	60	65	68	71	73	74	
11	3	24	30	44	53	63	69	72	74	76	78	81
$\bar{x}$	332	20	32	48	58	64	68	70	72	73	75	81
Region I: Male												
1	67	21										
2	105	19	30									
3	113	20	33	47								
4	35	19	30	46	55							
5	14	22	33	45	58	64						
6	21	20	32	48	59	65	67					
7	8	20	30	42	55	62	65	67				
8	3	22	33	45	55	60	63	66	66			
9	5	24	30	40	50	58	64	68	69	72		
10	1	20	26	42	55	59	61	64	66	69	70	
11	1	21	28	36	51	55	59	61	64	66	68	70
$\bar{x}$	373	20	31	46	56	63	66	66	68	71	69	70
Region II: Female												
1	45	19										
2	24	20	28									
3	3	23	34	42								
4	2	25	36	50	57							
5	1	22	33	45	61	68						
6	1	24	39	53	64	67	71					
$\bar{x}$	76	20	30	46	60	67	71					
Region II: Male												
1	62	20										
2	27	20	27									
3	5	23	33	47								
5	1	19	29	38	56	60						
$\bar{x}$	95	20	28	45	56	60						
Region III: Female												
1	42	21										
2	43	22	31									
3	14	21	28	37								
4	1	25	29	33								
$\bar{x}$	100	21	30	37								
Region III: Male												
1	56	22										
2	29	21	26									
3	9	23	28	32								
$\bar{x}$	94	22	27	32								

TABLE 2.—Results of Duncan's new multiple range test, including probability values, comparing mean back-calculated lengths at age of weakfish, *Cynoscion regalis*, between regions. Connecting bars indicate no significant differences ($P > 0.05$); *N* is given in parentheses.

	Region			
Age	I	II	III	*P*
1	20 (752)	20 (171)	22 (194)	0.001
2	32 (615)	29 (63)	28 (96)	0.001
3	47 (408)	46 (12)	35 (24)	0.001
4	57 (212)	59 (5)		0.015
5	64 (147)	63 (3)		0.559
6	67 (112)	71 (1)		0.299
7	69 (63)			
8	71 (41)			
9	73 (25)			
10	75 (11)			
11	78 (4)			

occurred in the first year for both sexes (Table 3). Growth of weakfish from Region III was highest at 22 cm, while Regions I and II to the north each averaged 20 cm in the first year. Growth rate in Region III declined steadily after the first year. Growth in Regions I and II decreased in the second year to 10 and 7 cm, but increased to 14 and 9 cm during the third year. Thereafter growth rate declined, reaching a low of 2 cm in the 11th year for Region I and 4 cm in the 5th year for Region II.

Initial growth in weight was slower than length (Table 4). Back-calculated lengths at age were converted to weight using the GM functional regression (Ricker 1973):

TABLE 3.—True growth (cm) represented as the mean of annual increments between next-to-last and last back-calculated lengths at age for individual weakfish, *Cynoscion regalis*

Region and sex	Age 0 • 1	• 2	• 3	• 4	• 5	• 6	• 7	• 8	• 9	• 10	• 11
I. Female	20	10	14	12	7	5	3	3	2	2	2
Male	20	11	13	12	7	4	3	1	2	2	2
II Female	19	7	8	7	3	4					
Male	20	6	10	—	5						
III Female	21	7	5								
Male	22	6	2								

TABLE 4.—Annual increments in gutted weight (g) of weakfish, *Cynoscion regalis*, by region and sex, based on the equation ln gutted wt = 4.705 + 2.984 ln TL.

Region and sex	Age 0 • 1	• 2	• 3	• 4	• 5	• 6	• 7	• 8	• 9	• 10	• 11
I Female	80	150	634	742	603	335	241	276	248	136	478
Male	80	172	576	584	566	326	220	227	366	122	241
II Female	59	119	295	508	736	481					
Male	69	100	576	714	341						
III Female	80	163	244								
Male	92	71	92								

$$\ln \text{gutted wt} = -4.705 + 2.984 \ln \text{TL}$$
$$r^2 = 0.983 \quad n = 418$$

A covariate analysis indicated that the equation adequately described the length-weight relationship for both sexes ($P < 0.001$). In Regions I and II, growth in weight was lowest during the first year but increased steadily reaching maximum gain at age 4, except Region II females in which maximum weight increase occurred during the fifth year. Region III had the highest initial weight gain, but the rate of increase to maximum size, at age 3, was reduced. Annual weight increase was greater for females in Region I, although the age of maximum gain was the same for both sexes. In Region II, annual growth in weight was greater for males, but maximum growth was attained at an earlier age than for females.

Growth was described by the von Bertalanffy growth curve (Fig. 4), $L_t = L_\infty = (1 - \exp(-k\,(t - t_0))$. Parameters for the three regions are described in Table 5.

Von Bertalanffy growth curves were fit to mean back-calculated lengths for each sex in Region I and compared with the Hotelling T^2 test. Differences in growth parameters k, L_∞, and w_∞ were not significant between sexes ($P < 0.05$). The parameter t_0 was significantly different between sexes ($P < 0.05$), but the value of t_0 is not considered biologically revelant (Galluci and Quinn 1979). Therefore, growth in Region I could be described by a single set of growth

TABLE 5.—Von Bertalanffy growth parameters for weakfish, *Cynoscion regalis*, by region.

Region and sex	L_∞	t_0	k	w_∞
I: Male	82.8	0.056	0.28	5,309
Female	82.3	0.005	0.26	5,202
Both sexes	82.6	0.031	0.27	5,273
II	68.6	0.051	0.35	3,026
III	40.0	−0.500	0.55	608

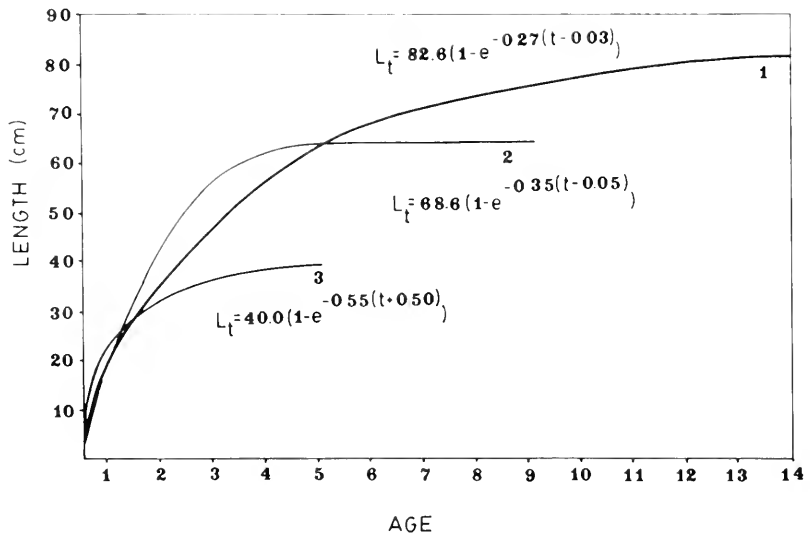

FIGURE 4.—Von Bertalanffy growth curve fitted to mean back-calculated lengths at age of weakfish, *Cynoscion regalis*, for Regions I-III (sexes combined).

parameters. No statistical comparisons of growth curves were made between regions because of the large variance around parameters in Regions II and III.

Historic Growth

Weakfish in the New York Bight showed a general increase in length at age between 1929, 1952, and 1980-81. Back-calculated lengths at age were compared using a Student's t-test with variances of the 1980-81 data applied to the historic data (Table 6). The application of the 1980-81 variances to the historic data provided a more sensitive test of differences than would have been otherwise possible. Literature values (Perlmutter et al. 1956) were significantly smaller ($P < 0.001$) than present mean lengths at age, with the exceptions that age 1 females and age 6 males of 1952 and age 1 males of 1929 were not significantly different from our values. After age 1, lengths at age of weakfish in 1980-81 were greater than in 1952, which were greater than in 1929. Maximum size was greatest in 1980-81 at 80 cm, followed by 64 cm in 1952 and 52 cm in 1929. Longevity was not consistent with maximum mean length at age. Weakfish in 1952 were not >6 yr old (male) while an 8-yr-old male was captured in 1929 and an 11-yr-old in 1980. Thus, larger but younger fish were caught in 1952 than in 1929, whereas 1980-81 fish were larger and older than those caught in 1929 or 1952.

Fishery Age Structure

Age-size composition of the commercial trawl fishery varied substantially with gear type and season. An age-length key was applied to randomly collected length frequencies to determine age structure of the fisheries in the Delaware Bay area. Spring (May-July) landings from midwater trawls consisted of fish from ages 1-10, with 85% of the catch being >55 cm and age 5. Fall catches (August-November) by otter trawls were primarily 1-yr-olds, 25-35 cm, with occasional fish as old as 7 yr (Fig. 5). Young-of-the-year fish (<20 cm) were removed from the otter trawl catches by culling. Size-frequency data of juvenile weakfish from NMFS groundfish surveys were compared with commercial fisheries data. Collections were made with otter trawls similar to those used in the commercial fisheries. The analysis of available NMFS length-frequency data was limited to areas north of Chesapeake Bay (Fig. 5). In July and August 1979, the data were primarily 1-yr-old weakfish, 20-30 cm. In September-October samples of 1978 and 1979, young-of-the-year weakfish predominated. Two length modes of young-of-the-year weakfish <20 cm were evident, undoubtedly because the juveniles were composed of individuals resulting from several spawning waves of adults (Daiber 1957; Shepherd 1982). This bimodality of juvenile lengths is reduced to a single mode by age 1, because of growth convergence or high mortality of the smaller juveniles during migration.

TABLE 6.—Comparison of 1929 and 1952 growth of weakfish, *Cynoscion regalis*, in the New York Bight to 1980-81 values for each sex. Historic mean values weighted by N.

Age	$\bar{x}_{1929}$	N	$\bar{x}_{1952}$	N	$\bar{x}_{1980\text{-}81}$	N	s	t_{1929}	t_{1952}
MALES									
1	20	209	21	341	20	373	3.47	1.001	2.308*
2	26	174	28	136	31	303	6.48	8.111***	7.375***
3	30	124	36	47	46	181	6.59	27.764***	9.357***
4	32	104	48	11	56	78	5.43	29.390***	4.690***
5	36	89	56	4	63	51	4.75	32.003***	2.841**
6	41	67	64	2	66	35	3.32	36.127***	1.895
7	44	35	—		66	17	2.67	27.999***	
8	52	10	—		68	9	2.65	12.580***	
FEMALES									
1	19	190	20	401	20	332	3.53	3.427***	−0.764
2	26	172	28	115	32	269	6.87	8.799***	5.489***
3	30	132	36	49	48	187	7.15	22.148***	10.285***
4	34	114	48	13	58	95	6.07	28.505***	5.390***
5	38	91	56	5	64	63	5.43	28.899***	3.213***
6	41	56	64	1	68	50	4.47	30.922***	5.113***
7	43	29	—		70	31	4.51	23.543***	
8	44	7	—		72	23	4.73	13.852***	

*** significant differences $P < 0.001$.
** significant differences $P < 0.01$.
* significant differences $P < 0.05$.

DISCUSSION

Geographic variation in growth with a general tendency toward larger sizes in cooler latitudes is a common occurrence among many marine organisms (Wimpenny 1941). This phenomenon is particularly well illustrated in some marine invertebrates such as the Pacific cockle, *Clinocardium nuttalli* (Conrad) (= *Cardium corbis*) (Weymouth and Thompson 1930). Clinal variations in size have also been described for fishes such as Atlantic menhaden, *Brevoortia tyrannus* (June and Reintjes 1959), American shad, *Alosa sapidissima* (Leggett and Carscadden 1978), and croaker, *Micropogonias undulatus* (White and Chittenden 1977).

Weakfish follow a similar pattern of increasing size toward the northern end of the range. Weakfish in Region I (Cape Cod, Mass., to Ocean City, Md.) were largest at each age, and attained a greater maximum size and longevity. Growth of weakfish in Region III (Virginia Beach, Va., to Cape Fear, N.C.) was lowest, and fish from Chesapeake Bay, Region II (Ocean City, Md., to Virginia Beach, Va.), had intermediate growth. There was a discrepancy of 49 cm and 7 yr between the largest northern and southern fishes.

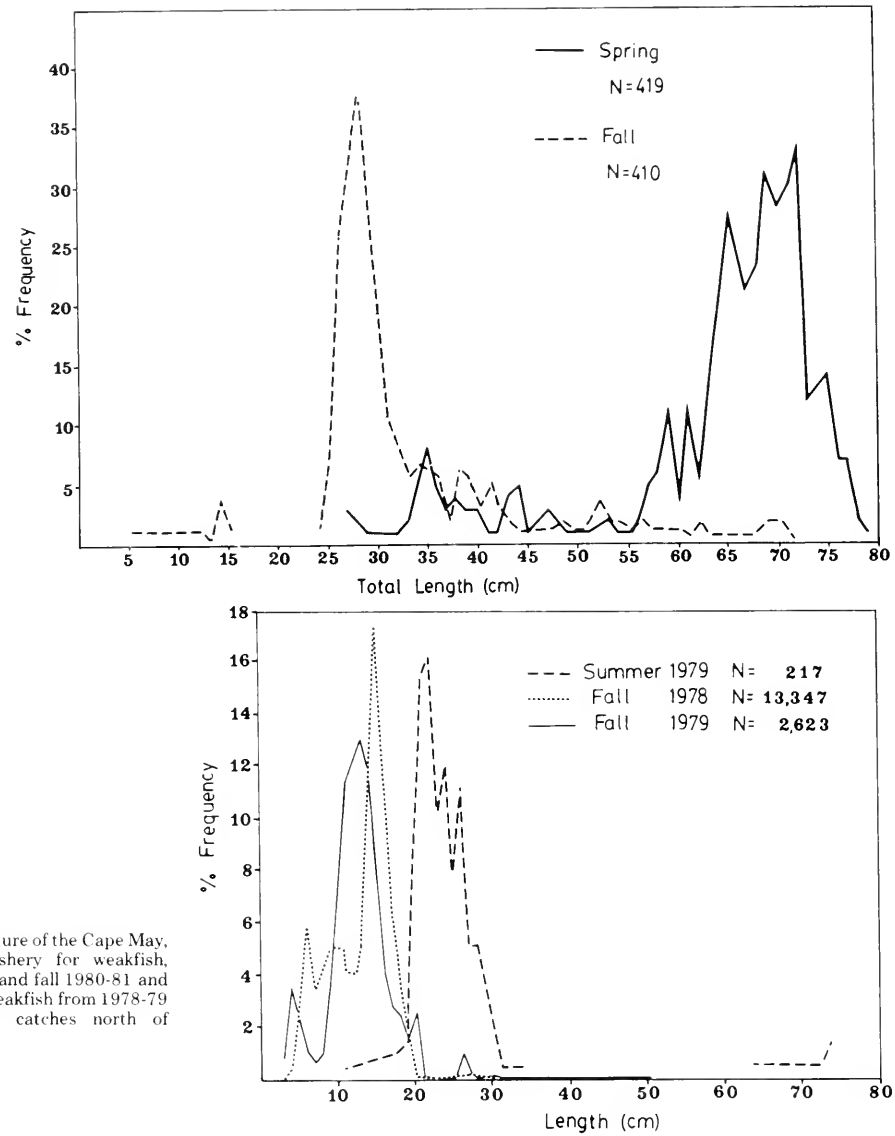

FIGURE 5.—(Top) size structure of the Cape May, N.J., commercial trawl fishery for weakfish, *Cynoscion regalis*, in spring and fall 1980-81 and (bottom) size structure of weakfish from 1978-79 NMFS groundfish survey catches north of Chesapeake Bay.

Merriner's study of weakfish (1973) in North Carolina estuaries found only small weakfish, few greater than age 4 and 44 cm which agrees well with our results. Nesbit (1954) and Perlmutter et al. (1956) also noted larger weakfish at northern latitudes.

Growth variations have been attributed to such factors as density-dependent mechanisms, temperature (Nikolsky 1963), variable energetic costs of migration and spawning (Glebe and Leggett 1981), and variable prey availability (Jones and Johnston 1977). Weakfish seasonal migrations occur in conjunction with movements of the 16°-24°C isotherms (G. Shepherd, unpubl. data); therefore, annual variation in temperature encountered by fish in the three regions is inadequate to account for the noted growth differences. We know of no data to indicate that weakfish density varies enough between regions to create drastic growth variations by the compensatory mechanism, although the density of all fish species could be a factor.

Glebe and Leggett (1981) have shown that growth variations can result if fish in different regions are required to make varying energetic commitments between gonad and somatic growth and seasonal

migration. Presumably, seasonal migrations to take advantage of ephemeral resources (Morse 1980) must be completed in a limited time, and longer migrations would require greater energy reserves. Because swimming speed is a function of body size (Marshall 1966), larger (faster growing) fish would be better able to bear the high energy cost and complete the migration, and would thus be favored by selection. However, the penalty imposed by increased somatic growth to cope with migration would be decreased annual gonad growth and fewer gametes produced annually. Therefore, the life history strategy of migratory fish might be to assure survival by varying the energetic commitment between somatic and gonad growth according to migration cost.

These factors may explain much of the geographic variation in weakfish growth. The seasonal movements of weakfish follow a northward and inshore route in spring to spawning grounds, and feeding continues while inshore during summer and early fall before migrating offshore in mid to late fall to southern overwintering areas. The energy required for migration of northern fish to southern waters would be greatest due to the distance traveled. Therefore, northern fish emphasize somatic growth and longevity to maximize chances of surviving migration and producing gametes. Increased chances of survival for larger individuals and greater longevity result in an increased number of spawning opportunities, to offset the losses in annual gonad production. By increasing lifetime spawning frequency, this strategy has the added benefit of increasing chances for survival of gametes introduced into less environmentally predictable northern estuaries. In contrast, southern fish have little distance to migrate, so the energetic requirements for the journey are proportionately less. Because a smaller size is less of a handicap in migration, the growth strategy is shifted to increased gonad growth. This is indicated in the greater fecundities at length for southern fish (Shepherd and Grimes[5]). Greater emphasis on reproduction may increase adult mortality (Gerking 1959), causing the decreased longevity we observed in southern weakfish. This tradeoff between gonadal and somatic growth should not become effective until the onset of maturity. This is, in fact, the case in weakfish, as growth differences between regions become evident only after age 1, which is the approximate age at maturity (Merriner 1973). It should be noted that the cumulative gamete production for these two life history strategies is approximately the same (Shepherd and Grimes footnote 5), thus the size differences between northern and southern weakfish do not appreciably alter the reproductive potential of the species.

Growth of southern-origin weakfish may also be limited by the availability of certain prey items. Jones and Johnston (1977) wrote that fishes pass through a series of food niches during a lifetime, and the upper limits of growth are determined in part by the optimal size for exploiting the final food niche available in a given environment. Prey availability may limit maximum size of most southern weakfish to 40-50 cm. Food habit studies by Welsh and Breder (1923) and Merriner (1975) have shown that weakfish shift prey preference to menhaden at about 35-40 cm. This size range approaches the maximum sizes of weakfish for southern waters (L_∞ = 40 cm). Stratification of menhaden by age-size with latitude has been documented along the east coast, with 1-yr-olds predominant in the south and older, larger fish further north (June and Reintjes 1959). The implication is that net energy for southern weakfish feeding on small menhaden is insufficient for growth beyond $\simeq$40 cm. Thus maximum size limitation of weakfish is imposed by the energy available in the final food niche. The energy saved from short migrations may be utilized to maximize reproduction before reaching the size limitations imposed by feeding. Northern fish, on the other hand, may migrate north and take advantage of a final food niche that allows superior growth.

The variations in growth may result from differences between genetically distinct groups. Our findings of three or more or less distinct body-scale relationships in Regions I, II, and III may indicate different stocks (Rojo 1977). Similar stock separations have been suggested by Perlmuter et al. (1956) and Seguin (1960). However, the body-scale relations in our study varied clinally, and such morphological characters have been shown to display clinal variation with no apparent genetic discontinuity (Katz et al. 1983). The genetic basis of these growth differences remains a topic for future research.

Historic Variations in Growth

Weakfish populations have fluctuated widely over the last several decades, and growth rates have varied similarly, but most noticeably since the population decline of the 1960's. For example, in weakfish from the New York Bight, age 4 females in 1929 were 34 cm compared with 48 cm in 1952 and 58 cm

[5]Shepherd, G., and C. B. Grimes. In prep. Reproduction of weakfish, *Cynoscion regalis*, in the New York Bight and evidence for geographically specific life history characteristics. Unpubl. manuscr. Rutgers University, New Brunswick, NJ 08903.

in 1980 (Perlmutter et al. 1956). Longevity has changed from 8 yr in 1929 and 6 yr in 1952 to 11 yr in 1980. Average weight per fish in recreational catches has likewise increased from 480.8 g in 1960 to 1,510.5 g in 1974 (Wilk 1979).

The trend toward increasing growth rate may be a manifestation of increased growth following the severe population decline of the 1960's. Botsford (1981) demonstrated with several species that individual growth rates will increase (compensatory growth) following a severe decline in abundance, and when the population is allowed to recover it will respond by maintaining increased growth rates and slightly lower biomass, but never regain the abundance levels experienced previous to the decline.

Present abundance of weakfish in the Middle Atlantic Bight seems to be approaching levels comparable to the predecline period of the 1950's (Murawski 1977[6]; Wilk 1981), while growth rates have increased over the same timespan (Table 5). These trends in abundance, the severe decline followed by a recovery, and changes in individual growth rates have followed the predicted pattern of density-induced growth compensation. Circumstantial evidence for Delaware Bay density-dependent growth changes has also been noted by Seagraves (1981).

Length-frequency data of fisheries in the Delaware Bay region suggest that current levels of exploitation may lead to decline in weakfish abundance. Commercial midwater trawl and recreational fisheries put greatest emphasis on catching the largest, and consequently the most fecund, fish during the spring fishing season. In the fall, young-of-the-year weakfish are recruited into the otter trawl fishery and constitute a large percentage of the catch, as indicated by the NMFS length-frequency data. These small fish have no market value, so are discarded from the commercial catches and likely suffer a high mortality. Therefore, fishing results in a reduction of the present and future spawning stock. It remains to be seen whether this reduction in spawning stock will cause a reduction of the weakfish population, reminiscent of the 1950's and 1960's.

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INTERRELATIONSHIPS BETWEEN JUVENILE SALMONIDS AND NONSALMONID FISH IN THE COLUMBIA RIVER ESTUARY

GEORGE T. MCCABE, JR., WILLIAM D. MUIR, ROBERT L. EMMETT, AND JOSEPH T. DURKIN[1]

ABSTRACT

Interrelationships between juvenile salmonids—coho salmon, *Oncorhynchus kisutch*; chinook salmon, *O. tshawytscha*; and steelhead, *Salmo gairdneri*—and nonsalmonid fish were studied in the Columbia River estuary during 1980. Nonsalmonid species were numerically dominant in pelagic and intertidal areas of the lower estuary. In pelagic and intertidal areas of the upper estuary, juvenile salmonids, particularly subyearling chinook salmon were proportionally important. Nonsalmonid species commonly associated with juvenile subyearling chinook salmon included American shad, *Alosa sapidissima*; Pacific herring, *Clupea harengus pallasi*; northern anchovy, *Engraulis mordax*; surf smelt, *Hypomesus pretiosus*; longfin smelt, *Spirinchus thaleichthys*; peamouth, *Mylocheilus caurinus*; threespine stickleback, *Gasterosteus aculeatus*; shiner perch, *Cymatogaster aggregata*; Pacific staghorn sculpin, *Leptocottus armatus*; and starry flounder, *Platichthys stellatus*. Commonly associated species were generally defined only in reference to subyearling chinook salmon because, of all the juvenile salmonids, subyearling chinook salmon were clearly the most abundant and available in sizable numbers for the longest time. Predation on juvenile salmonids by nonsalmonids and other juvenile salmonids was insignificant. Significant diet overlap occurred among subyearling and yearling chinook salmon, coho salmon, and steelhead during the spring. American shad, threespine stickleback, and starry flounder had significant diet overlaps with juvenile salmonids.

The Columbia River system is an important producer of Pacific salmon (*Oncorhynchus* spp.) and steelhead, *Salmo gairdneri*, in North America (Chaney and Perry 1976; Bohn and Stockley 1981). Salmonids (wild and hatchery) originating from the Columbia River system provide fish for both river and ocean fisheries (recreational and commercial). Historically, the world's largest migration of adult chinook salmon, *O. tshawytscha*, occurred in the Columbia River (Van Hyning 1973). Dam construction, poor logging and agricultural practices, overfishing, and pollution have severely reduced adult salmonid returns to the Columbia River system. Efforts to improve the runs, such as large hatchery releases of juveniles, collection and transportation of juveniles at selected dams, and the installation of dam spillway deflectors to reduce nitrogen supersaturation have enhanced adult returns, but failed to increase them to historical levels. There is concern by some resource managers that significant losses of juvenile salmonids may be occurring in the ocean and/or estuary. They feel these losses may be due to predation or competition for the same food organisms by nonsalmonid fish.

No published information is known to exist on the interrelationships between juvenile salmonids and nonsalmonid fish throughout the Columbia River estuary; this paper helps fill that void. Our objectives were to document the following: 1) The proportional abundance of salmonids and nonsalmonids in various estuarine habitats, 2) the nonsalmonid fish species associated with juvenile salmonids, 3) the length characteristics of nonsalmonids and juvenile salmonids, 4) predation on salmonids, and 5) prey consumption and possible competition between salmonids and nonsalmonids in similar habitats.

METHODS AND MATERIALS

Study Area

The study was carried out in the Columbia River estuary between River Kilometers 3 and 62 (Fig. 1). The estuary is a drowned river mouth with delta islands in the upper portion. Salinity intrusion in the estuary fluctuates considerably because of changing river flows and tide conditions. Vertical salinity gradients exist in parts of the estuary, with the highest salinities in deep water near the bottom (Neal 1972; McConnell et al. 1981).

We divided the estuary into upper and lower areas (Fig. 1); these two areas were further divided into pelagic and intertidal habitats. Pelagic and intertidal areas of the upper estuary were classified as freshwater. The lower estuary was classified as a mixed zone, with salinities ranging from 0 to 33‰ depend-

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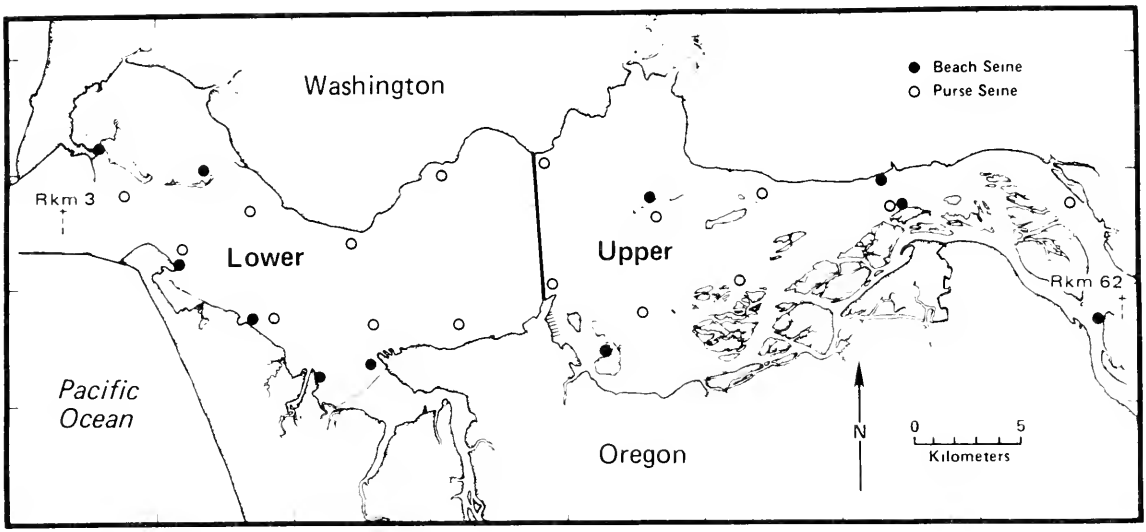

FIGURE 1.—Sampling sites in the upper and lower areas of the Columbia River estuary.

ing upon distance from the river mouth, river flow, and tidal stage. Saline water penetrates along the river channels into sections of the upper estuary at times; however, in most instances, our sampling was associated with fresh water. Habitats we called intertidal often consisted of both intertidal and some subtidal areas.

Sampling

Two beach seines were used to sample in intertidal areas. The seines were 50 m long; one was 4.0 m and the other 3.4 m deep at their deepest points. Both nets contained panels with the following mesh sizes (stretched): 19.0, 12.7, and 9.5 mm. Knotless mesh was used in the bunt to minimize scaling of fish (this was also true in the purse seine). The fishing method was similar to that described by Sims and Johnsen (1974). Beach seining was done at various tide stages.

A 200 m long by 9.8 m deep purse seine was employed to collect pelagic species. Mesh sizes (stretched) in the seine included 19.0 and 12.7 mm. Purse seine sets were made for 5 min in an upstream direction during various stages of the tide.

Collapsible hoop nets and trawl nets were also used, but captured comparatively few salmonids.

Monthly sampling throughout the estuary was performed from February 1980 through January 1981. The effort involved 11 beach seine and 16 purse seine sites (Fig. 1). Five intertidal sampling stations (beach seine) were in the upper estuary and six in the lower. Eight of the pelagic sampling sites (purse seine) were in the upper estuary and eight in the lower. Before each sampling effort, water temperature, conductivity, and salinity were recorded using a Beckman,[2] Model RS5-3 salinometer and probe.

Fish were identified and enumerated, and a random subsample of up to 50 fish of each species or stock was measured to the nearest millimeter (total length) and weighed to the nearest gram. Subyearling and yearling chinook salmon were separated using length-frequency histograms. The number and total weight were recorded for those species with over 50 individuals in a single sample effort.

A representative subsample of five individuals of each species was selected from each purse seine and beach seine set for stomach analysis. Fish taken for stomach analysis were injected with a 20% buffered Formalin solution soon after capture to preserve stomach contents. Injected fish were weighed and measured at the laboratory. Stomachs were then removed from the fish and placed in vials containing 70% ethyl alcohol.

Fish stomach contents were examined in a watch glass using a 10× binocular dissecting microscope. Food organisms were identified to the lowest practical taxon and weighed to the nearest 0.0001 g after blotting and air drying for 10 min.

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

Data Analysis

Because subyearling chinook salmon were the most frequently caught salmonids and were available in sizable numbers from March through September, we chose to compare all other species (including other juvenile salmonid species) in relation to them. We assigned one of three abundance categories: Common, occasional, or uncommon. A common species occurred in 50% or more of the sampling efforts (in which juvenile salmon were captured) and equaled 50% or more of the total number of subyearling chinook salmon captured in that habitat. An occasional species occurred in more than 20% of the sampling efforts and equaled more than 10% of the total number of subyearling chinook salmon. An uncommon species occurred in 20% or less of the sampling efforts and equaled 10% or less of the total number of subyearling chinook salmon. Fish were not separated by age-classes, except yearling and subyearling chinook salmon.

Food habit data from April through September were combined into two periods—spring (April through June) and summer (July through September). Diet descriptions and comparisons are not presented for February, March, and October. Principal prey items for each fish species were determined by calculating the Index of Relative Importance (IRI) modified from Pinkas et al. (1971):

$$\text{IRI} = (N + W)F$$

where N = numerical percentage of a prey item
W = weight percentage of a prey item
F = frequency of occurrence percentage of a prey item.

Any prey item with an IRI value >50 was considered a principal prey for a given species. Digested food was not included in this calculation.

To assess possible food competition, diet overlap of associated species was measured using the formula developed by Morisita (1959) and modified by Horn (1966):

$$\hat{C}_\lambda = \frac{2 \sum_{i=1}^{s} X_i \cdot Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

where $\hat{C}_\lambda$ = overlap coefficient
s = number of food categories
X_i = proportion of the total diet of fish species X contributed by food category i (by biomass)
Y_i = proportion of the total diet of fish species Y contributed by food category i (by biomass).

Values of $\hat{C}_\lambda$ range from 0 to 1, with 0 indicating no overlap and 1 indicating complete diet overlap. A value of 0.6 is considered significant diet overlap (Zaret and Rand 1971).

RESULTS

Juvenile chinook salmon (subyearling and yearling); coho salmon, *O. kisutch*; and steelhead were the most common salmonids in the estuary (Table 1). Subyearling chinook salmon were the most abundant and were available in quantity for the longest time (March through September). Catches of juvenile chum salmon, *O. keta*; sockeye salmon, *O. nerka*; and cutthroat trout, *S. clarki*, were small; consequently, they will not be included in the analysis of intercompetition. The low incidences of these species indicate their small estuarine populations when compared with steelhead and chinook and coho salmon.

TABLE 1.—Numbers of juvenile salmonids collected in four habitats of the Columbia River estuary from March to September 1980.

	Habitat				
	Pelagic		Intertidal		
Species	Upper estuary	Lower estuary	Upper estuary	Lower estuary	Total
Chum salmon	1	0	16	4	21
Coho salmon	695	617	71	12	1,395
Sockeye salmon	15	14	0	0	29
Chinook salmon					
subyearling	1,858	1,627	1,816	730	6,031
yearling	512	243	29	4	788
Cutthroat trout[1]	16	9	7	0	32
Steelhead	278	253	1	1	533

[1]Includes some adults.

Proportional abundances of juvenile chinook salmon (subyearling and yearling), coho salmon, steelhead, and nonsalmonids are shown by month in Figure 2. If fewer than 10 subyearling chinook salmon were collected, then no comparisons were made. In pelagic areas of the upper estuary, juvenile salmonids were numerically important from April through August, with a substantial decline in September. Yearling chinook salmon were an important part of the catch in April and May, coho salmon in May and June, and steelhead in May. Subyearling chinook salmon were important from May through August.

In the pelagic area of the lower estuary, nonsalmonids were clearly numerically dominant. Periodically this portion of the estuary contained large schools of marine fish, such as Pacific herring, *Clupea*

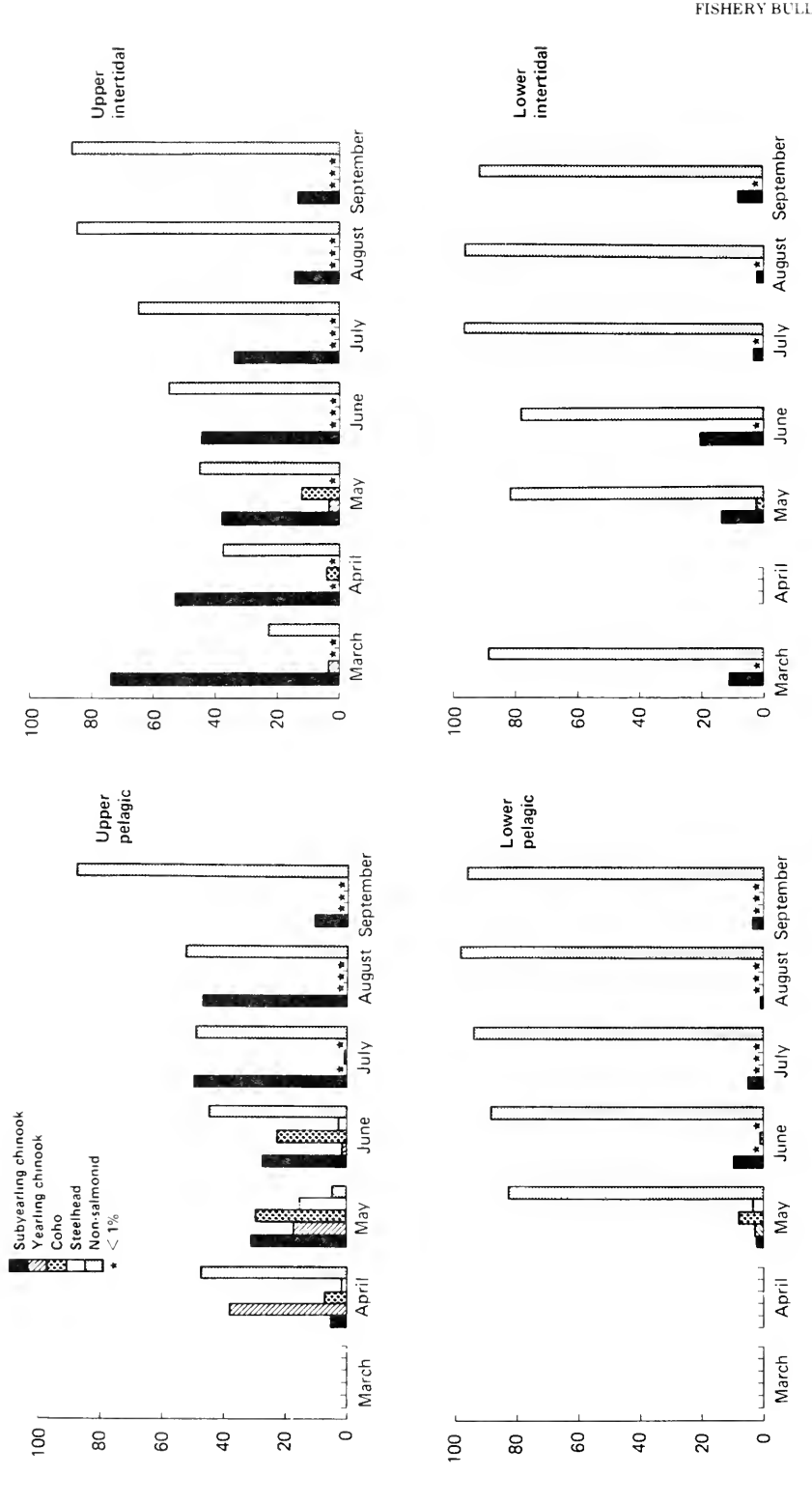

FIGURE 2.—Proportional abundances of fish collected in four habitats of the Columbia River estuary in 1980.

harengus pallasi, and northern anchovy, *Engraulis mordax*.

In intertidal areas of the upper estuary, subyearling chinook salmon was the only abundant salmonid species; its importance was considerably reduced by August.

Catches in intertidal areas of the lower estuary were dominated by nonsalmonids; however, in the intertidal areas, subyearling chinook salmon were more important than in the pelagic zone. Although large numbers of salmonids were captured in the pelagic and intertidal areas of the lower estuary (Table 1), their importance was masked by the large number of marine nonsalmonids.

Thirteen species including yearling chinook salmon were commonly associated with subyearling chinook salmon during at least one of the months in the two seasonal periods in the Columbia River estuary (Table 2).

Juvenile coho salmon were captured primarily in pelagic areas; however, they were occasionally collected in intertidal areas (Table 1). Yearling chinook salmon and steelhead in particular were almost exclusively in pelagic areas.

Length characteristics of subyearling chinook salmon and the commonly associated species are shown in Table 3. Most common species in the pelagic zone of the upper estuary were longer than the subyearling chinook salmon, whereas in the pelagic zone of the lower estuary many of the species were shorter or the same. In the intertidal areas of the upper estuary, only starry flounder, *Platichthys stellatus*; threespine stickleback, *Gasterosteus aculeatus*; peamouth, *Mylocheilus caurinus*; and American shad, *Alosa sapidissima*, were commonly associated with subyearling chinook salmon and all of their mean lengths were shorter. In intertidal areas of the lower estuary, many of the common species were

TABLE 2.—Fish associated with subyearling chinook salmon in the Columbia River estuary from March through September 1980. (C = commonly, O = occasionally, and U = uncommonly associated with subyearlings; * = commonly associated species; J = juveniles; and A = adult.)

	March-June 1980				July-September 1980			
	Pelagic		Intertidal		Pelagic		Intertidal	
Species	Upper estuary	Lower estuary	Upper estuary	Lower estuary	Upper estuary	Lower estuary	Upper estuary	Lower estuary
River lamprey, *Lampetra ayresi*	—	U	—	—	—	U	—	U
Pacific lamprey, *Lampetra tridentata*	—	U	—	U	—	—	—	—
White sturgeon, *Acipenser transmontanus*	—	U	—	U	U	U	—	—
*American shad, *Alosa sapidissima*	C	C	U	U	C	C	C	U
*Pacific herring, *Clupea harengus pallasi*	—	C	—	O	O	C	—	C
*Northern anchovy, *Engraulis mordax*	—	C	—	U	—	C	—	O
Chum salmon (J), *Oncorhynchus keta*	U	—	U	U	—	—	—	—
*Coho salmon (J), *Oncorhynchus kisutch*	C	C	O	O	U	U	U	U
Coho salmon (A)	—	—	—	—	U	U	—	—
Sockeye salmon (J), *Oncorhynchus nerka*	U	U	—	—	—	—	—	—
*Chinook salmon (Yr), *Oncorhynchus tshawytscha*	C	C	U	U	U	—	U	—
Chinook salmon (A)	—	U	U	—	U	U	—	—
Cutthroat trout, *Salmo clarki*	U	U	—	—	U	U	U	—
*Steelhead (J), *Salmo gairdneri*	C	C	U	U	—	U	—	—
Steelhead (A)	—	—	U	—	—	—	U	—
Whitebait smelt, *Allosmerus elongatus*	—	U	—	—	—	O	—	—
*Surf smelt, *Hypomesus pretiosus*	U	C	—	C	—	O	—	C
*Longfin smelt, *Spirinchus thaleichthys*	U	C	—	U	C	C	—	—
Eulachon, *Thaleichthys pacificus*	—	—	U	O	—	—	—	—
Common carp, *Cyprinus carpio*	—	—	U	U	U	—	U	—
*Peamouth, *Mylocheilus caurinus*	C	U	U	U	O	O	C	O
Northern squawfish, *Ptychocheilus oregonensis*	U	—	U	—	—	—	U	—
Largescale sucker, *Catostomus macrocheilus*	U	—	U	U	—	—	O	U
Pacific hake, *Merluccius productus*	—	U	—	—	—	—	—	—
Pacific tomcod, *Microgadus proximus*	—	U	—	—	U	O	—	U
*Threespine stickleback, *Gasterosteus aculeatus*	C	O	O	C	O	O	C	O
Yellow perch, *Perca flavescens*	—	—	—	—	—	—	—	U
Redtail surfperch, *Amphistichus rhodoterus*	—	U	—	—	—	U	—	U
*Shiner perch, *Cymatogaster aggregata*	—	C	—	C	O	C	O	C
Walleye surfperch, *Hyperprosopon argenteum*	—	U	—	—	—	—	—	—
Silver surfperch, *Hyperprosopon ellipticum*	—	U	—	—	—	—	—	U
Pile perch, *Rhacochilus vacca*	—	—	—	—	—	U	—	—
Pacific sandfish, *Trichodon trichodon*	—	U	—	—	—	—	—	—
Snake prickleback, *Lumpenus sagitta*	—	U	—	—	—	U	—	U
Lingcod, *Ophiodon elongatus*	—	U	—	—	—	—	—	—
Prickly sculpin, *Cottus asper*	—	—	U	U	U	U	U	U
*Pacific staghorn sculpin, *Leptocottus armatus*	U	U	O	C	U	O	O	C
Speckled sanddab, *Citharichthys stigmaeus*	—	—	—	—	—	—	—	U
Butter sole, *Isopsetta isolepis*	—	—	—	O	—	—	—	—
English sole, *Parophrys vetulus*	—	—	—	O	—	—	—	O
*Starry flounder, *Platichthys stellatus*	O	U	C	C	O	O	C	C
Sand sole, *Psettichthys melanostictus*	—	U	—	U	—	U	—	U

TABLE 3.—Total length (mm) characteristics of subyearling chinook salmon and commonly associated species captured in four habitats of the Columbia River estuary in 1980. N = total number captured.

Species	March			April			May			June			July			August			September		
	$\bar{X}$	2SE	N	$\bar{X}$	2SE	N	$\bar{X}$	2SE	N	$\bar{X}$	2SE	N	$\bar{X}$	2SE	N	$\bar{X}$	2SE	N	$\bar{X}$	2SE	N
Upper pelagic																					
Subyearling chinook				86	2.2	31	100	0.8	493	95	2.0	205	100	1.6	557	128	1.8	366	119	1.6	203
Yearling chinook				178	3.8	210	149	2.6	278												
Coho				139	4.4	41	147	1.6	469	145	2.1	168									
Steelhead							203	4.2	246												
American shad										187	11.8	173				236	10.0	230	186	12.2	260
Longfin smelt																			97	3.4	710
Peamouth										194	10.2	108									
Threespine stickleback				55	1.6	177															
Lower Pelagic																					
Subyearling chinook							102	1.6	138	103	1.2	696	104	1.6	444	126	2.4	216	125	2.4	122
Yearling chinook							148	2.4	195												
Coho							149	1.4	509												
Steelhead							207	3.6	234												
American shad							172	7.2	287							239	4.0	567	242	9.6	87
Pacific herring							152	2.6	4,264	153	4.2	721	114	4.2	944	108	2.8	8,331	107	3.2	1,366
Northern anchovy										149	1.8	4,530				142	3.0	2,357	141	5.2	1,386
Surf smelt							83	5.8	107												
Longfin smelt							100	2.8	245	111	1.6	660	83	2.8	5,164	93	4.2	176			
Shiner perch							105	3.8	150				108	2.4	357	94	4.0	368	78	3.2	83
Upper intertidal																					
Subyearling chinook	69	2.0	214	77	2.6	136	85	2.4	181	75	1.6	709	82	1.4	303	98	1.8	112	125	2.6	161
American shad																			62	1.6	270
Peamouth																71	6.0	242	88	6.2	232
Threespine stickleback																42	1.6	156	49	1.2	252
Starry flounder										49	3.6	725	56	5.6	423	57	2.8	237	71	3.8	132
Lower intertidal																					
Subyearling chinook	73	3.0	18				92	2.6	58	75	1.2	405	85	2.2	192	97	4.0	28	120	5.8	25
Pacific herring													74	1.4	569	93	1.6	156			
Surf smelt										86	1.2	428				119	4.6	90			
Threespine stickleback	53	2.6	19				55	1.6	37												
Shiner perch										105	3.8	504	64	3.2	3,960	70	3.0	649	73	1.4	148
Staghorn sculpin	58	10.2	22				58	2.4	186							92	11.0	17	100	4.2	22
Starry flounder	138	14.4	89				118	9.2	89							105	14.2	60	100	5.6	82

shorter, or no longer than, subyearling chinook salmon.

About 5,000 stomachs from 50 species of fish collected from February through October 1980 were analyzed. There were only two predations on juvenile salmonids—two yearling chinook salmon each ate a subyearling chinook salmon. Juvenile subyearling chinook salmon preyed on nonsalmonid fish, chiefly in the lower estuary. Nonsalmonid fish consumed by subyearlings included Pacific sand lance, *Ammodytes hexapterus*; northern anchovy; longfin smelt, *Spirinchus thaleichthys*; and whitebait smelt, *Allosmerus elongatus*. Principal prey items accounted for an average of 93% of the diet biomass for all fish species with a range of 53-100%. Principal prey items of juvenile salmonids and commonly associated nonsalmonids were invertebrates, chiefly crustaceans (Figs. 3, 4); fish were eaten but they were never the only prey.

Figures 5 and 6 show the degree of diet overlap between salmonids and commonly associated species. In the pelagic areas during spring, all the salmonids except steelhead (upper pelagic) had significant diet overlap values ($\geq$0.6). Salmonid species had significant diet overlap values with American shad in the lower estuary and threespine stickleback in the upper estuary. In the intertidal areas during spring, significant diet overlap occurred only between subyearling chinook salmon and starry flounder. Significant diet overlap in the spring was primarily due to the importance of *Corophium salmonis* and *C. spinicorne* as prey items. In summer there was no significant fish diet overlap.

On 18 May 1980, Mount St. Helens erupted and deposited large amounts of volcanic ash and sediments into the Columbia River, thereby increasing the turbidity of the estuary. For a short time, the increased sediment loads and high turbidities reduced the amount and variety of food items eaten. By July 1980, turbidities returned to lower levels.

DISCUSSION

Some of the same species associated with juvenile chinook salmon in the Columbia River estuary were found in similar associations in other Pacific Northwest estuaries. Conley (1977), working in Everett Bay in Puget Sound, Wash., caught many shiner perch, *Cymatogaster aggregata*; Pacific staghorn sculpin, *Leptocottus armatus*; and starry flounder in intertidal areas along with juvenile chinook salmon. Myers (1980), working in Yaquina Bay,

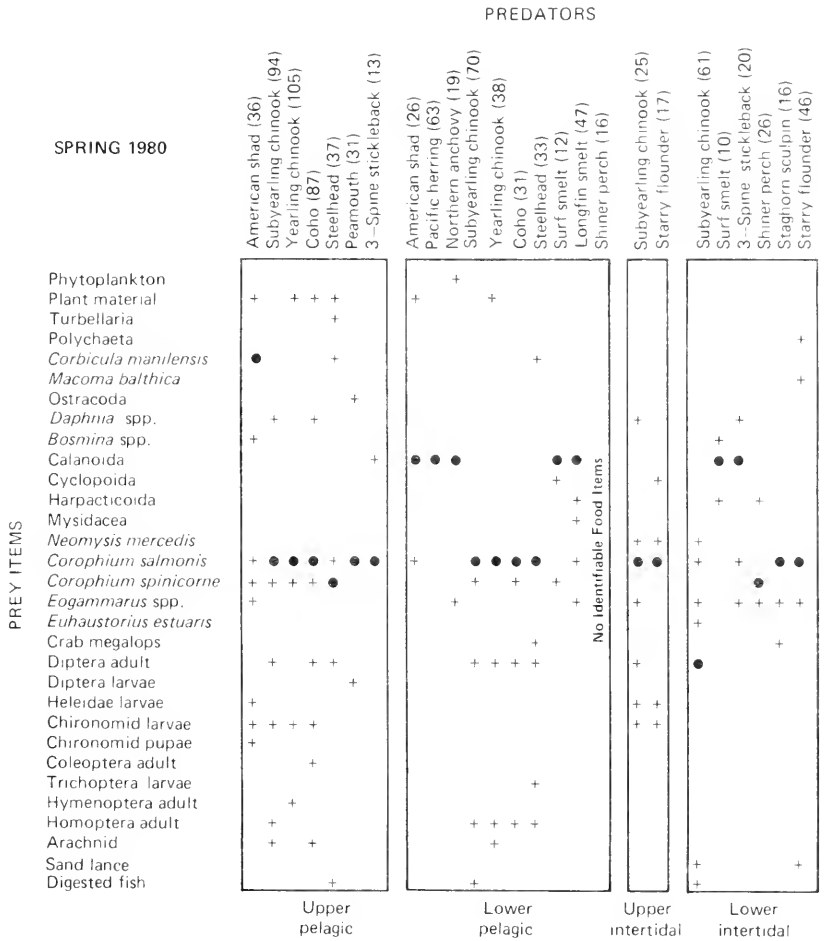

FIGURE 3.—Principal prey items of juvenile salmonids and commonly associated nonsalmonids captured in four habitats of the Columbia River estuary during spring 1980. A principal prey item has an IRI value >50; the prey item with the highest IRI value for each species is indicated by a solid circle. Number of stomachs examined is shown in parentheses.

Oreg., found that Pacific herring, shiner perch, northern anchovy, and surf smelt, *Hypomesus pretiosus*, were abundant at her beach seine sites. Durkin et al.[3] found that shiner perch, Pacific herring, surf smelt, and northern anchovy were commonly associated with subyearling chinook salmon in intertidal areas of the lower Columbia River estuary.

Considering the nonsalmonid species commonly associated with subyearling chinook salmon and their size characteristics, nonsalmonid predation on subyearlings in the Columbia River estuary should be minimal. American shad, Pacific herring, surf smelt, longfin smelt, peamouth, threespine stickleback, and shiner perch are essentially invertebrate and/or plant eaters. Large Pacific staghorn sculpins and starry flounder could eat subyearling chinook salmon; however, the large individuals of these species are usually not found in intertidal areas of the estuary. Normally the large sculpins and flounders are found in deep demersal habitats of the Columbia River estuary. Although many researchers have studied the use of the estuarine areas as nursery and feeding areas for salmonids (Mason 1974; Levy and Levings 1978; Reimers et al. 1978; Sibert 1979; Healey 1980; Myers 1980), few have documented the food habits of associated nonsalmonid estuarine fish

[3]Durkin, J. T., S. J. Lipovsky, G. R. Snyder, and M. E. Tuttle. 1977. Environmental studies of three Columbia River estuarine beaches. Unpubl. manuscr., 78 p. Northwest and Alaska Fisheries Center Hammond Field Station, National Marine Fisheries Service, NOAA, P.O. Box 155, Hammond, OR 97121.

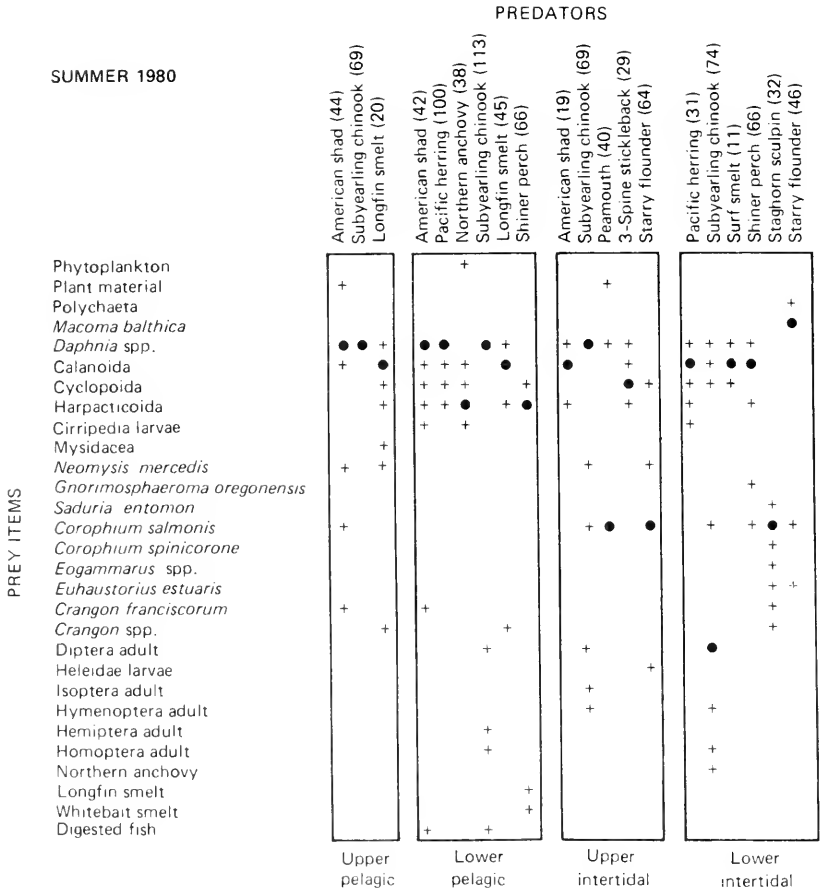

FIGURE 4.—Principal prey items of juvenile salmonids and commonly associated nonsalmonids captured in four habitats of the Columbia River estuary during summer 1980. A principal prey item has an IRI value >50; the prey item with the highest IRI value for each species is indicated by a solid circle. Number of stomachs examined is shown in parentheses.

that could prey on salmonid species. Dunford (1975, cited by Levy and Levings 1978) found Pacific staghorn sculpins feeding on salmonids.

Our sampling gear was less effective for capturing adults than juveniles; however, we feel that our samples indicate the relative importance of the various sized fish in the estuary. Larger fish, i.e., adult salmon, steelhead, and American shad, may have swum under or around the sides of the purse seines as we were sampling. Another possible sampling bias, at least in the lower estuary, was the tidal stage at which we sampled. Beach seining was not generally done at high tide because it was impractical due to beach configuration. Possibly more salmonid predators move into mixed intertidal areas during high tide. Even with all the possible biases, if there were any large populations of predators of juvenile salmonids in the estuary, we should have caught more than we did. The logical conclusion is that the estuary represents a sanctuary from fish predators for juvenile salmonids.

The food habits of salmonids differ from estuary to estuary. Unlike the Columbia River estuary where *C. salmonis* and *Daphnia* spp. were the primary prey, Myers (1980) found fish to be the primary prey for juvenile chinook and coho salmon in Yaquina Bay, Oreg. Although *C. salmonis* was important prey in the Sacramento-San Joaquin Delta, *Neomysis mercedis* was also important for juvenile chinook salmon (Sasaki 1966). In the Squamish River estuary, British Columbia, *N. mercedis* and *Anisogammarus* (= *Eogammarus*) *confervicolus* were the primary prey for juvenile chinook and coho salmon (Levy and Levings 1978). In the Sixes River estuary, Oreg., *C.*

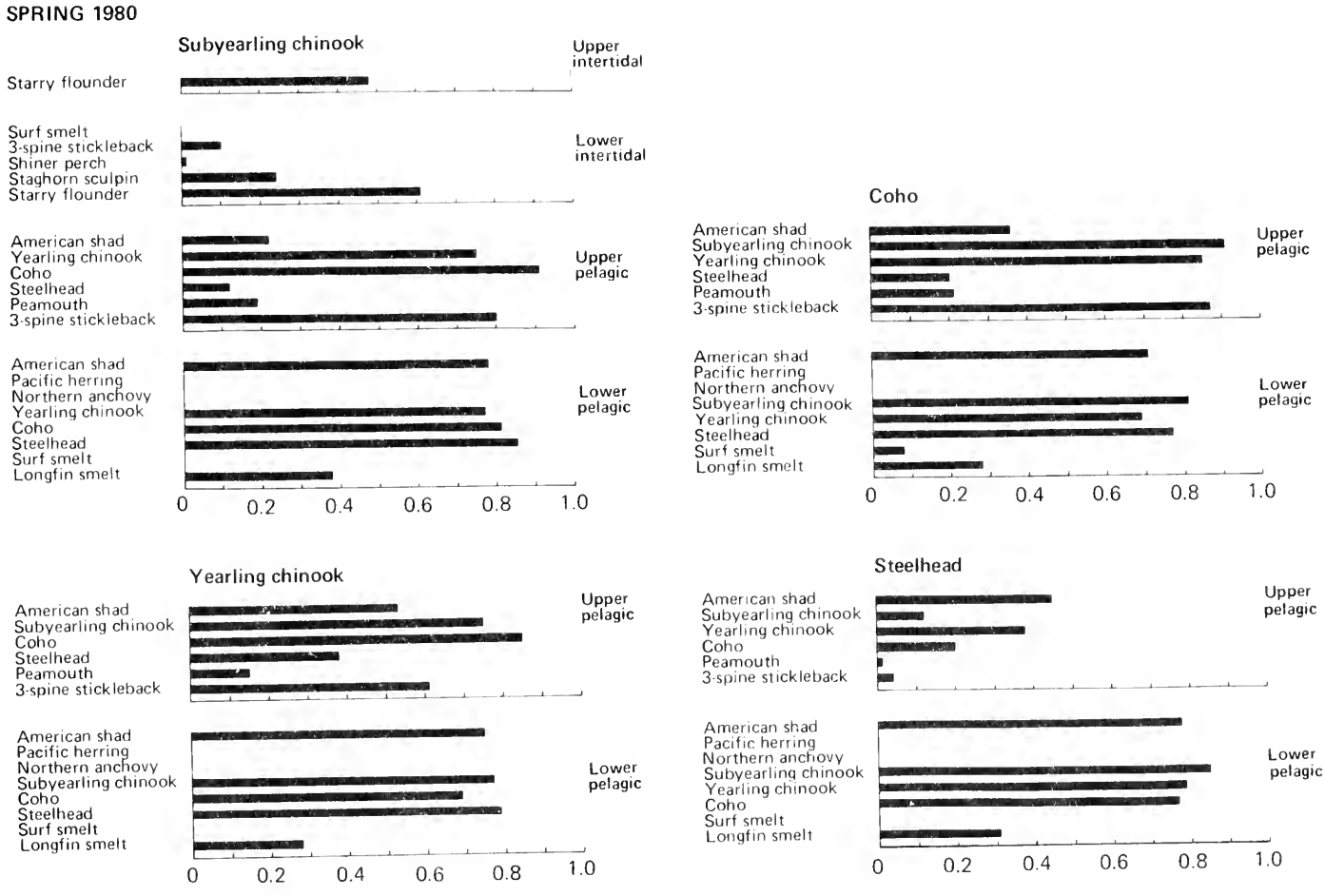

FIGURE 5.—Diet overlaps between juvenile salmonids and commonly associated species in the Columbia River estuary during spring 1980. Overlap values were calculated using Morisita's (1959) equation modified by Horn (1966).

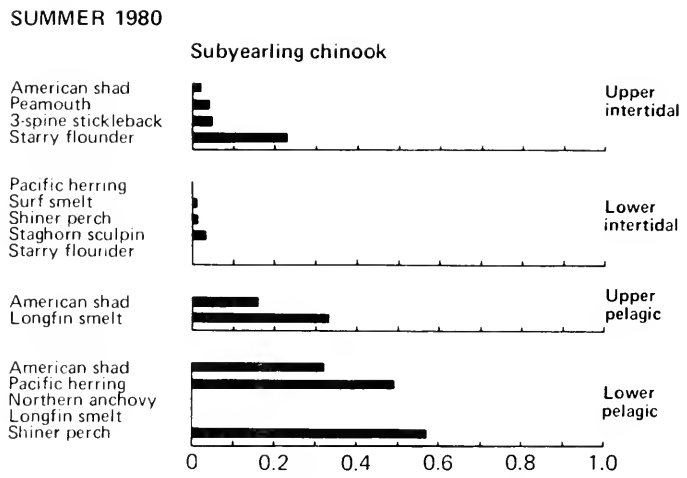

FIGURE 6.—Diet overlaps between subyearling chinook salmon and commonly associated species in the Columbia River estuary during summer 1980. Overlap values were calculated using Morisita's (1959) equation modified by Horn (1966).

spinicorne and *C. salmonis* were found to be important prey for juvenile chinook salmon (Reimers et al. 1978). Although the principal prey items differ in each estuary, the estuaries do provide important feeding habitat. Estuarine feeding and growth play an important role in salmonid and nonsalmonid life histories (McHugh 1967; Mason 1974; Levy and Levings 1978; Healey 1980).

Research indicates that at low prey abundances various prey sizes are eaten as encountered, but at higher densities larger prey are selected by predators (Ivlev 1961; Werner and Hall 1974). We believe the high diet overlap between fish in the spring is related to the occurrence of an abundant food resource (principally *C. salmonis*). In the summer when *Corophium* abundance apparently was lower, predators shifted to feeding primarily on zooplankton and diversified their diets, thus keeping diet overlap at a minimum. McConnell et al. (1978) also noted reduced abundance of *C. salmonis* in the diets of subyearling chinook salmon in the upper Columbia River estuary during the summer.

Information explaining why *C. salmonis* was an important prey in spring and not in summer is lacking. It was apparent that migrating salmonids and many nonsalmonids were intensely harvesting this food resource. This predation may have affected *Corophium* abundance. Levings and Levy (1977) and Nelson (1979) showed that fish predators could be a controlling factor in estuarine amphipod populations. Also, the huge deposition of sediment that resulted from the eruption of Mount St. Helens probably reduced *C. salmonis* populations in the Columbia River estuary (Emmett 1982).

Juvenile salmonids and nonsalmonids share the same habitats. Both nonsalmonids and subyearling chinook salmon utilize intertidal areas of the estuary as feeding and resting areas. Undoubtedly the estuary serves as a sanctuary for many juvenile nonsalmonids as well as for juvenile salmon. Intertidal shallow areas of the estuary typically support rich populations of benthic invertebrates, which are important prey items.

Like the intertidal areas, the pelagic sections of the estuary are utilized by juvenile salmonids and nonsalmonids as feeding places. Many of the juvenile salmonids in the pelagic areas are probably migrating actively to the ocean. Myers (1980) found that the mean length of wild juvenile chinook salmon captured in the channel areas was greater than that of those collected along the shoreline. Gear selectivity may have caused this anomaly; however, if it did not, then Myers (1980) felt that the small juvenile chinook salmon may be rearing along the beaches, then migrating into channel areas at a larger size.

The interrelationships of various species in estuarine habitats will probably change from year to year. Yet we feel the general picture of the fish communities in the estuary in regards to juvenile salmonids will remain virtually unchanged, unless detrimental artificial alterations are made. This estuary serves as a sanctuary (from other fish predators) for juvenile salmonids, along with being an important feeding area for some subyearling chinook

salmon. The juvenile salmonids share the same estuarine habitats with many other species, both freshwater and marine.

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GROWTH OF LARVAL ATLANTIC COD, *GADUS MORHUA*, AND HADDOCK, *MELANOGRAMMUS AEGLEFINUS*, ON GEORGES BANK, SPRING 1981[1]

GEORGE R. BOLZ AND R. GREGORY LOUGH[2]

ABSTRACT

A study of the otoliths of larval Atlantic cod and haddock collected on Georges Bank in spring of 1981 provided information on growth and development during the first 2 months of life for these species. Exponential growth curves of length at age were fitted based on daily increment deposition which agreed with prior laboratory results and the few reported field studies. The faster growth rate (3.4% per day) of haddock larvae collected in May compared with that of cod larvae (2.6% per day) collected in April appeared to be due to the higher water temperature rather than to species-specific differences in rate of growth. Based on the microstructure of the otoliths, it was estimated that both species remained in the yolk-sac phase for 2-8 days followed by an 8-11 day period of slow growth during the transition to successful active feeding.

One of the major hypotheses of fisheries biology is that the extent of mortality during the larval phase greatly influences the size of a year class (Moser 1981). Since mortality is best described as a function of age and abundance, it is very important to be able to determine accurately the age of the larvae. Until Pannella (1971, 1974) demonstrated that the otoliths found in the semicircular canals of larval fish are composed of daily rings or increments, the only methods available for aging field-caught larvae were indirect ones based on inference, e.g., cohort analysis or growth curves generated by laboratory rearing experiments. Although the mechanisms controlling the rhythmic secretion of calcium and carbonate ions into the protein matrix of the otolith are as yet incompletely known (Watabe et al. 1982), many recent studies have demonstrated that the periodic increments formed are of a daily nature for the most part (Taubert and Coble 1977; Wilson and Larkin 1980; Schmidt and Fabrizio 1980; Tanaka et al. 1981; Mugiya et al 1981; Townsend and Graham 1981; Rosenberg and Laroche 1982; Laroche et al. 1982; Campana and Neilson 1982; Lough et al. 1982).

In addition to containing an age record, otoliths can provide other information on the life history of larval fish (Radtke 1980; Brothers 1981; Brothers and McFarland 1981). Physiological changes or growth disturbances often are indicated on the otolith by thick, dark bands or check rings (Radtke and Waiwood 1980; Geffen 1982). An examination of the area and the number of increments enclosed by these checks can provide insight on the duration and related environmental conditions of the early stages of larval fish. The relative width of individual increments, or small groupings of increments, provides a possible index to the daily or weekly feeding success of the larvae (Methot 1981). By knowing the precise age, hatching dates can be established and analyzed to assess yearly or population differences in the survival of larvae in relation to spawning time and location.

The work reported here was undertaken to derive accurate growth curves for larvae of Georges Bank Atlantic cod, *Gadus morhua* L., and haddock *Melanogrammus aeglefinus* L., from the field based on an analysis of their increment formation. Also, from the standpoint of understanding their larval ecology, it was important to determine what additional information might be revealed in the microstructure of cod and haddock otoliths on species differences and on stage of development in relation to environmental conditions. This study was conducted as part of the MARMAP program of the Northeast Fisheries Center, which measures long-term changes in the variability of the fish-stock abundance off the northeast coast of the United States (Sherman 1980).

METHODS

Cod and haddock larvae were collected on two larval fish dynamics cruises (Lough and Laurence 1982)

[1]MARMAP Contribution MED/NEFC 82-64, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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

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conducted by the Northeast Fisheries Center's RV *Albatross IV* on southeastern Georges Bank during spring 1981 (14 April-1 May-1June). Sample dates and station location where larvae were selected for otolith analysis are shown in Figure 1 and Table 1. The samples were collected with either 1) a continuous double-oblique haul [3] using a 61 cm bongo net sampler (0.505 and 0.333 mm mesh) deployed to a maximum depth of 100 m, or 2) a MOCNESS[4] fitted with 0.333 mm mesh nets which sampled discrete vertical layers from the bottom of the water column to the surface. Stations with high densities of cod and haddock larvae in good condition were selected during the cruises for a study of larval otoliths. Larvae were removed immediately following the haul and preserved in 95% ethanol. Temperature data for each station were obtained from surface bucket readings, expendable bathythermograph traces, or MOCNESS profiles.

In the laboratory, larvae selected for analysis were representative of the entire size-range collected. The standard length, as well as several other morphometric measurements, of each larva was measured to the nearest 0.1 mm prior to removal of their otoliths. The

[3]Gear configuration and other details can be found in Posgay and Marak (1980).

[4]Multiple Opening/Closing Net and Environmental Sensing System, after Wiebe et al. (1976).

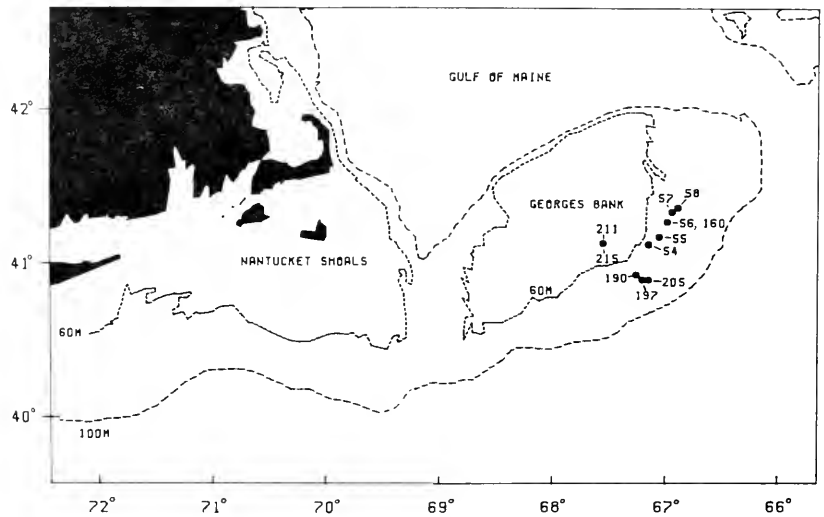

FIGURE 1.—Station locations for larval Atlantic cod and haddock specimens collected for otolith analysis aboard the RV *Albatross IV* during two cruises in the spring of 1981 (14 April-1 May; 19 May-1 June) on southeastern Georges Bank.

TABLE 1.—Station information for larval cod and haddock specimens collected for otolith analysis by 61 cm bongo net (0.505 mm mesh) oblique hauls (6B5) and 1 m MOCNESS (0.333 mm mesh) discrete vertical hauls (1M3) aboard the RV *Albatross IV* during two cruises in the spring of 1981 (14 April-1 May; 19 May-1 June) on southeastern Georges Bank.

Station	Lat N	Long. W	Date (GMT)	Time (GMT) (Night or day)	Gear	Bottom depth (m)	Temp. (°C) at 20 m	No. larvae	Mean standard length (mm)	Mean no. otolith increments
Cod Larvae										
54	41°10′	67°06′	24 April	1235 (D)	6B5	62	5.8	19	12.4	38.2
55	41°13′	67°02′	24 April	1330 (D)	6B5	62	5.8	10	12.2	38.3
56	41°18′	66°58′	24 April	1450 (D)	6B5	66	5.7	16	11.0	32.6
57	41°22′	66°55′	24 April	1630 (D)	6B5	66	5.8	13	11.1	33.6
58	41°26′	66°51′	24 April	1840 (D)	6B5	71	5.7	12	12.6	39.5
160	41°22′	67°00′	26 April	0645 (N)	1M3	63	4.9	29	16.8	44.8
Haddock Larvae										
190	40°57′	67°19′	22 May	0300 (N)	1M3	76	6.7	8	8.4	22.4
197	40°55′	67°13′	25 May	1200 (D)	1M3	80	6.9	16	4.6	12.1
205	40°55′	67°09′	26 May	1130 (D)	1M3	80	6.8	6	5.8	12.1
211	41°11′	67°35′	27 May	1200 (D)	1M3	49	8.2	27	9.4	27.9
215	41°12′	67°36′	27 May	2330 (N)	1M3	40	8.2	19	8.1	23.2

2 sagittae, 2 lapilli, and, when possible, 2 asterisci were dissected from the larvae and mounted whole on microscope slides with Permount[5]. The growth increments on most of the otoliths were discernible without any further preparation.

The largest of the otolith pairs, the sagittae, were then viewed under a Zeiss compound microscope with transmitted light. The number of growth increments were counted from the image projected by a drawing tube onto a Zeiss MOP Digital Image Analyzer System. This method was found to be superior to the microscope-television system used in previous studies (Lough et al. 1982) in terms of both increment resolution and the time necessary for repetitive counts. Depending on the size of the otolith, magnifications used ranged from 400× to 1,000×. Three counts were made on one of the 2 sagittae from each larvae, and those otoliths with a repeatable increment count of ≥95% were used in the growth analysis. The other sagitta was counted once for comparison.

The following measurements were made routinely on each sagitta to the nearest micron (Fig. 2): 1) Anterior and posterior radii from the center of the otolith nucleus to the outer edge of the otolith (otolith length); 2) diameter of the sagitta perpendicular to the length (lateral diameter); 3) diameter of the nucleus; 4) diameter of that portion of the otolith deposited prior to yolk-sac absorption as defined by Radtke and Waiwood (1980); and 5) planar surface area of the entire otolith. Diameters and planar surface areas of the lapilli and asterisci also were measured.

In order to distinguish faint increments within and immediately outside of the nuclear check, several otoliths of both cod and haddock larvae were examined by using a scanning electron microscope (SEM). After securing the otoliths to a microscope slide with Clear 2-Ton epoxy, they were ground with 1 μm diamond polishing compound. The grinding procedure was monitored periodically by viewing the otolith under a compound microscope. Next, the otoliths were etched with 10% HCl for 5-15 s. The epoxy containing the ground and etched otolith was removed from the slide, attached with double-sided tape to SEM viewing stubs, and sputter-coated with gold-palladium using a Tousimis Samsputter-2A.

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

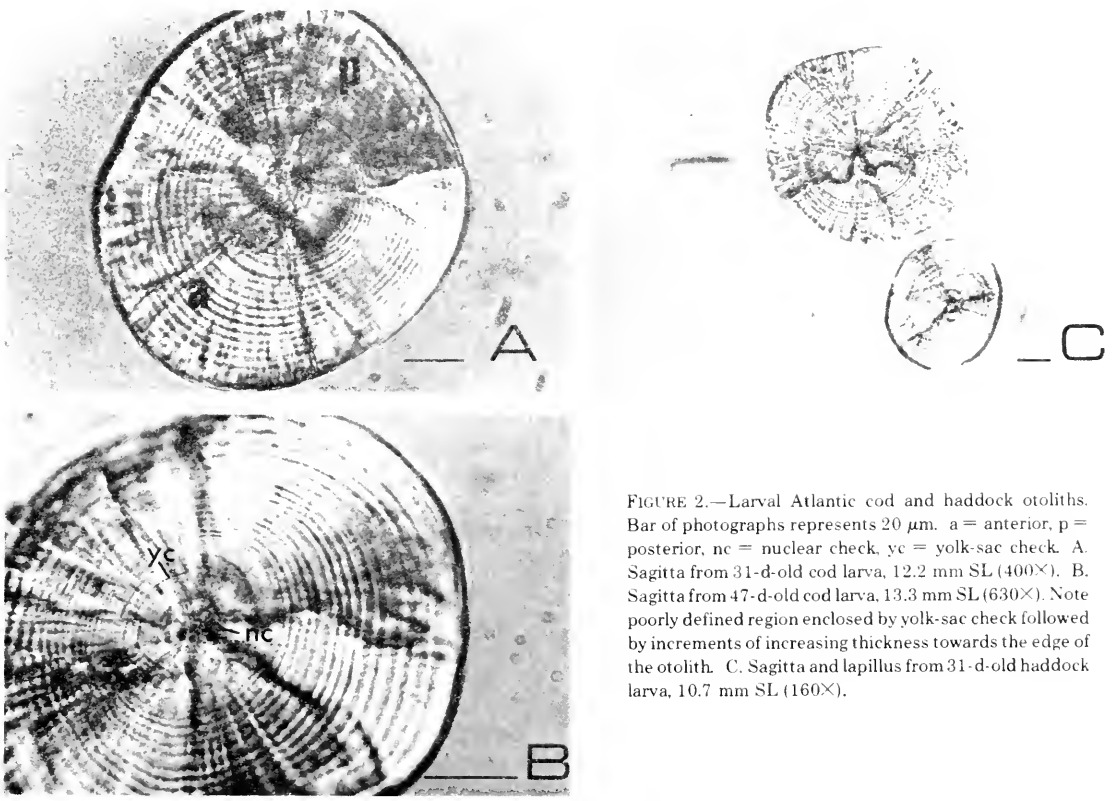

FIGURE 2.—Larval Atlantic cod and haddock otoliths. Bar of photographs represents 20 μm. a = anterior, p = posterior, nc = nuclear check, yc = yolk-sac check. A. Sagitta from 31-d-old cod larva, 12.2 mm SL (400×). B. Sagitta from 47-d-old cod larva, 13.3 mm SL (630×). Note poorly defined region enclosed by yolk-sac check followed by increments of increasing thickness towards the edge of the otolith. C. Sagitta and lapillus from 31-d-old haddock larva, 10.7 mm SL (160×).

The otoliths were viewed and photographed with a Semco Nanolab-7 SEM.

Radtke and Waiwood (1980) have shown that cod larvae shrink in length as much as 15% within 15 min of death and another 5% following preservation in ethanol. The amount of shrinkage was dependent on the size of the larvae. In order to correct for shrinkage, an algorithm developed by Theilacker (1980) for estimating the differential shrinkage of northern anchovy, *Engraulis mordax*, larvae with length was applied in this study to both cod and haddock larvae:

$$\ln L = \ln X_1 + 0.289e^{-0.434X_1X_2^{-0.680}}$$

where L = standard length (mm) of the larvae prior to death and alcohol fixation;
X_1 = standard length (mm) of the preserved specimen; and
X_2 = length of handling time (min) from death until preservation (assumed to be about 20 min in the present study).

Although cod and haddock larvae are less fusiform in shape than northern anchovy, the percentage of shrinkage with length agrees closely with the findings of Radtke and Waiwood (1980). It therefore appeared reasonable to use Theilacker's (1980) algorithm as a correction factor for the size range of larvae collected in this study. All lengths referred to in the results and discussion portions of this paper are reported as corrected lengths unless otherwise stated.

RESULTS

Growth of Atlantic Cod and Haddock Otoliths

The inner ear of adult teleosts contains three otoliths within its membranous labyrinths: 1) The sagitta located within its sacculus; 2) the lapillus housed within the utriculus; and 3) the asteriscus situated within the lagena. When viewed under a compound microscope with transmitted light, the otoliths of cod and haddock larvae were composed of a series of light and dark rings (Fig. 2) which corresponds to the heavily calcified incremental zones and the organic-rich discontinuous zones of Watabe et al. (1982). The sagittal increments (1 incremental and 1 discontinuous zone) were segregated into three or more regions delimited by distinctly thicker, darker, discontinuous zones referred to as checks or check rings. The innermost region or nucleus had a mean diameter of 16.2 μm (SD = 2.8) in cod and 14.7 μm (SD = 6.8) in haddock. When viewed under SEM, the nucleus was composed of a central amorphous core surrounded by a more structured area in which 1 or 2 irregular increments (Fig. 3) were discernible in some specimens. Proceeding outward from the nuclear check ring were 2-8 faint increments bounded by a discontinuous zone which appeared to be synonymous with the yolk-sac check found by Radtke and Waiwood (1980) in larval cod otoliths and with the "first heavy ring" noted by Geffen (1982) in otoliths of herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*). The mean diameter of the area enclosed by the yolk-sac check was 27.2 μm (SD = 3.8) in cod and 23.5 μm (SD = 2.8) in haddock. Between the yolk-sac check and the edge of the otolith were an average of 8 (haddock) to 11 (cod) increments of ≤ 1 μm followed by thicker rings of 1-3 μm.

The sagittae and lapilli of an individual larva contained about the same number of increments, and both pairs of otoliths were present in all cod and haddock, regardless of length. In larvae <7.0 mm SL, the sagitta and lapillus were both circular with centrally positioned nuclei and were of equal size. Cod larvae with a 10.0 mm SL had sagittae with maximum diameters 1.8 times greater than those of the lapilli, and by 25.0 mm in length the difference had further increased to 2.3 times (Fig. 4). The same trend was evident in haddock larvae, and sagittae in larvae with a 10.0 mm SL had a maximum diameter 1.5 times greater than that of the lapilli. Growth of the sagitta was relatively greater in the anterior-posterior plane, and the otolith was oval in the larger larvae. The lapillus remained roughly circular; however, deposition was not uniform and the nucleus became eccentric in larger larvae (Fig. 3).

No discernible asterisci were present in cod larvae with sagittae having >37 increments. Extrapolation from the plot of otolith diameter vs. standard length (Fig. 4) indicated that the asteriscus first appeared when the larvae reached a length of about 9.0 mm. Once initiated, the asteriscus grew more rapidly than the lapillus and would be expected to surpass it at a length of 90 mm. No asterisci were found in the haddock larvae examined.

Atlantic Cod and Haddock Larval Growth

Figure 5 is a plot of the standard lengths (range: 7.8-24.9 mm) of 99 cod larvae vs. their number of sagittal increments (range: 13-66). Assuming that the num-

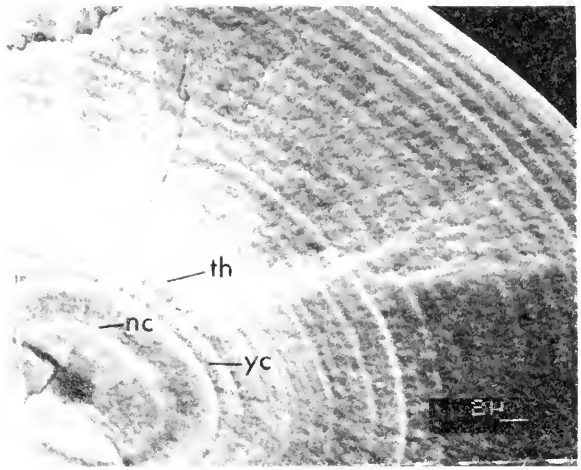

FIGURE 3.—Scanning electron micrograph of sagitta from 30-d-old haddock larva, 9.5 mm SL. Note the 1-2 poorly defined increments enclosed by the nuclear check (nc), the faint increments between the nuclear and yolk-sac (yc) check marks, and the series of very thin increments (th) immediately encircling the yolk-sac check.

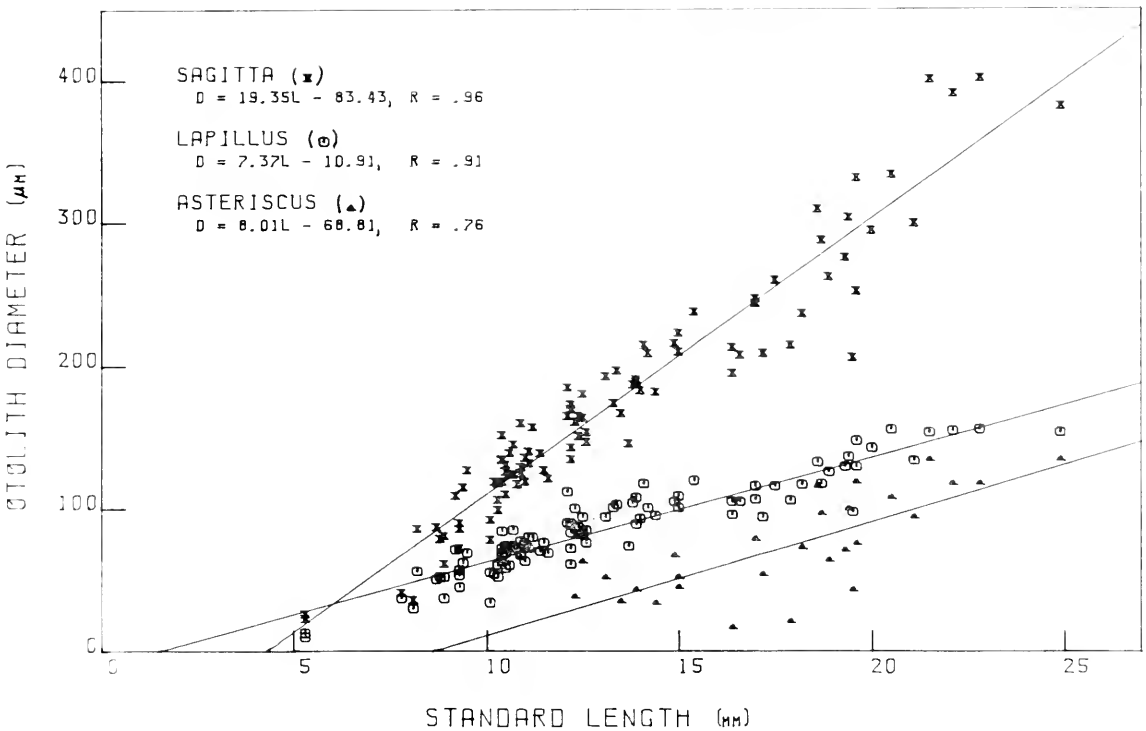

FIGURE 4.—Plot of otolith diameter:standard length fitted with linear regression lines for the three pairs of otoliths (sagitta, lapilli, and asterici) dissected from the inner ear of larval Atlantic cod.

ber of increments equals days from hatch (Radtke and Waiwood 1980; Gjösaeter and Tilseth 1982), cod growth through the first 2 mo of life may best be described by the exponential relationship:

$$L = 4.82e^{0.0250R}, r = 0.92 \quad (1)$$

where L = standard length in mm, and
R = number of days (increments) from hatch.

The average growth rate of cod larvae was 0.18 mm/d through the first month and 0.28 mm/d through 2

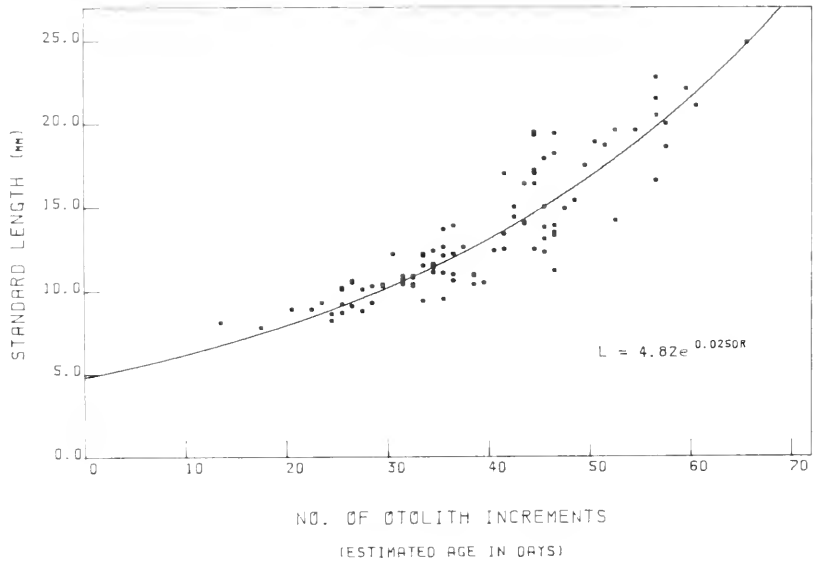

FIGURE 5.—Exponential growth curve and equation fitted to plot of standard length: no. of otolith increments (estimated age in days) for 99 Atlantic cod larvae collected during spring 1981 on southeastern Georges Bank.

mo. Growth continued exponentially from the predicted hatch length of 4.82 mm through the size range of larvae collected with no indication of a cessation in rate. Based on otolith age, hatching dates for the cod larvae analyzed extended from 19 February to 5 April (see Figure 7).

An exponential growth curve also resulted when the standard lengths (range: 3.5-12.7 mm) of 76 haddock larvae were plotted against their otolith increment counts (range: 5-36 (Fig. 6)):

$$L = 3.54e^{0.0346R}, r = 0.96. \quad (2)$$

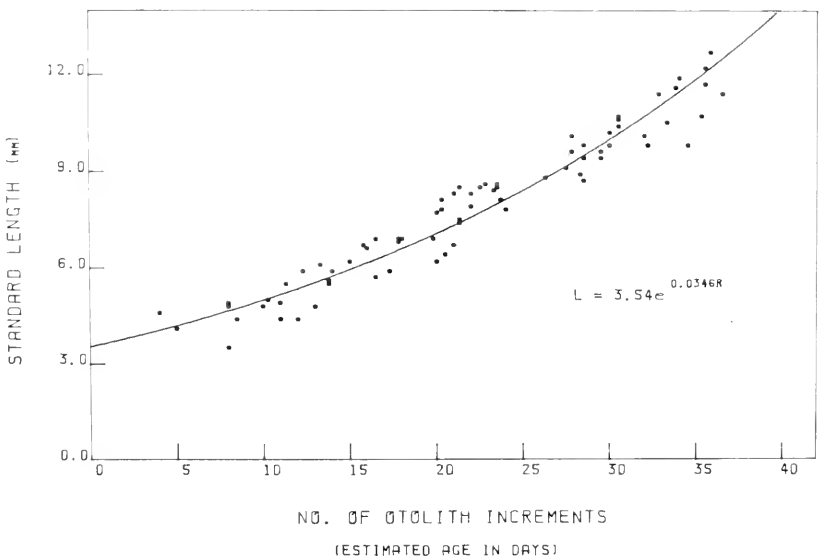

FIGURE 6.—Exponential growth curve and equation fitted to plot of standard length:no. of otolith increments (estimated age in days) for 76 haddock larvae collected during spring 1981 on southeastern Georges Bank.

As with the cod, larval haddock growth was exponential from the predicted hatch length of 3.54 mm through the size range analyzed (12.7 mm). For the first month of life, haddock grew at an average rate of 0.21 mm/d. Hatching dates for the haddock larvae occurred from 21 April to 21 May (Fig. 7).

In both cod and haddock larvae, it was not always possible to determine accurately the number of increments deposited prior to the yolk-sac check; consequently, size at hatch could be slightly less than predicted. However, since an average of only 3 increments were noted between the nuclear and yolk-sac checks in the clear otoliths, any error incurred would have little effect on the calculated growth curves.

DISCUSSION

The present work on cod and haddock concurs with the day-increment relationship found in many recent studies of fish otoliths (Mugiya et al. 1981; Tanaka et al. 1981; Uchiyama and Struhsaker 1981; Watabe et al. 1982; Lough et al. 1982). The exponential growth rates generated by the regression of standard length on otolith age (increments) agree with the findings of most previous field (Anderson 1982) and laboratory analyses of cod and haddock larvae. Length-at-age data for Southern New England cod from laboratory rearing experiments (Laurence et al. 1981) were highly correlated ($r = 0.98$) with the growth model derived for cod larvae in the present study. A 35-d-old cod larva raised at the maximum feeding ration of 3 prey/ml had an uncorrected length of 10.75 mm which closely agrees with the estimated length from the growth curve of 10.52 mm. Gjösaeter and Tilseth (1982) depict an otolith from a preserved 5.1 mm North Sea cod larva with the same number of increments (9) as predicted by the growth model. However, Steffensen's (1980) work on daily growth increments of juvenile East Baltic cod does not agree with these studies. The number of increments recorded by him are much lower for a given length than were found in the present analysis, e.g., a 60 mm fish with only 46 increments. His results should be viewed with caution, as he states that the central portion of his otoliths was blurred and "that an unknown number of growth zones in the central part of the otolith have escaped detection."

It is necessary to examine the central portion of the otolith carefully in order to establish when daily increment formation is initiated, as there is considerable variation between species (Brothers et al. 1976). The intercept values of 4.82 mm for cod and 3.54 mm for haddock derived from the growth model fall within the range of reported hatching lengths for the two species collected previously in the Gulf of Maine (Colton and Marak 1969). An intercept of 4.75 mm calculated from length-at-age data for larval and juvenile cod collected in Woods Hole, Mass., and tabulated by Bigelow and Schroeder (1953) also compared closely with the estimate for cod larvae. Brothers and McFarland (1981) noted 3 diffuse

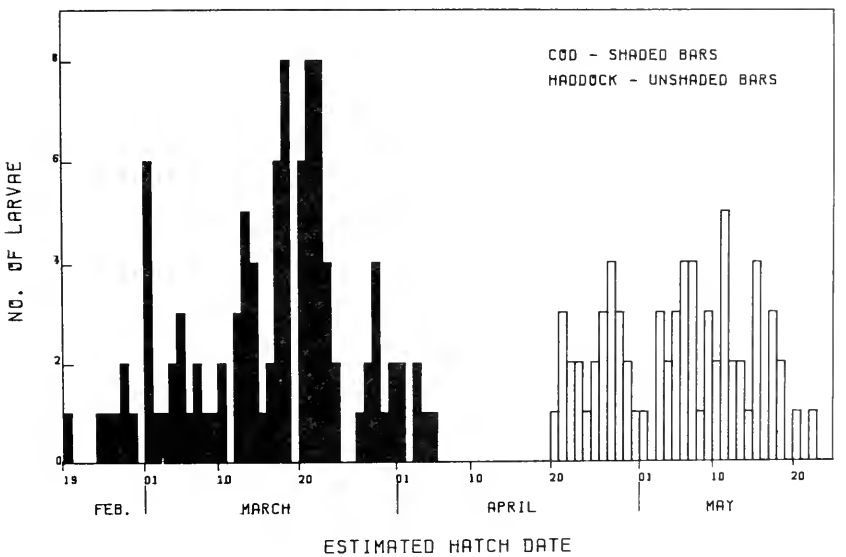

FIGURE 7.—Estimated hatch dates for Atlantic cod and haddock larvae collected during spring 1981 on southeastern Georges Bank based on otolith age (no. of daily increments).

increments in the otolith core of French grunt, *Haemulon flavolineatum*, and speculated that they may have been deposited during the egg stage, and Radtke and Dean (1982) found that laboratory-reared mummichogs, *Fundulus heteroclitus*, deposited 2 or 3 increments prior to hatching. It therefore seems reasonable to infer that the 2 or 3 irregular increments found inside the nucleus of cod otoliths by SEM analysis also were formed at some point during the approximately 20-d incubation period (Radtke and Waiwood 1980) prior to hatching. The subsequent exclusion of these innermost increments from the growth model, combined with the calculated intercept values, supports the findings of Radtke and Waiwood (1980) that cod larvae begin daily growth-ring formation at hatch. The similarity of the otoliths and growth patterns of cod and haddock warrants the conclusion that daily increment formation for haddock larvae also begins at hatch.

Checks or check rings, exceptionally dark and thick discontinuous zones, are the primary landmarks present in larval otoliths and have been used extensively to date growth disturbances, injury, poor feeding, and environmental conditions (Taubert and Coble 1977; Radtke and Waiwood 1980; Lough et al. 1982; Radtke and Dean 1982; Geffen 1982). If the discontinuous zone represents a fixed period during the day when calcium deposition into the organic matrix slows or ceases as postulated by Watabe et al. (1982), check rings would be a reflection of a disturbance in the daily metabolism of the larval fish. Change from one life history stage to another would represent one such possible disturbance. The nuclear check formed at hatching and the yolk-sac check were the two major check rings found in the otoliths of cod and haddock larvae. Radtke and Waiwood (1980) noted the presence of a check deposited at the time of yolk-sac absorption in laboratory-reared cod larvae, and they remarked on its similarity to the metamorphic checks found by Bailey et al. (1977) in capelin, *Mallotus villosus*. Although the increments deposited between the nuclear and yolk-sac checks were faint and difficult to discern with the light microscope, it was possible to make counts on the clearer specimens and by SEM techniques. The average number of increments in this zone for both cod and haddock larvae was 3 with a range of 2-8. Radtke and Waiwood (1980) found that it took cod larvae 4 d at 4°C to reach yolk-sac absorption, and in Laurence's (1978) rearing experiments cod and haddock had completed yolk-absorption by 7 d at 7°C., Ellertsen et al. (1980) found that yolk exhaustion for Arcto-Norwegian cod occurred within 8 d of hatching at 5°C and that feeding was initiated 2-4 d prior to this when the jaw apparatus became completely functional. This close correspondence between rearing experiments and the present field study supports the proposition that the observed check was deposited at, or shortly before, the completion of yolk absorption and that the increments between it and the nuclear check approximate the number of days spent in the yolk-sac phase.

Because the early life history of the Atlantic cod and haddock larvae analyzed took place over an extended area and period of time, it is impossible to accurately know the temperatures at which hatching and larval growth occurred. However, based on the temperatures recorded during the two collecting cruises, it can be estimated that water temperature ranged from 4° to 6°C for cod and 6° to 8°C for haddock. The derived growth models estimate that cod grew in length at an average of 2.6%/d and haddock at 3.4%/d. Anderson (1982) recently found that a rise in the growth rate of cod larvae collected on the Flemish Cap "closely paralleled increasing surface water temperatures." Laboratory rearing experiments (Laurence 1978; Laurence et al. 1981) also found that growth for cod and haddock was positively correlated with temperature and that cod larvae grew in length about 0.62%/d faster at 7°C than at 5°C. If this percentage increase is incorporated into the cod growth model, the average rate of growth would be 3.2%/d, and most of the difference between the cod and haddock growth curves could be accounted for (Fig. 8). The similarity of these results agrees with that of Laurence (1978) in which he found no major differences between the growth rate of the two species at similar food levels, although haddock growth was slightly higher than cod at all temperatures.

Ring deposition appears to be endogenously controlled with the daily light-dark cycle acting as the primary triggering mechanism (Watabe et al. 1982). Environmental variables, such as temperature and day length, and feeding success are thought to be reflected in the relative width of the individual increments (Taubert and Coble 1977; Radtke 1980; Methot 1981). Since the thin otolith increments deposited immediately after the yolk-sac check ring represent a short period of time and are a constant feature throughout the extended hatching season, these thin daily increments were probably a reflection of the adjustment to active feeding rather than to an abrupt change in the environment. It is also known that the length of the yolk-sac phase and the adjustment to completely active feeding are somewhat dependent on temperature (Laurence 1978; Ellertsen et al. 1980); therefore, the greater number

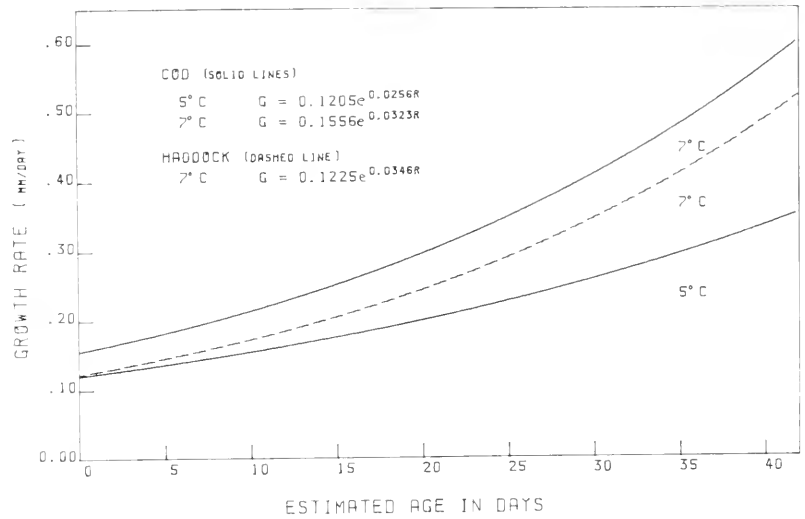

FIGURE 8.—Growth comparison of larval Atlantic cod and haddock at different temperatures. The 5° C curve for cod and the 7° C for haddock are based on an analysis of the no. of daily increments counted on otoliths from larvae collected during the spring of 1981 on southeastern Georges Bank. The 7° C curve for cod is hypothetical and incorporates the percent per day increase in growth for a 2° C temperature rise found in laboratory rearing experiments (Laurence 1978; Laurence et al. 1981).

of these thin increments found in cod (11) than in haddock (8) may have been due in part to slower growth in the cooler, late-winter water. It is also possible that the larger diameter of the yolk-sac check ring in cod (27.2 μm) than in haddock (23.5 μm) was indicative of the cod larvae having spent a longer period of time in the yolk-sac phase. However, more extensive SEM work on the region between the nuclear and yolk-sac check rings is needed to confirm the exact number of daily increments for a large sample size.

ACKNOWLEDGMENTS

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DISTRIBUTION OF FISHES IN SEAGRASS MEADOWS: ROLE OF MACROPHYTE BIOMASS AND SPECIES COMPOSITION[1]

ALLAN W. STONER[2]

ABSTRACT

Large spatial variation was found in the abundance and species composition of ichthyofauna in seagrass meadows of Apalachee Bay and Indian River lagoon, Florida. Abundance of fishes was a direct function of aboveground seagrass biomass in Apalachee Bay where seagrass meadows were dominated by turtlegrass, *Thalassia testudinum*, but the relationship did not hold across monospecific beds of *T. testudinum*; manatee grass, *Syringodium filiforme*; and shoal grass, *Halodule wrightii*, in Indian River lagoon. Rather, the shoal grass site, with lowest seagrass biomass, yielded the largest number of fishes, while manatee grass, with biomass near that of shoal grass, had fewest fishes. Across seagrass species, blade density was a better predictor of fish abundance than seagrass biomass. Seasonal patterns of fish abundance at all of the sites were related to macrophyte biomass. Although lowest numbers of fish species were collected at an unvegetated site, species richness was not related to seagrass biomass or blade density; habitat heterogeneity appeared to be more important. Abundance of prey and protection from piscivorous predators were hypothesized as the best explanations for high fish abundance associated with high seagrass biomass and with shoal grass. Differential distribution in pinfish, *Lagodon rhomboides*, of various size classes was related to foraging behavior of individual trophic stages.

The great abundance and diversity of ichthyofauna in seagrass meadows are well established (Hoese and Jones 1963; Kikuchi 1966; Adams 1976; Weinstein and Heck 1979; Robertson 1980), but little is known concerning the mechanisms which control the distribution and diversity of fishes within beds. Although a few researchers have compared the ichythofauna of vegetated and unvegetated substrata (Briggs and O'Connor 1971; Weinstein et al. 1977; Orth and Heck 1980) and changes in fish communities associated with pollution-induced reductions in seagrass cover have been examined (Kikuchi 1974; Livingston 1975), studies have not been designed specifically to test the role of seagrass biomass in the organization of fish assemblages. Only one study has examined ichthyofauna of different seagrass species (Martin and Cooper 1981). Such investigations require seagrass beds of different blade density or species composition within a restricted geographic range and beds which are characterized by similar physical and chemical conditions.

In this study I first discuss the ichthyofauna of four beds which have different seagrass biomass. Then, I compare the fish assemblages collected at three beds characterized by monotypic stands of three seagrass species. The criteria for similar physical-chemical conditions were met within each of the two systems studied (Apalachee Bay and Indian River lagoon, Florida). Patterns of abundance, species composition, species richness, and fish size are discussed in terms of the life history of individual fish species, abundance of prey at the sites, and foraging behavior of numerically dominant species.

METHODS

Sampling Sites

Trawl surveys were made in two Florida localities: Apalachee Bay in the northern Gulf of Mexico and Indian River lagoon, 8 km north of Fort Pierce, on the east coast of Florida. Apalachee Bay is shallow and open to the Gulf of Mexico with seagrass beds (primarily turtle grass, *Thalassia testudinum*, and lesser amounts of manatee grass, *Syringodium filiforme*) which cover hundreds of square kilometers. Four stations were chosen on the basis of long-term macrophyte data for the area (Zimmerman and Livingston 1976, 1979) and are identical to the stations discussed by Stoner (1980a). Fenholloway station 11 (F-11) was characterized by a very sparse and patchy seagrass flora with a mean aboveground biomass of only 9.3 g dry wt/m^2. Station F-11 will be termed the unvegetated site. Fenholloway 12 (F-12) had a mean macrophyte biomass of 141 g dry wt/m^2;

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the seagrass cover here was occasionally broken by a bare sand substratum. Econfina 10 (E-10) and 12 (E-12) had standing crops of 215 and 320 g dry wt/m^2, respectively, and were characterized by continuous, uniform seagrass cover. All of the stations were polyhaline, about 1.2 m in depth, and characterized by low levels of water color and turbidity. The physical-chemical and sedimentological similarity of the Apalachee Bay stations was established in an earlier report (Stoner 1980a).

Seagrass beds in Indian River lagoon are composed of three different species. Large monospecific stands of *Thalassia testudinum* (110 g dry wt/m^2), *Syringodium filiforme* (48 g dry wt/m^2), and shoal grass, *Halodule wrightii* (34 g dry wt/m^2) were sampled near the western shore of the lagoon in shallow (1.0 m) polyhaline water. The beds were adjacent to one another and biomass values were representative of beds in the lagoon. Biweekly sampling showed that the Indian River stations were statistically similar to each other in depth, salinity, temperature, and other water conditions (Stoner 1983).

Biological Collections

In Apalachee Bay, fishes were collected with a 5 m otter trawl (1.9 cm mesh wing; 0.6 cm mesh liner) which was towed in a straight line near permanent station markers at a speed of 2 kn for 2 min. Seven replicate tows were made at each bed on a monthly basis from December 1976 through November 1977. The seven-trawl strategy was found to be appropriate for an asymptotic accumulation of species (Livingston 1975). In Indian River lagoon, a smaller net and a more rigid trawl strategy were required so that only monospecific seagrass beds were sampled. A 3 m otter trawl, with mesh identical to that used in Apalachee Bay, was towed at 2 kn in a straight line between floats at the ends of a 70 m transect or in a line close to and parallel to the line of the floats. Seven replicate tows were made at each bed on a quarterly basis after preliminary analysis showed that the seven replicates yielded an asymptotic species accumulation curve for fishes. Despite the restricted area of a trawl site, replicate tows did not overlap in the area covered and no change in species composition was observed over the collection period which normally spanned several hours. Collections were made at midday in October 1979, and in January, April, and July 1980. Because the efficiency of capturing fishes (Ryan 1981) and invertebrates (Greening and Livingston 1982) varies diurnally and because certain species move to and from seagrass beds on a diurnal basis (Randall 1965; Ogden and Buckman 1973; Ogden and Zieman 1977), midnight collections were made at the Indian River stations. Two tows were made at each bed in January and in July. All fishes reported in this study were preserved in a Formalin[1]-seawater mixture, identified to species, counted, and measured for standard length (SL).

Macrophyte collections were made at each bed and on each date of fish collection. As described by Livingston et al. (1976), aluminum hoops (0.25 m by 0.25 m) were thrown haphazardly into the sampling site and all macrophytes within each hoop were collected by diving. Eight replicates were collected including leaves, stems, roots, and rhizomes. Samples were placed in plastic bags and taken to the laboratory for identification and weighing. Plants were divided into aboveground and belowground parts, dried at 80 -100 C for 12 h, and weighed by individual species and fractions. For an estimate of blade density at Indian River beds, the number of seagrass blades in each sample was determined and extrapolated to yield numbers of seagrass blades per square meter.

Certain limitations are inherent in the present study. The inefficiency of trawl sampling is known (Kjelson and Johnson 1978), and it is not possible to provide abundance data in absolute terms; only a comparison of collections is valid. It may also be argued (correctly) that trawl efficiencies decrease with seagrass biomass. Although visual surveys of ichthyofauna, made in Apalachee Bay and in Indian River lagoon during the surveys, helped to confirm the spatial patterns of abundance for large, mobile species, visual surveys are rarely quantitative and underestimate the abundance of cryptic species. Low water transparence further restricted the value of visual surveys in the two sampling areas.

RESULTS

Role of Seagrass Biomass

A total of 8,002 fishes representing 53 species were collected in the 12-mo survey in Apalachee Bay. The total number of individuals collected at a given station, however, varied from 714 to 3,171 (Table 1) and was a direct function of mean macrophyte biomass ($r = 0.988$; $P < 0.001$) (Table 2). The close linear relationship was largely a result of a linear increase in abundance of pinfish, *Lagodon rhomboides* ($r = 0.998$; $P < 0.001$); however, when all other species

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

TABLE 1.—Abundance of the 20 most numerous fishes at four seagrass sites in Apalachee Bay, Fla. Values are the total number of fish collected and percentages (in parentheses) of the total catch for each station. Macrophyte biomass (g dry wt/m²) for each station is given in parentheses.

Species	Station F-11 (9.3)		F-12 (141)		E-10 (215)		E-12 (320)	
Lagodon rhomboides	122	(17.1)	1,050	(57.0)	1,568	(68.9)	2,131	(67.2)
Leiostomus xanthurus	364	(51.0)	92	(5.0)	153	(6.7)	15	(0.5)
Bairdiella chrysoura	15	(2.1)	204	(11.1)	116	(5.1)	148	(4.7)
Diplodus holbrooki	0		97	(5.3)	87	(3.8)	179	(5.6)
Syngnathus floridae	0		40	(2.2)	47	(2.1)	145	(4.6)
Monacanthus ciliatus	5	(0.7)	52	(2.8)	4	(0.2)	127	(4.1)
Centropristis melana	0		58	(3.1)	23	(1.0)	98	(3.1)
Orthopristis chrysoptera	11	(1.5)	48	(2.6)	17	(0.8)	42	(1.3)
Haemulon plumieri	0		27	(1.5)	19	(0.8)	61	(1.9)
Paraclinus fasciatus	34	(4.8)	17	(0.9)	37	(1.6)	13	(0.4)
Micrognathus crinigerus	8	(1.1)	17	(0.9)	44	(1.9)	4	(0.1)
Eucinostomus argenteus	6	(0.8)	11	(0.6)	30	(1.3)	19	(0.6)
Monacanthus hispidus	0		20	(1.1)	7	(0.3)	35	(1.1)
Chilomycterus schoepfi	6	(0.8)	21	(1.1)	4	(0.2)	25	(0.8)
Gobiosoma robustum	32	(4.5)	7	(0.4)	15	(0.7)	2	(0.1)
Cynoscion nebulosus	10	(1.4)	10	(0.5)	13	(0.6)	11	(0.3)
Opsanus beta	15	(2.1)	9	(0.5)	19	(0.8)	0	
Urophysis floridana	16	(2.2)	14	(0.8)	7	(0.3)	4	(0.1)
Syngnathus scovelli	20	(2.8)	8	(0.4)	5	(0.2)	1	(0.05)
Eucinostomus gula	8	(1.1)	8	(0.4)	2	(0.1)	1	(0.05)
Other species	42	(6.0)	31	(1.8)	59	(2.6)	110	(3.5)
Total number of individuals	714		1,841		2,276		3,171	
Total number of species	34		36		33		32	

TABLE 2.—Summary of statistics from regression analyses for Apalachee Bay, Fla., fishes. R values are Pearson correlation coefficients; N is the total number of fish collected; F values are for tests of regression significance by analysis of variance.

Regression	R	N	F value	Significance
Tested as a function of mean macrophyte biomass				
Total number of fishes	0.988	4	576.21	$P < 0.001$
Number of pinfish	0.998	4	440.25	$P < 0.001$
Number of non-pinfish	0.882	4	7.00	$P < 0.10$
Tested as a function of macrophyte biomass, all dates examined separately				
Total number of fishes	0.572	48	22.31	$P < 0.001$
Number of pinfish	0.565	48	21.52	$P < 0.001$
Number of non-pinfish	0.380	48	7.75	$P < 0.01$

were combined, a similar positive relationship with seagrass biomass was found ($r = 0.882$; $P < 0.10$). The dominant fish at the unvegetated site (F-11) was spot, *Leiostomus xanthurus*, most of which were juveniles (10-20 mm SL). Silver perch, *Bairdiella chrysoura*, was most abundant at station F-12; the same was true for pigfish, *Orthopristis chrysoptera*, although numerical differences among the stations were small (Table 1). Fishes that increased in abundance with seagrass biomass or were most abundant at the most heavily vegetated site (E-12) included spot-tail pinfish, *Diplodus holbrooki*; dusky pipefish, *Syngnathus floridae*; fringed filefish, *Monacanthus ciliatus*; planehead filefish, *M. hispidus*; southern sea bass, *Centropristis melana*; and white grunt, *Haemulon plumieri* (Table 1); of these six species, only *M. ciliatus* was collected at the unvegetated site.

The total number of fishes collected per unit effort (seven trawls) was lowest in winter months (December, January, and February) and highest between May and August, except at the unvegetated site where peak fish abundance occurred in February (Fig. 1). A brief abundance of juvenile spot and pinfish at station F-11, as they moved from offshore spawning sites to the marshes of the Fenholloway estuary, was responsible for the winter peak in total fish abundance at that station. After the brief transience of early juveniles, a consistently low number of fishes characterized the unvegetated site. At vegetated stations, the abundance of pinfish and spot continued to increase after initial recruitment of juveniles until midsummer.

Because of major seasonal patterns in the abundance of fishes and macrophytes in Apalachee Bay (Figs. 1, 2), two tests of the relationship between these biotic components were made. In the first test, using the 48 points available for 12 collections at four stations, total numbers of fishes, numbers of pinfish, and numbers of non-pinfish all proved to be weak linear functions of macrophyte biomass (Table 2). The second test, using the four stations as separate points on a month-by-month basis, found significant positive correlations between fish abundance and seagrass biomass during certain periods (Table 3). Pinfish abundance was closely related to seagrass biomass between May and October, the season during which first-year pinfish use the benthic habitat for a nursery ground. Total fish abundance showed a similar positive correlation with seagrass standing crop from

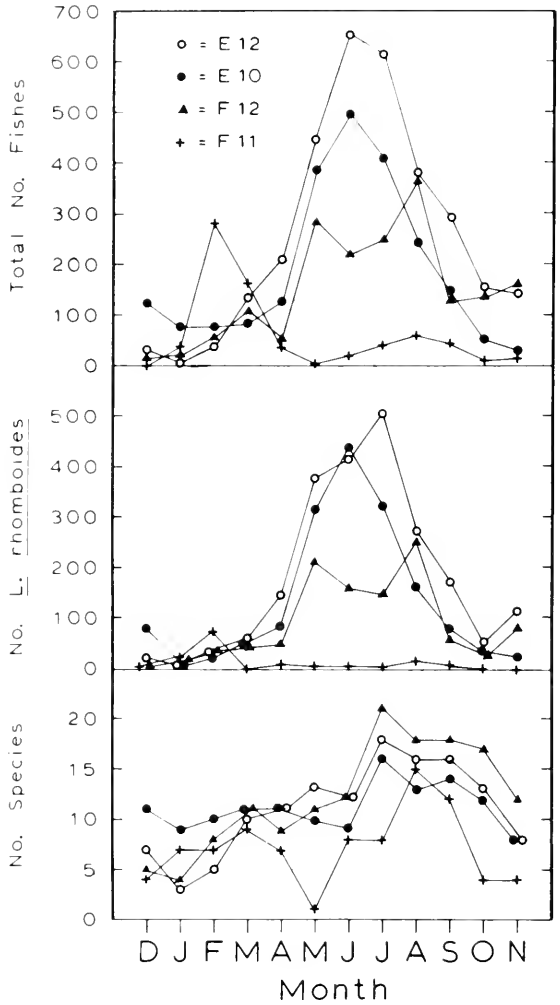

FIGURE 1.—Seasonal patterns of fish abundance and species richness at four seagrass sites in Apalachee Bay, Fla. Station F-11 (mean macrophyte biomass = 9.3 g dry wt/m²; F-12 (141 g dry wt/m²); E-10 (215 g dry wt/m²); E-12 (320 g dry wt/m²).

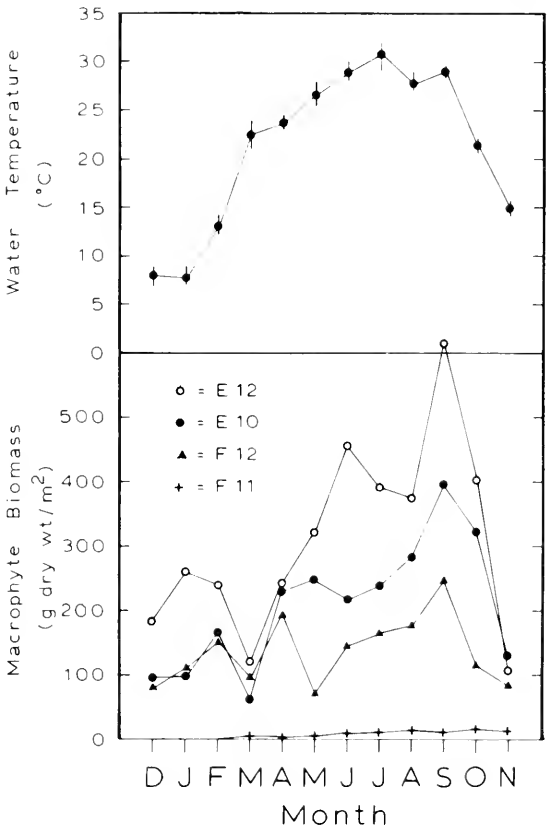

FIGURE 2.—Seasonal patterns in water temperature (mean and range) and seagrass biomass at four sites in Apalachee Bay, Fla.

TABLE 3.—Summary of statistics from regression analyses for abundance of fishes tested as a function of macrophyte biomass at four seagrass stations in Apalachee Bay, Fla. R values are Pearson correlation coefficients, with significance indicated; F values are for tests of regression significance using analysis of variance; n equals 4 for all regressions.

Sample period	All fish species		Pinfish		Non-pinfish	
	R	F	R	F	R	F
January	−0.385	0.35	−0.773	2.96	−0.242	0.12
February	−0.978***	43.18	−0.964***	26.35	−0.981***	50.24
March	−0.408	0.40	−0.808	3.76	0.609	1.18
April	0.699	1.91	0.776	3.03	0.443	0.49
May	0.900**	8.48	0.929**	12.55	0.709	2.02
June	0.950**	18.49	0.930**	11.79	0.959***	22.93
July	0.997***	305.96	0.988***	85.28	0.907**	8.46
August	0.870*	6.32	0.893*	7.31	0.848*	5.42
September	0.965***	27.30	0.976***	40.58	0.923**	11.53
October	0.481	0.60	0.836*	4.63	0.241	0.12
November	0.342	0.27	0.429	0.45	0.128	0.03
December	0.236	0.12	0.197	0.08	0.302	0.02

* = $P < 0.10$; ** = $P < 0.05$; *** = $P < 0.01$.

May to September, and non-pinfish abundance was significantly correlated with macrophyte biomass from June to September. Curiously, with all three fish categories, correlation coefficients gradually changed from negative in January to positive in the summer and fall when fishes and macrophytes were most abundant, and back to insignificant in December (Table 3).

Seasonality of fishes in Apalachee Bay was also a function of water temperature (Fig. 2) at the three vegetated sites. The correlation was strongest at station E-12 ($r = 0.857$; $F = 24.79$; $P < 0.001$) but was also significant at stations F-12 ($r = 0.717$; $F = 9.51$; $P < 0.01$) and E-10 ($r = 0.611$; $F = 5.29$; $P < 0.05$). The relationship was not observed at the unvegetated site ($r = -0.165$; $F = 0.251$; $P > 0.10$)

because of the heavy winter passage of juvenile spot and pinfish.

The number of fish species collected in Apalachee Bay was highest in July and August, concurrent with peaks in total abundance (Fig. 1). Total number of species, however, ranged only from 32 at station E-12 to 36 at F-12, and there was no significant relationship between macrophyte biomass and species richness on either a spatial or seasonal basis.

Analysis of length-frequency data for pinfish, using ontogenetic stages discussed in earlier studies of the species (Stoner 1980b; Stoner and Livingston 1984) revealed differences in size-frequency distribution among the populations found at the four stations in Apalachee Bay (Table 4). At the unvegetated site, the pinfish population was dominated by fish in the 11-15 mm class (51.6% of the total) which appeared primarily in February and March. Among the vegetated sites, however, the number of small juveniles (16-35 mm) increased with seagrass biomass, as did the number of large juveniles (36-80 mm). The number of pinfish >80 mm decreased with seagrass biomass at the vegetated sites, but were also relatively uncommon at the unvegetated site.

TABLE 4.—Distribution of *Lagodon rhomboides* at four seagrass sites in Apalachee Bay, Fla., based on size class. SL is standard length of fish; *N* is the total number of fish collected in a size class.

SL	Station							
	F-11		F-12		E-10		E-12	
(mm)	*N*	%	*N*	%	*N*	%	*N*	%
11-15	63	51 6	12	1 1	35	2 2	30	1 4
16-35	15	12 3	299	28 3	569	36 3	884	41 5
36-80	35	28 7	649	61 3	881	56 2	1,181	55 4
>80	9	7 4	99	9 4	83	5 3	36	1 7

Role of Seagrass Species

A total of 2,580 fishes representing 37 species were collected during daytime sampling at three stations in Indian River lagoon (Table 5). Unlike collections made in Apalachee Bay, spatial variation in the abundance of fishes was not related to seagrass biomass (Tables 6, 7); rather, fish abundance varied widely with seagrass species, independent of macrophyte biomass. The lowest number of individuals was found in beds of *Syringodium filiforme* (Table 5). Two and one-half times more fish were collected in *Halodule wrightii* where seagrass biomass was always lowest (Table 6), and an intermediate number of fishes were collected in *Thalassia testudinum* where highest macrophyte abundance occurred consistently. Analyzed by individual collection date, the *Halodule* bed supported greater total numbers of fishes than did the other two seagrass beds, except in October when equal numbers were collected in *Halodule* and *Thalassia* (Table 8). *Thalassia* and *Syringodium* beds supported statistically similar numbers of fishes except in October. As in Apalachee Bay, *Lagodon rhomboides* was the numerically dominant species in seagrass meadows of Indian River lagoon (Table 5). Except in October, the *Halodule* bed supported a significantly greater number of pinfish than the other two beds (Table 8). The *Syringodium* bed consistently yielded fewest pinfish, but mean values per trawl were similar to those from the *Thalassia* bed in January and July.

TABLE 5.—Abundance of the 10 most numerous fishes at three seagrass beds in Indian River lagoon, Fla. Values are the total number of fish collected and percentages (in parentheses) of the total catch for each bed type. Mean macrophyte biomass (g dry wt/m²) for each bed type is shown in parentheses.

Species	Syringodium (48)	Thalassia (110)	Halodule (34)
Lagodon rhomboides	265 (51 0)	576 (76 4)	898 (69 0)
Eucinostomus gula	45 (8 6)	16 (2 1)	145 (11 1)
Orthopristis chrysoptera	35 (6 7)	58 (7 6)	86 (6 6)
Gobiosoma robustum	100 (19 2)	12 (1 6)	14 (1 0)
Syngnathus scovelli	32 (6 2)	18 (2.4)	38 (2 9)
Bairdiella chrysoura	5 (1 0)	19 (2 5)	23 (1 8)
Lutjanus griseus	8 (1 5)	7 (0 9)	10 (0 8)
Chilomycterus schoepfi	1 (0 2)	12 (1 6)	4 (0 3)
Eucinostomus argenteus	2 (0 4)	1 (0 1)	12 (0 9)
Syngnathus louisianae	2 (0 4)	3 (0 4)	10 (0 8)
Other species	25 (4 8)	33 (4 4)	62 (4 8)
Total no. of individuals	520	758	1 302
Total no. of species	24	26	32

TABLE 6.—Aboveground biomass and blade density of macrophytes at three seagrass beds in Indian River lagoon, Fla. Values are mean ± SD (n = 8).

Seagrass bed	October	January	April	July
Seagrass biomass (g dry wt/m²)				
Halodule	25 7 ± 6 5	17 8 ± 1 9	23 2 ± 8 3	66 8 ± 19.8
Thalassia	69 4 ± 9 2	73 0 ± 20.3	99 4 ± 25.7	197 4 ± 52 4
Syringodium	49 9 ± 7 9	28 4 ± 8 5	23 4 ± 4 2	86 8 ± 27.1
Seagrass blade density (no./m²)				
Halodule	8,389 ± 1,878	6,111 ± 1,878	10,589 ± 2,752	11 611 ± 3,029
Thalassia	2,044 ± 218	1,856 ± 296	2,344 ± 493	2,400 ± 734
Syringodium	3,767 ± 489	2,722 ± 455	2,411 ± 206	4,178 ± 1,065

TABLE 7.—Summary of statistics from regression analyses for Indian River fishes. R values are Pearson correlation coefficients; N is the total number of fish collected; F values are for tests of regression significance by analysis of variance.

Regression	R	N	F value	Significance
Tested as a function of macrophyte biomass				
Total number of fishes	−0.021	12	0.005	$P > 0.10$
Tested as a function of macrophyte blade density				
Total number of fishes	0.769	12	14.42	$P < 0.01$
Number of pinfish	0.733	12	11.58	$P < 0.01$
Number of non-pinfish	0.596	12	5.51	$P < 0.05$
Total number of fishes				
October	0.318	3	0.11	$P < 0.10$
January	0.989	3	43.88	$P < 0.01$
April	0.998	3	199.39	$P < 0.001$
July	0.916	3	5.18	$P < 0.10$

TABLE 8.—Daytime abundance of fishes and fish species in three seagrass beds in Indian River lagoon, Fla. Values are mean numbers per trawl sample ± SD ($n = 7$). * and + indicate mean values that were not statistically different on a given date (ANOVA and Duncan's multiple range test, $P < 0.05$; F values are provided).

Seagrass bed	October	January	April	July
Number of individuals, all species				
Halodule	*53.1 ± 15.5	24.1 ± 10.3	50.1 ± 18.2	63.4 ± 19.2
Thalassia	*51.1 ± 9.9	* 3.9 ± 1.5	*21.3 ± 7.3	*31.9 ± 13.9
Syringodium	25.6 ± 11.0	* 4.9 ± 2.7	*19.1 ± 6.8	*22.0 ± 11.1
	($F = 9.21$)	($F = 20.13$)	($F = 11.01$)	($F = 12.49$)
Number of pinfish				
Halodule	*34.7 ± 8.4	13.2 ± 7.4	36.6 ± 10.8	44.7 ± 17.1
Thalassia	*39.3 ± 9.1	* 2.3 ± 1.4	15.0 ± 6.9	*26.0 ± 9.5
Syringodium	17.4 ± 6.5	* 1.1 ± 0.9	2.3 ± 1.6	*17.0 ± 5.4
	($F = 12.33$)	($F = 13.78$)	($F = 12.53$)	($F = 8.73$)
Number of individuals, excluding pinfish				
Halodule	*18.4 ± 9.8	10.9 ± 5.5	*13.6 ± 5.7	14.0 ± 8.0
Thalassia	*11.9 ± 3.1	* 1.6 ± 1.4	6.3 ± 3.8	* 5.9 ± 4.2
Syringodium	8.1 ± 5.2	* 3.7 ± 1.9	*16.9 ± 6.2	* 7.9 ± 3.2
	($F = 3.63$)	($F = 11.64$)	($F = 6.15$)	($F = 3.5$)
Number of species				
Halodule	* 6.0 ± 1.8	* 4.7 ± 0.7	* 5.7 ± 1.2	6.9 ± 2.8
Thalassia	* 5.9 ± 2.4	+ 2.4 ± 1.3	+* 4.0 ± 1.9	* 3.7 ± 1.1
Syringodium	* 5.0 ± 2.1	+*3.7 ± 1.4	+ 3.0 ± 0.7	* 4.1 ± 1.6
	($F = 0.40$)	($F = 5.79$)	($F = 10.13$)	($F = 4.30$)

The number of species collected per trawl varied little among the stations (Table 8); however, certain compositional differences were evident in the collections from different sites. *Orthopristis chrysoptera*, *Bairdiella chrysoura*, and *Syngnathus louisianae* increased in abundance from *Syringodium* to *Thalassia* to *Halodule* beds; however, because of wide variation in the numbers collected in replicate trawls, differences in catch among the beds were not significant statistically (ANOVA, $P > 0.10$). The gerreids, *Eucinostomus gula* and *E. argenteus*, were most abundant in *Halodule* beds in October and January (ANOVA, $P < 0.05$), the only months during which they were caught in large numbers. Both species were uncommon at the *Thalassia* bed. Code goby, *Gobiosoma robustum*, was abundant only at the *Syringodium* bed. Although other species were collected in nearly equal numbers in the three seagrass species, *Halodule* yielded mean abundances of non-pinfish higher than those from *Thalassia* and *Syringodium* in January and July (Table 8). *Thalassia* and *Syringodium* yielded statistically similar numbers of non-pinfish in October, January, and July.

Despite major differences in the gross morphology of the three seagrass species, blade density (Table 6) proved to be a better predictor of fish abundance than macrophyte biomass. Using all station-date combinations, there was a significant positive correlation between total number of fishes collected, number of pinfish, and number of non-pinfish (Table 7). Despite low sample numbers ($n = 3$), collections made in January, April, and July showed surprisingly close, and statistically significant, correlations between total number of fishes collected at a given site and macrophyte blade density (Table 7).

Although the *Halodule* bed yielded a higher total number of species (32) than the *Thalassia* and *Syringodium* beds (26 and 24, respectively), the number of species collected was a direct function of the number of individuals collected and may be artifactual. Differences in number of species collected per trawl were rarely significant (Table 8).

Length-frequency analysis of pinfish populations at Indian River stations (Table 9) showed that each of the three smallest size classes increased in total numbers from *Syringodium* to *Thalassia* to *Halodule* beds, but relatively small populations of fish >80 mm were uniformly distributed over the three habitats. Within-site analysis indicated that nearly 95% of the pinfish population on the *Syringodium* bed were > 35 mm; numerically, smaller fish were much more important at the *Thalassia* and *Halodule* beds, making up 14 and 23.1% of the total, respectively. Consequently, mean pinfish size decreased from *Syringodium* to *Thalassia* to *Halodule* beds, and numbers of individuals increased.

Night collections in Indian River lagoon yielded much larger numbers of fish per trawl than daytime collections in all three of the seagrass beds (Table 10); mean values for all fish species were between two and five times greater at night. The same was true for pinfish as well as non-pinfish. Although only two

TABLE 9.—Distribution of *Lagodon rhomboides* at three seagrass beds in Indian River lagoon, Fla., based on size class. SL is standard length of fish; N is the total number of fish collected in a size class.

SL (mm)	*Syringodium* N	*Syringodium* %	*Thalassia* N	*Thalassia* %	*Halodule* N	*Halodule* %
11-15	1	0.3	2	0.3	7	0.7
16-35	13	4.9	79	13.7	201	22.4
36-80	217	81.9	460	79.4	659	73.4
>80	34	12.9	38	6.6	31	3.5

trawls were made for night collections, as opposed to seven in the daytime, variation around the mean values was low; the three beds yielded no statistically similar collections of pinfish or total number of individuals. There were, however, no significant differences among the three beds in numbers of non-pinfish individuals or numbers of species collected. Although night collections yielded higher numbers of individuals than daytime collections, there were few qualitative differences between samples. In January, the relative abundance of pinfish was slightly greater in night collections than in daytime collections in *Halodule* and *Syringodium*; there were slight decreases at all stations in July (<14%) (Tables 8, 10). Certain cryptic species, such as *Syngnathus scovelli*, *Gobiosoma robustum*, and *Myrophis punctatus*, were more abundant in night collections than in daytime samples, but only one species, sea catfish, *Arius felis*, was captured only at night.

DISCUSSION

Comparisons of vegetated and unvegetated habitats have demonstrated the importance of seagrass habitats to a wide variety of juvenile fishes (Reid 1954; Livingston 1975; Weinstein et al. 1977; Orth and Heck 1980). From the present study, it is clear that there is a close relationship between structural complexity of a seagrass bed and patterns of fish abundance. Aboveground biomass was a good indicator of ichthyofaunal abundance in one type of meadow (*Thalassia*), but when examining monotypic beds of several seagrass species, blade density, rather than biomass, proved to be best correlated with fish abundance.

The observed relationships between fish abundance and structural complexity or type of seagrass meadow are governed by the dispersal of fishes to the beds, habitat preferences of the fishes, and their survival in the meadows. Because most of the fishes on temperate seagrass beds are seasonal residents (Kikuchi and Pérès 1977) and because the majority are juveniles, seasonal abundance is related to time of spawning. Many of the most numerous seagrass associates, including *Lagodon rhomboides*, *Leiostomus xanthurus*, *Bairdiella chrysoura*, and *Diplodus holbrooki*, spawn offshore in midwinter (Brady 1981). Differential dispersal of larvae to various field sites, therefore, could have a major influence on the abundance of fishes at a given field location. In a study of ichthyoplankton in Apalachee Bay, Brady (1981) found highest numbers of fish eggs and larvae at station F-12 which yielded the smallest trawl collections of all vegetated sites. Lowest numbers of eggs and larvae were collected at station E-12 where juvenile and adult fishes were most abundant. Similarly, there was no correlation between the abundance of eggs and larvae as determined by Brady and the number of juveniles and adults collected by trawl for species such as *L. rhomboides* and *L. xanthurus*. Clearly, differential dispersal of eggs and larvae does not explain the distributional pattern for juvenile and adult fishes in Apalachee Bay. Because late postlarval fish were collected at all stations in Indian River lagoon and because the sites were in very close proximity (all within a radius of 300 m), differential dispersal of fishes seems unlikely to explain ichthyofaunal differences among sites in the lagoon.

Individual fish species or age groups may actively seek particular habitat types. Two characteristics of seagrass meadows attract fishes—abundance of food and shelter. In earlier studies (Stoner 1980a) it was shown that spatial patterns in the abundance of benthic macroinvertebrates in Apalachee Bay are directly related to seagrass biomass. Because the benthic samples were taken concurrently with fish collections, and on the same stations, strong circumstantial evidence exists for a functional relationship between food abundance and fish distribution. Also, experimental data on the foraging behavior of *Lagodon rhomboides* (Stoner 1982) provide support for the hypothesis that predator and prey distribution may be related to predatory efficiencies of the fishes. *Lagodon rhomboides* was found to be most successful in capturing amphipod prey in habitats composed of *Halodule*; capture rate

TABLE 10.—Nighttime abundance of fishes and fish species in three seagrass beds in Indian River lagoon, Fla. Values are mean numbers per trawl ± SD ($n = 2$). * indicate mean values that were not statistically different on a given date (ANOVA and Duncan's multiple range test, $P < 0.05$; F values are provided).

Seagrass bed	January	July
Number of individuals, all species		
Halodule	43.0 ± 7.0	126.0 ± 20.0
Thalassia	21.5 ± 7.5	88.0 ± 8.0
Syringodium	12.0 ± 3.0	49.0 ± 9.0
	($F = 6.62$, $P < 0.10$)	($F = 8.76$)
Number of pinfish		
Halodule	30.0 ± 7.0	89.0 ± 11.0
Thalassia	12.0 ± 2.0	60.0 ± 7.0
Syringodium	5.0 ± 1.0	28.5 ± 5.5
	($F = 9.24$)	($F = 13.72$)
Number of individuals, excluding pinfish		
Halodule	*13.0 ± 0	*37.0 ± 9.0
Thalassia	* 9.5 ± 5.5	*28.0 ± 1.0
Syringodium	* 7.0 ± 2.0	*20.5 ± 3.5
	($F = 0.80$)	($F = 2.17$)
Number of species		
Halodule	*3.5 ± 0.5	* 5.5 ± 0.5
Thalassia	*2.5 ± 0.5	* 4.0 ± 1.0
Syringodium	*3.0 ± 0	* 3.5 ± 0.5
	($F = 1.50$)	($F = 2.17$)

was significantly lower in *Thalassia*; and lowest efficiency of predation occurred in *Syringodium*. Therefore, low biomass and high predatory success in the *Halodule* bed would make it the habitat of choice for pinfish and probably other consumers of small invertebrates. Herbivorous pinfish adults, which show a distinct dietary preference for *Syringodium* over other seagrasses (Stoner 1980b), showed largest relative abundance at the *Syringodium* site.

Predation experiments also showed that predatory efficiency is less affected by dense seagrass for small juvenile pinfish than for large juvenile and subadult size classes (Stoner 1982); therefore, the inverse relationship between abundance of large pinfish and seagrass biomass in Apalachee Bay may be a function of decreasing predatory efficiency in heavy seagrass. Conversely, small pinfish, adept at picking small prey from among seagrass blades, show an abundance pattern directly related to seagrass biomass and, hence, food abundance. In correspondence with these observations, it is interesting to note that negative correlations of fishes with seagrass biomass in January, February, and March occurred with numerical dominance by early juvenile fishes which feed in the water column or on small invertebrates of the sediment such as harpacticoid copepods (Stoner 1980b; Livingston 1982). Positive correlations occurred during months when collections were dominated by benthic carnivores (May to October). This observation provides more evidence for the utility of the "ontogenetic trophic unit" concept proposed by Livingston (1980) and Stoner (1980b).

As a more parsimonious explanation of the apparent relationship between fish abundance and seagrass biomass or species, individual fishes may simply prefer areas of high blade density, regardless of seagrass species. The selective advantage of such a habitat preference would be obvious if heavy losses to predation or shortages of appropriate food types occur outside the beds. Careful experimentation will be required to determine which mechanisms are involved in the choice of habitat by seagrass-associated fishes.

Heck and Orth (1980) have suggested that high abundance and species richness of fishes and motile invertebrates in seagrass meadows are, at least, partially due to protection offered by seagrass blades. Experimental evidence for this conclusion exists for crustaceans (Nelson 1979; Coen et al. 1981; Stoner 1982), and it is likely that small fishes are rapidly removed from unvegetated and sparsely vegetated habitats by large, piscivorous predators. Large piscivores are abundant in the seagrass meadows of Apalachee Bay (e.g., *Cynoscion nebulosus*) and are known to consume juvenile fishes such as *Lagodon rhomboides* (Ryan 1981). The predatory efficiency of most fishes would be reduced with increasing seagrass biomass or blade density. Seine hauls conducted by Gilmore[4] near the trawl stations in Indian River also yielded large numbers of piscivorous fishes which could have a significant effect on populations of smaller fishes such as *L. rhomboides*, *Eucinostomus* species, and *Orthopristis chrysoptera*. Fifty-three percent of all seine hauls yielded snook, *Centropomus undecimalis*, 41% contained great barracuda, *Sphyraena barracuda*, and 62% contained large grey snapper, *Lutjanus griseus*. Because these piscivores found in the seagrass meadows are visual predators relying on high speed, increasing blade density probably hinders both prey detection and capture. The relatively low density of thin *Syringodium* blades undoubtedly increases foraging efficiency of large predators. Despite low biomass, high blade density in *Halodule* beds (often over 10,000 blades/m^2) may provide excellent protection for small and/or juvenile fishes. High biomass and long, wide blades of *Thalassia* may provide better protection for juveniles than *Syringodium*, despite low blade densities.

Seagrass biomass had very little effect on the species richness of ichthyofauna in Apalachee Bay, unlike the relationship shown for invertebrates (Heck and Wetstone 1977; Stoner 1980a). Rather, species richness and occurrence of certain species appeared to be related to the presence of particular microhabitats. Highest species richness was found at the site with low plant biomass (station F-12), where there is a patchy distribution of grasses with occasional clumps of red algae and sponges. The importance of the red algal microhabitat has been reported for fishes from both Apalachee Bay (Stoner and Livingston 1980) and Indian River lagoon (Kulczycki et al. 1981). Similarly, Weinstein and Heck (1979) found that latitudinal variation in the richness of seagrass-associated ichthyofauna was related to the presence of non-seagrass habitats such as coral reefs and mangroves. Consequently, increasing habitat heterogeneity within beds may be more important than seagrass biomass, species, or blade density in determining species richness in fish communities.

Although certain, highly mobile predators such as sharks are known to move into seagrass meadows of Apalachee Bay and the total number of fishes collected per trawl increases, the smaller resident species appear not to leave the beds at night (Ryan 1981) as some do in tropical regions where regular diurnal

[4]R. G. Gilmore, Staff Scientist, Harbor Branch Foundation, Inc., R.R. 1, Box 196, Fort Pierce, FL 33450, pers. commun. April 1981.

movement of fishes and invertebrates between seagrass beds and coral reefs is common (Randall 1965; Ogden and Buckman 1973; Ogden and Zieman 1977). In Apalachee Bay, lack of diurnal change in species composition probably relates to the enormous size of the meadow (continuous for hundreds of square kilometers) and the fact that no alternative habitats are in close proximity except for occasional patches of bare sand or mud. Despite the smaller, band or patchlike nature of seagrass beds in Indian River lagoon, the ichthyofauna found there were also full-time residents. An examination of the food habits of temperate seagrass-associated fishes (Carr and Adams 1973; Livingston 1982) indicates that most consume prey items normally found among the macrophytes. Also, most appear to be visual predators which rest near bottom at night (pers. obs.), taking advantage of the shelter provided by the seagrass blades. It would appear, therefore, that fishes in the temperate regions examined do not move to and from seagrass beds, except for a few species of nocturnal predators which move into the beds at night. Increased catches at night are most likely related to inactivity of many species and the resultant elevation in capture efficiency.

Because trawl efficiency probably decreases with seagrass biomass, fish populations in Apalachee Bay would have been underestimated most severely at the most heavily vegetated station E-12 and least at station F-11; therefore, the relationship between seagrass biomass and fish abundance is probably even more pronounced than that demonstrated. In Indian River lagoon, seagrass biomass was similar at the *Syringodium* and *Halodule* beds, but the high density of *Halodule* blades might serve to reduce trawl efficiency as would high biomass at the *Thalassia* bed. Estimates of fish abundance at the *Halodule* and *Thalassia* beds, therefore, may be low, in relative terms. Because the limited collections made at night yielded much higher numbers of fishes and more clearly separated the stations in Indian River lagoon, future trawl studies should be conducted at night despite the inherent difficulties. New surveys in other areas would be particularly valuable in establishing the universality of relationships observed between fishes and seagrass biomass and seagrass species.

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REDESCRIPTION OF LARVAE OF THE PIGFISH, *ORTHOPRISTIS CHRYSOPTERA* LINNAEUS (PISCES, HAEMULIDAE)

WILLIAM WATSON[1]

ABSTRACT

A size series of larval pigfish, *Orthopristis chrysoptera*, was assembled from specimens collected from the lower Cape Fear River Estuary, North Carolina, and from the gulf coast of Texas. Larvae are rather heavily pigmented, principally along the ventral midline. Specimens up to about 9 mm SL have 13 to 19 ventral melanophores along the tail with those between the 19th and 22d myomeres typically larger. A dorsal melanophore usually is present above the largest ventral melanophore. At about 9 mm SL midlateral pigmentation begins near the peduncle and internal pigment appears posteriorly above and below the vertebral column. By about 15 mm SL a distinct pattern of dorsal, lateral, and ventral longitudinal stripes is present. Pigfish larvae may be separated from similar cooccurring species by various combinations of pigment pattern, very small preopercular spines, and myomere and fin ray counts.

Larval development of the pigfish, *Orthopristis chrysoptera*, was described by Hildebrand and Cable (1930) based on reared yolk-sac stage larvae and older field specimens collected near Beaufort, N.C. They described yolk-sac stage larvae as having a barred pattern, with dorsal and ventral melanophores on the trunk at the level of the anus and at midtail, but stated that preserved larvae between about 3 and 15 mm were unpigmented. Scotton et al. (1973) illustrated a 12.3 mm larva with series of melanophores along the ventral and lateral midlines of the tail, and a few dorsally on the head. Johnson (1978) summarized these earlier descriptions, but added no new information.

Pigfish larvae collected from the lower Cape Fear River Estuary, N.C., differed from Hildebrand and Cable's (1930) description in that they maintained the barred pattern well past the yolk-sac stage, and had considerable pigment along the ventral midlines of the gut and tail throughout the larval period. Pigfish larvae from the northern Gulf of Mexico were examined subsequently and found to be pigmented in these same areas.

Since larval pigment of pigfish is heavier and more persistent than previously described, larval development (emphasizing pigment) is redescribed here, based principally on specimens from the Cape Fear River Estuary. Specimens larger than 9.2 mm are from the northern Gulf of Mexico, since larvae of this size were not taken in the Cape Fear River Estuary.

MATERIALS AND METHODS

Larvae were collected from the lower Cape Fear River Estuary in May and June 1977 with 0.5 mm mesh nets of approximately 0.6 m^2 mouth area, towed at ca. 0.5 m/s (Copeland et al 1979[2]). Samples were fixed immediately in the field in unbuffered 5-10% Formalin,[3] and the pigfish larvae subsequently removed were stored in 2.5% seawater-Formalin.

Larvae were examined under a dissecting microscope equipped with an ocular micrometer. Counts and measurements (made to the nearest 0.04 mm and reported to the nearest 0.1 mm) were made on the left side. The following dimensions were recorded: Total length, standard length, head length, snout length, eye diameter, preanal length, and depth at pectoral fin insertion. These measurements are defined by Saksena and Richards (1975). Lengths given in the text refer to standard length unless otherwise specified. Drawings were made with the aid of a camera lucida. All specimens were lightly stained with alizarin to aid in drawing and in counting fin rays and preopercular spines. Two larvae (11.8 and 13.2 mm) were cleared and stained following the method of Hollister (1934).

Descriptions are based on 19 Cape Fear and 4 Gulf of Mexico specimens; 26 additional postflexion Gulf of Mexico specimens were briefly examined for

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[2]Copeland, B. J., R. G. Hodson, and R. J. Monroe, 1979. Larvae and postlarvae in the Cape Fear Estuary, N. C., during operation of the Brunswick Steam Electric Plant 1974-1978. Report 79-3 to Carolina Power and Light Co., Raleigh, N.C.

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

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pigmentation and found to conform with the description given here.

DESCRIPTION OF LARVAE

Pigmentation

The pigfish larva in the late yolk-sac stage (2.5 d; 3 mm) illustrated by Hildebrand and Cable (1930, fig. 27) is shown with large dorsal and ventral melanophores at myomeres 18-19, and a smaller pair at myomeres 9-10. Just after the yolk-sac stage, larvae from the Cape Fear River Estuary retain dorsal melanophores at myomeres 9-10 and between myomeres 18 and 21. The anterior dorsal melanophore rarely persists beyond 4 mm, while the posterior one (sometimes two) usually remains throughout the larval period (present in 13 of the 19 Cape Fear specimens; Figs. 1 and 2). This posterior dorsal melanophore(s) lies at the terminus of the dorsal fin in older larvae. About concurrently with completion of the dorsal fin (ca. 10.9 mm) additional melanophores develop posteriorly, forming a pigment patch just behind the fin. More patches are sub-

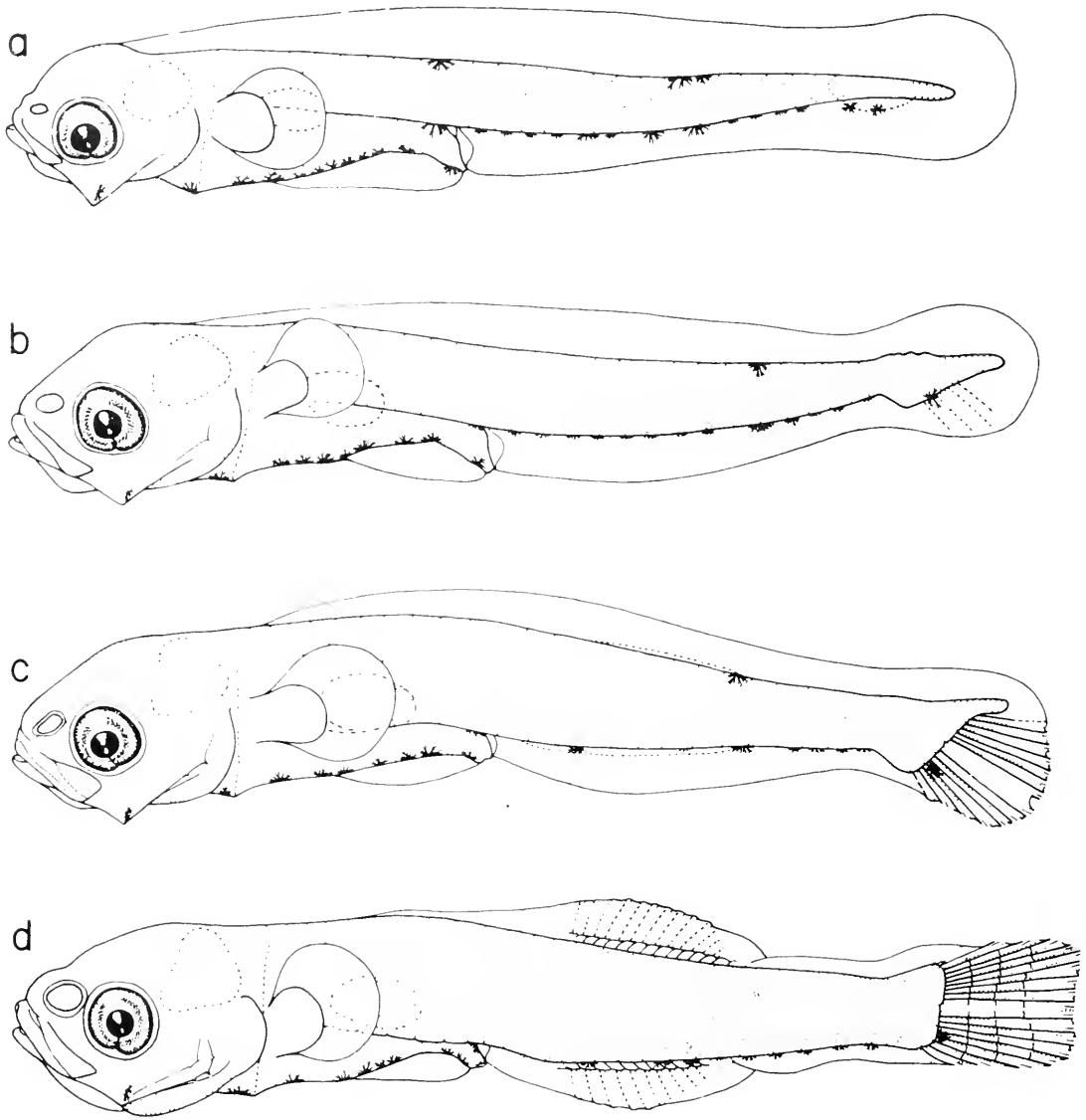


FIGURE 1.—*Orthopristis chrysoptera*; a, 4.2 mm; b, 5.6 mm; c, 6.4 mm; d, 7.3 mm. All specimens are from North Carolina.

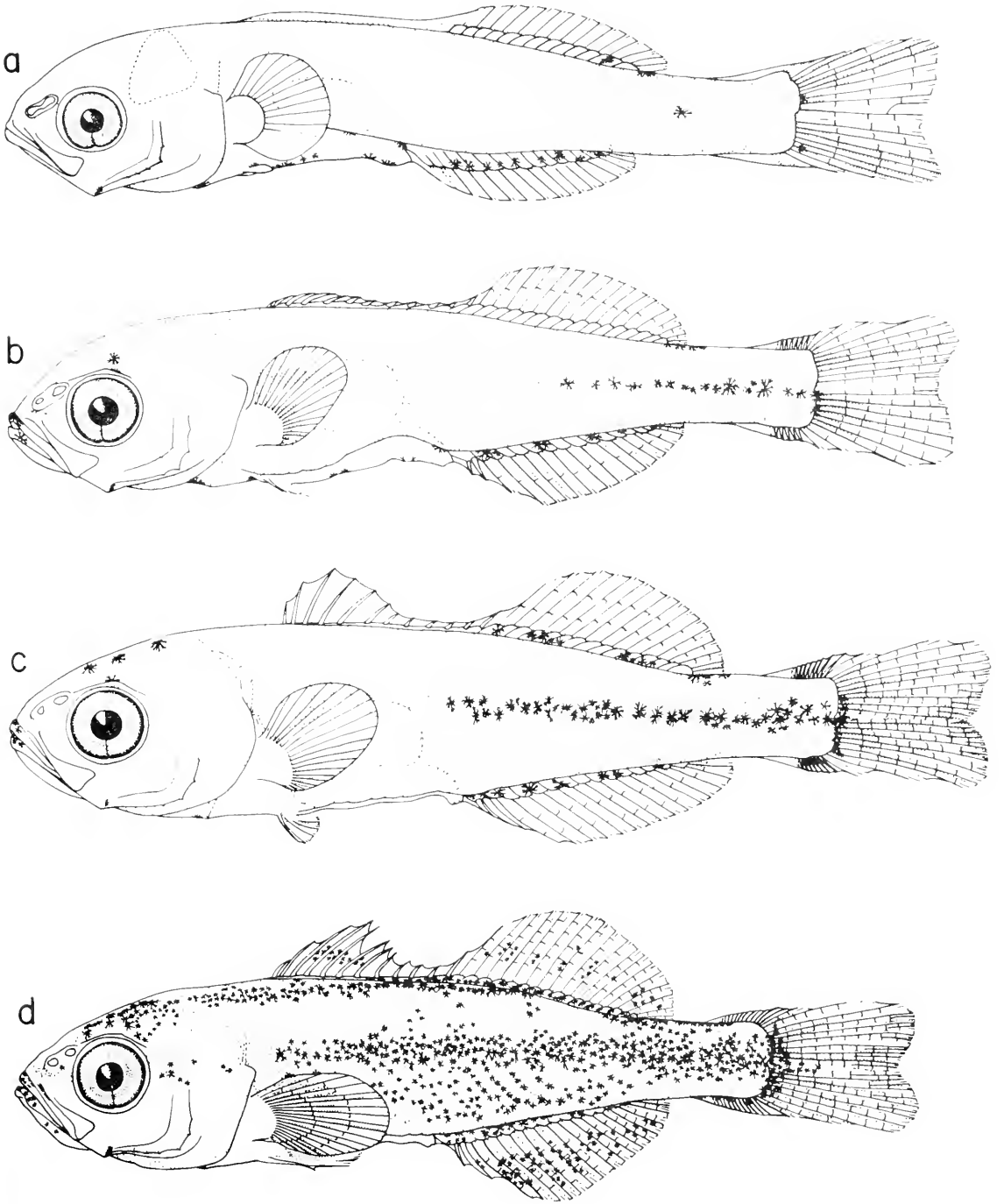


FIGURE 2.—*Orthopristis chrysoptera*: a. 9.2 mm; b. 11.1 mm; c. 12.7 mm; d. 15.8 mm. Specimen "a" is from North Carolina; specimens "b" through "d" are from the gulf coast of Texas.

sequently added from posterior to anterior along the dorsal fin ray bases (Fig. 2c) so that by the end of the larval period (ca. 16 mm) a continuous pigment line lies along each side of the dorsal midline. Melanophores develop on the membrane between the dorsal fin rays at this time (Fig. 2d).

Ventral tail pigment through most of the larval period consists of 12 to 17 melanophores arrayed along the length of the tail. Those at myomeres 17 to 21 (usually at 19 to 21) are distinctly larger, usually dendritic (Fig. 3), and correspond to the posterior ventral melanophore illustrated by Hildebrand and Cable (1930) in a 3 mm specimen. Larvae smaller than 5.7 mm typically have two or three enlarged ventral melanophores, while larger specimens have none to two. These lie at the posterior end of the anal fin in larger specimens. Melanophores behind the developing anal fin base (except the last melanophore) extend internally during notochord flexion. Those between the anus and myomere 19 or 20 extend internally early in larval development, but tend to move downward onto the developing anal fin ray bases during late flexion. They usually are located entirely along the sides of the anal fin ray bases in postflexion larvae (Figs. 2, 3). The last ventral melanophore is associated with the developing caudal complex and becomes located along the lower hypurals during notochord flexion. Melanophores proliferate along the distal hypural edge in postflexion larvae, forming a bar. Near the end of the larval period melanophores extend from the bar along the central caudal rays. At this time, melanophores also develop on the membranes between the dorsal and anal fin rays (Fig. 2d).

Lateral pigment is first evident in postflexion larvae (ca. 7.3 mm) as an internal melanophore above the notochord at myomere 20 or 21. Melanophores are added, first ventrally and then laterally, along the vertebrae both caudad and cephalad. The cephalad extension proceeds more rapidly. Hildebrand and Cable (1930, fig. 33) apparently illustrated this internal pigmentation in an 11 mm specimen, but did not mention it in the text. External pigment develops posteriorly along the lateral midline soon after the beginning of the cephalad extension of the vertebral melanophores (Fig. 2a). This external pigment proliferates both cephalad and caudad (more rapidly cephalad), but always lags behind the vertebral pigment (Fig. 2b). When the lateral pigment band reaches the level of the anus, it begins to widen as well (Fig. 2c), forming a broad lateral stripe from the opercular margin onto the central caudal fin rays by the

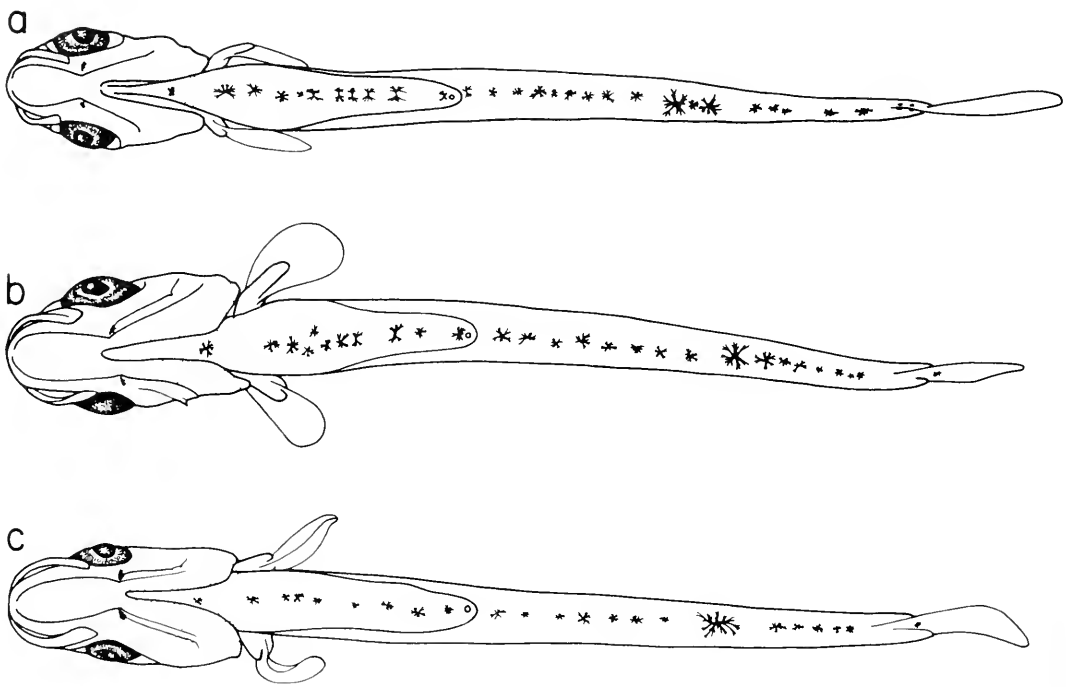


FIGURE 3.—Ventral view of *Orthopristis chrysoptera*; a, 4.2 mm; b, 5.6 mm; c, 6.4 mm; d, 7.3 mm; e, 9.2 mm;

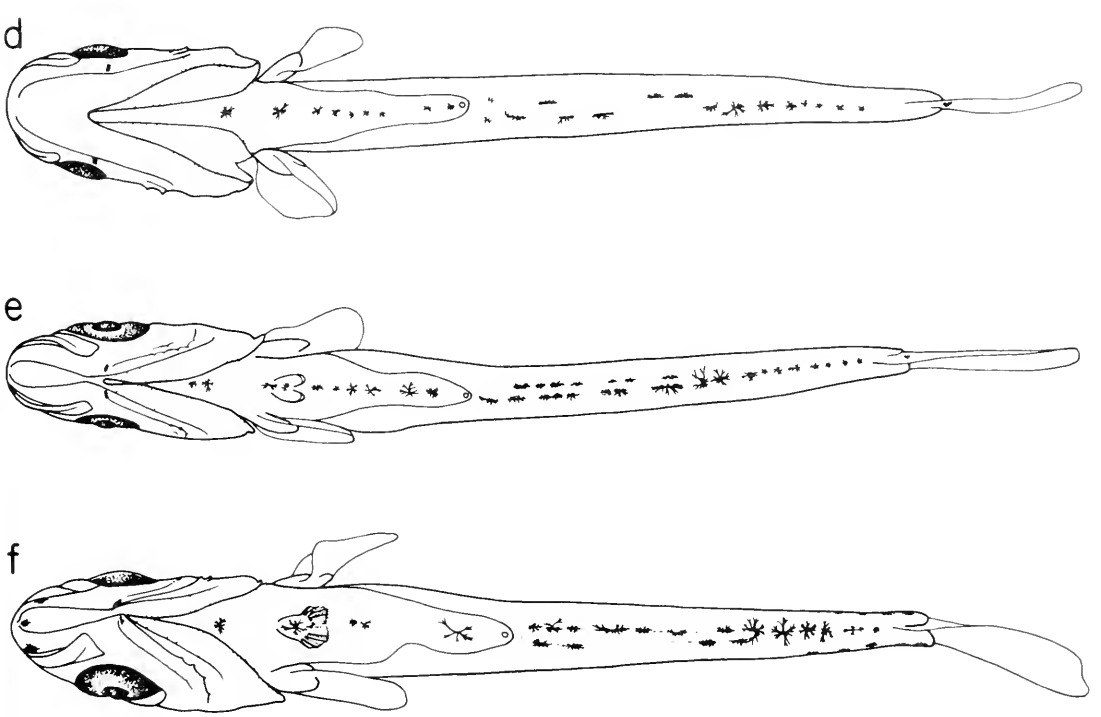
end of the larval period (Fig. 2d). Myoseptal melanophores develop late in the larval stage, particularly on the lower half of the body between about the level of midgut and the peduncle.

The gut and isthmus are moderately pigmented along their ventral midlines through notochord flexion: 6 to 11 melanophores are arrayed between the cleithral symphysis and the anus (Fig. 3). This number decreases in postflexion larvae, but at least one melanophore remains between the pelvic fin bases together with two or three between the pelvic bases and anus. One or two midline melanophores precede the cleithral symphysis throughout larval development.

Dorsal visceral pigment through most of the larval period consists of a single large melanophore over the hindgut where it turns down at the 9th or 10th myomere, and several melanophores over the posterior dorsal surface of the swim bladder. Occasionally a second melanophore lies over the hindgut between these areas. Swim bladder pigment extends forward to cover the entire dorsal surface during late postflexion. At this same time pigment proliferates over the hindgut and anterior to the swim bladder to form a band continuous with the vertebral pigment.

Pigfish larvae retain a melanophore at the angle of the lower jaw throughout the larval period. A melanophore may sometimes occur under the hindbrain before notochord flexion but this typically is absent until after notochord flexion. Pigment proliferates rapidly under the hindbrain in postflexion larvae, forming a continuous line with the vertebral and dorsal gut pigment. Pigment develops on the roof of the mouth during late postflexion, completing an internal stripe extending the length of the body. Near the end of the larval period pigment develops around the posterior midbrain and anterior hindbrain. Pigment may appear along the upper lip at ca. 9 mm, but is not consistently present until ca. 11 mm. Pigment develops along the lower lip at ca. 11 mm. External melanophores appear at the nostril and behind the eye at the end of the larval period, completing a nearly continuous external midlateral stripe extending along the entire length of the fish (Fig. 2d).

Dorsal head pigment first develops above the midbrain in postflexion larvae (Fig. 2b) at ca. 11 mm. This pigment proliferates rapidly to form longitudinal head stripes which become continuous with the dorsal trunk stripes by the end of the larval period (Fig. 2d). Pigfish larvae at this stage, although more heavily pigmented, display nearly the same pattern described by Hildebrand and Cable (1930).



f. 11.1 mm. Specimens "a" through "e" are from North Carolina; specimen "f" is from the gulf coast of Texas.

Morphology

Measurements of the 23 larvae examined are summarized in Table 1. All body parts measured increase relative to standard length with increasing larval length. However, these changes are small. The greatest changes are in body depth and preanal length relative to standard length, from means of 0.15 and 0.47, respectively, for preflexion-stage larvae to means of 0.21 and 0.52, respectively, for postflexion-stage larvae. Despite these small changes in proportions, the relationships of body parts with standard length are adequately described by straight lines (Table 2). These pigfish larvae are slightly more robust than those described by Hildebrand and Cable (1930).

The sequence of fin ray differentiation is as follows: Principal caudal, second dorsal and anal, pectoral, first dorsal, pelvic, and secondary caudal. Differentiation of the first anal fin ray into the third anal fin spine is delayed until after the larval stage. The following description of fin development refers to discernible, but not necessarily ossified, structures.

Fin development generally is as described by Hildebrand and Cable (1930). The caudal anlage is developing in the smallest specimen examined (3.8 mm). Notochord flexion begins between 4.8 and 5.5 mm and is complete by ca. 7 mm. Principal caudal fin rays begin developing during notochord flexion, with the full complement of 9 + 8 attained just after flexion (Table 3). Secondary caudal rays begin to develop after ca. 9.2 mm but before 10.9 mm, with the full complement of 13 + 12 present at the end of the larval period (ca. 16 mm).

Anal and dorsal fin anlagen develop simultaneously during late flexion (between ca. 5.8 and 6.2 mm). The dorsal fin base initially extends between myomeres 14 and 19 but elongates to between myomeres 4-5 and 20-21. Differentiation of second dorsal fin ray supports begins at 6.4 to 7.0 mm followed by the rays at 7.2 to 9.0 mm. Dorsal spines develop between 9.0 and 10.9 mm. The full dorsal fin complement of 12 spines and 15 to 17 soft rays is acquired by 10.9 mm. The anal fin base initially lies between myomeres 11-12 and 19, and ultimately extends caudad to myomere 20-21. Anal fin ray support differentiation begins almost simultaneously with the second dorsal fin ray supports. Anal fin rays are first discernible between 7.2 and 9.0 mm. All anal fin elements are present by ca. 10.9 mm but the third anal spine does not ossify from the first ray until well into the juvenile stage (at ca. 31 mm).

Pelvic fin buds appear near the end of notochord flexion, and pelvic fin rays begin differentiating at ca. 10.9 mm. The full complement of elements (I,5) is present by ca. 11.1 mm (Table 3).

Upper pectoral fin rays first differentiate in postflexion larvae at ca. 9.0 mm. The full complement of 19 rays is present at the end of the larval period.

The first preopercular spine appears at the angle in preflexion larvae (ca. 4.8 mm). A second spine is added on the lower preopercular margin during flexion (ca. 6.2 mm) and a third on the upper margin just after flexion (ca. 7.3 mm). Fourth and fifth spines subsequently appear along the lower and upper margins, respectively. A second, more anterior, row of one to three very small preopercular spines may develop during notochord flexion. All of these spines are short: The longest is no more than 10% of the eye diameter.

All gill rakers are present by ca. 13.2 mm (5 upper + 1 + 11 lower).

TABLE 1.—Summary of measurements (in mm) of larval *Orthopristis chrysoptera*. Specimens between dashed lines are undergoing notochord flexion.

Total length	Standard length	Preanal length	Head length	Snout length	Eye diameter	Depth
—	3.8	1.8	0.7	0.2	0.2	0.6
4.2	4.0	1.9	0.9	0.2	0.3	0.6
4.4	4.2	2.0	0.8	0.2	0.3	0.6
4.9	4.8	2.3	1.1	0.3	0.3	0.7
5.0	4.8	2.3	1.2	0.4	0.4	0.7
—	5.5	2.6	1.2	0.3	0.4	0.8
—	5.5	2.6	1.2	0.3	0.4	0.8
5.8	5.6	2.6	1.3	0.3	0.4	0.8
—	5.7	2.6	1.3	0.3	0.4	0.8
—	5.7	2.7	1.4	0.4	0.4	0.9
6.0	5.8	2.7	1.7	0.4	0.4	0.8
—	6.2	3.2	1.5	0.4	0.4	1.0
7.1	6.4	3.2	1.6	0.4	0.4	1.0
—	6.4	3.2	1.6	0.4	0.5	1.1
8.1	7.0	3.6	1.9	0.5	0.5	1.2
8.4	7.2	3.7	1.6	0.6	0.6	1.4
8.4	7.3	3.7	2.0	0.5	0.5	1.3
—	8.8	4.6	2.6	0.7	0.8	1.8
10.5	9.2	4.6	2.6	0.6	0.7	1.7
[1]12.8	10.9	6.1	3.0	0.8	1.0	2.2
[1]12.7	11.1	6.0	3.2	0.8	1.0	2.4
[1]15.1	12.7	7.0	3.8	1.0	1.2	2.9
[1]18.5	15.8	8.7	4.8	1.3	1.5	3.8

[1]Specimens from Texas

TABLE 2.—Summary of regressions of measurements of body parts (y) on standard length (x) of larval *Orthopristis chrysoptera*.

y	n	r	Regression equation
Preanal length	23	0.998	$y = -0.573 + 0.590x$
Head length	23	0.995	$y = -0.575 + 0.343x$
Snout length	23	0.986	$y = -0.152 + 0.091x$
Eye diameter	23	0.993	$y = -0.184 + 0.103x$
Depth at pectoral fin origin	23	0.993	$y = -0.636 + 0.272x$

TABLE 3.—Summary of counts from larval *Orthopristis chrysoptera*. Specimens between dashed lines are undergoing notochord flexion. The presence of a fin anlage is denoted by "A".

Standard length (mm)	Myomeres		Caudal fin rays			Dorsal fin		Anal fin rays	Pectoral fin rays	Pelvic fin rays
	Precaudal	Caudal	Dorsal secondary	Primary	Ventral secondary	Spines	Rays			
3.8	9	17		A						
4.0	10	16		A						
4.2	9	18		A						
4.8	9	17		A						
4.8	9	17		4						
5.5	10	16		A						
5.5	10	16		A						
5.6	10	16		A						
5.7	10	16		A						
5.7	9	17		4						
5.8	10	16		10						
6.2	10	16		12			A	A		
6.4	10	16		12			A	A		
6.4	10	16		14			A	A		Bud
7.0	9	16		16			A	A		Bud
7.2	10	17		17			14	12		Bud
7.3	10	16		17			A	A		
8.8	10	16		17			A	A		Bud
9.2	10	16		17			14	13	10	Bud
[1]10.9	11	15	8	17	7	XII	16	11.14	17	14
[1]11.1	12	14	8	17	7	XII	16	11.14	17	15
[1]12.7	12	14	9	17	8	XII	15	11,14	19	15
[1]15.8	12	14	13	17	12	XII	17	11.15	19	15

[1]Specimens from Texas

IDENTIFICATION

Larvae of haemulids resemble those of several other families, most notably gerreids, lutjanids, sparids, and some sciaenids. Gerreids, lutjanids, and sparids can be separated from haemulids by myomere count: 24 versus the 26 or 27 of haemulids. Sciaenids have 24 to 29 vertebrae (most species have 25) but are deeper bodied and often have a shorter gut than the described haemulid larvae. Sciaenids frequently have heavier preopercular armature as well (Johnson 1978). Counts of dorsal soft fin rays allow easy separation of older specimens: Most sciaenids have 19 or more while the western Atlantic haemulids have 18 or fewer (Miller and Jorgenson 1973).

Postflexion specimens of *Orthopristis chrysoptera* are easily separated from other haemulids with which they may occur by using anal fin ray counts. No other species has more than 11 soft rays (Table 4). Separation of smaller specimens may be much more difficult, since larvae of most of the western Atlantic haemulids are undescribed.

Larval *Haemulon plumieri*, described by Saksena

TABLE 4.—Fin ray and vertebral counts of haemulid species which may occur with *Orthopristis chrysoptera* along the Atlantic and gulf coasts of the United States.

Species	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Vertebrae	Source[1]
Anisotremus virginicus	XII, 16-17	III,10-11	17-18	10+16-17	1,2
A. surinamensis	XI-XII,16-18	III,9	18-19	10+16	1,2
Conodon nobilis	XII,13	III,7		10+16	1
Haemulon album	XII-16-17	III,5-8	18-19	10+16	1,3
H. aurolineatum	XIII,14-16	III,7-9	16-18	10+16	1,3
H. chrysargyreum	XII,12-14	III,9-10	15-17	10+16	1,3
H. flavolineatum	XII,14-15	III,7-9	16-17	10+16	1,3
H. macrostomum	XII,15-17	III,8-9	17-18		3
H. melanurum	XII,15-17	III,7-9	16-18	10+16	1,3
H. parrai	XII,16-19	III,8-9	16-17		3
H. plumieri	XII,15-17	III,8-9	16-17	10+16	1,3
H. sciurus	XII,15-17	III,8-9	15-17		3
H. striatum	XIII,12-15	III,7-9	17-19	10+16-17	1,3
Orthopristis chrysoptera	XII-XIII,15-16	III,12-13	19	10-16	1,4,5
Pomadasys crocro	XIII,11-12	III,7			4

[1] 1 Miller and Jorgenson (1973)
2 Hoese and Moore (1977)
3 Courtenay (1961).
4 Walls (1975).
5 This study.

and Richards (1975), closely resemble *O. chrysoptera*. *Haemulon plumieri* larvae between the end of yolk-sac absorption and late flexion lack the dorsal trunk pigment typically present in *O. chrysoptera*, and apparently lack the enlarged midventral trunk melanophore(s) at all sizes (Saksena and Richards 1975). Both species develop preopercular spines at about the same size, but *H. plumieri* acquires more, with those in the posterior series larger than the corresponding spines of *O. chrysoptera*.

Larvae of other species of *Haemulon* have not been described. Assuming that they resemble *H. plumieri*, the combination of slightly different trunk pigment and somewhat longer preopercular spines may allow separation of smaller specimens. Larvae of the Atlantic species of *Conodon* and *Pomadasys* have not been described. A juvenile (17.3 mm) *Conodon nobilis* illustrated by Heemstra (1974) has rather long preopercular spines, suggesting that this character may be useful in separating the larvae. Likewise, if larval *Pomadasys* from the Atlantic resemble larval *Pomadasys* from the Indo-Pacific, then they also may be distinguished from *O. chrysoptera* by having more, and longer, preopercular spines (Nellen 1973; Leis[4]).

De Sylva (1970) illustrated a 16.5 mm specimen of *Anisotremus virginicus* which was deeper bodied and much more lightly pigmented than *O. chrysoptera* of the same size. *Anisotremus virginicus* is being described from reared larvae by Potthoff et al.[5] The similarity between *A. virginicus* and *A. davidsonii* from the eastern Pacific (Watson and Walker[6]) indicates that *Anisotremus* can be separated from *O. chrysoptera* by being deeper bodied (mean depth 25% of SL for *A. davidsonii* vs. mean depth 17% of SL for *O. chrysoptera*) and by having more and longer preopercular spines than *O. chrysoptera*.

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COHERENCE IN ZOOPLANKTON OF A LARGE NORTHWEST ATLANTIC ECOSYSTEM[1]

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ABSTRACT

Mesoscale measurements of zooplankton of the continental shelf off the northeast United States reveal previously unreported large-scale temporal and spatial coherence in the Gulf of Maine, on Georges Bank, off Southern New England, and in the Mid-Atlantic Bight. Unlike the apparent decline in zooplankton over the 30 years reported for the North Atlantic and North Sea, the zooplankton of the northeast shelf have not undergone any large-scale change in abundance or species composition since initial measurements made 70 years ago. Recent declines in fish populations of the shelf appear related more directly to excessive fishing mortality than to any changes in the abundance of zooplankton.

Zooplankton in marine ecosystems function as links between primary producers (phytoplankton) and predatory populations of fish, marine birds, and mammals. Mesoscale changes in zooplankton abundance have been associated with disruption of predator-prey relationships resulting in economically disastrous declines in fish stocks (Glover 1957; Glover et al. 1961; Williamson 1961; Jacobsen 1980). Although it has been demonstrated that large-scale (100-1,000 km) seasonal and annual variability in abundance of zooplankton has been associated with advective processes in the northeast Pacific and northeast Atlantic (Wickett 1967; Colebrook 1977, 1978a, b), we have not observed any large-scale changes in abundance of zooplankton off the northeast coast of the United States. The region has been under investigation since the turn of the century, but previous studies of zooplankton have been limited to restricted areas of the northeast shelf and covered relatively short periods of time (Fish 1925, 1936a, b; Bigelow 1926; Clarke and Zinn 1937; Bigelow and Sears 1939; Clarke 1940; Clarke et al. 1943; Deevey 1952, 1956, 1960; Grice and Hart 1962; Sherman 1968, 1970, 1976; Malone 1977; Judkins et al. 1980).

METHODS

Our findings are based on 32 surveys of zooplankton conducted by the United States, Poland, Soviet Union, and German Democratic Republic between 1977 and 1981, as part of a joint MARMAP study of the ecosystem of the northeastern shelf (Sherman 1980). Between 6 and 8 surveys were done per year. Sampling was done in four subareas: Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight, each characterized by distinct bathymetry and circulation (Emery and Uchupi 1972; Butman et al. 1982) (Fig. 1). Zooplankton were collected at an average of 129 locations per survey situated 25-35 km apart, resulting in a total of 3,568 samples. The time-series analyzed for each subarea is shown in Figure 2. At each sampling location, tows for zooplankton, using a paired bongo-type sampler (Posgay and Marak 1980) with 60 cm openings and nets of 0.333 and 0.505 mm mesh, covered the water column obliquely from 5 m above bottom to the surface. These nets were towed at ship speeds from 1.5 to 3.5 kn, and were lowered at a wire speed of 50 m/min and retrieved at 20 m/min. Water filtered through the net was measured with a flowmeter and a time-depth recorder was used to measure the towing profile of the sampler.

Zooplankton samples were sorted, identified, and counted at the Plankton Sorting Center, Szczecin, Poland. The biomass of zooplankton is expressed as cc/100 m^3 of water strained; numerical abundance is expressed as numbers of zooplankters/100 m^3 of water strained. Patterns of abundance of the dominant zooplankters are based on the analysis of the size-fraction retained in the 0.333 mm net, which primarily captured late juvenile and adult copepods.

RESULTS

Coherent Patterns of Biomass

Displacement volumes expressed as cc/100 m^3 of

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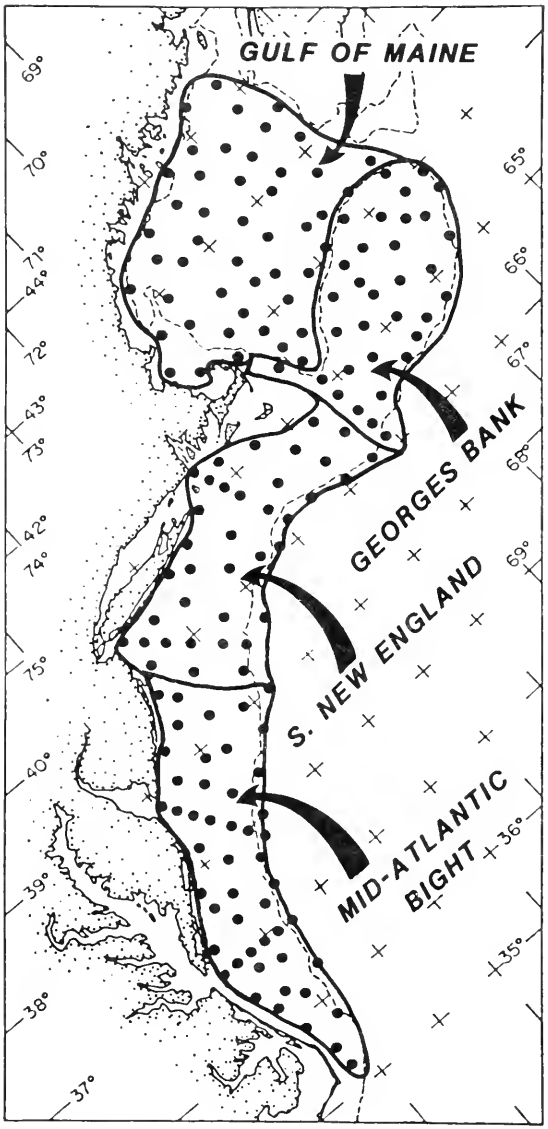


FIGURE 1.—The four geographic areas of the northwest Atlantic sampled for zooplankton during MARMAP operations from 1977 to 1981, with MARMAP station locations indicated by dots.

water strained are used to represent standing stocks of zooplankton. The seasonal patterns of zooplankton biomass observed each year and compared with the 5-yr means in each of the subareas, were coherent (Fig. 2a). The term coherent is used here to describe the recurring seasonal patterns of zooplankton biomass in which annual deviations from the 5-yr mean are insignificant at the 0.05 level (Table 1). On Georges Bank, the annual peak in spring (May) is followed by a sharp decline from late spring (June) through summer (August), and less precipitous decline from late summer through autumn to an annual low in winter. In the Gulf of Maine seasonal changes are not as pronounced as on Georges Bank, with the annual low in winter. The greatest change in biomass begins in April and reaches its annual high in May. From July until November, the standing stock does not undergo marked change, but declines gradually from November to a winter low in February. In Southern New England, zooplankton biomass is bimodal: an initial pulse occurs in May followed by a low in July, and a second peak occurs in August, followed by a decline in autumn and winter. In the Mid-Atlantic Bight biomass increases from an annual low in winter to an annual high in autumn.

TABLE 1.—Summary of probability statistics for the two-tailed Fisher-sign test for year-to-year coherence in the zooplankton volumes, dominance, and three dominant species—*Calanus finmarchicus*, *Pseudocalanus minutus*, and *Centropages typicus*. Annual departures from the MARMAP 5-yr mean annual cycle were tested for each subarea. The ranges of the probability of the Fisher-sign statistic are tabulated. Of the 100 tests (5 yr × 4 areas × 5 variables) only four reject the null hypothesis at 0.05 significance. H_0: annual cycle = 5-yr mean cycle; * = significant difference in the year indicated in parentheses.

Survey variable	Subarea			
	Gulf of Maine	Georges Bank	Southern New England	Mid-Atlantic Bight
MARMAP				
Volume	0.344-0.875	0.031-0.910	0.227-0.656	0.109-0.812
Dominance	0.145-0.773, 0.007* (78)	0.109-0.500	0.172-0.637	0.188-0.500
C. finmarchicus	0.344-0.773	0.109-0.891	0.500-0.656	0.188-0.812
P. minutus	0.344-0.773	0.188-0.891, 0.984* (79)	0.344-0.656, 0.992* (79)	0.500-0.812
C. typicus	0.227-0.891	0.344-0.891, 984* (77)	0.227-0.891	0.500-0.891

Coherence in Dominance

The Fager and McGowan (1963) index was used to identify the dominant zooplankters in each subarea by season. Of the 394 taxa in the samples, 50 were dominant in at least one location in one or more seasons. Summary statistics for all taxa, including rank, abundance, dominance, median abundance, and Delta-mean abundance (Pennington 1983), are available from the authors. Twelve taxa, all copepods, comprised 85% of the dominance—*Calanus finmarchicus*, *Pseudocalanus* sp., *Centropages typicus*, *Metridia lucens*, *Temora longicornis*, *Centropages hamatus*, *Acartia clausi*, *Acartia tonsa*, *Acartia* spp. (*A. clausi-A. longiremis*), *Oithona* spp., *Calanus* spp., and *Paracalanus parvus*. Among these 12 taxa, *Calanus finmarchicus*, *Pseudocalanus minutus*, and *Centropages typicus* accounted for 75% of the total dominance.

Species Shifts in Dominance

Although the three species co-occur on the shelf, their temporal and spatial patterns of dominance are different. These patterns are coherent among the 5 yr. The proportion of the total zooplankton accounting for these three dominant species is shown for each subarea as a function of time in Figure 2b. In the Gulf of Maine and over Georges Bank, *C. finmarchicus*, a species that overwinters in the cooler, deep waters of the Gulf of Maine (Bigelow 1926), is dominant in spring and early summer. During early autumn, when temperatures in the upper layer are warmest, dominance shifts to *C. typicus*, a species which undergoes greatest egg production in water warmer than 13° C (Dagg 1978). The shift from *C. finmarchicus* to *C. typicus* dominance occurs earlier (in late summer) on Georges Bank, where the change in abundance is of greater magnitude and persists to early winter. In the southern portion of the shelf, the dominance of *C. finmarchicus* in late spring is replaced by *P. minutus*, *C. typicus*, and other less-abundant zooplankters, including other copepods, cladocerans, larval echinoderms, salps, and barnacle larvae in Southern New England and principally cladocerans in the Mid-Atlantic Bight. Annual deviations in the dominance patterns of *C. finmarchicus*, *P. minutus*, and *C. typicus* from the 5-yr mean were insignificant at the 0.05 level in 95% of the comparisons made within the subareas (Table 1).

The numerical abundance of the three copepods were coherent within the envelope of one standard error of the mean and within the mean range in each of the subareas during the 5 yr (Fig. 2c). The zooplankton standing stocks, dominance patterns, and abundance levels of the principal species in each of the four subareas are different. The spring peak in zooplankton standing stock in the Gulf of Maine and on Georges Bank (Fig. 2a) is represented by *C. finmarchicus* in the Gulf of Maine and a combination of *C. finmarchicus* and *P. minutus* on Georges Bank, (Fig. 2b, c); the shift to *C. typicus* dominance in autumn is not of sufficient magnitude to register a secondary pulse in standing stock in the Gulf of Maine or Georges Bank.In Southern New England waters the bimodal peaks in zooplankton standing stock are represented by *C. finmarchicus* and *P. minutus* dominance in spring and early summer followed by large-scale *C. typicus* swarming in late summer and autumn (Fig. 2b, c). Further south in the Mid-Atlantic Bight, *C. finmarchicus* abundance is diminished, and is replaced by *P. minutus* and *C. typicus* in late winter and early spring, followed by an increase in the standing stock of zooplankton from summer through autumn (Fig. 2a) related to the growing abundance of cladocerans and other zooplankters in summer and large-scale swarming of *C. typicus* in autumn (Fig. 2b, c). Deviations from the 5-yr mean temporal patterns of abundance of the three dominant copepods were not significant at the 0.05 level in 95% of the comparisons (Table 1).

DISCUSSION

Observations on the zooplankton of the northeastern continental shelf made during the past half century (Bigelow 1926; Bigelow and Sears 1939; Grice and Hart 1962; Judkins et al. 1980) can be divided into four periods: 1) The first measurement of volumes and species abundance made by Bigelow between 1912 and 1920, 2) the volume measurements by Bigelow and Sears from 1929 to 1932, 3) the volume and species measurements of Grice and Hart in 1960, and 4) the more contemporary measurements of species abundance made by Judkins et al. in 1975. Data from these studies were converted where possible from volumes per standard haul and volumes per square meter to volumes per 100 m^3; data from stations showing evidence of net clogging due to large amounts of gelatinous zooplankton, large number of organisms >2.5 cm length, or sampling gear and methods differing significantly from MARMAP methods were excluded. Throughout the sampling periods the mean seasonal zooplankton values of the earlier investigators were not significantly different from the mean values of the contemporary MARMAP data base (Table 2). The greatest range in biomass from year to year is on Georges Bank and is likely related to variability in retention of zooplankton resulting from the seasonal formation and decay of the Georges Bank gyre (Butman et al. 1982). In the earlier studies (Bigelow 1926; Bigelow and Sears 1939; Grice and Hart 1962; Judkins et al. 1980) copepods were the predominant zooplankters: *Calanus finmarchicus* and *Pseudocalanus minutus* were the most abundant species in the spring, with a shift to *Centropages typicus* in late summer and autumn. These three species are important links in the energetics of the shelf ecosystem since they provide food for larval, juvenile, and adult fish (Sherman and Honey 1971; Sherman and Perkins 1971; Marak 1974; Sherman et al. 1981b; Cohen and Lough 1982).

Our results provide evidence that the biomass and species compositon of zooplankton have not changed substantially over the past 70 yr. The persistent patterns of abundance and species dominance reflect coherence within the range of interannual variability observed since the early part of the century. These

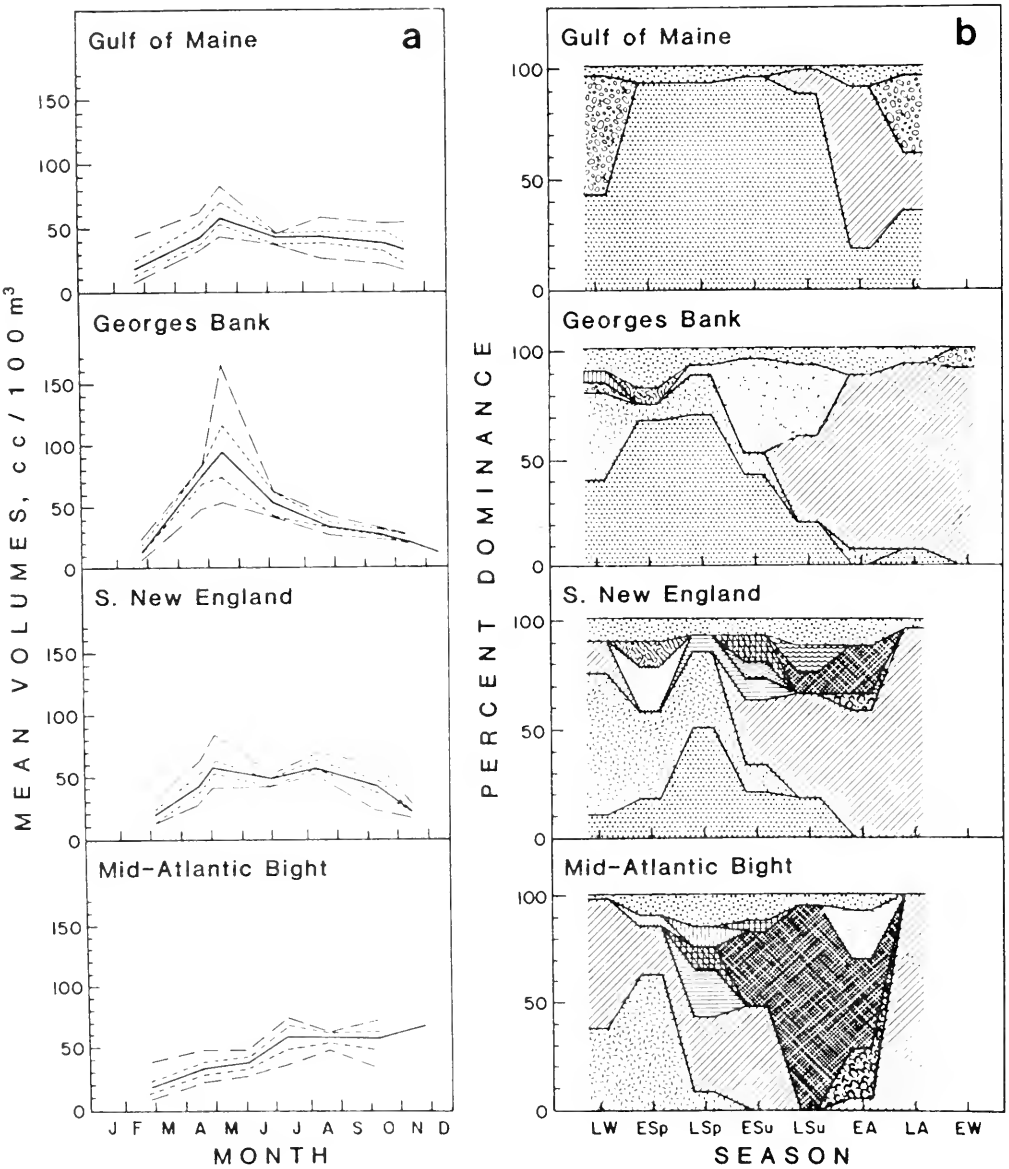
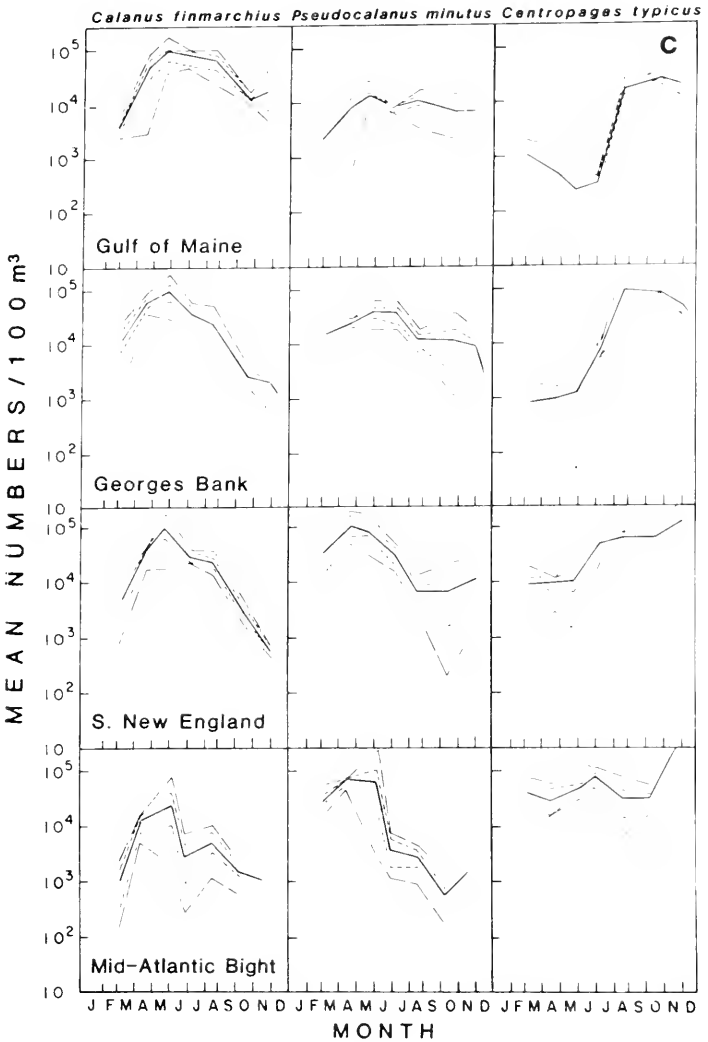


FIGURE 2.—Patterns of zooplankton coherence in four northeastern U.S. continental shelf subareas—Gulf of Maine, Georges Bank, Southern New England, and the Mid-Atlantic Bight. (a) Seasonal patterns in mean zooplankton standing stock (cc/100m³) for the 5-yr MARMAP time-series; (b) seasonal patterns of dominance of zooplankters by subarea shown as a percentage of the samples with a dominant taxon on the 5-yr MARMAP time-series; (c) seasonal pulses in abundance of the three dominant copepod species—*Calanus finmarchicus*, *Pseudocalanus minutus*, and *Centropages typicus* (no./100 m³)—in each of the subareas for the 5-yr time-series. LW = late winter, ESp = early spring, LSp = late spring, ESu = early summer, LSu = late summer, EA = early autumn, LA = late autumn, EW = early winter, in panel b.



For b section

_____ = seasonal changes in mean abundance; ----- = one standard error above and below the mean; —— —— = minimum and maximum range above and below the mean, in panels a and c. = Calanus finmarchicus; = Pseudocalanus minutus; = Centropages typicus; = Centropages hamatus; = Penilia avirostris; = other (taxa <5%); = Metridia lucens; = Sagitta elegans; = Balanidae; = Temora longicornis; = Acartia sp.; = Calanus sp.; = Evadne nordmanni; = Appendicularia; = Doliolidae; = Brachyura; = Echinodermata; = Thaliacea.

TABLE 2.—Comparisons of zooplankton volumes (cc/100 m³) by subarea between MARMAP data and the earlier studies on the northeast continental shelf. No significant differences were found between MARMAP data and earlier studies in comparisons of displacement volumes (Kruskal-Wallis $P > 0.05$). Volumes reported by Bigelow (1926) for late summer on Georges Bank were relatively high compared with those for the same season in MARMAP data. However, Bigelow's sampling was heavily biased towards the northeast peak of Georges Bank. The range of mean displacement volumes for that region in the MARMAP data is 24.4-191.7 cc/100 m³.

	Late winter	Early spring	Late spring	Early summer	Late summer	Early autumn	Late autumn	Early winter
Gulf of Maine								
MARMAP 1977-1981	10.9-47.0	34.6-65.2	44.0-83.2	40.3	31.8-58.0	23.3-57.5	18.4-53.9	
Bigelow 1912-1920	17.8				25.5-47.7			
P	0.380				0.248			
Georges Bank								
MARMAP 1977-1981	11.4-24.0	50.2-86.5	56.2-166.0	46.2-65.8	31.4-43.9	25.8-37.2	23.2-28.8	13.9
Bigelow 1912-1920	23.8				74.9			
P	0.655				0.157			
Southern New England								
MARMAP 1977-1981	13.2-33.5	32.0-66.5	46.7-85.4	43.4-54.4	57.4-69.2	24.2-60.9	21.4-28.4	
Bigelow and Sears 1929-1932	8.7-19.5	59.6-72.3	42.5-93.0	40.3-89.3		38.0-40.6		
P	0.180	0.101	0.631	0.157		0.770		
Grice and Hart 1960	12			40	61	38	14	
P	0.143			0.180	0.770	0.380	0.157	
Mid-Atlantic Bight								
MARMAP 1977-1981	11.8-39.6	25.2-51.5	29.5-50.9	41.0-73.2	50.4-66.0	37.4-76.0	70.1	
Bigelow and Sears 1929-1932	33.6-39.1	27.0-48.7	24.7-75.1	38.6-52.4 0.248		44.8		
P	0.180	0.655	0.715			0.380		

findings are in contrast with the 30-yr decline in zooplankton including the copepod component reported for large areas of the North Atlantic and North Sea (Colebrook 1978b). It appears that the climatic changes influencing the zooplankton decreases in the northeast Atlantic are more pronounced in the open ocean areas of the North Atlantic drift which in turn have greater impact on plankton in the North Sea (Colebrook 1978a, b, 1982; Garrod and Colebrook 1978). Based on MARMAP studies of the Northeast Fisheries Center, we have not detected large-scale influences of Gulf Stream eddies on populations of zooplankton or ichthyoplankton on the northwest Atlantic shelf (Laurence and Burns 1982; Cohen et al. 1982).

The fish stocks representing the mid-size predator component of the ecosystem of the northeast continental shelf have declined recently. During the period 1968 through 1975, the biomass of principle fish species declined about 50%. The decline was correlated with heavy fishing mortality (Clark and Brown 1977). The relative stability observed in both zooplankton standing stock and species composition when considered in relation to the decline in finfish biomass and subsequent population explosion of fast-growing, short-lived, zooplanktivorous sand eel (Sherman et al. 1981a) suggests that the reductions in fish abundance are not attributable to a lack of food at the lower end of the food chain. It appears that fishing mortality has imposed greater perturbations on fish populations of the northeast shelf than any changes in the abundance of zooplankton.

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THE MUD CRAB, *PANOPEUS HERBSTII*, S.L. PARTITION INTO SIX SPECIES (DECAPODA: XANTHIDAE)

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ABSTRACT

The "forms" of the mud crab, *Panopeus herbstii*, s.l., recognized by M. J. Rathbun are rediagnosed as four full species: *P. herbstii*, s.s., from oyster beds of the eastern United States; *P. simpsoni* from that habitat in the Gulf of Mexico; *P. obesus* associated with salt marshes in the Carolinian Province of the southeastern and southern United States; and *P. lacustris* from the intertidal and shallow littoral of the tropical west Atlantic. *Panopeus austrobesus* is newly diagnosed from south of Cabo Frio, Brazil, and *P. meridionalis* from Uruguay. Distinction of these six species is based on morphometry supplemented by color pattern and electrophoretic analysis of hemocyanins. A key for identification is given.

The xanthid crab, *Panopeus herbstii* H. Milne Edwards, s.l. (sensu lato), is recognized as an important member of the American oyster, *Crassostrea virginica* (Gmelin), community. It has been characterized as a selective feeder preferring small oysters over barnacles and large oysters (McDermott and Flower 1952), predatory on oysters and barnacles and potentially the most destructive of mud crabs occurring on New Jersey oyster beds (McDermott 1960), fifth in percent of total biomass on intertidal oyster reefs (Bahr 1976), and the most commonly captured decapod crustacean on Delaware oyster reefs (Maurer and Watling 1973). Menzel and Hopkins (1956) stated that *P. herbstii*, s.l., is a significant oyster predator in Louisiana and that along with *Menippe mercenaria* (Say) it is large enough to kill significant numbers of adult oysters in Florida (Menzel and Nichy 1958). It has also been determined as a consumer of *Cliona celata* Grant, the boring sponge parasitic in oysters (Guida 1976), a detritovore capable of feeding on barnacles and oyster spat (Kendall[2]), and, though an abundant associate on oyster reefs of Alabama, a commensal and scavenger rather than predator (May 1974). Whetstone and Eversole (1978) found *P. herbstii* to be a predator on hard clams, *Mercenaria mercenaria* (Linnè), and Seed (1980) found that both this crab and the blue crab, *Callinectes sapidus* Rathbun, are significant predators on the Atlantic ribbed mussel, *Geukensia* (= *Modiolus*) *demissa* (Dillwyn). McDonald (1982) contrasted the life history pattern of predatory *P. herbstii* with that of the smaller, more omnivorous *Eurypanopeus depressus* (Smith) in South Carolina. Dame and Vernberg (1982) evaluated the suggestion of Dame and Patten (1981) that mud crabs (e.g., *P. herbstii*) are one of the major controlling components in an oyster reef system, even though the amount of energy flowing through such predators is low in comparison with that moving through other elements of this system, and calculated the energetics of a population of *P. herbstii* in a South Carolina oyster reef on the basis of population density, size structure, standing crop, respiration, and production. The chelae of this and similar species of the family Xanthidae are strikingly adapted for cracking shelled prey, but the exact ecological roles of *Panopeus* species that occur in marine mollusk communities of the eastern and southern United States have been obscured because of imprecise identifications.

Panopeus herbstii has been a species complex from its initial misidentification and illustration as *Cancer panope* by Say (1817-18), through its later description as new in the new genus *Panopeus* by H. Milne Edwards (1834-40), and in a succession of specific and varietal treatments summarized by Rathbun (1930), Williams (1965), Holthuis (1979), and Manning and Holthuis (1981). Rathbun (1930) recognized four primary forms (*typica*, *obesa*, *crassa*, and *simpsoni*) which she believed represented extremes or perhaps environmental types connected by intergrades, but which were not subspecies, although there was a geographic component in her evaluation of material studied. The geographic range of the forms was listed as: form *typica*, Massachusetts to Cedar Keys, Fla.; form *obesa*, South Carolina to southern Brazil; form *crassa*, west Florida to central Brazil; form *simpsoni*, primarily Gulf of Mexico but also South Carolina where it was considered to intergrade with form *typica*.

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[2] Kendall, D. R. 1974. The ecology of the macrobenthos of a tidal creek, St. Simons Island, Georgia. Unpubl. M.S. Thesis, 212 p. Emory Univ., Atlanta, GA 30322.

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Now, three independent investigations which concern elements of this complex have produced results which bear on the status of these forms. The emphasis and method of each study are different, but each employs reference specimens from the crustacean collection of the U.S. National Museum of Natural History. The results of the studies are arranged here as a trilogy. To simplify nomenclature, the first (this paper) presents a taxonomic revision of the complex but rests in part on evidence in the following parts; the second (Sullivan et al. 1983) employs electrophoretic analyses of hemocyanins in the four forms (species) from the Carolinas, the gulf coast of Louisiana and Florida, and the Florida Keys; the third (Reames and Williams 1983) deals with morphological and ecological features of two forms (species) in local populations from southern Alabama.

This paper contains specific diagnoses of these populations partly conceived by Rathbun (1930) through designation as "forms" and includes diagnoses of two additional species from the southern part of the range; it also gives full synonymies of published descriptions with variant spellings of names and critical distributional records, outlines geographic distributions, and provides a key for determination. Some of the older records already included in published synonymies can be associated with nominal species by place of origin.

MATERIALS AND METHODS

Conclusions are based on results presented in Sullivan et al. (1983) and Reames and Williams (1983), on study of specimens in the crustacean collection of the U.S. National Museum of Natural History, Smithsonian Institution (USNM), on type materials in the Yale Peabody Museum (YPM), and photographs of type material in the Museum National d'Histoire Naturelle, Paris (PM).

Form and ornamentation of the carapace have been the main bases for distinguishing "varieties" in this complex in the past, but imprecision in setting limits for the variations led earlier workers to arrive at identities which form improbable species distributions over a broad range of latitude between the northern and southern temperate regions. Factors that contributed to these interpretations include ill-defined "varietal" differences as well as allometric changes, sexual dimorphism, and wear of exoskeletal parts. To increase the number of definitive characters, other features such as shape and ornamentation of the chelipeds and color pattern were employed, although the ranges of variation were increased by these additions. To avoid the consequent confusion, distributional patterns were outlined by noting the occurrence of "typical" specimens in a large series; once that framework was perceived, the variants could be recognized as such and placed properly.

Mensuration data are treated in two ways. Species diagnoses include proportional measurements, i.e., one measure expressed as a percent of another. Minimum values, maximum values, and arithmetic means are presented in a table to supplement the accounts of each species. In order to test for differences among species, the analysis of covariance (ANCOVA) procedure is used. This procedure tests null hypotheses concerning 1) overall coincidence, 2) equality of slopes, and 3) equality of intercepts of two or more regression equations. If hypothesis 1 is rejected at a prespecified level ($P = 0.05$ in this study), hypotheses 2 and 3 are then tested. If the null hypotheses concerning the slopes or intercepts of three or more groups are rejected, the Newman-Keuls multiple range test (MRT) is used in order to determine which regressions are different from others. It is not uncommon for the ANCOVA procedure to reject a null hypothesis in which the MRT procedure is unable to detect differences. It is generally accepted that the ANCOVA procedure is a more powerful test than the MRT.

Statistical tests were performed on the DEC System 10 Computer[1] of the National Marine Fisheries Service, using computer programs written and maintained by Joseph L. Russo for the NMFS Systematics Laboratory.

All statistical procedures and notation used in this investigation follow those presented by Zar (1974), with the exception that the probability associated with the calculated value of the F statistic of the ANCOVA procedure is generated by the computer programs which for the purpose of simplification and clarity is used instead of the calculated value of the F statistic with its associated numerator and denominator degrees of freedom. The independent variable used for all regressions is carapace width.

First pleopods of male crabs were studied with the aid of a light microscope and scanning electron microscope.

Citations in synonymies are limited to descriptive or distributional accounts that can be associated with species. Many references that cannot be assigned to species with certainty are not included.

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

SPECIES ACCOUNTS

Panopeus austrobesus new species

Figure 1

Panopaeus herbstii.—Heller 1868:16 (Brazil, locality).
Panopaeus herbstii.—Ortmann 1893b:475 (part).
Panopeus herbstii forma obesa.—Rathbun 1930:336 (part, specimens from south of Cabo Frio, Brazil).
Panopeus herbstii forma crassa.—Rathbun 1930:336 (part, specimens from south of Cabo Frio, Brazil).
Panopeus herbstii.—Coelho and Ramos 1972:190 (part).—Williams 1984:412 (part).

Material examined.—Specimen lots in USNM recorded by Rathbun (1930) under *P. herbstii* (catalog number only) plus material added since that time.

Brazil: 47847, 47851, 59457, 59458, 59459, 59460, 59461, 59462, 59465.—75661. 2M juv.; Ilha Paqueta; W. L. Schmitt, 23 August 1925.—75663. 1F (ovig.); Ilha Govenador; W. L. Schmitt, 1 September 1925.—75603. 5 juv.; Santos, on muddy beaches between canals 4 and 5; W. L. Schmitt, 13 September 1925.—75654. 3M, 1F, 3 juv.; Santos estuary; W. L. Schmitt, 13 September 1925.—75653. 1M juv.; Paranagua; W. L. Schmitt, 2 October 1925.—75662. 1M juv.; Paranagua; W. L. Schmitt, 3 October 1925.

Types.—The following are designated and labelled as types deposited in the crustacean collection of the USNM: 59462. Holotype male, cl 26.5 mm, cw 38.7 mm, Paranagua, Brazil, sandy mud flats, under scattered rocks; W. L. Schmitt, 3 October 1925.—191147. 7M, 2F, same lot of specimens as above and considered as paratypes.

Diagnosis.—Carapace with few transverse lines of granules, slightly coarsened granules on ocular and hepatic regions and along anterolateral slopes (length 64.2-72.9% width, $\bar{x}$ 68.8). Coalesced first and second anterolateral teeth of carapace separated by very shallow notch, broadly rounded second tooth usually but not always exceeded by acute first tooth; remaining teeth outstanding in large adults, less so in smaller specimens, third tooth with rounded to rectilinear tip, fourth swept forward and acute, fifth much smaller, acute and directed anterolaterad; arc drawn along tips of first 4 teeth diverging laterally from arc drawn along bases of notches between teeth. Chelipeds microscopically granular, sometimes more conspicuously so along anterior edge of carpus, granules on outer surface of palm often arranged in obsolescent rugose pattern. Major chela with teeth on fixed finger varied in size, one or more distal to level of basal tooth on dactyl enlarged, with cusps raised above straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger) (Fig. 2); cusps of teeth on fixed finger tending to be well separated, seldom worn, their external faces sometimes prominent but not noticeably bowed outward from axis of finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

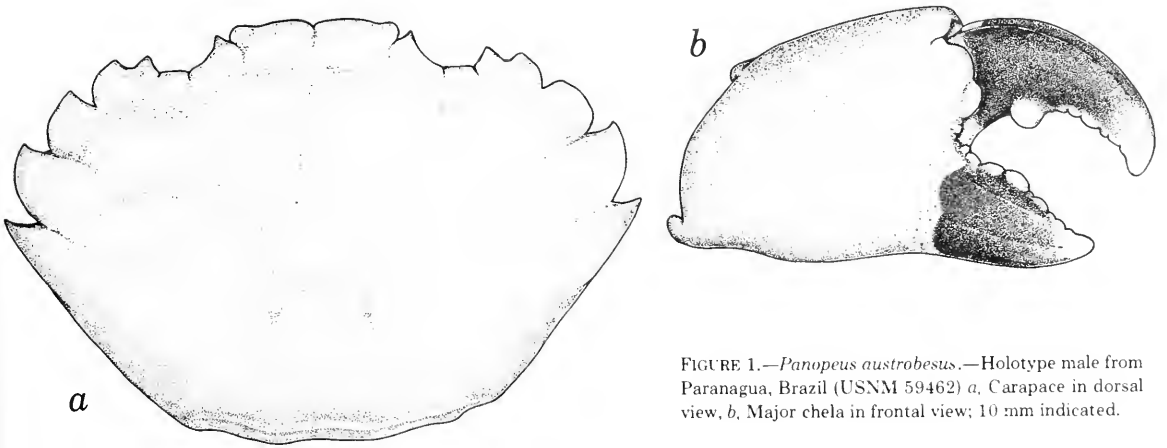

FIGURE 1.—*Panopeus austrobesus*.—Holotype male from Paranagua, Brazil (USNM 59462) *a*, Carapace in dorsal view, *b*, Major chela in frontal view; 10 mm indicated.

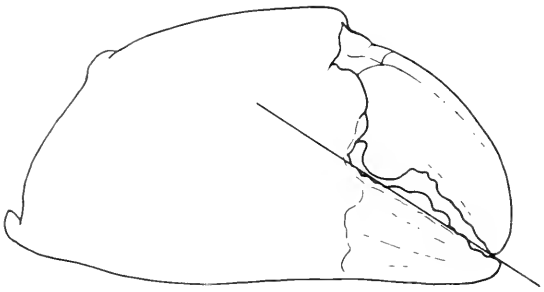

FIGURE 2.—Major chela showing straight line drawn between angle at juncture of fixed finger with anterior margin of palm and tip; cusps of some teeth raised above line in this example (*Panopeus lacustris*).

TABLE 1.—Basic statistics for length percent width of carapace in six species of *Panopeus* from the western Atlantic Ocean.

Species	*N*	Min.	Max.	Mean	SD
herbstii	50	98.8	77.0	73.2	1.64
simpsoni	50	68.2	77.1	73.5	2.04
meridionalis	7	70.1	74.0	71.7	1.21
obesus	53	59.3	75.5	70.1	2.43
lacustris	57	64.5	78.5	69.3	2.10
austrobesus	44	64.2	72.4	68.8	1.57

areolations of the carapace and its transverse lines of granules are less distinct than in that species. The chelipeds, however, are more smoothly granulated than in *P. lacustris*, recalling the surface of chelae in the *simpsoni-herbstii* group; but the tooth pattern of the fixed finger has a striking similarity to that of *P. obesus*.

Panopeus herbstii H. Milne Edwards, s.s.

Figure 3

Cancer panope.—Say 1817:58, pl. 4, fig. 3 (misidentified).

Panopeus herbstii H. Milne Edwards 1834:403.—Lucas 1840:90.—Gibbes 1845:63, 69.—1850b:175 (part, not Key West material).—Leidy 1855:149.—Smith 1869a:276 (part, the South Carolina and E. Florida material).—1869b:34 (part, list).—Coues 1871:120.—Kingsley 1878:318 [3] (part).—1880:393 (part).—A. Milne Edwards 1878-1880:308 (part), pl. 27, fig. 2, 2*a*.—R. Rathbun 1884:772 (part).—Benedict and Rathbun 1891:358 (part), pl. XIX, fig. 1, pl. XXIII, figs. 10(?), 12.—Rathbun 1905:6.—1930:335 (part, *forma typica*), text figs. 52, 53; pl. 156, figs. 1-2.—Fowler 1912:404, pls. 122-123.—Hay and Shore 1918:437 (part), pl. XXXIV, fig. 9.—Lunz 1937:13 (part).—McDermott and Flower 1952 2:48-49.—Williams 1965:196 (part), fig. 180.—1974:34, fig. 97 (key).—1984:412, fig. 326 (part).—Williams and Wigley 1977:11 (part, distribution).—Gosner 1971:543, 550 (key), fig. 21.61A.—Van Engel and Sandifer 1972:160 (list).—Felder 1973:pl. 9, fig. 21.—Young 1978:182 (list).—Holthuis 1979:159 (selection

TABLE 2.—Linear regression analysis for width (x) and length (y) in millimeters of the carapace for samples of five species of *Panopeus* from the western Atlantic Ocean.

Species	Data pairs	Mean x	Mean y	Min.	Max.	SD	Slope	Y intercept	r^2
herbstii	50	26.06		12.10	46.80	63.075			0.9952
			19.04	8.70	33.60	33.255			
							0.71337	0.44276	
simpsoni	50	22.21		11.10	44.00	80.687			0.9957
			16.34	7.80	33.50	44.065			
							0.73741	−0.04489	
obesus	53	31.96		15.40	50.90	77.889			0.9893
			22.36	9.90	36.30	37.047			
							0.68597	0.43766	
lacustris	57	37.90		14.80	56.80	157.590			0.9953
			26.08	10.60	38.80	68.181			
							0.65622	1.20575	
austrobesus	44	30.81		18.50	51.30	56.659			0.9924
			21.14	13.20	35.10	23.383			
							0.63977	1.41792	

Color.—Occasionally with random spots on external side of palms.

Known range.—Region of Rio de Janeiro, Brazil, to Florianopolis, Brazil (and probably southward).

Name.—The specific name is derived from the Latin "australis," southern, and "obesus," in reference to its similarity to *P. obesus*.

Remarks.—*Panopeus austrobesus* has carapace dimensions and outstanding anterolateral teeth that almost exactly match those of *P. lacustris*, although

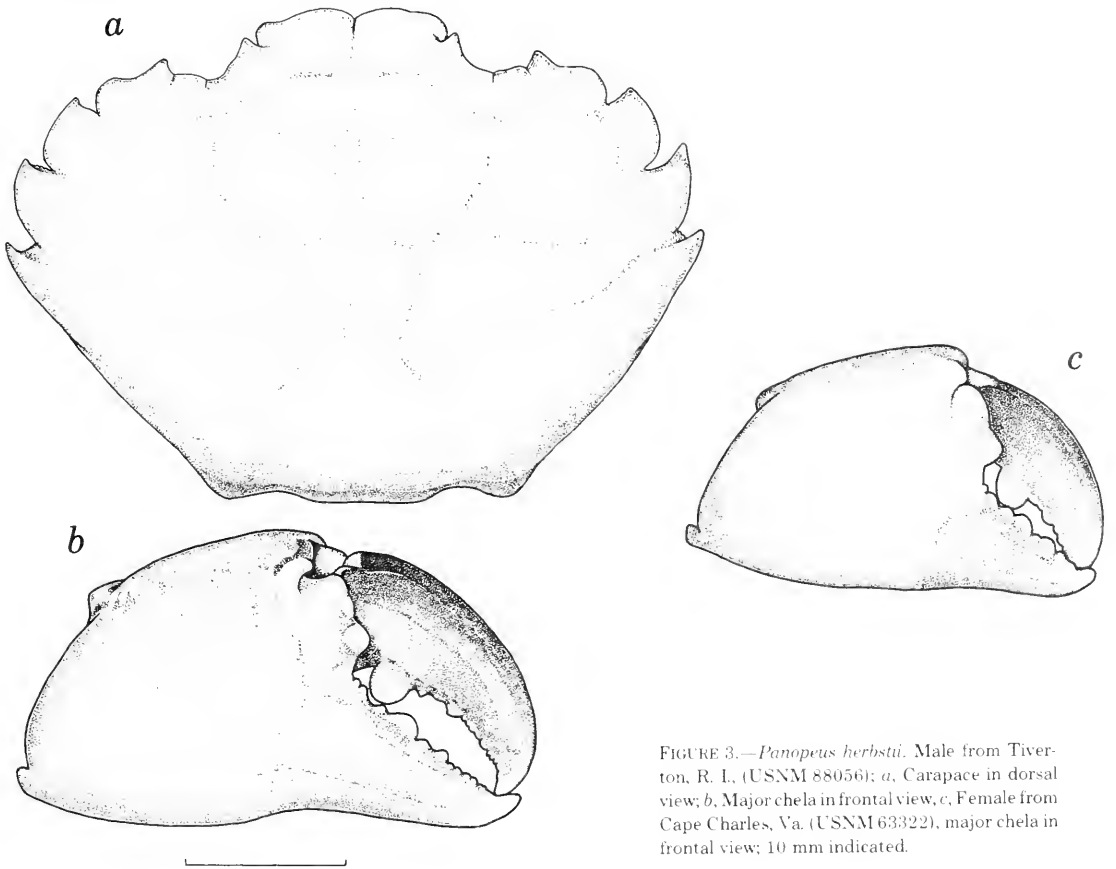

FIGURE 3.—*Panopeus herbstii*. Male from Tiverton, R. I., (USNM 88056); *a*, Carapace in dorsal view; *b*, Major chela in frontal view, *c*, Female from Cape Charles, Va. (USNM 63322), major chela in frontal view; 10 mm indicated.

of lectotype).

Panopeus herbsti.—DeKay 1844:5.—Ryan 1956:147 (part, in eastern USA) pl. 1, fig. C; text figs. 3, 4B, 5B, 9A.—McDermott 1960:201-210, fig. 1.—Schwartz and Cargo 1960:201-203.—Wass 1961:XII-14 (list).—1963:44 (list).—1965:41 (list).—Smith 1964:119 (key).—Maurer and Watling 1973:161, 179.

Panopeus Herbstii.—Gibbes 1845:69 (? no locality).—1850a:23.—Stimpson 1860:444.—Smith 1873:547.—Verrill et al. 1873:547 (part).

Panopaeus herbsti.—Ortmann 1893a:57 (part).

Eupanopeus herbstii.—Rathbun 1900b:138 (key, part).—1905:6.

Panopeus simpsoni.—Rathbun 1930:338-339 (part, material from Virginia to South Carolina).

Panopeus (Eupanopeus) herbstii.—Miner 1950:522, pl. 167, colored pl. XII, 5.

Material examined.—Lots of specimens in USNM recorded by Rathbun (1930) under *P. herbstii* (catalog numbers only) plus material added since that time.

Massachusetts: 173575. 1M; Sippewisset Marsh, West Falmouth, 41°34′45″N, 70°38′22″W, 1 m, muddy sand; C. Wheeler, 28 June 1979.

Rhode Island: 4539.—88056. 7M, 4F; Sakonnet River, N side of Stone Bridge, Tiverton; F. A. Chace, Jr., 4 September 1948.

Connecticut: 15690.

New Jersey: 75626. 1F (ovig.); Mullica River; H. G. Richards, 6 July 1931.—75624. 1F; Thorofare, Atlantic City; H. G. Richards, 14 August 1931.—75625. 2M; Great Egg River; H. G. Richards, 13 August 1931.—76154. 1M; Cape May Point; H. G. Richards, 20 March 1932.—63321. 2 juv.; Prissy-Wick Shoal off Cape May; H. G. Richards.

Delaware: 191148. 2M, 1F; Wreck N Roosevelt Inlet and Nantauxent Point; W. Amos, 1952-56.

Maryland: 56266.

Virginia: 22328, 48850, 56267, 56268, 56386, 56837, 57139.—75595. 3M, 1F; Smith's I., from

oyster bed 0.5 mi S of light at low tide; J. P. E. Morrison, 6 July 1935.—191149. 1F (ovig.); Wachapreague; 24 July 1943.—63322. 1F; Cape Charles, near wharf; H. G. Richards.—63323. 1F (juv.); Cape Charles; H. G. Richards.—63324. 2F; Cape Charles, near wharf; H. G. Richards.—74600. 5M; York River, 6 ft; J. B. Engle, U.S. Bur. Fish., 21 October 1936.—75628. 1F; Yorktown; J. B. Engle, U.S. Bur. Fish.—75668. 1F; Yorktown; J. B. Engle, U.S. Bur. Fish.

North Carolina: 62538, 62539, 62540.—60607. 1M; Hatteras; A. J. Poole and R. Kellogg, May 1927.—191172. 2M; Pivers I., Beaufort; J. B. Sullivan, 10 July 1978.—84428. 2M; Fort Macon, Beaufort, under stones in muddy zone just above low water on breakwater; T. A. and A. Stephenson, Stn. BM(N)39, 1947.

South Carolina: 15726, 15741, 15762, 15780, 15782, 26150, 42881, 45502, 51022, 56265, 59938.—75667. 1M; Dewees I.; G. R. Lunz, Jr., 15 May 1934.

Florida: 56838.—99909. 2F; Bridge over Matanzas River, Crescent Beach; D. K. Caldwell et al., 1 December 1954.—170017. 1M; Sebastian Inlet, Indian River Co.; on sabellariid reef S side under bridge, intertidal; R. H. Gore, 7 May 1974.

Locality uncertain: 56840. 2F; east coast of North America; Boston Society of Natural History.—75596. 1M, 5F (1 ovig.); O. Bryant, Boston Soc. Nat. Hist.

Diagnosis.—Coalesced first and second anterolateral teeth of carapace separated by shallow rounded notch, second tooth broader than but not so prominent as first tooth; third and fourth anterolateral teeth curved anteriorly; fifth tooth much smaller than fourth, acute and swept forward or hooked anteriorly. Carapace length 66.8-77.0% width, $\bar{x}$ 73.2. Chelipeds superficially smooth but actually finely granulate on upper surface of carpus; lower outer surface of palms light colored (pink, buff, or yellowish, rarely mottled reddish); major chela with cusps of teeth on fixed finger usually either reaching or falling below straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger); anterior margin of palm with distance between crest at base of dactyl and tip of condylar tooth lateral to base of dactyl 0.70 or less length of fixed finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Dull olive, brown-green, dirty gray or slate color, sutures between regions sometimes lighter, and some tendency to variegated dark pattern on lighter background. Chelipeds darker with variegation coarse on upper parts, sometimes spotted claret brown, blotching extending about halfway down sides of articles, lower half and underparts light; fingers black. Third maxillipeds of males and about half of females with red or burgundy spot near base of inner surface of ischium. (Specimens from Beaufort, N.C.; Hay and Shore 1918; Rathbun 1930.)

Type-locality.—"Inhabits oyster beds, &c . . . often found on oysters (*O. virginica*) in our markets" [by implication the eastern United States] (Say 1817:58). Holthuis's (1979) selection of the specimen figured by Say (1817, pl. 4, fig. 3) as the lectotype for *P. herbstii* restricts the nominal species to the common mud crab occurring on oyster bars of the eastern United States.

Known range.—The known geographic range of this species, represented by the material listed above, is shallow intertidal and subtidal waters of the eastern United States from Boston Harbor, Mass., to Indian River County, southeastern Florida.

Remarks.—See general discussion below.

Panopeus lacustris Desbonne

Figure 4

Panopeus lacustris Desbonne 1867:28.

Panopeus herbstii.—Gibbes 1850b:176 (part, Key West material).—Smith 1869a:276 (part, the Bahamian material).—Kingsley 1880:393 (part).—Rathbun 1884:772 (part).—Benedict and Rathbun 1891:358 (part, the Bermuda, Caribbean, and Brazilian material).—Young 1900:132.—Rathbun 1924:14.—Chace 1940:34.—Chace and Hobbs 1969:154, figs. 46c, 47.—Holthuis 1959:207.—Edmondson 1962:277, fig. 20c (?).—Coelho 1966:163 (habitat).—1970:53 (habitat).—Coelho and Ramos 1972:190 (part).—Fausto Filho 1966:33 (occurrence).—Bonnelly de Calventi 1974:27 (list).—Markham and McDermott 1981: 1273 (list).—Williams 1984:412 (part).

Panopeus Herbstii.—Smith 1869b:34 (part, listing).—von Martens 1872:89.—Verrill et al. 1874:547 (part).—A. Milne Edwards 1880:13 (Brazil locality).

Panopeus herbstii var. *obesus* Smith 1869a: 278 (part, the Aspinwall material).

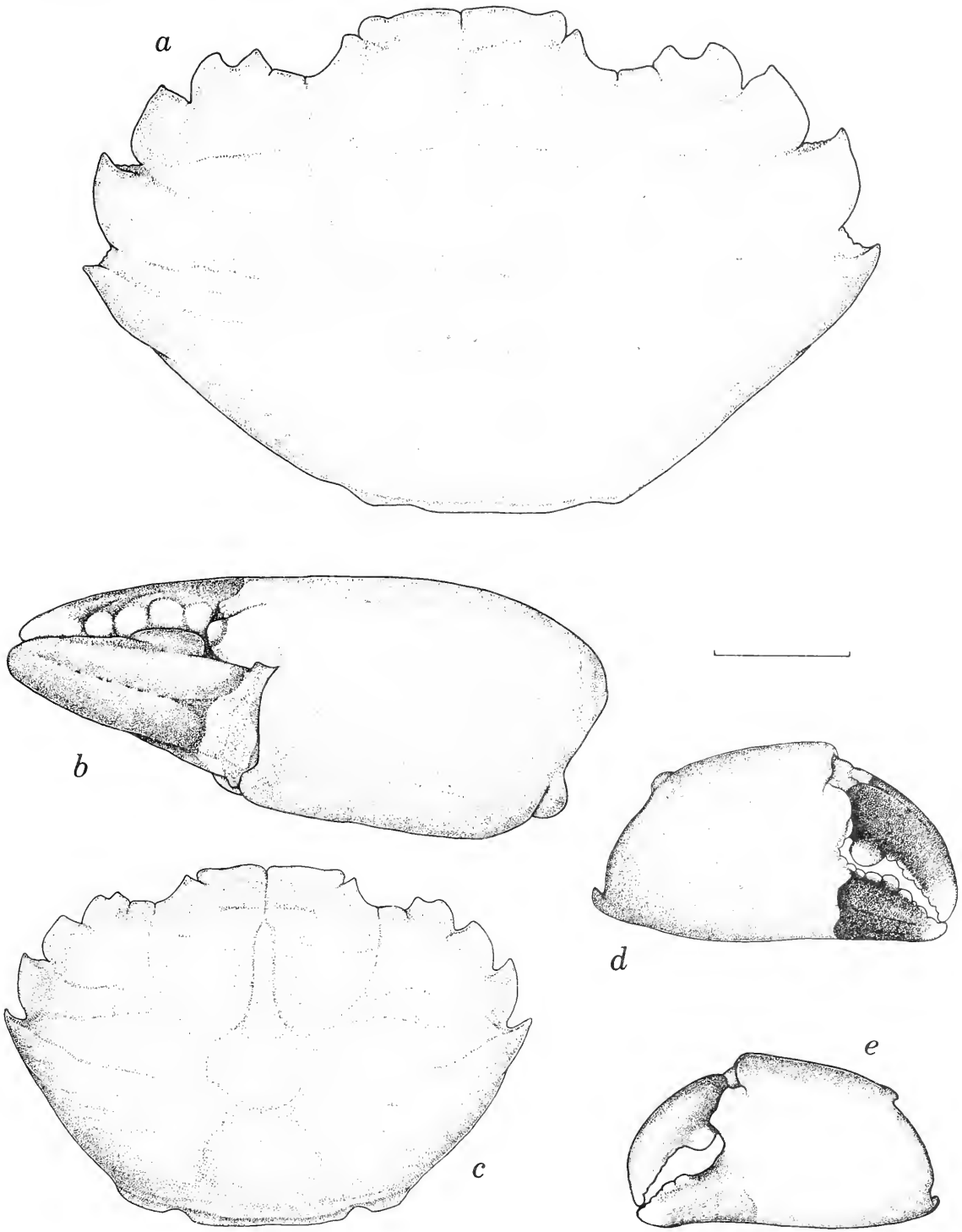

FIGURE 4.—*Panopeus lacustris*. Male from southern Florida (USNM 75643); *a*, Carapace in dorsal view; *b*, Major chela in oblique dorsal view showing broadened "molar" teeth on fixed finger. Female from St. Croix, W.I.; *c*, Carapace in dorsal view; *d*, Major chela in frontal view. *e*, Male from Panama (YPM 470), major (left) chela in frontal view, teeth of fixed finger worn. 10 mm indicated.

Panopeus Herbstii granulosus A. Milne Edwards 1880:309.

Panopeus crassus A. Milne Edwards 1880:313, pl. 57, figs. 1, 1*a*; 2, 2*a*.—Benedict and Rathbun 1891:383.

Panopeus herbstii granulosus.—Benedict and Rathbun 1891:383.—Young 1900:134.

Panopaeus herbsti.—Ortmann 1893a:57 (part).—1893b:475 (part).

Eurypanopeus herbstii.—Rathbun 1897:18 (listing)

Eupanopeus herbstii.—Rathbun 1898:273.—1900a: 140.—1901:28.

Panopeus herbstii obesus.—Young 1900:134.

Eupanopeus Herbstii, var. or subspecies, *minax* Verrill 1908:348, text fig. 15; pl. 15, fig. 2.

Panopeus herbstu [sic].—Gundlach et al. 1917:564, fig. 16.

Panopeus herbstii forma crassa.—Rathbun 1930:336, pl. 157, fig. 3.—1933:61, fig. 53.

Panopeus herbsti.—Coelho 1971:283 (habitat).

Material examined.—Lots of specimens in USNM recorded by Rathbun (1930) under *P. herbstii* (catalogue numbers only) plus material added since that time.

Bermuda: 25825, 43046.—94239. 1M; Harrington Sound; T. A. Stephenson, Stn. BRH-21.—94240. 2M; Ferry Reach; T. A. Stephenson, Stn. BRM-3.—143596. 2M; Riddells Bay, algal mat; J. E. Pearson, July 1972.

Florida: 2077, 9254, 9296, 15412, 15419, 59456, 59937, 61122, 62541, 62542, 62544.—170016. 1M; Sebastian Inlet, Indian River Co., on sabellariid reef S side under bridge, intertidal; 19 June 1974.—170015. 1M, 1 juv.; Sebastian Inlet, Indian River Co., on sabellariid reef S side under bridge, intertidal; R. H. Gore, 1 November 1974.—170014. 1M, 2 juv.; Sebastian Inlet, Indian River Co., on sabellariid reef S side under bridge, intertidal; R. H. Gore, 9 December 1975.—170013. 1F; Link Port, Indian River, St. Lucie Co., intertidal; R. H. Gore, 8 December 1975.—170018. 1M, 3F (2 ovig.); Ft. Pierce, Jim Island mud flats in grass beds, intertidal; R. H. Gore, 26 June 1972.—75643. 1M; vicinity of Coral Gables; J. F. W. Pearson.—75656. 1F; vicinity of Coral Gables; J. F. W. Pearson.—191150. 1M; Big Pine Key, southeast point, beach rock, littoral fringe; Gosner, Stn. 257, 16 January 1968.—75613. 1F; Key West; U.S. Bur. Fish.—75614. 1F; Key West; U.S. Bur. Fish.—75645. 1M; Key West; U.S. Bur. Fish.—75649. 1M, 2F; Key West; U.S. Bur. Fish.—75655. 1F (ovig.); Key West; U.S. Bur. Fish.—75611. 1M; Marquesas Key; A. S. Pearse, 11 August 1930.—75642. 1M; Tortugas; W. L. Schmitt, 1932.—75644. 1M, 1F; Tortugas, from *Porites* clumps, low tide after supper; W. L. Schmitt, 2 July 1931.—72270. 1M juv.; Long Key, Tortugas; W. L. Schmitt, 30 July 1924.—75594. 1F; Bush Key, Tortugas, N point; W. L. Schmitt, 18 June 1932.—75622. 1M; Bush Key, Tortugas; W. L. Schmitt, 27 July 1931.—75659. 1M; W side of Bush Key Reef, Tortugas; W. L. Schmitt, 20 August 1924.—191151. 1M, 2F; Bush Key; W. L. Schmitt, 24 August 1924.—71026. 2F; Fort Jefferson, Tortugas; under coral debris at and near top of moat; A. S. Pearse, 21 June 1931.—75610. 1M; Fort Jefferson, Tortugas; Dexter, 4 August 1930.—75608. 2M, 2F (1 ovig.); Cook Key (west coast); Springer, 13 March 1936.—75615. 1M, 1F; Caxambas-Marco Cut, not bicolored in life; Springer, 13 March 1936.—75607. 1F(juv.); Caxambas-Marco Cut near Coon Key; Springer, 13 March 1936.—75609. 1F, 1 juv.; Marco-Caxambas Cut near Coon Key; Springer, 13 March 1936.

East Coast of United States: 75597. 1M, 1F; Univ. Iowa.

Mexico: 191152. 1M; Beach Champoton, Campeche; ASP, 13 July 1932.

Bahamas: 20710, 23829, 57008.—88658. 2F; Bimini; A. S. Pearse, 16 October 1948.—88659. 2 juv.; Bimini; A. S. Pearse, 29 October 1948.—75658. 1M; Spanish Wells; Univ. Iowa.

Cuba: 24329, 48551, 48553, 48559, 53343, 58393, 59896.—99955. 1F; Laguna Choco, E of Xanadu, Hicacos Pen., Matanzas Prov.; W. L. Schmitt, 24-25 January 1957.

Jamaica: 15654, 19591, 41750, 42933, 59472, 61366, 61587, 62537, 62543.—72777. 1F, 1 juv.; the Palisades, Kingston Harbor; W. G. Lynn, 1 July 1936.

Puerto Rico: 24246, 24266, 24268.

Virgin Islands: 72358. 1M, 2F, 1 juv.; St. Croix, Fairplain str. below bridge, under stones in gravelly bank; H. A. Beatty, 1935-36.—73327. 1M, 2F; St. Croix, Salt River Lagoon; Smithsonian-Hartford Exped. 10 April 1937.—75641. 1F (ovig.); St. Croix, on mangroves bordering Shoys Lagoon; H. A. Beatty, 1937.—75646. 1M, 2F (ovig.); St. Croix; H. A. Beatty.—75606. 1M (juv.); St. Croix, on mangroves bordering Shoys Lagoon; H. A. Beatty.—75045. 3M, 3F; Mangrove I., Salt River, St. Croix; W. L. Schmitt, 10 April 1937.

Leeward Islands: 58037.—75619. 1M; Pillars of Hercules, Antigua; Barbados-Antigua Exped. Univ. Iowa, 1918.

Barbados: 58036.

Trinidad: 7640, ?56759, 57012.—137742. 3M, 2F; Caroni Swamp, Colorite Swamp, mangrove roots; J. Stanley, 5 January 1970.

Dutch West Indies: 7585, 42979, 56889.—191173. 1M; Netherlands Antilles; Gosner, September 1968.

Panama: 44180, 44181, 59319.—191153. 1M; Laguna de Chirigui; F. Richardson, 2 April 1936.—139587. 2F; Canal Zone, Ft. Sherman, Shimmey Beach, intertidal; L. G. Abele, 8 February 1969.—139588. 1M; Canal Zone, Galeta Island, small lagoon; L. G. Abele, 14 May 1969.—139589. 1F; Canal Zone, Galeta Island, mangrove swamp, intertidal; L. G. Abele, 24 May 1969.—139590. 2M; Canal Zone, Galeta Island, mangrove swamp, intertidal; L. G. Abele, 14 July 1969.—153994. 7M, 4F; Canal Zone, Galeta Island, mangrove swamp; L. G. Abele, 14 July 1969.—153995. 3M; Canal Zone; L. G. Abele, 1971.—155266. 3M, 1F (ovig.); Canal Zone, Coco Solo Airfield, along seawall, 0.5 m; L. G. Abele, 4 January 1969.—155269. 3M, 1F; Canal Zone, Galeta Island, reef next to lab.; L. G. Abele, 11 March 1969.—155267. 1F (ovig.); Canal Zone, Galeta Island, reef next to lab.; L. G. Abele, 11 March 1969.—155270. 1M; Canal Zone, Galeta Island, mangroves; L. G. Abele, 14 July 1969.

Colombia: 7562, 25655.

Brazil: 25732, 25733, 25734, 40584, 40585.—75553. 1M; Recife, Pernambuco; von Ihering.—75593. 1F, 2 juv.; Bom Successo, Minas Geraes; D. Cochran.—90367. 1F; Ilha do Fundito, 22°50′30″S, 43°14′W, Rio de Janeiro; L. de Oliveira, 15 January 1947.

Hawaii: 81729. 1M, 1F; Pearl Harbor, Oahu; C. H. Edmondson, 1940.—95605. 1M; Maunalua Bay, Oahu, sand flats; C. H. Edmondson, 6 February 1953.—99169. 1F; Pearl Harbor, Oahu; C. E. Cuttress, 22 April 1950.

YPM 470. 1M, 1F; Aspinwall [= Colón, Panama].

Diagnosis.—Carapace with transverse lines of granules, coarse granules on ocular and hepatic regions and along anterolateral slopes, length 64.5-78.5% width, $\bar{x}$ 69.3. Coalesced first and second teeth of carapace often separated by deep rounded notch, second broader than first but tips almost equally prominent (variable in form); remaining teeth outstanding (especially in adults), tips usually rectangular to acute; arc drawn along tips of first four teeth diverging laterally from arc drawn along base of notches between teeth. Chelipeds bearing distinct closely crowded granules, especially along anterior edge of carpus and on upper and outer surface of palm (often in obsolescent rugose pattern); distinct reticulate pattern of color on outer surface of palm, usually continued over its lower half, and accented with random scatter of spots, mainly in upper half (may be faded but evident after long preservation). Major chela with teeth on fixed finger varied in size, a group distal to level of basal tooth on dactyl enlarged with cusps raised above straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger); cusps in proximal "molar area" of fixed finger broad, often impacted, and worn severely, their external faces and external side of finger swollen, flared, or bowed outward from axis of finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Usually lighter in color than russet colored *P. obesus*, often grayish dorsally, cream ventrally and on lower parts of chelae. Reticulate pattern on outer surface of chelae as in *P. obesus* and sometimes with scattered spots on this surface.

Type-locality.—The lagoons of Guadeloupe, hiding under rocks.

Known range.—The known geographic range of this species, represented by material listed above, is shallow and subtidal waters from Bermuda and extreme southern Florida, through the West Indies, and along the continental margin of the Caribbean Sea and South America to Cabo Frio, Brazil. The species has been introduced in Hawaii, and, according to a report by Edmonson (1962), apparently has been known on the California coast for a number of years. It is often associated with mangroves as well as coarse substrates.

Remarks.—Desbonne's (1867) description clearly applies to what is here recognized as a single species of this *Panopeus* complex in the tropical western Atlantic, and his long suppressed name, rather than A. Milne Edwards' *P. crassus*, has priority.

The large series of study specimens in the USNM was augmented by excellent photographs of a syntype male of *Panopeus crassus* A. Milne Edwards from Bahia which was kindly supplied to me from the Museum National d'Histoire Naturelle by M. J. Forest. Parenthetically, measurements for a male given in the original description (cl 36 mm, cw 65 mm) of *P. crassus* depart considerably from the shape of any specimens measured by me, but the dimensions of the carapace of the figured male correspond to those of the male from Bahia in the Paris Museum (cl 36 mm, cw 56 mm), suggesting that digits in measure-

ment of width recorded in the original text were transposed.

Smith's (1869a) syntypes of *Panopeus herbstii* var. *obesus* from Aspinwall are actually *P. lacustris*, a male, cl 21.3, cw 30.2, with left major chela, and an immature female, cl 16.1, cw 23.2, with right major chela. The carapace of each specimen, while somewhat inflated, shows the slight surface sculpture, transverse lines of granules, granular frontal and anterolateral slopes characteristic of *P. lacustris*, and most noticeably its outstanding curved but pointed anterolateral teeth, the third and fourth being most characteristic; the first and second tooth are coalesced but well separated by a moderate notch, the rather acute first tooth being one-fourth to one-third as wide as the much more rounded second and slightly exceeding it in each case. The front is fairly prominent in both specimens and granular along its edge.

In both specimens, the molar teeth of the crushing chela are strong, coalesced, broadened, raised, bowed laterally from the longitudinal axis of the finger, and opposed by a well-developed dactylar tooth. In both specimens, the molar area of the fixed finger is worn, noticeably so in the male. The minor chela of the female is typical for a specimen of this size, but that of the male is relatively slender, the fingers somewhat more decurved than normal, and the tip of the dactyl broken off. The right third walking leg of the female is missing and the left first and right third to fifth walking legs missing in the male.

No color is evident except for the slightly brownish gray fingers of the chelae, with their lighter tips and tooth cusps, but the fingers of the regenerated minor chela of the male are darker than others. There is faint indication of the reticulate color pattern on the large chela of each specimen.

Other remarks are given in the general discussion below.

Panopeus meridionalis new species

Figure 5

Material examined.—USNM 99846, holotype male, cl 19.4 mm, cw 26.9 mm, Montevideo and Punta Carretas, rock coast of Rio de la Plata, Uruguay; C. S. Carbonell, 1955.—191154. 2M, 4F; same lot of specimens as above and considered as paratypes.

Diagnosis.—Carapace relatively narrow, length 70.1-74.0% width, $\bar{x}$ 71.7. Coalesced first and second anterolateral teeth usually separated by very shallow notch, tip of acute first tooth exceeding that of second; third and fourth teeth strongly curved forward, acute, anterior margin of each concave; fifth much smaller than fourth, slightly curved forward. Chelipeds finely granulate on upper surface of carpus and palm; lower outer surface of palms appearing light colored in preserved material. Major chela with teeth on fixed finger varied in size, one or more teeth on fixed finger distal to level of basal tooth on dactyl enlarged, with cusps raised above straight line drawn between angle at juncture of finger with anterior margin of palm and tip (= length of fixed finger); cusps of teeth on fixed finger rather well separated, not broad, seldom worn, their external faces not flared or bowed outward but aligned along axis of finger.

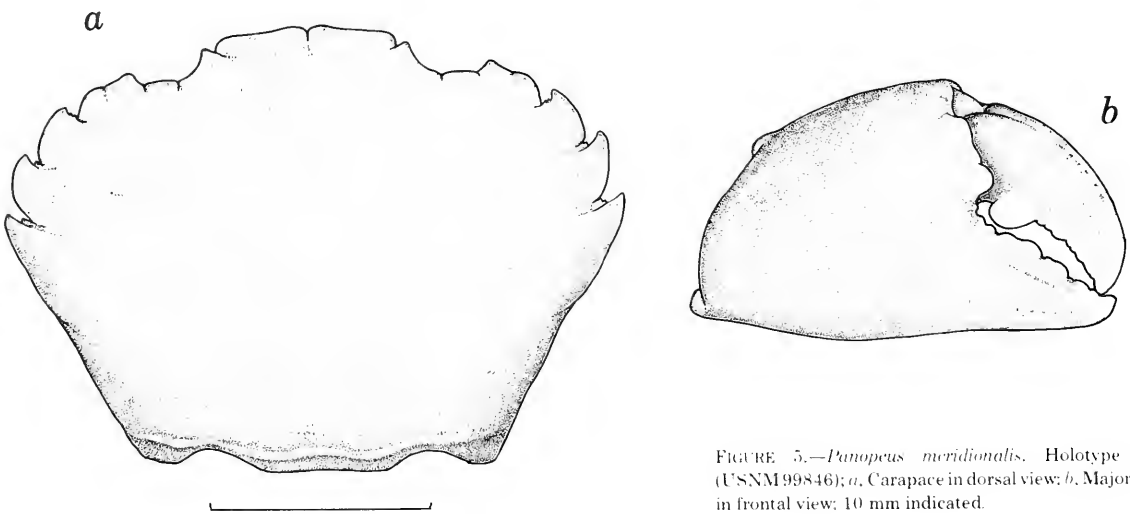

FIGURE 5.—*Panopeus meridionalis*. Holotype male (USNM 99846); *a*, Carapace in dorsal view; *b*, Major chela in frontal view; 10 mm indicated.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Third maxillipeds of males with red spot near base of inner surface of ischium. No other reliable color pattern is evident in preserved material.

Known range.—The only specimens known are those from the type-locality.

Name.—The specific name is derived from the Latin "meridionalis" southern, in reference to the extreme southern distribution.

Remarks.—This species has acute, forwardly swept anterolateral teeth that recall those of *P. simpsoni* from the Gulf of Mexico. Granulation of the chelipeds is smooth as in *P. simpsoni* and *P. herbstii*, but the tooth arrangement on the fixed finger of the major chela is closer to that of *P. obesus* or *P. austrobesus*. *Panopeus meridionalis* thus occupies an intermediate position between the *herbstii-simpsoni* group and the *obesus, austrobesus, lacustris* group of this genus.

Panopeus obesus Smith, new rank

Figures 6, 7

Panopeus herbstii var. *obesus* Smith 1869a:278 (part, the Egmont Key specimen).—Coues 1871:120.—Kingsley 1878:318 [3] (part).

Panopeus herbstii.—Kingsley 1880:437 (part).—Rathbun 1884:772 (part).—Hay and Shore 1918: 437 (part).—Lunz 1937:13 (part).—Williams 1965: 196 (part).—1984:412 (part).—Felder 1973:69 (part, key).—Powers 1977:102 (part, notes).

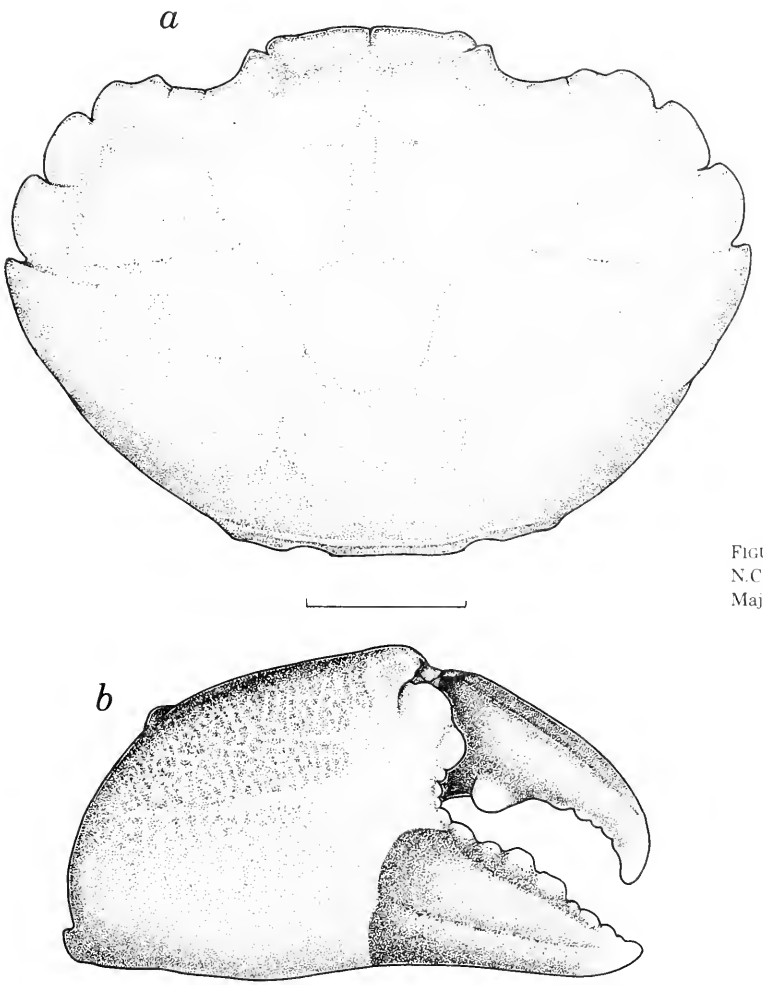

FIGURE 6.—*Panopeus obesus*. Male from Beaufort, N.C. (USNM 191157); *a*, Carapace in dorsal view; *b*, Major chela in frontal view; 10 mm indicated.

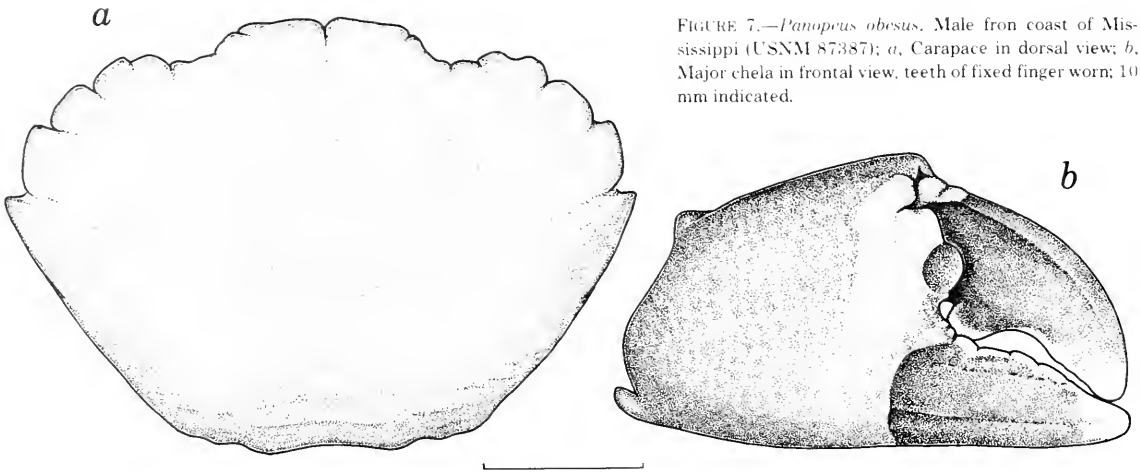

FIGURE 7.—*Panopeus obesus*. Male fron coast of Mississippi (USNM 87387); *a*, Carapace in dorsal view; *b*, Major chela in frontal view, teeth of fixed finger worn; 10 mm indicated.

Panopeus Herbstii obesus (variety).—A Milne Edwards 1880:309.

Panopeus herbstii forma obesa.—Rathbun 1930:335, pl. 156, fig. 3.

Paneopeus herbstii forma *obesa*.—Behre 1950:24 (list).

Panopeus herbstii forma *obessa* Heard 1982:50, fig. 56*a-c*.

Material examined.—YPM 901. Lectotype F; Egmont Key, Fla.; col. E. Jewett.

Specimen lots in USNM recorded by Rathbun (1930) under *P. herbstii* (catalog numbers only) plus material added since that time.

North Carolina: 191155. 1M, 1F; sea wall near Pivers I., Beaufort, Carteret Co.; J. B. Sullivan and W. Kirby-Smith, 22 March 1978.—191156. 1M; Pivers I., Beaufort; J. B. Sullivan, 8 April 1978.—191157. 1M; Pivers I., Beaufort; J. B. Sullivan, 10 May 1978.—191158. 2M; Pivers I., Beaufort; J. B. Sullivan, 10 July 1978.—75243. 2M, 1F; Bogue Sound, Morehead City; Shoemaker and Bell, 3 September 1934.

South Carolina: 15784, 57011.

Georgia: 89063. 1M; Georgia coast; State Game and Fish Comm. 1948?

Florida: 15417, 15421, 15742, 15768, 39122, 42849, 56379, 57846, 59840.—72840. 2M; Lemon Bay, Englewood; S. Springer, January 1936.—72841. 2F; Lemon Bay, Englewood; S. Springer.—72851. 8M, 1F; Lemon Bay, Englewood; S. Springer.—78379. 2M, 2F (ovig.); near Sarasota; Bass Biol. Lab., 17 May 1938.—173113. 2M; Sope Hoppy, FSU Marine Lab.; B. Hazlett, June 1978.—81368. 1M; Pensacola Beach; R. O. Christianson, 16 October 1939.

Mississippi: 87387. 1M; Gulf Coast Research Lab. [?]; J. F. Walker, summer 1948.

Louisiana: 2256, 56839.—64150. 1M; Grand Pass, Lake Borgne; S. Springer.—75647. 1M, 2F (1 ovig.); E and Grand Terre Is.; in heavy mangrove roots; E. H. Behre.

Diagnosis.—Carapace noticeably arched dorsally, with few if any transverse lines of granules, coarse granules on ocular and hepatic regions and along anterolateral slopes, length 59.3-75.5% width, $\bar{x}$ 70.1. Coalesced first and second anterolateral teeth of carapace usually separated by shallow rounded notch, second tooth broader than and sometimes more prominent than first; remaining teeth usually rounded, not outstanding (but variable in this respect), fifth tooth shorter than fourth; arc drawn along tips of first 4 teeth converging laterally with arc drawn along bases of notches between teeth. Chelipeds microscopically granular over most of surface (often in obsolescent rugose pattern) but bearing distinctly coarser, closely crowded granules along anterior edge of carpus and on upper and outer surface of palm; distinct reticulate pattern of color on outer surface of palm usually continued over its lower half (may be faded but evident after long preservation). Major chela with teeth on fixed finger varied in size, one or more distal to level of basal tooth on dactyl enlarged, with cusps raised above straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger); cusps of teeth on fixed finger rather well separated, not broad, seldom worn, their external faces not flared or bowed outward but aligned along axis of finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Male somewhat slate blue to dull maroon dorsally, lighter on cardiac and intestinal regions, buff or tannish lines more or less separating regions. Chelipeds with same color as carapace, densest dorsally but breaking into a reticulate pattern of color made up of discrete dark spots on light background on both inner and outer sides of palm, carpus, and merus, continued nearly to ventral side but spots becoming progressively more widely spaced and lighter ventrally; palm with inner and outer central longitudinal stripe relatively colorless, thin proximally but widening distally, a much thinner light line below this on outer side; fingers brown, color continued slightly but variably on palm, tips light. Walking legs tinted dorsally somewhat as carapace but lighter distally (becoming somewhat olive). Eyestalks with alternate longitudinal stripes of broad gray and narrow dull olive, cornea dark. Antennules with dark and lighter slate blue banding, tipped by off-white brush. External maxillipeds with patches of darker and lighter slate blue banded by off-white on merus; ischium with internal burgundy spot near base variable in size. Tips of raised parts on lower side of legs and venter off-white.

The reticulate pattern on the outer surface of the palm may fade but basically remains after long preservation in 70% ethanol. (From specimens at Beaufort, N.C., and preserved in the USNM.)

Type-locality.—The type-locality is hereby restricted to Egmont Key (mouth of Tampa Bay), Fla.

Known range.—The known geographic range of this species, represented by material listed above, is marsh edge, shallow intertidal, and subtidal waters of the Carolinian Province from environs of Beaufort, N.C., to Georgia (and perhaps northeastern Florida), and from Sarasota County, Fla., to Louisiana. D. L. Felder[4] has records of the species from Texas and northeastern Mexico. Reames and Williams (1983) and Sullivan et al. (1983) show that the species is mainly associated with marshlands of the Carolinian Province.

Remarks.—Smith (1869a) included syntypic material from Aspinwall (= Colón, Panama) in the type-series of his variety, but it is evident, after examination of that type-series in the YPM, that the Panama material is *Panopeus lacustris*. The Egmont Key specimen is a well-preserved immature female, cl 8.7 mm, cw 13.0 mm, which lacks one leg, the first walking leg on the left side.

The general shape of the carapace fits that for *P. obesus* at this stage of development: smooth dorsally, branchial areas somewhat inflated, arched anteroposteriorly; anterolateral teeth rounded at apices, first two being almost completely coalesced; front not prominent.

The chelipeds are representative of a large series of the specimens examined, though not fully developed at this size. The right major chela has a well-developed tooth row on the fixed finger with proximal molar area prominent, not broadened, and with cusps somewhat sectorial in nature, forming a row in line with the trend of the finger. The minor chela has a somewhat damaged fixed finger, the distal one-fourth having apparently been broken off but healed; otherwise it is characteristic.

There is no indication of color or color pattern, except for brownish gray darkening of the fingers on both chelae, with tips of fingers and cusps of teeth lighter, and a definite faded internal basal oval spot on the ischium of the third maxillipeds.

Other remarks are given in the general discussion below.

Panopeus simpsoni Rathbun, new rank

Figure 8

Eupanopeus herbstii.—Rathbun 1900b:138 (key, part).

Panopeus herbstii forma simpsoni Rathbun 1930:337, pl. 157, figs. 1-2.—Martin et al. 1984:537-602, figs. 10*b*, 11*b*, 13*b* ii, 14, 18, 23*b* ii, 24, 25, 33*b* ii, 34, 35, 36, 46, 47.

Panopeus herbstii.—Rathbun 1930:340-342 (part, *forma typica* from Gulf of Mexico and Bahahamas).—Behre 1950:24 (list).—Williams 1965:196 (part).—1984:412 (part).—Felder 1973:69 (part, key).—Powers 1977:102 (part, notes).

Panopeus herbstii forma *typica.*—Behre 1950:24 (list).

Panopeus herbstii forma Stimpson.—Pounds 1961:4 (list), pl. IX, fig. 2.—Leary 1964 and 1967:44 (list), unnumbered plate and fig., p. 39.

Panopeus herbstii forma *simpsoni.*—Heard 1982:50, fig. 55*a-c*.

[4]Darryl L. Felder, Associate Professor, Department of Biology, University of Southwestern Louisiana, Lafayette, LA 70504, pers. commun. 1981-82.

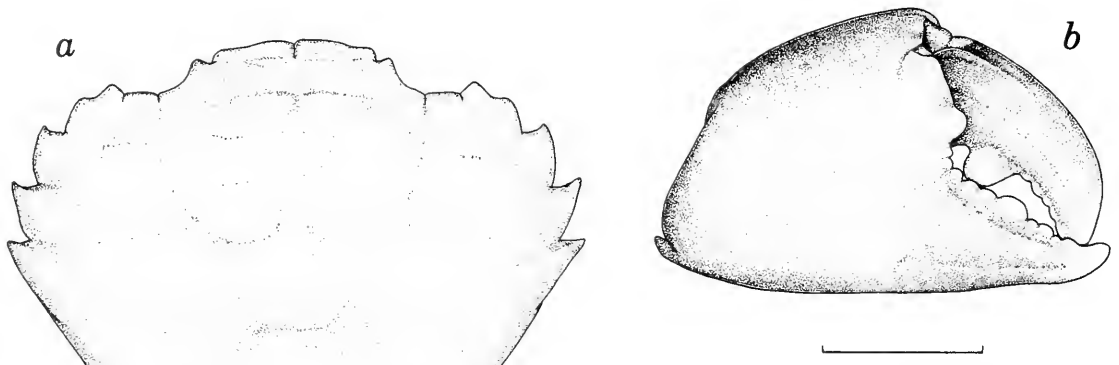

FIGURE 8.—*Panopeus simpsoni*. Holotype female (USNM 56382); *a*, Carapace in dorsal view; *b*, Major chela in frontal view; 10 mm indicated.

Material examined.—Specimen lots in USNM recorded by Rathbun (1930) under *P. herbstii* (catalog numbers only) plus material added since that time.

Florida: 6433, 6985, 15413, 15637, 56360, 56382, 56841, 60806, 60919, 61377, 62545.—75648. 1M; Key West; U.S. Bur. Fish.—15415. 1M; South Florida; D. Stearns.—110390. 1M; Tampa Bay; Bur. Com. Fish., 31 July 1962.—65615. 1M; near Wakulla, among oysters; B. C. Marshall, July 1931.—75650. 1M, 1F (ovig.); Apalachicola; A. S. Pearse, 16 June 1935.—75652. 5M, 6 juv.; St. Vincents Bar, Apalachicola; A. S. Pearse, 25 September 1935.—75651. 1F parasitized with *Sacculina*; Hagen's Flats, Apalachicola; A. S. Pearse, 9 January 1936.—89451. 1F (ovig.); Picalyne Bar, Apalachicola; A. S. Pearse, Stn. 319, 9 August 1935.—99860. 1M, 2F; Intracoastal Waterway, 3.5 mi E Interarity Point, Pensacola; F. Berry & A. Mead, 15 August 1953.

Louisiana: 64149. 1M; Grand Pass, Lake Borgne; S. Springer.—98142. 1F; Lake Pontchartrain, 0.5 mi off Bayou St. John, 33 ft; R. M. Darnell, 3 November 1954.—75627. 1M; Grand Isle, Landry's Oyster Reef; E. H. Behre, 12 June 1936.—81369. 9M, 14F (2 ovig.); Bay des Ilettes; E. H. Behre, 13 July 1939.

Texas: 17101, 20639, 33029, 33030.—191174. 2M, 1F; Lower Lavaca Bay, Sand Point Reef; B. D. King III, 4 October 1966.—63275. 1M; Corpus Christi; M. E. Quisenberry.

Locality unknown: 60805. 1M; *Fish Hawk*, U.S. Bur. Fish. tin tag #174.

Types.—The following are designated and labelled as types deposited in the crustacean collection of the USNM: 56382, holotype female, cl 35.9 mm, cw 35.2 mm, Saint George's Sound, Apalachicola, Fla.; E. Danglade, *Fish Hawk* col., 16 July 1915; 191159, 6M, 1F, transferred from above lot and considered as paratypes.

Diagnosis.—Carapace relatively narrower than that of most other species in complex, length 68.2-77.1% width, $\bar{x}$ 73.5. Coalesced first and second anterolateral teeth separated by deep rounded notch, adjacent slopes of each tooth nearly equal and tip of second nearly as advanced as that of first; fourth tooth not curved forward as much as third; fifth much smaller than fourth, usually projecting straight anterolaterally but sometimes slightly swept forward or hooked anteriorly. Chelipeds superficially smooth but actually finely granulate on upper surface of carpus and palm; lower outer surface of palm light colored (buff or yellowish); major chela with cusps of teeth on fixed finger usually either reaching or falling below straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger); anterior margin of palm with distance between crest at base of dactyl and tip of condylar tooth lateral to base of dactyl 0.80 or more times length of fixed finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Carapace light olive to yellowish or variegated grayish brown on lighter background. Chelipeds with darker of these colors on carpus and palm dorsally, often in mottled pattern (but not reticulated pattern of dots) extending about halfway down inner and outer surface; lower half of palm

yellowish to cream or off-white; fingers brown with white on tips and edges of teeth, shades of light brown to tan on inner surface of fingers. Walking legs variegated as carapace. (From color slide by D. L. Felder; see also Reames and Williams 1983.) Third maxillipeds of males with red spot near base of inner surface of ischium, females lacking spot (Heard 1982).

Known range.—The known geographic range of this species, represented by the material listed above, is shallow intertidal and subtidal waters of the northern Gulf of Mexico: Key West, Fla. (1 doubtful lot); Lee County, Fla., to Corpus Christi, Tex.

Remarks.—See general discussion below.

Key to species of *Panopeus* in the "*herbstii* complex."

Characters of major chelae refer to original or fully regenerated state.

1a. Major chela with cusps of teeth on fixed finger not reaching above imaginary straight line drawn between tip and angle at juncture of finger with anterior margin of palm (= length fixed finger) 2

1b. Major chela with cusps of teeth near midlength of fixed finger reaching above an imaginary straight line drawn between tip and angle at juncture of finger with anterior margin of palm (= length fixed finger) 3

2a. Coalesced anterolateral teeth 1-2 separated by shallow rounded notch, 2 broader than but not so prominent as 1; 4 curved forward as much as 3; 5 much smaller than 4, acute and hooked forward; palm with distance between crest at base of dactyl and tip of cusp lateral to base of dactyl 0.7 or less length of fixed finger ..... *P. herbstii*

2b. Coalesced anterolateral teeth 1-2 separated by deep rounded notch, adjacent slopes of each about equal, 2 nearly as prominent as 1; 4 not curved forward as much as 3; 5 much smaller than 4, usually projecting straight anterolaterally, sometimes slightly hooked; distance between crest of palm and tip of cusp lateral to base of dactyl 0.8 or more length of fixed finger ..... *P. simpsoni*

3a. Major chela with cusps of teeth in "molar area" of fixed finger very broad, often coalesced and worn, their external faces often flared or bowed outward .... *P. lacustris*

3b. Major chela with cusps of teeth in "molar area" of fixed finger somewhat enlarged but separated from each other, in line with axis of finger, not bowed outward 4

4a. Anterolateral teeth 3-5 definitely swept forward, acute, anterior margins noticeably concave (especially 3-4) .... *P. meridionalis*

4b. Anterolateral teeth 3-4 curved but not noticeably swept forward, anterior margin of at least 3 rectangular and often rounded 5

5a. Anterolateral teeth more or less prominent, arc drawn along tips of first 4 teeth diverging laterally from arc drawn along bases of notches between teeth ..... *P. austrobesus*

5b. Anterolateral teeth usually rounded, not prominent, arc drawn along tips of first 4 teeth converging laterally with arc drawn along bases of notches between teeth. ..... *P. obesus*

DISCUSSION

The *Panopeus herbstii*, s.l., complex of mud crabs occurring in intertidal and shallow littoral regions of the western Atlantic, especially in estuaries and lagoons, is a discouragingly close-knit group of species with few clear-cut characters. Before the diagnoses offered above were developed, the extent of the differences was unknown (but indicated by several authors), although ground work for making such determinations was laid by finding evidence for specific differences in morphometry and ecology between local populations of *P. obesus* and *P. simpsoni* in the northern Gulf of Mexico (Reames and Williams 1983) and comparably strong evidence for specific differences in hemocyanins and ecology among *P. herbstii*, s.s., *P. lacustris*, *P. obesus*, and *P. simpsoni* in the southeastern United States (Sullivan et al. 1983). The question then was: Were these differences paralleled by morphological evidence that applied to the whole complex throughout the geographic range? Answer was sought by reevaluation of a large series of specimens, including statistical analysis of certain measurements and study of the first male pleopods at high magnification.

The first pair of pleopods in males of many brachyurans exhibit characters that are useful in distinguishing species, but study of these structures in this series by light microscopy and scanning electron microscopy shows no consistent differences.

Carapace length and width were recorded for *P.*

herbstii, s.s., *P. simpsoni*, *P. obesus*, and *P. lacustris* from throughout their ranges as determined from the series in the USNM. Characters of the chelae were noted as these measurements were made, and it was seen that the specimens assorted into two apparent groups: 1) Those with major chelae in which cusps on the fixed finger almost always reached or fell below (rarely exceeded) a straight line drawn between its tip and the angle formed by its base and the anterior margin of the palm—the *herbstii-simpsoni* group, and 2) those with major chelae in which some cusps on the fixed finger were raised above or exceeded such a line (if the chela was not regenerating or otherwise altered)—the *lacustris-austrobesus-obesus* group.

Members of the first group have a carapace which is relatively narrower than those of the second group (Tables 1-2, Fig. 9), *P. simpsoni* being the narrowest of all, (a point made by Rathbun 1930), the regression line describing this width-length relationship cutting across analogous lines for the other species. Moreover, the major chela of *P. simpsoni* is relatively larger than that of *P. herbstii*, an observation that is difficult to quantify but one that can be expressed by the relationship of the height of the anterior margin of the palm (i.e., region above articular condyle of dactyl) to the length of the fixed finger. This relationship is greater in *P. simpsoni* (≥ 0.80) than in *P. herbstii* (≤ 0.70). In addition, both of these species have similarly smooth surface granulation; variably mottled dorsal coloration; and third maxillipeds with a basal red spot on the internal surface of the ischium in males, in about 50% of female *P. herbstii* (see Williams 1965), but never in females of *P. simpsoni* (see Heard 1982).

Rathbun (1930) conceived the center of distribution for *P. simpsoni* to be the northern Gulf of Mexico, but she considered some specimens from South Carolina to belong to this group as well and found specimens of *P. herbstii* from Virginia to vary toward *P. simpsoni*. *Panopeus herbstii* exhibits considerable variation in form of the anterolateral teeth, some specimens from South Carolina resembling in acuteness those of *P. simpsoni*, as do other specimens from as far north as New Jersey. Among such variants are females with internal red spots on the ischium of the third maxillipeds. On the whole, the Atlantic *P. herbstii* is morphologically distinct from the Gulf of Mexico *P. simpsoni*, as confirmed by electrophoretic patterns of the respective hemocyanins (Sullivan et al. 1983).

Members of the second group are relatively larger and more robust than those of the first group, more coarsely granular on carapace and chelipeds, and they share curious veined or reticulate patterns of coloration on the outer surface of the chelae which often extend from the upper to lower margin of the palms. This pattern is rarely seen in members of group 1. Both males and females have a proximal red spot on the inner surface of the ischium of the third maxilliped.

Teeth of the fixed finger of the major chela (except for certain regenerated examples) are developed into a conspicuous raised "molar area" in the proximal and middle parts of the prehensile edge. This development is extreme in *P. lacustris* in which teeth of the molar area are impacted, often worn flat at their crowns, and broadened such that their lateral faces and that of the adjacent finger are bowed or swollen laterally. This development is seen in either right- or left-handed individuals, but some, evidently with chelae in an intermediate stage of development or regeneration, do not exhibit the extreme molar development. *Panopeus obesus* has the molar area developed but its teeth are not impacted or conspicuously broadened and are arranged in line with the axis of the finger; the fingers are relatively longer than those of *P. lacustris*. A counterpart to the tooth pattern of *P. obesus* is found in *P. austrobesus*..

The carapace of *P. obesus* tends to be tumid, with rounded anterolateral teeth; *P. lacustris* has a less tumid carapace, with regions often well developed and angular anterolateral teeth; the carapace of *P. austrobesus* resembles the latter, but is somewhat less strongly developed. Rathbun (1930) tacitly recognized this southern Brazilian population in that

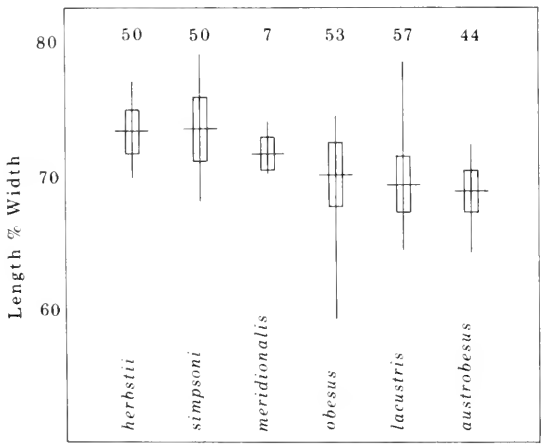

FIGURE 9.—Proportional values and basic statistics for length percent width for samples of six species of *Panopeus* from the western Atlantic. Top row of numbers = N in samples, vertical bars = range, horizontal bars = mean, open rectangles = SD.

she placed most of those specimens which she examined in or near form *obesa*.

A sixth species, represented by a very small sample, is intermediate between the two groups discussed above. Its superficial resemblance to *P. simpsoni* in narrowness of carapace, surface granulation, and lack of a basal red spot on the inner surface of the ischium of the third maxilliped in females is offset by prominence of the molar area aligned with the axis of the fixed finger of the major chela.

The species thus are separable on the basis of carapace width-length relationships, with considerable overlap (Table 1, Fig. 9), which are reinforced by a second character, the shape and dentition of the fixed finger of the major chela. The somewhat obscured width-length relationships are presented as linear regressions for samples of five of the species in Table 2. These were tested with the ANCOVA procedure, but sample size for the sixth, *P. meridionalis*, was too small to allow comparable treatment. At $P = 0.05$, there is a significant difference in linear regression of samples of the groups (species) ($F = 34.4647$* with 4, 252 df). The hypothesis that the slopes for this regression are equal is rejected ($F = 24.6288$* with 4, 244 df) as is the hypothesis that the intercepts are equal ($F = 31.5588$* with 4, 244 df). The Newman-Keuls MRT procedure is able to separate these five species into only four significantly different but overlapping groups. The test thus has limited utility for discrimination, merely restating what was known from visual inspection, and emphasizing the fact that other characters must be used in combination with carapace dimensions in making species determinations.

The ranges of these species fit known zoogeographic distribution patterns for many littoral decapod crustaceans (Perez Farfante 1969; Williams 1965). The tropical species, *P. lacustris*, is widespread from Bermuda and southern Florida through the Caribbean Sea to the region of Cabo Frio, Brazil, and flanked by apparent cognates to the north and south. *Panopeus herbstii*, s.s., is associated with oyster beds along the Atlantic coast of the United States from Boston Harbor to southeastern Florida; the closely related *P. simpsoni* occupies the same habitat in the Gulf of Mexico, and a similar species in Uruguay, *P. meridionalis*, may occupy a comparable niche. *Panopeus obesus*, associated mainly with salt marshes, is distributed in the Carolinian Province from Beaufort, N.C., to northeastern Florida, and from western Florida to northeastern Mexico. *Panopeus austrobesus* seems to be a southern counterpart of the latter, ranging from near Cabo Frio, Brazil, southward, although its precise habitat cannot be determined from the collection data at hand.

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ELECTROPHORETIC ANALYSES OF HEMOCYANINS FROM FOUR SPECIES OF MUD CRABS, GENUS *PANOPEUS*, WITH OBSERVATIONS ON THE ECOLOGY OF *P. OBESUS*

The mud crab, known until now as *Panopeus herbstii* H. Milne Edwards, s.l., of the family Xanthidae, has been regarded as a common intertidal species throughout much of its range in the western Atlantic. As such, it commonly has been used in ecological, physiological, and genetic studies (reviewed in McDonald 1977). Four morphological forms (Rathbun 1930) are recognized as species in the paper by Williams (1983), their ranges outlined, and habitat preferences shown.

As part of the study on the genetic control of hemocyanin production, we examined several hundred individuals from coastal North Carolina and found considerable evidence that two of these four forms represent separate gene pools. Additional field observations revealed that these two forms occupy distinct areas in the intertidal zone, exhibit behavioral differences, and consume different prey. However, morphological differences other than color appeared to be slight. Smaller collections of *Panopeus* were made at Charleston, S.C., Big Pine Key and St. Petersburg, Fla., and Grand Terre Island, La. These included individuals representing the species *P. herbstii* H. Milne Edwards, s.s., *P. lacustris* Desbonne, *P. obesus* Smith, and *P. simpsoni* Rathbun. Electrophoretic analyses of their hemocyanins provide data that are compatible with taxonomic treatment of each as a distinct gene pool.

Materials and Methods

Crabs were collected by hand at low tide from the intertidal zone. Although ecological studies were confined to the area around Pivers Island, Beaufort, N.C., additional material was collected at Harkers Island and Swansboro, N.C., and at the localities mentioned above. Crabs from Big Pine Key and Grand Terre Island were shipped by air to Beaufort. The remaining crabs were bled at the collecting sites and hemocyanin samples transported on ice to Beaufort. Electrophoretic analysis of hemocyanins was performed following dissociation to monomeric subunits according to the methods of Sullivan et al. (1974) and Sullivan and Tentori (1981). Stomach analyses were made by injecting 1 ml of Formalin[1] into the cardiac region of the crab at the time of collection, and later, following its removal, contents of the cardiac stomach were examined under a binocular dissecting microscope.

Results

In studying the electrophoretic patterns of hemocyanin from the forms of *P. herbstii*, s.l. (Fig. 1), we associated an aberrent pattern with the color morph now recognized as *P. obesus* (Williams 1983). Conditions of preparation and electrophoresis of hemocyanins cause the polymeric hemocyanin to dissociate into subunits (Sullivan et al. 1974). The patterns shown in Figure 1 represent monomeric hemocyanin subunits. Six loci are active in a fiddler crab, *Uca pugilator* (Bosc), but the polypeptides of-

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

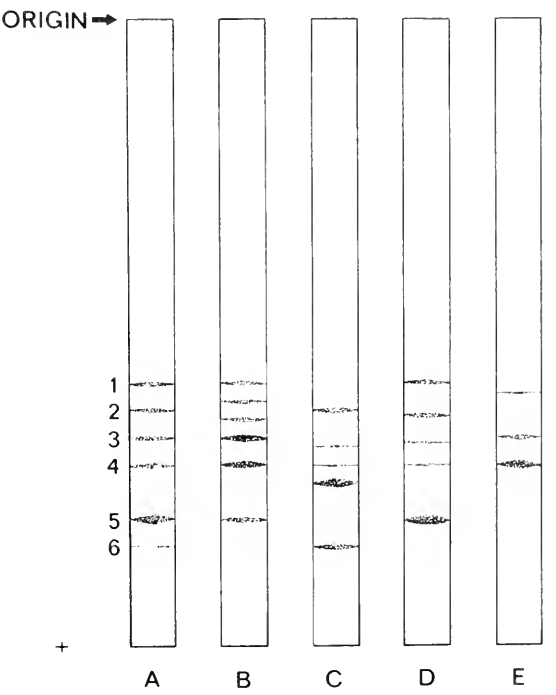

FIGURE 1.—Electrophoretic patterns of monomeric hemocyanins from *Panopeus herbstii*, s.s. (A), *P. obesus* (B), *P. lacustris* (C), *P. simpsoni* (D), and *Uca pugilator* (E) for comparison. Only one of several phenotypic patterns is shown.

ten overlay one another (Sullivan et al. in press). By comparison, in *P. herbstii*, s.s., at least six loci are also present with multiple alleles segregating at many of these loci (unpubl. data). The anodal zone of *P. obesus* differs from *P. herbstii*—most *P. obesus*' anodal zones (35 of 37 crabs examined) usually contain a single band, while in *P. herbstii* two bands are present in this zone (bands 5 and 6, Fig. 1). When double bands are present in *P. obesus* (because the individual is heterozygous at locus 5), the extra band does not align with band 6 but moves between bands 4 and 5. We are able to differentiate *P. obesus* from *P. herbstii* in every case by color pattern and by hemocyanin pattern. The hemocyanin pattern is extremely variable in both of these species, yet the differences described above were present in all individuals of *P. obesus* from Beaufort to St. Petersburg.

Electrophoretic analyses of the hemocyanins in specimens of *P. lacustris* ($n = 23$) from Big Pine Key, Fla., revealed five or six banded patterns which fell into seven phenotypic classes. This variable species shows a single major fast band, but it aligns with band 6 of *P. herbstii* instead of band 5. The remainder of the hemocyanin pattern is distinct when compared with those of the other forms (Fig. 1). Electrophoretic analyses of the hemocyanins in eight specimens of *P. simpsoni* from Louisiana reveals three phenotypic patterns which indicate polymorphism in this population also. Comparison of the patterns with those of *P. herbstii* reveals certain distinctions. A single fast band aligning with band 5 of *P. herbstii* is prominent in all gels. Band 6 is absent in all of the individuals of *P. simpsoni* which we examined. Comparison with *P. obesus* from the Carolinas and Florida reveals a similarity of electrophoretic mobilities but distinct intensity changes. In *P. obesus*, bands 3 and 4 are usually prominent; in *P. simpsoni*, band 5 is most prominent.

Our original samples ($n = 246$) of *Panopeus* from Beaufort, N.C., contained about 2% *P. obesus*. At Charleston, S.C., ($n = 38$) the frequency was 24%, and at St. Petersburg, Fla., ($n = 19$) it was 89% *P. obesus*. All individuals were collected in rocky areas or on oyster bars. Turner (1979) and Turner and Lyerla (1980) indicated that *P. obesus* was common in the upper intertidal at North Inlet, S.C., where the marsh grass, *Spartina*, grew in abundance. At Beaufort, N.C., our upper intertidal samples yielded virtually 100% *P. obesus*. A transect of an intertidal region containing both oyster rubble and *Spartina* revealed overlap for the two species only in the middle intertidal where oyster rubble and marsh grass were adjacent. *Panopeus obesus* was associated with burrows at the base of *Spartina* clumps; *P. herbstii* was in and under oyster shells. *Panopeus herbstii* alone occurred in the lower intertidal where only shells were present, and *P. obesus* alone was present in the upper intertidal where *Spartina* dominated; but in areas of lower salinity it appeared that *P. obesus* tended to displace *P. herbstii* on oyster bars.

Examination of adult females in June showed one ovigerous female out of five *P. obesus* whereas five of seven adult females of *P. herbstii* were ovigerous. Individuals of *P. obesus* appeared to live in burrows and would position themselves in the entrances to defend them. In general, *P. obesus* appeared more aggressive than *P. herbstii*. Stomach analyses of *P. obesus* revealed oyster spats (the primary food source of *P. herbstii*), shell and sea urchin fragments, and eggs and walking legs of *Uca pugnax* (Smith) and perhaps *Sesarma* sp., which are all primary food sources for *P. obesus*. Although the number of crabs examined was small, the ratio of the cheliped dactyl length (inner length, base to tip) divided by the carapace width averaged 0.25 for *P. obesus* and 0.22 for *P. herbstii*. If *P. obesus* does prey on other crabs in considerable numbers rather than mainly on oysters, one might expect a longer dactyl as compared with the oyster-feeding *P. herbstii*.

Discussion

Genetic variability at the hemocyanin loci in all populations of *Panopeus* which we have sampled complicates comparisons. Such variability is characteristic of many, but not all, temperate xanthid species (unpubl. data). Additionally, there are shifts in allelic frequencies in geographically separated populations, and the occurrence of local alleles is not unusual. However, in all areas where we have sampled two species, hemocyanin patterns can be designated as specific in spite of the "within-species" variability. Repeated sampling of the same individual over time has always yielded identical patterns, and the alleles at each locus are invariably in Hardy-Weinberg equilibrium.

We believe the evidence for the existence of two gene pools is very strong. In addition to hemocyanin data, Turner and Lyerla (1980) found unique alleles at the amylase, esterase, and malate dehydrogenase loci in the two South Carolina species. For instance, the most abundant amylase allele in *P. obesus* was not even present in adjacent populations of *P. herbstii*.

Habitat preferences are very clear in the Carolinas, at or near the northern limit of range for *P. obesus*. In western Florida, *P. obesus* is more abundant than it is in North Carolina and may occupy a broader range of habitats. Feeding habits in the two regions appear to

be dissimilar and breeding times may also differ. Detailed studies of the life histories of all the species in this complex are likely to reveal considerable differences. Unfortunately, the "forms" of *P. herbstii*, s.l., have been considered a single species and it is seldom possible to determine which "form" (= species) has been used in physiological, ecological, and behavioral experiments (McDonald 1977). The existence of four such similar species over a large range will undoubtedly provide an excellent opportunity for studies of their displacement and comparative biology.

Acknowledgments

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MUD CRABS OF THE *PANOPEUS HERBSTII* H. M. EDW., S.L., COMPLEX IN ALABAMA, U.S.A.

The mud crab, *Panopeus herbstii*, s.l. (sensu Rathbun 1930), occupies two distinct habitats in the Mobile Bay region of Alabama—the intertidal marsh and intertidal to subtidal oyster (*Crassostrea virginica* (Gmelin)) reef (Heard 1982). This paper presents an analysis of morphological attributes and ecological associations of these mud crabs, showing that the populations observed correspond to two sympatric species, *P. obesus* Smith and *P. simpsoni* Rathbun (Williams 1983).

Methods

Collection of mud crabs for morphological comparisons and feeding experiments was limited to 14 stations along southwestern Mobile Bay, Ala., and nearby eastern Mississippi Sound, from Dog River to Point of Pines, including Dauphin Island (Fig. 1), where *P. herbstii*, s.l., commonly occurs in a salinity range of 14 to > 20 ppt (May 1974). Figure 1 shows the location of stations which were sampled for crabs before destructive Hurricane Frederick struck in September 1978. The crabs, most numerous in waters with salinity >20 ppt, were sampled on four general types of substrate as follows: 1) Intertidal rubble (pieces of broken concrete over shell hash and silty sand at stations 1, 3, 4, 5, and oyster shell beach at station 2); collected by hand and in small mesh net from beneath pieces of cover. 2) Undercut marsh (mud eroded from beneath floating overhang of vegetation at edge of marsh leaving mat still attached to marsh sod at stations 6, 7, 8); overhanging mat was partly cut from bank with shovel and flipped over onto marsh to expose roots from which many small and some larger crabs were collected, mat then returned to water. 3) Mud bank (banks of hard mud

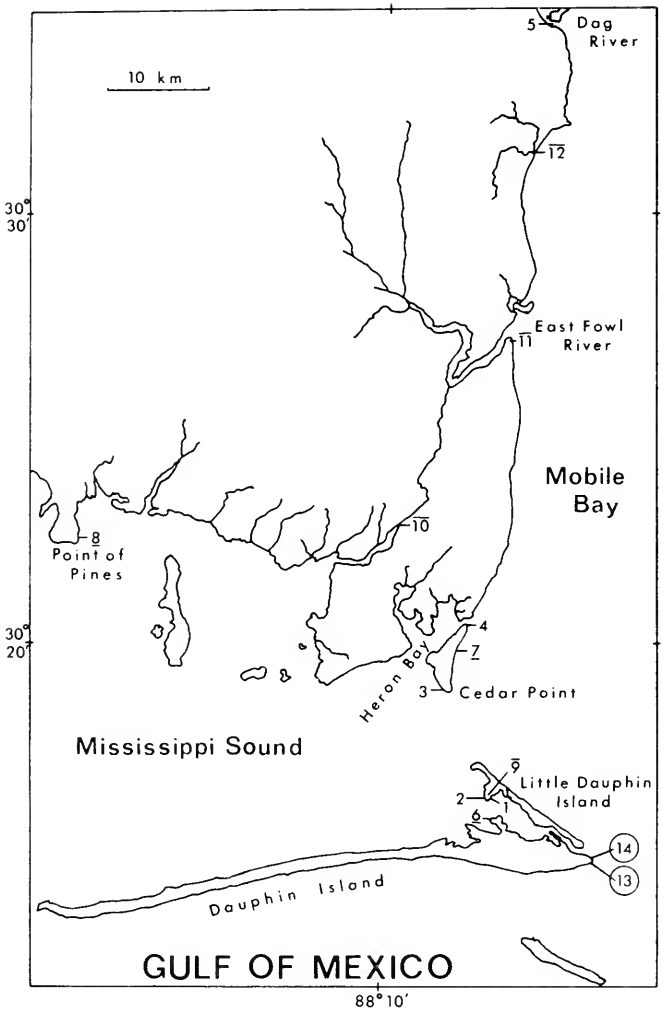

FIGURE 1.—Section of the northern Gulf of Mexico showing southwestern Mobile Bay and eastern Mississippi Sound with indicated prominent physical features and location of numbered sampling stations discussed in text. Station substrate types: unmarked = intertidal rubble and shell beach; underscored = undercut marsh; overscored = mud bank; encircled = jetty.

containing *Juncus* and *Spartina* roots and marsh mussel (*Geukensia*) shells, generally about 1 ft (30 cm) in depth from top of marsh surface to bottom of silty mud along tidal creeks at stations 9, 10, 11, 12); from burrows 2-4 ft (61-122 cm) long × 2-3 in (50-75 mm) in diameter; crabs captured at mouths of burrows, trapped near openings by inserting shovel behind crabs and breaking burrow open, or taken by hand from depths of burrows. 4) Jetty (among boulders and stones at stations 13, 14); crabs captured by hand intertidally, and subtidally with aid of mask and snorkel.

Physical and biological factors, along with color and behavior of mud crabs, were noted at each collection site. Mud crabs were preserved in the field for morphological studies or transported alive to the laboratory and maintained in seawater aquaria until used in feeding experiments. Three kinds of prey—oysters, snails, and crabs—associated with the crabs in nature were presented to both species in the aquaria.

Seven morphological characters were measured with a metric vernier caliper for statistical analysis (Fig. 2): Carapace, length in midline and greatest width; body depth; third maxilliped, length of merus and ischium; major chela, length and height of palm. Third maxillipeds of crabs with carapace lengths of <9 mm were not measured, nor were newly regenerated chelae. Male gonopods were examined with the aid of a light microscope and scanning electron microscope.

Statistical analyses were performed at the Computer Center of the University of Alabama, Mobile, using the MUSIC STATPAK program (Jarvis 1974),

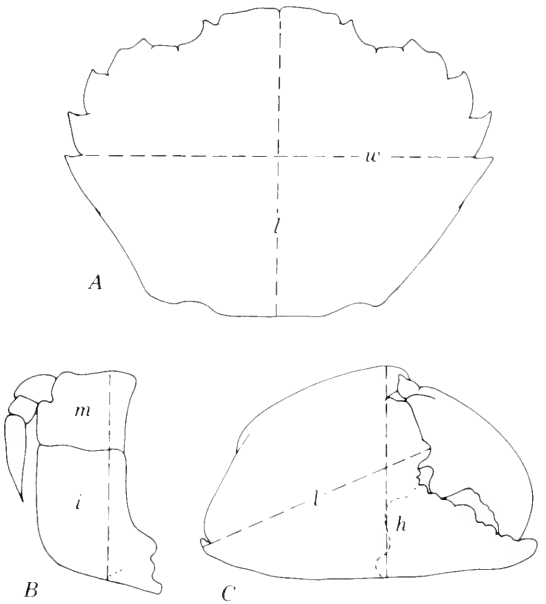

FIGURE 2.—Diagram of measurements made for analysis of morphometry. *A*, carapace, length (*l*), width (*w*); *B*, third maxilliped, length merus (*m*), ischium (*i*); *C*, palm of major chela, length (*l*), height (*h*).

and on the DEC System 10 Computer[1] of the National Marine Fisheries Service (NMFS), using computer programs written and maintained by Joseph L. Russo for the Systematics Laboratory, NMFS. The ANCOVA procedure follows that presented by Zar (1974), with the exception that the probability associated with the calculated value of the F statistic, for the purpose of simplification and clarity, is generated by the computer program instead of being calculated as a value of the F statistic with its associated numerator and denominator degrees of freedom.

Results

Ecology

Panopeus simpsoni occurs among oysters, rocks, and rubble. The crabs burrow in rubble, clearing out shallow depressions under pieces of cover, each excavation usually having more than one opening. When uncovered, the crabs again bury themselves in the substrate by wedging their flat bodies between loose shells. On jetties, this species occupies burrows, shallow depressions beside pieces of stone, and interstices among rocks and attached oysters. Collection of such individuals is difficult because they rapidly burrow among sharp oyster shells when disturbed.

Undercut marsh and mud bank stations exclusively yielded *P. obesus*. The burrows of this species are tubular, those in mud banks being the most intricate and often consisting of numerous interconnecting galleries. Each burrow generally has one or more openings at the surface of the marsh near the edge of a bank and a lower opening near the interface between hard and silty substrates. From the lower opening, a passage normally penetrates horizontally into the bank. This passage divides into one more or less vertical connection with the upper openings and another branch which angles downward at about 45°. The lower part of most burrows is <1 m long (about an arm's length), the end commonly being filled with soft, silty mud. The mud bank habitat contains many large adult *P. obesus*.

Burrows of larger mud crabs in the undercut marsh connect to both upper and lower surfaces of the marsh mat. Larger burrows are all vertical or nearly so, while smaller burrows are inclined or nearly horizontal. Juveniles (the majority of individuals in this habitat) live in the tangle of marsh roots on the lower surface of the mat.

Panopeus simpsoni occurs both inter- and subtidally (under pieces of rubble); *P. obesus* occurs only intertidally but does occupy habitats of *P. simpsoni* if suitable cover is available. For example, a large *P. obesus* was found among concrete rubble at one station but not burrowed under it as was *P. simpsoni*. Small *P. obesus* (carapace length about 10 mm) were also found among pebbles behind a stone jetty. The presence of young *P. obesus* in rocky *P. simpsoni* habitat tends to contradict the assumption by Benedict and Rathbun (1891) that dorsal curvature in the *P. obesus* carapace results from development in burrows.

Principal associated macroinvertebrates observed were *Sesarma cinereum* (Bosc), *S. reticulatum* (Say), *Uca* spp., and *Littorina irrorata* (Say) in the marsh; *Crassostrea virginica*, *Eurypanopeus depressus* (Smith), and *Balanus* spp. in the intertidal rubble and on jetties.

Stations north of Heron Bay (5, 10, 11, and 12, Fig. 1) had salinities which were too low (<14 ppt) to support populations of either species.

Panopeus obesus fed actively on oysters, snails, and crabs which were offered to them in captivity; *P. simpsoni* consumed the offered prey least actively. Both species fed on small American oysters, *Crassostrea virginica* (up to 5 cm long). A crab would grasp the oyster in its chelae and begin to chip around the edges of the valves with its major chela. As soon as an

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

opening could be found between the valves, the crab would insert fingers of the major chela into the opening and utilize the large basal tooth on the dactyl to repeatedly crush one valve. Once the valves remained open, the crab would pick out the flesh with its chelae.

Panopeus obesus was successful in feeding on the marsh periwinkle, *Littorina irrorata*, but *P. simpsoni* was unable to chip the shell aperture of the snail. *Panopeus obesus* initially chipped at the edge of the snail's shell aperture, and soon inserted fingers of the major chela into the opening which it had created. Repeated crushing with the dactyl opened the shell along a direct line toward and beyond the operculum. Once the crab was able to remove the operculum, it could feed on the flesh. Densities of *L. irrorata* were apparently related to those of *P. obesus*; where large individuals of the crab were abundant, few or no *L. irrorata* could be found.

Large *P. obesus* readily fed on *Sesarma cinereum*, *S. reticulatum*, and species of *Uca*, but less actively on *Eurypanopeus depressus*. Prey was entrapped by means of ambulatory legs and chelae. The less aggressive *P. simpsoni* fed on any of the crabs presented if they were sufficiently small.

Regardless of feeding intervals or molting occurrences, cannibalism in both species always resulted when medium to large individuals remained in a tank for extended periods (2-3 mo).

Only *P. simpsoni* was observed feeding in the field. One individual was observed feeding on algae and bryozoans encrusting rocks by tearing off bits of the encrustation with both chelae and passing these to the third maxillipeds.

Coloration

The two species of mud crabs from Mobile Bay can be identified by differences in coloration. *Panopeus obesus* is dark reddish brown dorsally and cream colored ventrally. The chelipeds exhibit a "veined" pattern extending from upper to lower margins on the external surface of the palm. These pigmentation sites coincide with muscle fiber attachments within the chelae. Fingers are dark brown.

Panopeus simpsoni is variably grayish brown dorsally, with or without a variable cream colored stripe (lacking, simple, broken, or staggered) posterior to the frontal margin; some individuals have a spotted appearance (grayish brown varying to dark brown with yellow-white areolations). Most are white to cream ventrally. Palms of the chelae are mottled with brown, gray, and yellow-white, fading to yellow-white ventrally; fingers are dark brown.

Males of both species of mud crabs have a large proximal red spot on the inner surface of the ischium of the third maxillipeds (color variably persistent after long preservation). The spot is present in all females of *P. obesus* but completely lacking in females of *P. simpsoni*.

Morphology

The carapace of *P. obesus* appears wider in relation to its length, is more convex dorsally along the anterior-posterior axis, and is armed with generally blunter anterolateral teeth than that of the relatively less bulky *P. simpsoni* (Rathbun 1930; Williams 1983). While differences in carapace morphology and color usually suffice to distinguish living or freshly preserved individuals of the two species, variations among individuals within the study area and throughout the entire geographic range indicate that these and other possible differences should be rigorously evaluated (Smith 1869; Rathbun 1930; Williams 1965).

The ecological interface between the two sympatric forms was considered to be the best place to test for possible differences between them, since it is the area in which intergradation might most likely occur. Nearly all of the measured mud crabs were collected at random from habitats in the intertidal zone. However, by imposing this limitation on the samples, the proportion of older (and larger) individuals in them may not reflect true proportions in the natural populations. (Larger individuals of *P. simpsoni* may occur subtidally but normally *P. obesus* did not occur there.) An intertidal rubble station in proximity to a mud bank sheltered many *P. simpsoni* as well as a small number of *P. obesus*. Intertidal mud banks yielded about 22% of the *P. obesus* (mainly larger individuals), but the overwhelming proportion of this form came from undercut marsh (mostly smaller individuals).

The means for each character except those of the palm (Table 1) were significantly greater ($P = 0.05$) in the *P. obesus* samples, although the smallest specimen of *P. simpsoni* was only 1 mm shorter than its *P. obesus* counterpart. The relationships between carapace length and width, carapace length and body depth, length of merus and ischium of the third maxilliped, and length and height of the palm of the major chela (Fig. 2) were analyzed by regression analysis (Table 2) and the ANCOVA procedure (Table 3). The coefficients of determination (Table 2) were >0.94 in all cases except one. The ANCOVA procedure (Table 3) showed a highly significant statistical difference between the species in each of these

TABLE 1.—Elementary statistics for samples of *Panopeus obesus* ($N = 209$) and *P. simpsoni* ($N = 200$) from Mobile Bay, Ala.; measurements in mm.

Character	Mean	SD	Max	Min.
P. obesus				
Carapace				
Length	16.6	7.60	38.9	5.7
Width	23.2	10.99	55.8	7.7
Body depth	10.9	5.29	27.8	3.7
Third maxilliped				
Length merus	2.5	0.86	4.8	1.2
Length ischium	4.5	1.58	9.4	2.4
Major palm				
Length	12.3	6.50	33.7	3.8
Height	8.2	4.44	23.2	2.4
P. simpsoni				
Carapace				
Length	14.8	4.38	26.2	4.7
Width	19.7	5.94	35.2	6.1
Body depth	9.0	2.96	16.7	2.4
Third maxilliped				
Length merus	2.1	0.45	3.8	1.0
Length ischium	3.9	0.88	6.7	2.0
Major palm				
Length	11.3	4.13	22.2	2.8
Height	8.2	3.15	16.6	1.9

able for subspecific status. After field observations in southwestern Alabama, it was apparent that the two forms which she recognized in that area differ markedly from each other, although no obvious external feature will distinguish every individual.

Color

There is a difference in the dorsal coloration of living animals, *P. obesus* being generally russet in tone whereas *P. simpsoni* is mottled gray. The chelae of *P. obesus* exhibit a "veined" pattern over the external surface of the palm whereas those of *P. simpsoni* are mottled brown, gray, and yellow-white, fading to cream color ventrally. The inner surface on the ischium of the third maxilliped bears a large, proximal red spot in both male and female *P. obesus*. The color of this spot is persistent in fluids which are commonly used for preserving study specimens, although it may fade after periods of storage. Males of *P. simpsoni* possess this spot but females lack it.

TABLE 2.—Regression statistics for samples of *Panopeus obesus* and *P. simpsoni* from Mobile Bay, Ala.; measurements in mm. First variable of each pair is independent (x).

Character	Data pairs	*Y*-intercept	Regression coefficient	SE regression coefficient	SE estimate	Coefficient of determination
P. obesus						
Carapace						
Length: width	209	−0.88316	1.44504	0.005	0.507	0.998
Length: body depth	209	−0.33666	0.67624	0.011	1.256	0.945
Third maxilliped (length)						
Merus: ischium	183	0.10077	1.77387	0.032	0.376	0.943
Major palm						
Length: height	181	−0.16787	0.68115	0.003	0.303	0.996
P. simpsoni						
Carapace						
Length: width	209	−0.24887	1.35075	0.008	0.515	0.992
Length: body depth	209	−0.66950	0.65737	0.007	0.446	0.976
Third maxilliped (length)						
Merus: ischium	183	0.69728	1.52849	0.064	0.435	0.755
Major palm						
Length: height	181	−0.35777	0.75729	0.006	0.312	0.990

pairs of attributes except for the slope of carapace length:body depth, but the *Y*-intercepts of those two lines differed significantly.

A number of other characters compared in preliminary tests are not included in this discussion because they provided minimum information for defining differences between *P. obesus* and *P. simpsoni*. These characters included statistical comparisons of the fifth pereopods of dactyl and propodus lengths, third maxilliped ischium and merus widths, major chelae, dactyl lengths and widths, frontal and frontoorbital widths, and shape of male gonopods.

Conclusions

Rathbun (1930) considered forms of the mud crab, *Panopeus herbstii*, s.l., to be distinct but unacceptable for subspecific status. After field observations in southwestern Alabama, it was apparent that the two forms which she recognized in that area differ markedly from each other, although no obvious external feature will distinguish every individual.

TABLE 3.—*F* statistics for results of ANCOVA comparing measured characters from samples of *Panopeus obesus* and *P. simpsoni* from Mobile Bay, Ala.

Character	df	Slope	*Y*-intercept
Carapace length:width	405	99.6812**	
Carapace length:body depth	405	1.9055(NS)	39.8751**
Third maxilliped, length merus:ischium	365	12.4791*	
Major palm, length:height	354	130.1565**	

* = significant at $P = 0.05$.
** = significant at $P = 0.01$.
NS = Not significant.

Morphometry

Panopeus obesus is a wider, deeper bodied form

than *P. simpsoni*, with relatively less massive chelae than the latter. Statistically, there is a significant ($P = 0.05$) difference between the two crabs (independent of size) in length and width of carapace, length and depth of body, length of merus and ischium of the third maxilliped, and length and height of the major palm.

Habitat

There is a relatively effective isolation of the two mud crabs by habitat. *Panopeus simpsoni* occurs intertidally or subtidally in association with the American oyster, but not usually in the marsh bank environment. *Panopeus obesus* occurs in marsh banks, but not subtidally. Both species inhabit intertidal rubble areas.

Feeding

Though food type for both species is similar, *P. obesus* is much more aggressive in capturing and consuming prey.

These findings reinforce the conclusion of Williams (1983) that *P. obesus* and *P. simpsoni* are specifically distinct.

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EFFECT OF TEMPERATURE ON RATE OF EMBRYONIC DEVELOPMENT OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*

Recent studies by the Northwest and Alaska Fisheries Center Auke Bay Laboratory of the National Marine Fisheries Service, Auke Bay, Alaska, have focused on causes underlying mortality of eggs and larvae of walleye pollock, *Theragra chalcogramma*, a species of considerable economic importance in Alaskan waters. One aspect of these studies is to predict age of walleye pollock embryos in samples from surveys at sea. Knowledge of age of embryos is necessary for estimating peak spawning time and daily production of eggs, and for predicting abundance and distribution of spawning fish. Because length of the incubation period is dependent on temperature of the water mass in which the eggs are developing (Hamai et al. 1971), embryo age (hours since fertilization) can be estimated provided water temperature is known.

In this study, we determined the relation between temperature and rate of development of walleye pollock embryos at constant incubation temperatures and at fluctuating temperatures (simulated). We then derived equations and a contour plot for estimating the age of an embryo (time from fertilization, in hours) at a given incubation temperature and stage of development. We also derived an equa-

tion to estimate hours to midpoint of the hatching interval.

Methods

On 4 April 1981, adult walleye pollock were trawled in Stephens Passage, southeastern Alaska (lat. 58°17'N, long. 134°42'W). One sexually mature female and one adult male were kept alive until spawned artifically in the laboratory, about 3 h later. The eggs were removed and fertilized according to the "dry" method (Kinne 1977).

Embryos were incubated about 4 h at 6°C to ensure that only viable eggs were used in the experiment. At the end of the 4-h period, each egg was examined visually before being transferred to an incubator. The incubators were then placed in water baths of the various experimental temperatures. By the time of the first observation, about 4 h later, water temperature in the incubators had reached experimental temperatures. Six groups of about 200 embryos each were incubated separately in identical incubators. Two of the groups were incubated at 6°C to provide an estimate of residual error. The other groups were incubated at 2°, 5°, 8°, or 11°C. These incubation temperatures fall within the range of incubation temperatures walleye pollock embryos usually encounter at sea.

The incubators were 3.5 l cylindrical containers made of black ABS (acrylonitrile-butadiene-styrene) plastic. Each incubator was filled with 2,500 ml of seawater (salinity 32.5‰) and covered with a clear Plexiglas[1] cover 3.2 mm thick. Seawater was not changed during the experiment. The incubators were kept in thermostatically controlled water baths at temperatures within ±0.2°C of the treatment temperature. Photoperiod was 12-h illumination and 12-h darkness. Illumination at the cover of each container was 170 lux (15.8 fc) from 60-W Soft White incandescent bulbs.

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

Embryos were removed from the containers at about 4-h intervals for the first day, then at least daily thereafter. The embryos were preserved in Gilson's fixative and later classified according to a seven-stage classification system, based on easily recognized developmental features (Table 1). For quantitative purposes, we used whole integers for midpoint of stages (Ferraro 1980). The start and end of each stage is quantified by adding or subtracting 0.5 to the stage number. We also recorded the time when larvae were first observed in culture vessels and the time when all embryos had hatched.

TABLE 1.—Stages of embryo development used for walleye pollock.

Stage I:	Fertilized egg without germ disc.
Stage II:	From germ disc through 32-cell stage
Stage III:	From 64-cell stage to completion of blastoderm.
Stage IV:	From germ ring to germ ring enveloping egg, but before completion of epiboly
Stage V:	From completion of epiboly to embryo extending at least three-fourths way around yolk and caudal region not directed off axis of embryo
Stage VI.	From caudal region slightly off axis of embryo to markedly off axis, and tip of tail just reaching embryo head
Stage VII.	Tip of tail extending beyond embryo head to hatching

Statistical Analyses

Because the embryos were incubated for 4 h at 6°C before they were placed in the incubation containers, the data were corrected (Table 2) for the delay in attaining experimental temperatures using Ferraro's (1980) method. In our experiment, the correction factor was the ratio of development time to Stage VII for embryos incubated at 2°, 5°, 8°, and 11°C relative to development time to Stage VII at 6°C (see Table 2 for derivations and Table 3 for corrected midpoint and duration of each stage).

We developed a general predictive equation with temperature-dependent coefficients to estimate the age of a walleye pollock embryo, given a stage of development and incubation temperature over the range of 2°-11°C. For each experimental temperature, the midpoint age (in hours) for each developmental stage was plotted against the stage (Fig. 1),

TABLE 2.—Derivation of correction factors to adjust development data for differences between experimental and pre-experimental temperatures (°C) in walleye pollock. See Table 1 for description of stages.

Item	2°	5°	6°	8°	11°
Hours (midpoint) to Stage VII (unadjusted data).	514	322	278	187	153
Ratio of hours to Stage VII relative to Stage VII at 6°C.	1.85	1.16	1.00	0.67	0.55
Hours from fertilization to transfer.	2.75	3.75	2.25	3.25	2.25
Expected age (in hours) at time of transfer to culture vessels. Line 2 × line 3.	5.09	4.48	2.25	2.18	1.24
Correction factor to unadjusted data. Line 4-2.25 h.	+2.84	+2.23	0	−0.07	−1.01

TABLE 3.—Midpoint (h) and duration (h) of stage of walleye pollock embryos for Stages I-VII at experimental temperatures 2°, 5°, 6°, 8°, and 11°C. See Table 1 for description of stages.

Stage	2°C		5°C		6°C		8°C		11°C	
	Midpoint (h)	Duration (h)	Midpoint (h)	Duration (h)	Midpoint (h)	Duration (h)	Midpoint (h)	Duration (h)	Midpoint (h)	Duration (h)
I	2	4	<1	1	<1	<1	<1	<1	<1	<1
II	12	16	8	14	8	14	5	8	4	6
III	58	76	38	44	35	40	25	30	22	28
IV	130	70	82	44	80	50	55	30	45	20
V	240	150	145	80	133	56	91	42	69	38
VI	382	136	230	90	205	90	149	72	111	46
VII	508	116	317	84	277	54	208	46	155	40

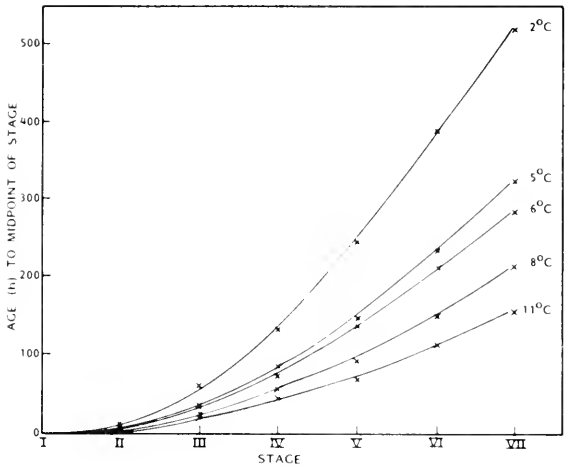

FIGURE 1.—Age-stage relation of walleye pollock embryos at 2°, 5°, 6°, 8°, and 11°C. Solid lines are regression lines of embryo age on developmental stage with experimental data adjusted for pre-experimental time and temperature; x's represent experimental data.

TABLE 4.—Regression equations for estimating age (in hours) of walleye pollock embryos at constant temperatures of 2°, 5°, 6°, 8°, and 11°C, where $\hat{Y}$ = predicted age and X = Stages I-VII. See Table 1 for description of stages.

Temperature (°C)	Regression equations
2	$\hat{y} = 50.0 - 73.4365X + 28.8571X^2 - 1.2778X^3$
5	$\hat{y} = 16.2857 - 27.5436X + 12.3512X^2 - 0.3194X^3$
6	$\hat{y} = 14.5714 - 25.9524X + 12.3036X^2 - 0.4583X^3$
8	$\hat{y} = 6.0286 - 12.3960X + 6.3286X^2 - 0.06111X^3$
11	$\hat{y} = 0.6000 - 5.0111X + 3.9119X^2 - 0.0056X^3$

TABLE 5.—The temperature-dependent coefficients, $a_0 \ldots a_3$, estimated from the least-square fits of the regression coefficients in Table 4. T = mean incubation temperature (°C). See Table 1 for description of stages.

$\hat{a}_0$	=	$75.867 - 14.8769\,T + 0.7368\,T^2$
$\hat{a}_1$	=	$-108.5209 + 20.0783\,T - 0.9770\,T^2$
$\hat{a}_2$	=	$41.4383 - 7.1494\,T + 0.3414\,T^2$
$\hat{a}_3$	=	$-1.9642 + 0.3958\,T - 0.0199\,T^2$

and the data were fitted to a third-degree polynomial model using stage as the predictor variable (Table 4). The regression equations in Table 4 were then used to derive the temperature-dependent coefficients, $a_0(T), \ldots, a_3(T)$, (Table 5), for the generalized predictive equation for embryo age,

$$\hat{y} = a_0(T) + a_1(T)X + a_2(T)X^2 + a_3(T)X^3 \quad (1)$$

where $\hat{y}$ = age (in hours), X = stage, and T = water temperature (°C). Equations for estimating the temperature coefficients are least square fits of the regression coefficients in Table 4 to a second degree polynomial model of temperature (Table 5). Over the temperature range of 2°-11°C, the standard error (obtained by comparing predicted with observed values) was normally distributed and equaled 3.03 h.

The temperature-dependent coefficients in our predictive model represent the rate (units: hours/stage) of embryogenesis in walleye pollock and are only meaningful when used in context with the embryo-staging classification in Table 1.

To verify that the curves in Figure 1 were different for each temperature, we statistically compared the curves for embryonic development at the two closest temperatures, 5° and 6°C. Cumulative measurements of development are dependent and violate assumptions underlying usual statistical comparisons among treatment groups. To avoid this problem of dependency, we transformed the development curves of embryonic development into time increments between midpoints of adjacent stages. Time increments are less correlated than cumulative measurements yet contain the same information (Box 1950). The time increments were then used as the dependent variable in the analysis of variance. The analysis of variance showed a significant temperature effect ($P < 0.01$) and significant interaction ($P < 0.05$), which indicates a real difference in development rates at 5° and 6°C.

To further substantiate that the generalized predictive Equation (1) is valid for estimating age of walleye pollock embryos at any stage over the temperature range of 2°-11°C, we regressed age (ln) as a function

of temperature for Stages II-VII. The slopes of the resulting straight lines (Fig. 2) were compared using a multivariate general linear hypothesis model (Morrison 1967), which regresses a vector of observations (development time of each stage) against temperature. The hypothesis of parallel slopes was not rejected ($P > 0.05$); therefore, the relation between age and temperature is probably independent of the stage of development.

To facilitate estimating age (time after fertilization, in hours) of walleye pollock embryos, we generated a contour plot (Fig. 3) from the generalized predictive Equation (1) over the temperature range of 2°-11°C for development Stages II-VII. For both contour plot and generalized predictive Equation (1), the estimates of age of walleye pollock embryos can be made more precise by refining the staging scheme (Table 1) into fractions of stage development. The qualitative estimates of stage fractions are quantified by adding or subtracting the proportion of stage development to the stage number.

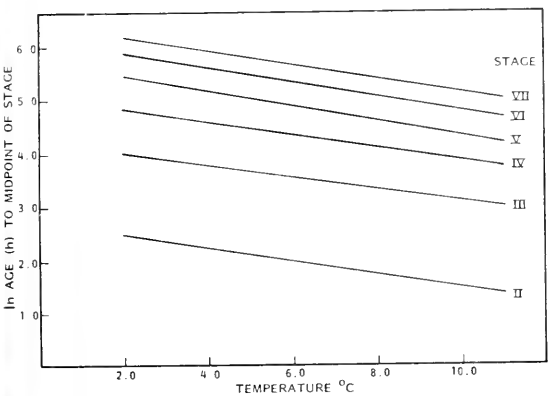

FIGURE 2.—Age-temperature relations of walleye pollock embryos, Stages II-VII.

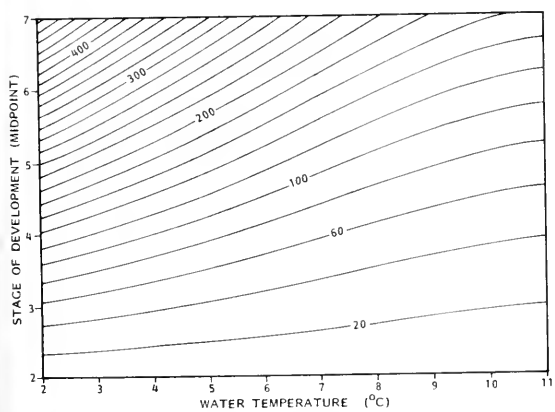

FIGURE 3.—Contours of predicted development time (h) of walleye pollock embryos as related to stage of development and water temperature (°C).

Similarity of the age-temperature relations among stages implies that embryo development is predictable regardless of whether water temperatures fluctuate or remain constant. We examined this implication mathematically by simulating stage of embryo development after 200 h given a mean temperature of 6°C. Examples of temperature variation used were 1) 100 h of embryo development at 4°C followed by 100 h at 8°C, 2) 100 h at 8°C followed by 100 h at 4°C, 3) 67 h at 2°C followed by 133 h at 8°C, and 4) 133 h at 8°C followed by 67 h at 2°C. We compared the simulations with 200 h of embryo development at constant 6°C. For various fluctuating temperatures, the mean of the simulations predicting stage of development was 6.08 with a standard error of 0.05. The value 6.08 corresponds closely to the computed stage of development of 6.06 for embryos reared at a constant temperature of 6°C. The standard error of 0.05 transforms into a standard error of 3.5 h in terms of development time and is similar to the standard error of 3.03 h of the generalized predictive Equation (1). The similarity of the standard errors (in hours) shows that temperature fluctuations exert a negligible decrease in accuracy of the generalized predictive Equation (1) and that an estimate of embryo development time based on mean temperature has the same reliability as an estimate based on a constant temperature. It should be noted, however, that mean development times were simulated and that estimates of mean development time based on empirical data are needed to verify the implication of the age-temperature relations.

We further substantiated that the mean of fluctuating temperatures could be used to estimate development time by comparing results from our generalized predictive equation with the development time observed by Hamai et al. (1971). Hamai et al. collected walleye pollock adults near Hokkaido, Japan, and reared the embryos from these fish at three different temperature ranges: 7.8°-14.5°C, 5.1°-10.6°C, and 0.0°-6.7°C. Only the temperature range 5.1°-10.6°C ($\bar{x} = 6.6$°C) and stage at completion of epiboly (our late Stage IV) were comparable with our data. We determined time to completion of epiboly over the temperature range 5.1°-10.6°C from their figure 3 (100 h). In our experiment, predicted development time to completion of epiboly at 6.6°C was similar (92 h) to time for completion of epiboly observed by Hamai et al.

The only other study on embryonic development of walleye pollock embryos comparable with ours is

Yusa (1954). Yusa described the development of walleye pollock embryos incubated at 6°-7°C. We classified Yusa's developmental data according to the stages of our Table 1 and calculated age (in hours) at 6.5°C to the midpoints of Stages II-VII. Rates of development of walleye pollock embryos were similar (Table 6) for both studies.

Our study was not designed to determine hatching time of individual walleye pollock embryos. Although we recorded the presence of larvae in culture vessels, we did not monitor distribution of hatching times.

A preliminary estimate of hours to hatching, however, can be derived using the midpoint age of the observed hatching interval, y, and the empirically derived Equation (1):

$$\ln \hat{y} = \frac{1}{a + bT} \qquad (2)$$

where least square estimates of a and b are $\hat{a} = 0.15012$, $\hat{b} = 0.00431$, and T = water temperature (°C). The estimated hours to midpoint of hatching using Equation (2) are similar to the observed midpoint ages at hatching (Table 7).

Conclusions

In general, walleye pollock embryos developed more rapidly at higher temperatures, as indicated by shorter time intervals between stages at higher temperatures (Fig. 1). Rates of embryonic development at the temperatures used in our study were significantly different from each other; however, the rates were similarly related to temperature regardless of stage of development (Fig. 3).

The age (in hours from fertilization) of a walleye pollock embryo at any stage of development (Table 1) can be estimated from the mean incubation temperature by 1) determining the temperature-dependent coefficients in Table 5 and then 2) solving the generalized predictive Equation (1). Together, these equations describe the relationship between age, stage of development, and temperature for walleye pollock at easily identifiable stages (Table 1) for temperatures within the range 2°-11°C. Simulated temperature fluctuations had no measurable effect on the accuracy of the generalized predictive equation; therefore, an estimate of the age of an embryo based on mean temperature apparently has the same reliability as an estimate based on a constant temperature. Although not as accurate as the equations, the contour plot (Fig. 3) can also be used to approximate the age (time from fertilization, in hours) of an embryo given a mean incubation temperature and stage of embryonic development. At 6.5°C, rates of development of walleye pollock embryos from Alaskan and Japanese waters are similar.

TABLE 6.—Age (time from fertilization, in hours) of walleye pollock embryos at 6.5°C to midpoints of development for Stages II-VII. Data from Yusa (1954) and this study.

	Age (h) at midpoint of stage					
Source	II	III	IV	V	VI	VII
Yusa 1954	7	20	60	133	213	267
This study	8	32	73	126	193	268
Difference (h)	−1	−12	−13	+7	+20	−1

TABLE 7.—Predicted and observed hours to hatching of walleye pollock embryos at temperatures of 2°, 5°, 6°, 8°, and 11°C.

	2°	5°	6°	8°	11°
Predicted hours	544	338	294	225	158
Observed hours	555	333	285	232	158
Hours difference	+11	−5	−9	+7	0

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HELMINTH PARASITISM OF THREE LARVAL FISHES IN THE NORTHERN GULF OF MEXICO[1]

Helminth infections of the pelagic larvae of marine fishes are ecologically germane to fisheries biology for two important reasons. First, endoparasites, although not likely to actively kill host larvae, may passively contribute to larval mortality by competing for nutrients and space in the alimentary canal (Rosenthal 1967) or by causing pathological lesions (Yamashita 1979), thereby compromising growth (May 1983). Because growth abets both feeding success and predator avoidance, it is linked with survival and therefore is an important factor in determining cohort size (Hunter 1981). Second, helminth infections can be useful indicators of trophic relationships because the life stages of cestodes and trematodes are transmitted through intermediate hosts before infection of the definitive host (see review in Campbell et al. 1980).

Given that larval fishes eat copepods, the vectors of many marine helminth infections (Cheng 1964; Gibson and Bray 1979), it should not be surprising that they are infected with cestodes and trematodes. Yet, despite extensive laboratory and field studies of larval fish feeding (see review in Hunter 1981), there are only incidental reports, none comprehensive, of helminth infections (Lebour 1918; Ogilvie 1927; Hentschel 1950; Bowers and Williamson 1951; Rosenthal 1967; Marak 1974; Mackenzie 1974; Yamashita 1979). Herein I report the prevalence and temporal variation of cestode and trematode infections in three species of larval fishes collected in the northern Gulf of Mexico: gulf menhaden, *Brevoortia patronus* Goode; spot, *Leiostomus xanthurus* Lacepède; and Atlantic croaker, *Micropogonias undulatus* (Linnaeus).

Methods

Larvae of gulf menhaden, spot, and Atlantic croaker were collected on four cruises in the northern Gulf of Mexico in December 1979, February 1980, December 1980, and February 1981. Cruises generally occupied three stations (at the 5.5, 27, and 55 m isobaths) along each of three transects (off of Galveston Bay, the Mississippi Delta, and Cape San Blas). Collections from three discrete depths taken at 0001, 0600, 1200, and 1800 h (CST) at each station with a Multiple Opening/Closing Net and Environmental Sensing System[2] (MOCNESS) (Wiebe et al. 1976) were fixed in 5% Formalin buffered with sodium borate. Nominal depths of the MOCNESS samples corresponded to strata just above the thermocline, in the middle of the upper mixed layer, and just below the surface. The MOCNESS was equipped with nine 1.0 by 1.4 m, 505 μm mesh nitex nets and with 0.25 by 0.35 m, 67 μm mesh nets "nested" inside.

Larvae of all three species were removed from MOCNESS samples, measured (notochord or standard length), and dissected, except when the total number of a species exceeded 30 larvae. In these cases, 30 larvae were chosen randomly from a numbered grid by consulting a table of random numbers. Contents of the entire alimentary canal, including parasites, were identified and enumerated. Helminths were stained with Mayer's paracarmine and mounted to aid in identification.

The cooccurrence of cestodes and trematodes was assessed by the index of affinity (Fager 1957; Fager and McGowan 1963). Independence in the prevalence of helminth infections was assessed by constructing four-way contingency tables (species of fish larvae × cohort × month × prevalence of infection) and by referring G^2 to a chi-square distribution (Fienberg 1970). In this log likelihood ratio test, 1×10^{-7} was added to each observed value in order to allow the use of natural logarithms with observed zero incidences.

Results and Discussion

Parasites

Two taxa of helminths were identified, a tetraphyllidean cestode of the *Scolex pleuronectis* complex and a digenean hemiurid trematode *Aphanurus* sp. All specimens of *S. pleuronectis* were plerocercoids with the exception of one juvenile that had undergone strobilization. *Aphanurus* sp. were late metacercariae or adults; gonads were developed but ova were never visible.

Helminths occurred primarily in the midgut; only 4 of 64 (6.2%) gulf menhaden and none of the spot and Atlantic croaker larvae had helminths in the hindgut (sensu Iwai 1969). Usually a single larva was infected by only one cestode and/or one trematode; 8 of 64 (12.5%) gulf menhaden larvae were infected simultaneously by as many as three helminths.

Cestode plerocercoids of the *S. pleuronectis* com-

[1]Contribution No. 83-31B, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, N.C.

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

plex are ubiquitous endoparasites of adult fishes (Appey and Burt 1982) including *Brevoortia tyrannus* (Meyers 1978). They also have been reported in the alimentary canal of *Clupea harengus* larvae (Rosenthal 1967). Plerocercoids of the *Scolex polymorphus* complex, a systematic composite that is similar to *S. pleuronectis*, infect a variety of fishes and invertebrates in the northern Gulf of Mexico (Overstreet 1978). Digenean hemiurid trematodes, but none of the genus *Aphanurus* (Lebour 1918; MacKenzie 1974; Yamashita 1979), have been reported in larval fishes of disparate taxa. *Aphanurus* sp. also infects adult *B. tyrannus* (Meyers 1978).

Prevalence of Infections

The cooccurrence of cestodes and trematodes in larval gulf menhaden did not indicate affinity. *Scolex pleuronectis* and *Aphanurus* sp. cooccurred in only 2 of 64 (3.1%) infected gulf menhaden larvae and never in the 1 spot or the 4 Atlantic croaker larvae; the theoretically expected coincidence of infection was 15%. The index of affinity was −0.02 where an index >50 is expected if species show positive affinity (Fager and McGowan 1963). Whereas Ogilvie (1927) reported that most *C. harengus* larvae in the North Sea were infected simultaneously with both a cestode and a trematode, Hentschel (1950) reported only cestode infections of *C. harengus* in the North and Baltic Seas. The present lack of affinity suggests that *S. pleuronectis* and *Aphanurus* sp. do not share a common intermediate host.

The prevalence of infections (Table 1) differed significantly among the three species of fishes (Tables 2, 3). *Scolex pleuronectis* infected 26 of 1,067 (2.4%) gulf menhaden and 2 of 235 (0.8%) Atlantic croaker larvae examined. No *S. pleuronectis* were found in spot larvae. *Aphanurus* sp. infected 38 (3.6%) gulf menhaden, 1 (0.5%) spot, and 2 (0.8%) Atlantic croaker larvae. The high prevalence of infection by both the cestode and the trematode in gulf menhaden larvae and the corresponding low or complete lack of infection by the cestode in spot and Atlantic croaker larvae imply that diets differ. The diets of these three species did differ significantly with the diet of gulf menhaden larvae the most distinct (Govoni et al. 1983). Gulf menhaden larvae ate a more diverse diet that included phytoplankters (mainly dinoflagellates) as well as zooplankters (including tintinnids, pelecypods, pteropods, and all stages of copepods). The diets of larval spot and Atlantic croaker were restricted to zooplankton. Significant differences in diet notwithstanding, the lack of adequate systematic definition (the *S. pleuronectis* complex), and the lack of tetraphyllidean and hemiurid host specificity confound relationships between helminth infections and diet among these larval fishes.

The prevalence of infections (Table 1) was lower than previously reported helminth infections of larval fishes caught at sea (Lebour 1918; Hentschel 1950; MacKenzie 1974). Previous reports have dealt with larger fish larvae that were exposed to helminth infection for longer periods (MacKenzie 1974) and

TABLE 1.—The prevalence of cestode (*Scolex pleuronectis*) and trematode (*Aphanurus* sp.) infection in larval cohorts of *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus* in the northern Gulf of Mexico.

Species	Winter	Month	Cestodes		Trematodes		Larvae examined	
			Infected	Uninfected	Infected	Uninfected	Number	Totals
Brevoortia patronus	1979-80	Dec.	1	163	2	162	164	
		Feb.	21	319	35	305	340	
		Σ	22	482	37	467	504	
	1980-81	Dec.	0	177	0	177	177	
		Feb.	4	382	1	385	386	
		Σ	4	559	1	562	563	
								1,067
Leiostomus xanthurus	1979-80	Dec.	0	13	0	13	13	
		Feb.	0	12	1	11	12	
		Σ	0	25	1	24	25	
	1980-81	Dec.	0	134	0	134	134	
		Feb.	0	37	0	37	37	
		Σ	0	171	0	171	171	
								196
Micropogonias undulatus	1979-80	Dec.	1	16	2	15	17	
		Feb.	0	18	0	18	18	
		Σ	1	34	2	33	35	
	1980-81	Dec.	0	151	0	151	151	
		Feb.	1	48	0	49	49	
		Σ	1	199	0	200	200	
								235

TABLE 2.—Tests of independence in the prevalence of cestode (*Scolex pleuronectis*) infection among larval *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus* collected in December 1979, February 1980, December 1980, and February 1981 in the northern Gulf of Mexico.

		Partial association		Marginal association	
Variable	df	G^2	Probability (%)	G^2	Probability (%)
Prevalence (P)	1	1,798.33	<0.001		
Month (M)	1	23.15	<0.001		
Cohort (C)	1	92.34	<0.001		
Species (S)	2	899.60	<0.001		
PM	1	12.09	<0.001	19.4	<0.001
PC	1	16.73	<0.001	23.83	<0.001
PS	2	2.38	>0.050	10.77	=0.010
MC	1	0.93	>0.050	32.80	<0.001
MS	2	181.92	<0.001	215.08	<0.001
CS	2	127.76	<0.001	160.98	<0.001
PMC	1	4.43	>0.050	1.34	>0.050
PMS	2	4.33	>0.050	0.81	>0.050
PCS	2	2.20	>0.050	0.00	>0.050
MCS	2	17.49	<0.001	15.34	<0.001
PMCS	2	0.05	>0.050		

TABLE 3—Tests of independence in the prevalence of trematode (*Aphanurus* sp.) infection among larval *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus* collected in December 1979, February 1980, December 1980, and February 1981 in the northern Gulf of Mexico.

		Partial association		Marginal association	
Variable	df	G^2	Probability (%)	G^2	Probability (%)
Prevalence (P)	1	1,700.74	<0.001		
Month (M)	1	23.15	<0.001		
Cohort (C)	1	92.34	<0.001		
Species (S)	2	899.60	<0.001		
PM	1	13.87	<0.001	23.57	<0.001
PC	1	58.80	<0.001	71.46	<0.001
PS	2	0.08	>0.050	12.24	<0.010
MC	1	0.39	>0.050	32.80	<0.001
MS	2	183.17	<0.001	215.08	<0.001
CS	2	126.11	<0.001	160.98	<0.001
PMC	1	0.10	>0.050	0.34	>0.050
PMS	2	8.71	>0.050	6.01	=0.050
PCS	2	0.14	>0.050	0.68	>0.050
MCS	2	18.04	<0.001	15.34	<0.001
PMCS	2	0.00	>0.050		

that ate greater numbers of copepods (Hentschel 1950). Copepods are the intermediate hosts of tetraphyllidean cestodes (Cheng 1950) and digenean hemiurid trematodes (Gibson and Bray 1979).

Although the prevalence of infections was low for all species, it became greater in gulf menhaden and Atlantic croaker larvae as length increased. No helminths were found in larval gulf menhaden or Atlantic croaker shorter than 5.01 mm. *Scolex pleuronectis* infected only 2 of 557 (0.4%) gulf menhaden larvae <15.01 mm long but 24 of 386 (6.2%) larvae between 15.01 and 20.00 mm; *Aphanurus* sp. infected no gulf menhaden larvae <15.01 mm, but 37 of 386 (9.6%) larvae between 15.01 and 20.00 mm.

The prevalence of *S. pleuronectis* and *Aphanurus* sp. infections (Table 1), being significantly (Tables 2, 3) greater in February than in December, particularly for gulf menhaden, may be related to differences in the corresponding size of larvae and to ontogenetic changes in their diets. Larger larvae, which had a higher prevalence of infection, were more abundant in February than in December. Spawning of gulf menhaden during these years was bimodal with peaks in late December and late January,[3] thus growth of cohorts resulted in longer larvae in February collections. Inasmuch as gulf menhaden larvae did not eat appreciable numbers of adult copepods until they had grown longer than 5.01 mm[2], one would expect a higher prevalence of helminth infection in months when larger larvae were more abundant. Since the length of the spot and Atlantic croaker larvae collected changed little from December to February, a seasonal trend in the prevalence of infection would not be expected.

Larval cohorts collected in the winter of 1979-80 (Table 1) showed a significantly greater prevalence of infection than larvae collected in 1980-81 for both *S. pleuronectis* (Table 2) and *Aphanurus* sp. (Table 3), but shifts in diet do not explain this difference. Gulf menhaden larvae exemplified this annual difference in infection owing to the greater number of larger larvae (>5.01 mm) collected and examined from both winters. Larval gulf menhaden ate a greater number and a greater diversity of copepods in the winter of 1980-81 than in 1979-80 (Govoni et al. 1983).

Whether gulf menhaden, spot, and Atlantic croaker larvae are definitive or paratenic (auxiliary) hosts for members of the *S. pleuronectis* complex or *Aphanurus* sp. are not known, due in part to the lack of systematic definition. In either case, the levels of infection in terms of the prevalence of infection as well as the parasite loads on individual larvae are lower than those that directly cause death of larval seabream (*Pagulus* = *Chrysophrys major*) in the laboratory (Yamashita 1979). Indirect effects of helminth infections (May 1983) on larval fish cohorts are not yet clear.

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[3]S. M. Warlen, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516, pers. commun. March 1982.

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EMPIRICAL USE OF LONGEVITY DATA TO ESTIMATE MORTALITY RATES

Various investigators have utilized compendia of life history parameters to develop equations for predicting values of difficult-to-estimate parameters from easily measured or estimated quantities. For example, Pauly (1979) developed multiple regressions to predict the natural mortality rate of fish from growth parameters and mean water temperature. Ohsumi (1979) developed linear regressions for estimating natural mortality of cetaceans from maximum length or maximum age. In this paper, a general regression equation is developed to predict the total mortality rate of fish, cetacean, and mollusk stocks from the maximum age.

It seems intuitive that longevity and mortality rate in a species should be inversely related since animals from a population with a high mortality rate would not survive long enough to reach old age. The nature of the relationship between mortality and maximum age is explored below.

Development of the Model

In fishery biology, it is generally assumed that, after some early life history stages, the mortality rate is constant. That is, the proportion reaching age t is given by

$$\frac{N_t}{N_0} = e^{-Zt} \qquad (1)$$

where Z is the constant instantaneous rate of mortality, N_t is the number surviving to age t, and N_0 is the initial number present so that N/N_0 is the proportion surviving to age t.

Suppose the longevity of a stock is defined as the age, t_L, to which a proportion, k, of the animals survive, where k is some arbitrarily small constant (e.g., 0.01). Then

$$k = e^{-Zt_L}$$

and

$$\ln(k) = -Zt_L. \qquad (2)$$

Equation (2) describes a hyperbola which can be linearized by plotting the mortality rate against $1/t_L$ or by plotting log (Z) against log (t_L).

In Equation (2), t_L is a quantile that is determined by aging the fish in the upper tail of a length-frequency sample. However, it is considerably easier to find the maximum age, t_{max}, in a sample (by aging just the largest few fish) than it is to estimate a quantile. Thus, it is of interest to know if Equation (2) will hold, at least approximately when t_{max} is substituted for t_L.

Tanaka (1960) plotted the mortality rate versus $1/t_{max}$ for five fish species and suggested that the apparently linear relationship deserves further investigation. Beverton (1963) and Bayliff (1967) made the same kind of plot for fishes in the families Clupeidae and Engraulidae, and Ohsumi (1979) investigated the situation within the Cetacea.

In this paper, plots of log (mortality) versus log (t_{max}) were investigated for three taxonomic groups comprising 134 stocks.

Data and Results

Data on the total mortality rates and the corresponding maximum observed ages were taken mainly from the compendia by Beverton and Holt (1959), Ohsumi (1979), and McBride and Brown (1980). Most of the data pertain to unexploited or lightly exploited stocks. All of the data are shown in Figure 1 and their sources are listed in Hoenig (1982). The data for the mollusks are shown separately in Figure 2.

Results of calculating ordinary least squares linear regressions on the log transformed data are given in the following table:

Taxonomic group	*Sample size*		*Slope*	*Intercept*			
	Stocks	*Species*	b	a	r^2	F	*df*
Mollusks	28	13	−0.842	1.23	0.78	91	1,26
Fish	84	53	−1.01	1.46	0.68	177	1,82
Cetaceans	22	13	−0.873	0.941	0.70	47	1,20
All	134	79	−0.982	1.44	0.82	595	1,132

The predictive equations are of the form

$$\ln(Z) = a + b \ln (t_{max}).$$

The four regression lines are very similar. The combined regression equation makes use of data over the widest possible range of ages (1-123 yr) and has the highest coefficient of determination (r^2). It is suggested that the combined regression equation be used for predictive purposes for all three groups.

Discussion

The high values of the coefficients of determination in the above regressions indicate that the equations have considerable predictive power. The relationship between mortality rate and maximum age appears to hold within a species as well. This is demonstrated by the data for 10 stocks of Pacific razor clam, *Siliqua patula*, and 6 stocks of Nuttall's cockle, *Clinocardium nuttallii*, shown in Figure 2.

In deriving the regression approach, it was assumed that the mortality rate does not vary with age. However, it is well known that in at least some groups of fish (e.g., sturgeons, Ricker 1975: ch. 2; clupeids and engraulids, Beverton 1963; and salmonids, Gerking 1957) the mortality rate appears to increase with age. Concave catch curves, suggestive of decreasing mortality rate with age, have sometimes been reported but these have usually been given other interpretations (Ricker 1975: ch. 2). In general, not much is known about the mortality rates among the oldest animals of most species (and how mortality might vary among taxa).

The regressions presented here are based largely on data from unexploited stocks. Since the scatter plots and regression statistics indicate a strong linear relationship between the maximum age and the mortality rate, the method works well for predicting mortality rates in unexploited stocks. If age truncation is a common phenomenon among the stocks for which data were available, then the application of this technique to heavily exploited stocks may result in an underestimate of the mortality rate.

Applications

The regression technique can be used in several distinct applications:

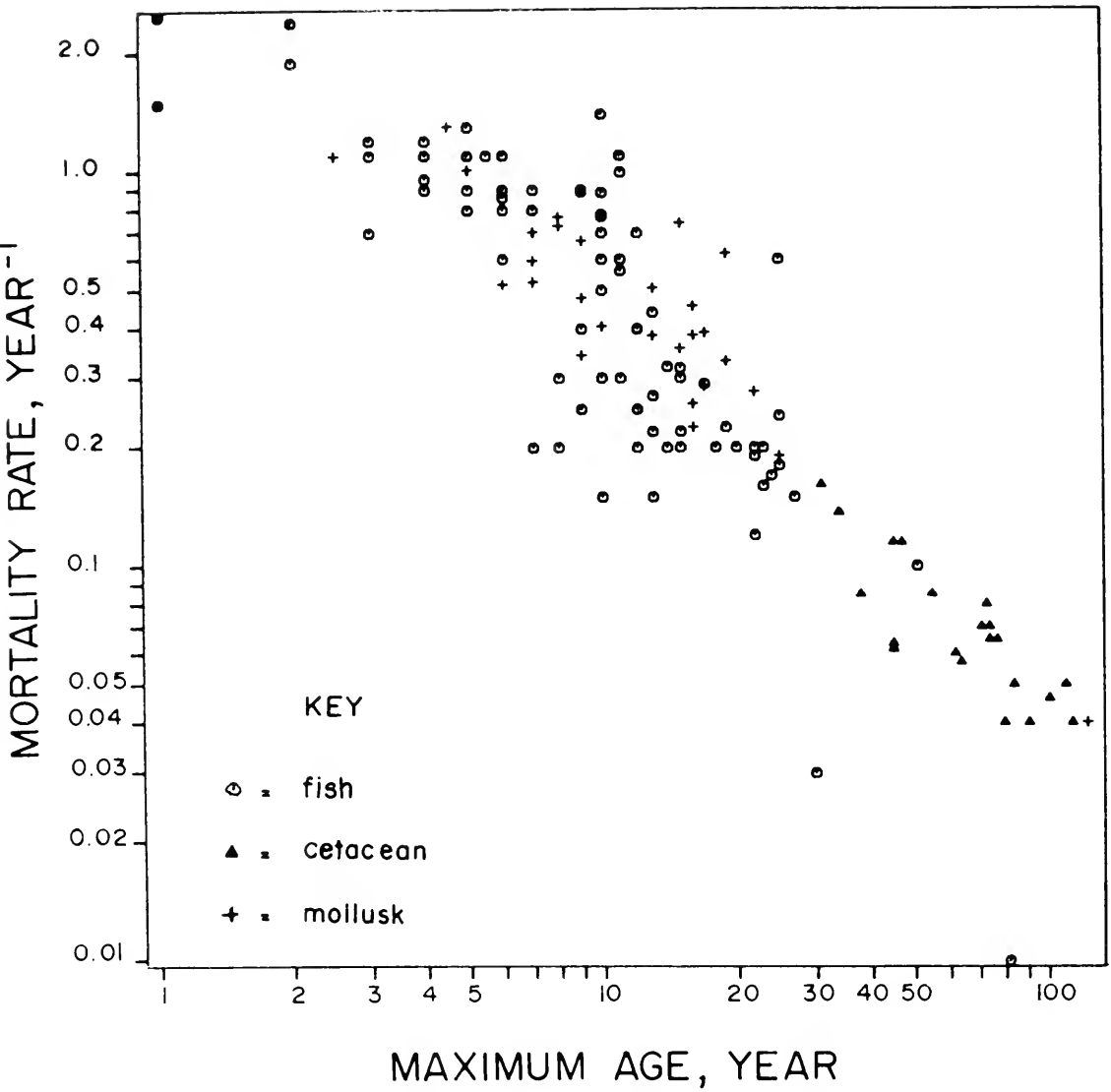

FIGURE 1.—Plot of instantaneous mortality rate (yr^{-1}) against maximum observed age (yr), both on logarithmic scales.

1) A quick preliminary estimate of the mortality rate can be obtained by aging just the largest few fish. This does not preclude aging the rest of the sample at a later date.

2) In some cases, the number of age determinations must be kept to a minimum because of time or cost constraints; e.g., determining the ages of tropical fishes may necessitate a tedious procedure of counting daily growth rings (Brothers 1980; Brothers et al. 1976).

3) The procedure can be used when the sample is not representative of the population. This can occur as the result of a particular sampling scheme or if the animals segregate by size.

4) An interesting application of the method is to cases where recruitment is highly variable. In an extreme case, Goldspink (1981) reported finding only three or four year classes in bream, *Abramis brama*, in three English lakes even though the maximum age found was 23 yr. A maximum age of 23 yr would normally indicate a mortality rate of 0.19. However, this is likely to be a maximal estimate, since older fish might have been found if there had happened to be a strong year class in an earlier year.

5) The technique can also be used to obtain a rough estimate of the mortality rate when the maximum age

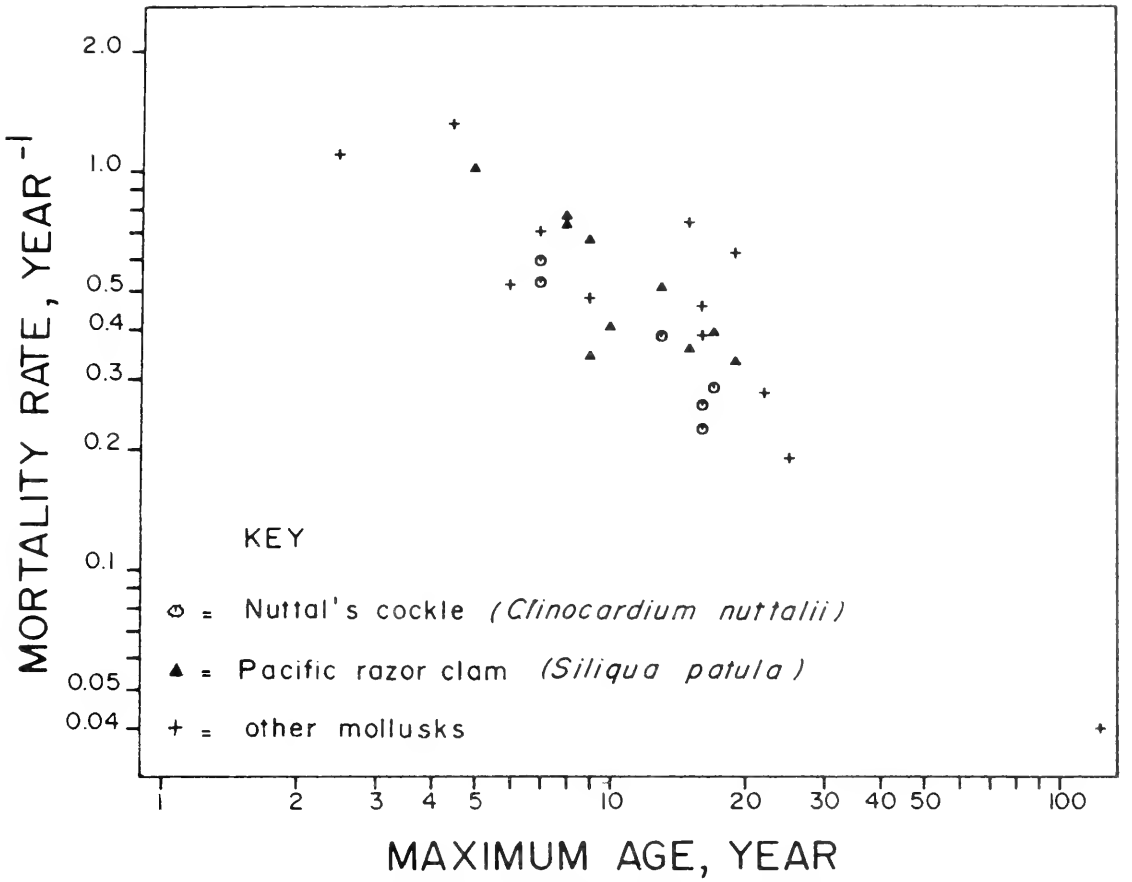

FIGURE 2.—Plot of instantaneous mortality rate (yr^{-1}) against maximum observed age (yr), both on logarithmic scales, for 28 stocks of mollusks.

is the only information available; e.g., McBride and Brown (1980) summarized the life history parameters of the major fish stocks in the western North Atlantic. For the following species McBride and Brown gave estimates of maximum age but not of natural mortality rates. The estimates provided here were calculated by the regression method.

Species	*Max age (yr)*	*Predicted M (yr^{-1})*
Ocean pout, *Macrozoarces americanus*	18	0.25
Scup, *Stenotomus chrysops*	19	0.23
Black sea bass, *Centropristis striatus*	20	0.22
White hake, *Urophycis tenuis*	23	0.19
Bull shark, *Carcharhinus leucas*[1]	28	0.16
Dusky shark, *Carcharhinus obscurus*[1]	30	0.15
Angler, *Lophius americanus*	30	0.15
Tilefish, *Lopholatilus chamaeleonticeps*	40-50	0.11-0.09

[1]Maximum ages for the sharks were taken from the growth study by Hoenig (1979). The estimates are believed to be conservative.

The major limitation of the technique is that the sample size is not taken into consideration. The maximum age observed depends on the number of animals in the sample since rare, old animals are more likely to be found in large samples. However, once a sample of, say, 200 animals has been examined, the maximum age tends to increase slowly with increasing sample size. The nature of the relationship between sample size and maximum age is examined in Appendix A. Because the sample size is not taken into consideration, it is not possible to attach confidence bounds to the estimates or to test hypotheses.

Another limitation is that the age structure will change slowly following a decrease in the mortality rate. Hence, the maximum age will remain depressed for several years resulting in an overestimate.

This regression technique appears to have considerable predictive power for estimating mortality. It is useful in a variety of situations where the data are limited. However, the statistical foundation underlying the technique is weak thus precluding the making

of critical comparisons. More sophisticated statistical methods, which implicitly take the sample size into consideration but which require stronger adherence to the assumptions of the exponential model, are discussed in Hoenig and Lawing (1982) and Hoenig (1983).

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APPENDIX A

Relationship Between Maximum Observed Age and Sample Size

Assume that life duration follows a two-parameter exponential distribution with probability density function

$$f(t) = Ze^{-Z(t-t_c)}$$

where Z is the instantaneous mortality rate, t is age, and t_c is the youngest age fully represented in the catch. Also assume a stable age distribution (i.e., that recruitment is continuous and constant). Under these restrictive conditions, the expected value of the maximum age in a sample of size n is given by (Johnson and Kotz 1970: 216)

$$E(t_{max}) = \frac{1}{Z} \sum_{i=1}^{n} \frac{1}{i} + t_c. \quad (1)$$

To see the effect of sample size on the maximum age more clearly, we can approximate Equation (1) by

$$\frac{1}{Z}\sum_{1}^{n}\frac{1}{i}+t_c \cong \frac{1}{Z}\int_{1/2}^{n+1/2}\frac{dX}{X}+t_c=\frac{\ln(2n+1)}{Z}+t_c.$$

Hence

$$E(t_{max}) \cong \frac{\ln(2n+1)}{Z}+t_c. \qquad (2)$$

Holt (1965) presented similar findings as an asymptotic result.

The expected value of the maximum age is shown in the table for three values of Z and several values of n when t_c equals 0.

$E(t_{max}) = \frac{1}{Z}\sum_{1}^{n}\frac{1}{i}$ for $Z =$

n	1.0	0.5	0.25
50	4.5	9.0	18.0
100	5.2	10.4	20.7
150	5.6	11.2	22.4
200	5.9	11.8	23.5
250	6.1	12.2	24.4
500	6.8	13.6	27.2
1,000	7.5	15.0	29.9

Increasing the sample size from 100 to 1,000 causes the expected value of the maximum age to increase by 43%. Increasing the sample size from 200 to 1,000 will cause a 27% increase.

If the mortality rate is higher for older fish, the maximum age will increase even more slowly with increasing sample size. For example, if the age structure is governed by the Gompertz equation, the maximum age in a sample tends to increase as the log of the log of the sample size (Beverton 1963).

Addendum

Dr. W. E. Ricker (pers. commun.) has suggested that a geometric mean (GM) regression would be more appropriate than the ordinary predictive (arithmetic mean, AM) regression for predicting values of log Z since both variables are naturally variable. The regression equation presented here can be converted to a GM line by dividing the slope (b) by the square root of the coefficient of determination ($|r|$) and passing the line through the point defined by the means of the log transformed values of Z and t_{max} (Ricker 1973). The means are: for mollusks, mean ($\ln(Z)$) = −0.821 and mean ($\ln(t_{max})$) = 2.465; for fish, −0.767 and 2.214; for cetaceans, −2.684 and 4.154; for all groups, −1.093 and 2.585.

GROWTH OF *GERYON QUINQUEDENS* (BRACHYURA: GERYONIDAE) JUVENILES IN THE LABORATORY[1]

The deep-sea red crab, *Geryon quinquedens* Smith, is a large brachyuran of commercial interest inhabiting the upper continental slope in the western Atlantic Ocean from Nova Scotia to Argentina (Scelzo and Valentini 1974). Studies of the biology of the species have concerned distribution, abundance, and bathymetric limits (Wigley et al. 1975; Haefner 1978); the ovarian cycle of adult females (Haefner 1977); and development and behavior of larvae in the laboratory (Perkins 1973; Rosowski 1979; Sulkin and Van Heukelem 1980; Kelly et al. 1982). Studies of the rate of growth of the species have been limited to inferential analysis of size-frequency data, and it appears that 13-15 molts are required for the crab to grow from a carapace width of 20 mm to the maximum size of 150 mm (Haefner 1978).

In this note we report results of a study of the effects of temperature on the rate of growth of juvenile red crabs in the laboratory.

Methods

Groups of juvenile red crabs were reared for nearly 1 yr at one of four temperatures: 6°, 9°, 12°, and 15°C. Temperatures were chosen to approximate those of bottom water at depths ranging from 200 to 2,000 m in the western North Atlantic (Haefner 1978). Each group at 6°, 9°, and 12°C consisted of five individuals. The crabs in these groups were the progeny of one female and resulted from laboratory-reared larvae. The group at 15° consisted of 25 crabs. These crabs were the progeny of another female whose larvae were also laboratory-reared.

During the experiment, juvenile red crabs were held in darkness at ambient pressure at 35‰ salinity. Diet consisted of frozen brine shrimp (*Artemia salina*), chopped mussel (*Mytilus edulis*), and clam (*Mercenaria mercenaria*), and bits of muscle from adult red crabs. Juveniles used in the experiment were subjected to experimental conditions upon molting from the megalopa stage to crab stage 1.

Crabs in groups at 6°, 9°, and 12°C were maintained individually in glass bowls (10.5 cm diameter) with a shallow layer of sand and a small piece of plastic tubing in which the crabs generally took up residence. The bowls were kept in aerated aquaria containing 25 l of filtered seawater. Upon molting to crab stage 4,

[1]Contribution No. 1425 from the Center for Environmental Studies, University of Maryland, Cambridge, Md.

each juvenile was transferred to a separate aquarium containing 1.5 l of seawater.

Crabs in the group held at 15°C were maintained in clear plastic boxes measuring 27 × 15 × 5 cm. Each box consisted of 18 chambers (each 4.5 × 5 × 5 cm). Crabs were maintained in individual chambers for the duration of the study.

In all cases, survival and molting were checked daily, and the red crabs were transferred weekly to clean culture vessels with clean seawater. Carapace width was measured with calipers after each molt. Measurements were taken at the widest dimensions of the carapace.

Results and Discussion

Our data show a linear relationship between carapace width and time over at least the first five postlarval molts (Fig. 1). This differs from results of some other studies of growth in crustaceans in which increase in carapace width was a logarithmic function of time (for review see Hewett 1974). However, Tagatz (1968) and Simpson (1961) have reported linear increases in carapace width in captive crustaceans.

We recognize that the growth rates determined in the present investigation may be biased by laboratory conditions (diet, substrate, and pressure differed from natural conditions) and, further, that the small sample size at 6°, 9°, and 12°C requires cautious interpretation of results. Nevertheless, we have shown that growth occurs very slowly at 6°C, a temperature characteristic of depths >500 m (Haefner 1978). Between 9° and 15°C, however, growth is five to six times more rapid than at 6°C. The relative independence of growth from temperature in the 9°-15°C range suggests that this is an optimal range for juvenile existence. These conclusions suggest that if

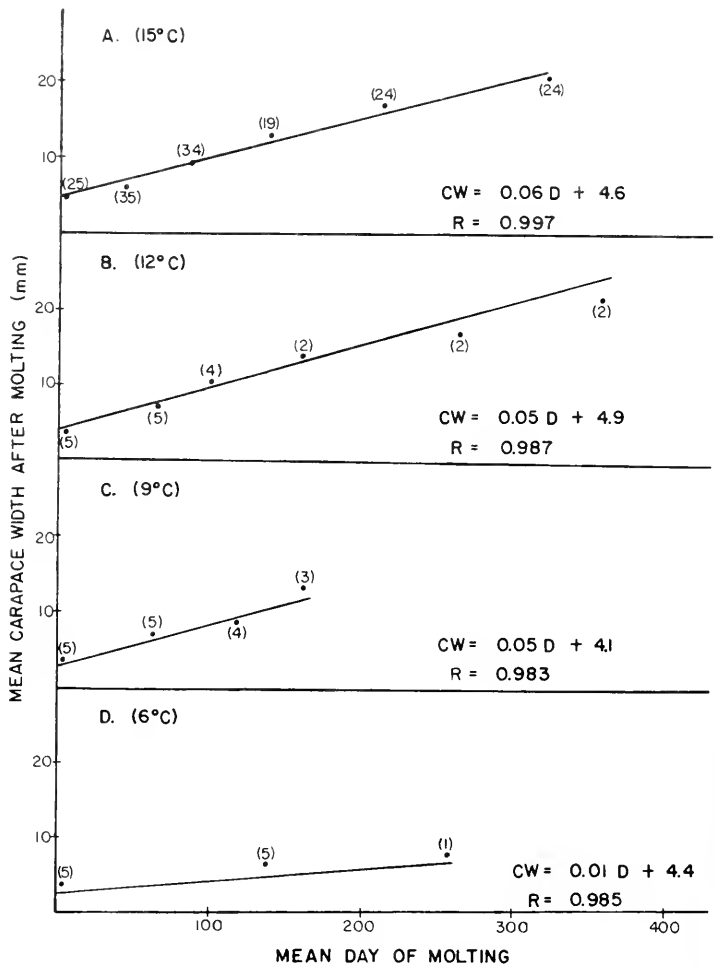

FIGURE 1.—Least-squares regression lines describing rate of increase in carapace width of juvenile red crabs, *Geryon quinquedens*. CW = carapace width; D = days postmetamorphosis. Numbers in parentheses adjacent to data points indicate number of crabs measured in calculating carapace width.

the settlement occurs at the base of the continental slope as suggested by Wigley et al. (1975) and Kelly et al. (1982), upslope migration to warmer water must occur quickly or else natural growth rates would be very slow.

Our growth equations predict that red crabs would enter the fishery (114 mm; Haefner 1978) in 5.3 yr at 15°C or in 6.0 yr at 9°-12°C. Maximum size of males is about 150 mm, and this would take 7.0 yr at 15°C, while females would require 6.5 yr to reach their maximum carapace width of 140 mm. However, there may be gender-related differences in growth rates, and our analysis does not take these into account (we were unable to determine gender in the juveniles). In any case, growth under natural conditions is probably somewhat greater than that in captivity (Winget et al. 1976), so our values represent maximum ages for crabs entering the fishery or reaching maximum size (Table 1). Crabs in our investigation reached a size of 20 mm in five postlarval molts at both 12° and 15°C. This, in combination with Haefner's (1978) results, suggests that the species undergoes 18-20 postlarval molts before reaching its apparent maximum size.

TABLE 1.—Predicted age (yr) of male red crabs, *Gerryon quinquedens*, entering fishery or reaching apparent maximum size. Based on laboratory measurements of growth of juvenile crabs.

Temperature (°C)	Age	
	Enter fishery	Maximum size
9-12	6.0	8.4
15	5.3	7.0

Acknowledgments

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AGE AND GROWTH OF DOLPHIN, *CORYPHAENA HIPPURUS*, AS DETERMINED BY GROWTH RINGS IN OTOLITHS

The dolphin, *Coryphaena hippurus* Linnaeus, is a large, schooling, pelagic fish with a worldwide distribution in warm seas. Its range extends from the Tasman Sea (Shcherbachev 1973) to Nova Scotia (Vladykov and McKenzie 1935). It supports important game and commercial fisheries in the Caribbean (Mahon et al. 1982), Southeastern United States (Beardsley 1967), East Africa (Williams 1956), Taiwan, Japan, China, and Hawaii (Hagood et al. 1981).

Growth rates of dolphin have been estimated using scale annuli (Beardsley 1967; Rose and Hassler 1968), modal progression of length-frequency distributions (Wang 1979), and captive fish of known age (Herald 1961; Beardsley 1971; Hassler and Rainville 1975; Hagood et al. 1981). However, scale annuli are not present in all dolphin populations (Schuck 1951; our study population) and are of limited use in aging a short-lived species. Modal progression of length frequencies, when appropriate, provides little information on intrapopulation growth variability; and fish growth in captivity is not necessarily representative of growth in the wild.

Daily rings on otoliths have now been used to age temperate and tropical fish (e.g., Pannella 1971, 1974; Brothers et al. 1976; Taubert and Coble 1977; Uchiyama and Struhsaker 1981; Rosenberg 1982; Campana and Neilson 1982). In this paper, we describe the sagittal otoliths of dolphin and suggest that they can be used to estimate age and growth in this species.

Materials and Methods

Dolphin were caught between January 1981 and June 1982, 10-40 mi offshore Barbados, using trolling lines for adults and surface gill nets for juveniles. Each fish was measured for standard length (SL) to the nearest mm. Monthly length-frequency distributions were drawn. Changes in mean length of a cohort were used to estimate the growth rate of adults.

The sagittal otoliths of the dolphins were removed from the sacculi, mounted on a glass slide in the syn-

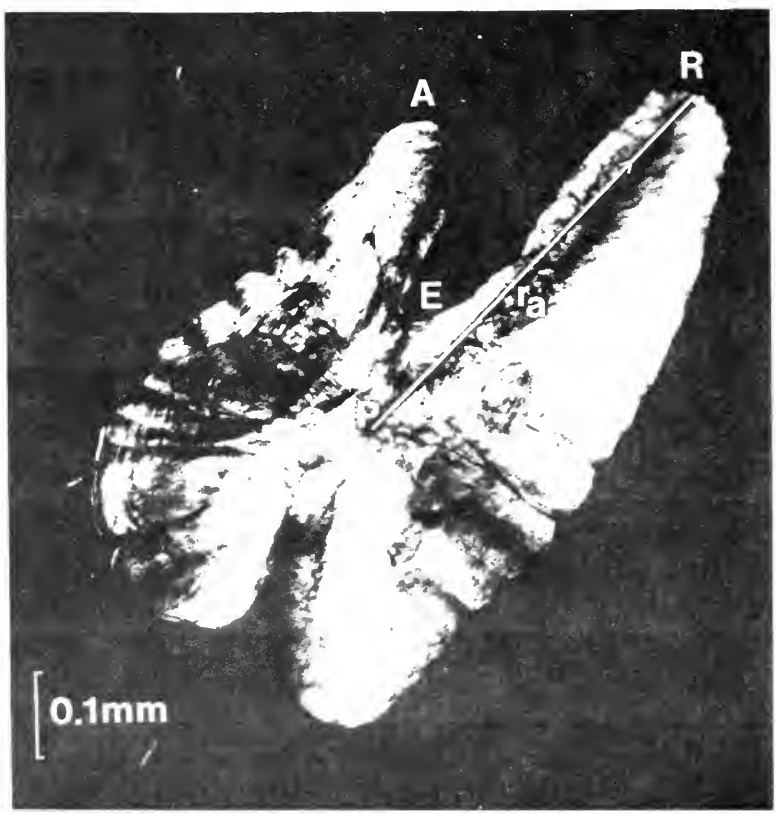

FIGURE 1.—Right sagitta of *Coryphaena hippurus* (307 mm SL) viewed from the lateral surface. R = rostrum, A = antirostrum, E = excisural notch, P = primordium, r_a = radial measurement.

thetic mounting medium Covermount, and viewed under a compound light microscope with bright field illumination at 100× and 400× magnification. A radial measurement from the primordium to the rostrum margin was taken on the right sagitta of each fish, to the nearest 0.01 mm.

The sagittae were thin enough that growth rings could be read with no further preparation. Five counts were made using both the right and left sagittae at 400× and repeat counts were made at 100×. A plot of fish standard length against the number of sagittal rings (N) was drawn, and from this an average growth rate was calculated.

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

Results and Discussion

The sagittae of *C. hippurus* are extremely small (2.6 mm in a fish of 1,100 mm SL). The rostrum is exaggerated and separated from the antirostrum by a deep V-shaped excisural notch (Fig. 1). Rings are clearly visible on the lateral or convex surface of the sagittae from the primordium to the margin (Fig. 2). These could be counted accurately on all specimens

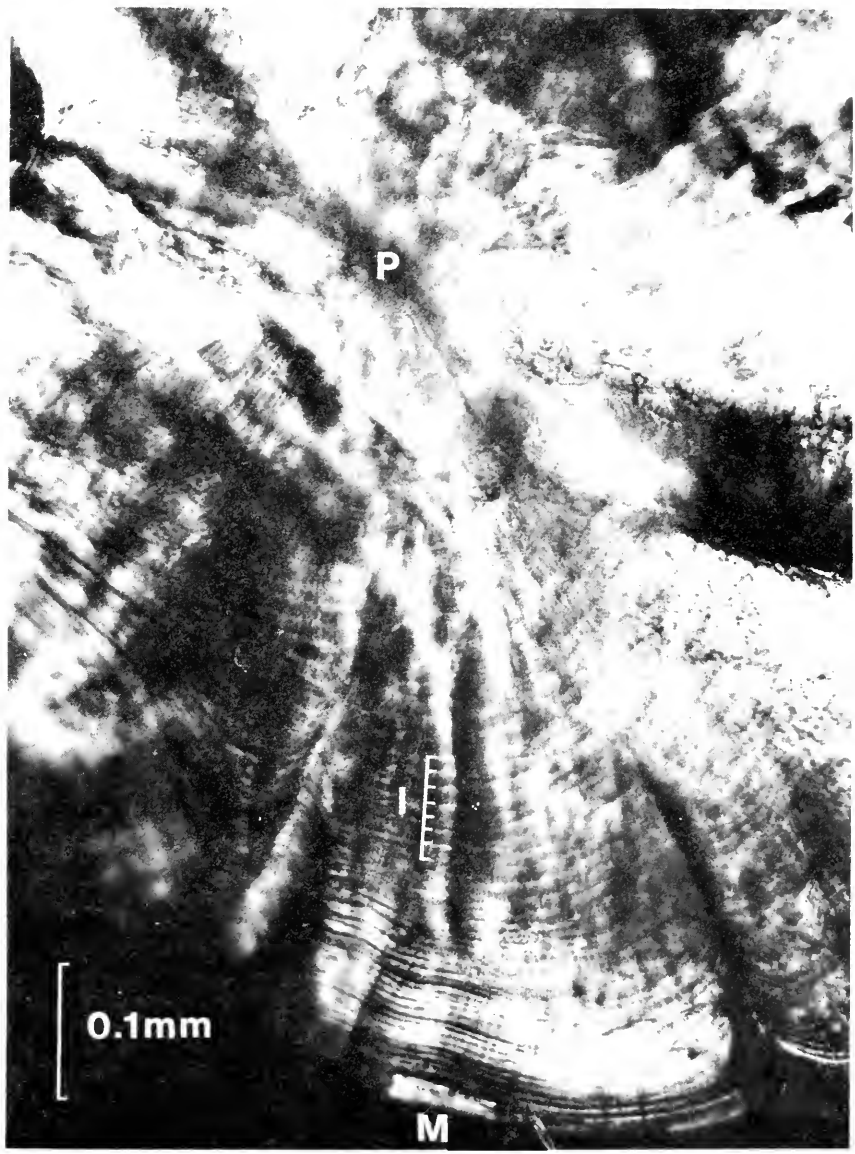

FIGURE 2.—Lateral surface of sagitta of *Coryphaena hippurus* showing 51 increments from the primordium to the margin. P = primordium, I = increments, M = margin.

(174-1,100 mm SL) at 100×.

There is a close correlation between the number of sagittal rings and fish standard length (mm SL) = $58.608 + 4.709N$; $r = 0.95$; Fig. 3). Assuming that the rings are daily, the average growth rate for all fish is 4.71 mm/d: the average growth rate for adults (size range 700-1,100 mm SL) is 1.43 mm/d (mm SL) = $711.574 + 1.425N$; $r = 0.57$; Fig. 3). Using changes in mean length of a cohort (Fig. 4), the average growth rate for dolphin of size range 600-1,200 mm SL is 1.53 mm/d.

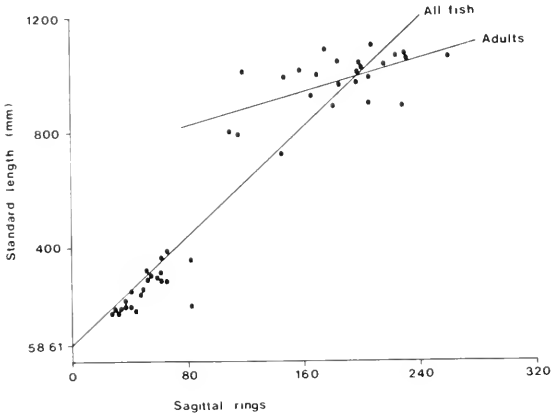

FIGURE 3.—The relationship of dolphin standard length to number of sagittal rings. The upper line (adults) represents the upper set of scatter points only.

The close correlation between number of sagittal rings and fish standard length suggests that ring formation is periodic. The similarity in growth rates obtained for the same population, using length-frequency distributions and the otolith rings, suggests that periodicity of the ring formation is daily.

Data published on growth rates of dolphin vary considerably (Table 1). These differences may reflect use of fish of different ages (the present study suggests that adults grow slower than juveniles), or may result from differences in aging techniques, in water temperatures, or in health and degree of provisioning of captive specimens.

We conclude by suggesting that daily rings occur in the otoliths of all sizes of dolphin fish (174-1,100 mm SL) and, therefore, that counts of otolith rings provide an alternative method of estimating age in this species. Moreover, since there is a linear correlation

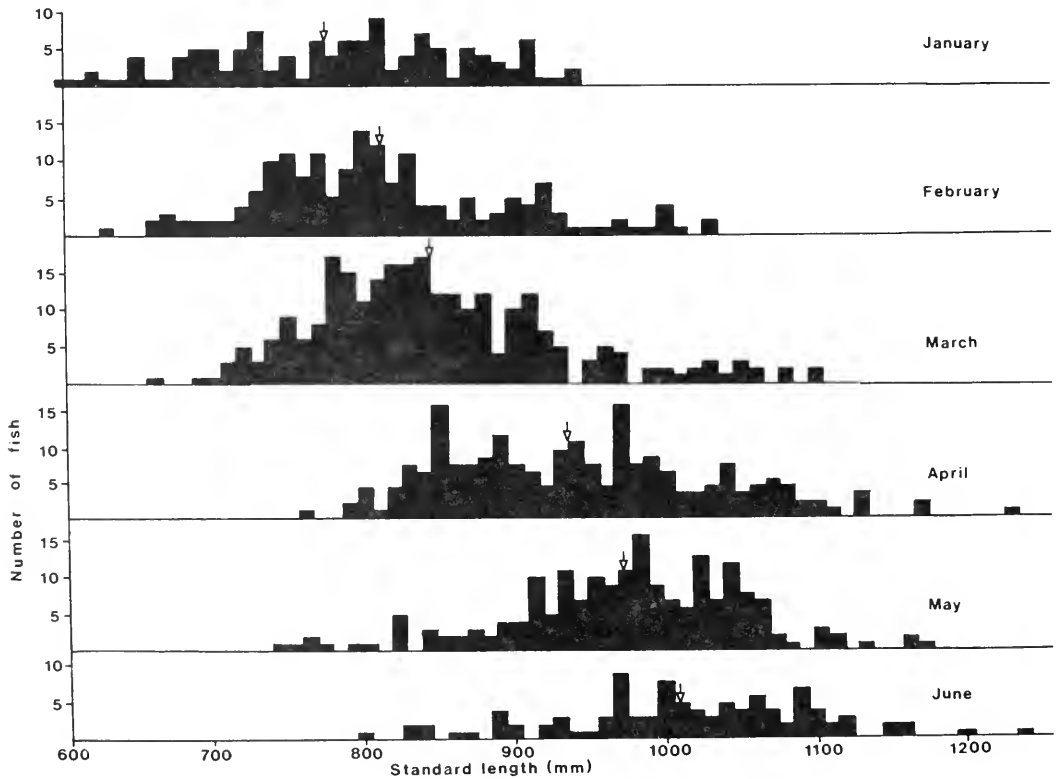

FIGURE 4.—Monthly length-frequency distributions of adult dolphin landed in Barbados between January and June.

TABLE 1.—Estimated growth rates of *Coryphaena hippurus*

Location	No. of fish	Aging method	1st year growth rate (mm SL/d)	Reference
Laboratory reared	26	days known	1.07	Hassler and Rainville 1975
North Carolina	593	scale annuli	1.64	Rose and Hassler 1968
Straits of Florida	121	scale annuli	1.82	Beardsley 1967
Waters adjacent to Taiwan	?	progression of size-frequency	2.96	Wang 1979
Laboratory reared	?	days known	3.03	Schekter[1]
Laboratory reared	94	days known	3.56	Hagood et al. 1981
Florida Marineland	2	days known	4.80	Herald 1961
Miami Seaquarium	1	days known	5.28	Beardsley 1971
Laboratory reared	30	days known	5.88	Hassler and Hogarth 1977

[1]Richard Schekter, Research Associate, Division of Biology and Living Resources, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, pers. commun. February 1982.

between sagittal radius and fish standard length ($r = 0.95$) and between sagittal radius and the number of rings ($r = 0.88$), it may be possible to estimate the length and age of a fish from the sagittal radius alone.

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A COMPARISON OF AERIAL, SHIPBOARD, AND LAND-BASED SURVEY METHODOLOGY FOR THE HARBOR PORPOISE, *PHOCOENA PHOCOENA*

A review of the status of harbor porpoise, *Phocoena phocoena*, in the U.S. waters of the western North Atlantic identified substantial information gaps in our knowledge about this species, and raised serious questions about the health of the North American population (Prescott and Fiorelli 1980). Significantly, no population estimate exists for *P. phocoena* in the western North Atlantic. Gaskin's (1977) estimate of 4,000 in the Bay of Fundy region is admittedly preliminary, and includes only a portion of the known range. Prescott and Fiorelli (1980) used winter stranding records from a single year to postulate a minimum mid-Atlantic regional population of 726 to 1,525 (between Long Island Sound and Cape Hatteras), but acknowledged that no information on stock or population discreteness exists for U.S. coastal waters.

Harbor porpoise are one of the smallest oceanic cetaceans, reaching a maximum size of about 2 m (Gaskin et al. 1974). They are also behaviorally innocuous, seldom leaping from the water, are usually found in small groups of 2-4, and generally avoid motor vessels (Amundin and Amundin 1974). These factors frustrate attempts to study the species, and it was necessary to establish and test survey methodology prior to undertaking a full-scale survey. An experiment was designed to estimate the fraction of visible harbor porpoises observed from aircraft, shipboard, and land-based survey platforms.

Between 4 and 12 August 1980, 30 to 34 persons from College of the Atlantic, the University of Guelph, and the New England Aquarium took part in this experiment in Head Harbor Passage, a narrow channel running NE-SW, bounded by Campobello Island (N.B.) on the east and a series of small islands and ledges on the west (Fig. 1). Head Harbor Passage was chosen for three reasons: 1) Harbor porpoise regularly inhabit the passage; 2) the passage is only 800 to 1,000 m wide, with many identifiable landmarks, which permits accurate orientation and navigation; and 3) the northwestern coast of Campobello Island provides easy access to land observation stations of nearly uniform height.

Methods

Four transect lines were established at 200 m intervals for a 5 km section of Head Harbor Passage (Fig. 1). Each transect line was surveyed by the survey vessel, the RV *Beluga*, a 12 m power vessel provided by the College of the Atlantic, and by the survey aircraft, an amphibious Cessna 185[1] provided by the U.S. Fish and Wildlife Service. Because of the difference in survey speed, the experiment required that the aircraft cover all four transects for each one the boat completed. For example, while the RV *Beluga* was enroute along Transect 3, the aircraft would survey Transects 1, 2, 3, and 4, in that order, and then break off until the boat had started surveying Transect 4. At that time the aircraft would cover all four transects again (Table 1).

Six land stations were set up on the coast of Campobello Island at about 500 m intervals. These stations were supplemented by additional stationary observation points at 500 m intervals on or near Spruce Island (across the passage). Two observers were posted at each station, to record location and movement of all harbor porpoise within sight. All land stations were oriented to true northwest, in order that overlapping sightings could be identified later. Sighting distances were estimated by the observers, based on a series of known distance calibration trials completed the first day using the vessel and a wooden life-size harbor porpoise model. During each transect, the 200 m interval made by the RV *Beluga* provided additional distance calibrations. In the final analysis of the data, only those observations from the 4 km survey area in view of the six Campobello Island land stations have been utilized, since the consistency of position and orientation of the boat stations across Head Harbor Passage were more variable and tide dependent.

Vessel transects were conducted with two observers and a recorder stationed on the bow (approximate height of eye about water = 2.5 m). Each observer was responsible for surveying 95° of horizon, from a point directly abeam of the survey vessel to a point 5° off the opposite bow. This pattern provided an

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

TABLE 1.—Summary of experiment on survey methodology for harbor porpoise, August 1980.

Date	Completed vessel transects	Completed aircraft transects	Operating no. of land stations
4 August	4	12	7
5 August	5	14	9
7 August	8	32	8
8 August	8	36	7
11 August	8	40	8
Total	33	134	

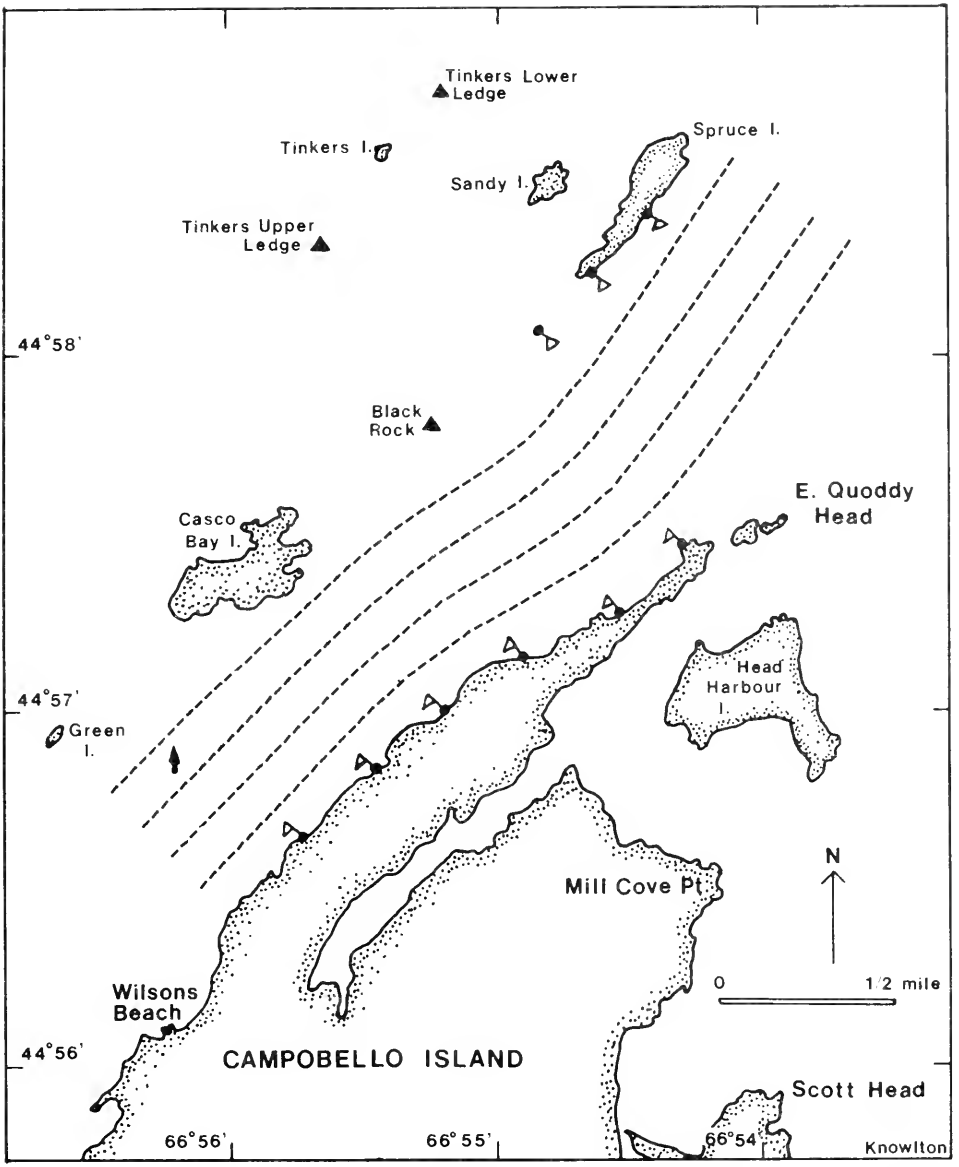

FIGURE 1.—Experimental survey transects through Head Harbor Passage are indicated by the dotted lines. Flags indicate the observation stations on each side of the passage.

overlap in viewing fields of 10°. Observers were changed after each transect to reduce fatigue. Navigation was accomplished by the use of radar and triangulation with landmarks. Vessel speed was 9 ± 2 kn, its variability caused by the strong tidal currents in Head Harbor Passage.

Aircraft transects were flown at an altitude of 229 m at 90-100 kn. Two experienced aerial observers and a recorder participated in each flight. Navigation and sighting locations were accomplished by triangulation on landmarks, including large orange markers at each land station. Visual survey techniques were similar to those employed in standard aerial surveys (Scott and Gilbert 1982). Because observers were looking specifically for harbor porpoise and because the survey area was limited by land masses, observers' search scans were restricted to within 630 m of the transect line. On two days of the experiment, observers noted the right angle distance of each sighting from the transect line by a handheld Suunto

inclinometer, categorizing sightings by 90° to 40° (< 200 m from the transect) or 40° to 20° (between 200 and 630 m from the transect).

Species identification problems were not a factor during the experiment since 1) all aerial and shipboard observers were experienced in *P. phocoena* observations; 2) land-based observers reported no other cetacean species in the vicinity during the entire week; 3) *P. phocoena*, although sometimes difficult to spot, once sighted has clear and unique field marks that make it easy to identify.

Results

Triangulation of land station sightings resulted in accurate plots of the harbor porpoise movements through the area for every set of four transects. Aircraft and shipboard sightings were then plotted using the same methods over the same time periods. The number of sightings made by aircraft and shipboard platforms were then compared independently against the number of sightings made by ground stations to test sightability from each platform. A "sighting" represents one or more porpoise. Analysis of observations by all platforms on all days show that average "sighting" group size was 1.94 to 2.39 porpoise per group (Table 2). Reported group size from moving platforms was generally lower than observed from the shore.

Comparison between aircraft and ground counts of the number of sightings of harbor porpoise groups indicated that the aircraft observers consistently sighted only 10 to 20% of the harbor porpoise groups available in the passage (Table 3). The shore-based observers, using aircraft sightings for comparison, were estimated to sight about 80% of the available harbor porpoises.

Comparison between shipboard and ground observations was more inconsistent because of smaller sample size (Table 4). Shipboard observers sighted about 50% of the harbor porpoises in the area and ground-based observers about 60%.

TABLE 2.—Mean number of harbor porpoise per group, as observed from the ground, boat, and aircraft, August 1980.

Platform	5 August	7 August	8 August	11 August	All days
Ground	3 81	1 72	2.19	2.03	2 39
Boat	2 46	1 75	1 33	1 44	1.98
Aircraft	4 00	2 00	1.66	1 47	1 94

Discussion

Analysis of the data shows that shipboard observers are more likely to see harbor porpoise than aircraft observers. Although vessels may not be as efficient as aircraft in terms of the amount of area covered, aircraft observers tend to miss porpoise because of their small size, the high survey speed, and limited effective survey width. Aircraft effectiveness appears to rise in high-density porpoise areas. However, the results suggest that shipboard surveys are the superior method in estimating harbor porpoise dis-

TABLE 3.—Numbers of groups of harbor porpoise observed by ground observers and from the air in Head Harbor Passage, New Brunswick, August 1980.

Observed from ground	Observed from aircraft								Total	
	5 August		7 August		8 August		11 August			
	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
Yes	2	19	0	7	4	23	8	37	14	86
No	0	—	0	—	1	—	2	—	3	—
	[1]P = 0.10		P = 0.00		P = 0.15		P = 0.18		P = 0 14	
	[2]G = 1 00		G = 1.00		G = 0.80		G = 0.80		G = 0.82	

[1]P = calculated probability of sighting from aircraft.
[2]G = calculated probability of sighting from ground

TABLE 4.—Numbers of groups of harbor porpoise observed by ground observers and from shipboard in Head Harbor Passage, New Brunswick, August 1980.

Observed from ground	Observed from shipboard								Total	
	5 August		7 August		8 August		11 August			
	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
Yes	7	3	1	0	1	5	2	2	11	10
No	2	—	1	—	0	—	4	—	7	—
	[1]S = 0 70		S = 1.00		S = 0.20		S = 0.50		S = 0.52	
	[2]G = 0.78		G = 0.50		G = 1.00		G = 0.33		G = 0.61	

[1]S = calculated probability of sighting from shipboard.
[2]G = calculated probability of sighting from ground.

tribution and abundance. In analysis of survey data, these results are a first approximation of correction factors that could be applied to aircraft and shipboard observations to provide more accurate estimates of harbor porpoise abundance, although caution should be exercised because of variable sighting conditions or animal behavior.

Further work on survey methodology should examine the effect of eye height, survey speed, and meteorological conditions upon survey results. Gaskin (1977) has discussed sea state and cloud coverage as factors in survey results, and Scott and Gilbert (1982) have examined several variables affecting aerial surveys, but the effects of glare on shipboard surveys and observer variability merit further attention. Also, the estimation by observers of distances from sighted porpoise to survey vessel needs clear definition for open-ocean surveys (Eberhardt 1978). Nevertheless, if survey methods similar to those described here are adhered to during the course of a survey, the results reported here are applicable, and useful in estimating porpoise abundance more accurately.

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TOLERANCE OF FIVE-DAY-OLD WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*, LARVAE TO THERMAL SHOCK[1]

The winter founder, *Pseudopleuronectes americanus* (Walbaum), is an important commercial and recreational fish generally found in waters with temperatures of 0° to 25° C and salinities of 4 to 30 ‰ (Pearcy 1962). The winter flounder ranges from northern Labrador to Georgia, but is most commonly found from the Strait of Belle Isle, northern shore of the Gulf of St. Lawrence, to Chesapeake Bay. A separate spawning population, or race, is found on Georges Bank (Bigelow and Schroeder 1953). Smith et al. (1975) indicated that there is a progression in spawning time from south to north initiated by increasing water temperature. Spawning generally occurs in estuaries and shoal waters in winter and early spring (Bigelow and Schroeder 1953) at temperatures of 3° to 10°C and salinities of 15 to 35‰ (Rogers 1976).

[1]Contribution No. 345, Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794.

Clusters of adhesive demersal eggs, 0.74 to 0.88 mm, are laid on sandy bottom (Bigelow and Schroeder 1953). Upon hatching, the planktonic larvae are 3 to 3.5 mm long. Metamorphosis occurs when the larvae reach lengths of 8 to 9 mm. The larvae remain free-swimming until prior to metamorphosis, when they become bottom oriented (Bigelow and Schroeder 1953).

In the planktonic state the larval stages are susceptible to the hazards of entrainment by steam electric generating stations, which usually use once-through cooling because it is the most economical method for condensing exhaust steam from turbines. However, cooling requires the passage of large quantities of water through the steam condensers. During its passage the temperature of the water is elevated by 5.5° to 23.3°C, while residence time may be as much as half an hour or longer, depending on the geometry and operational methods of the cooling system (Committee on Entrainment 1978).

The present study determines the temperature-time combinations which produce a thermal shock leading to significant mortalities in 5-d-old winter flounder larvae.

Materials and Methods

Winter flounder, collected from Narragansett Bay, were induced to spawn artifically by injecting freeze-dried carp pituitary hormone in saline into the back muscle below the dorsal fin (Smigielski 1975). Hormonal treatments were repeated daily until the mature ova were released. The fish were then stripped by hand. Fertilized eggs were secured from two females. An even layer of eggs was deposited on the bottom of a plastic bowl and then milt from several males was added. After fertilization, a dense suspension of diatomaceous earth (50 g/l) was mixed with the eggs to retard clumping (Smigielski and Arnold 1972). After the fertilized eggs remained in the slurry for 10 min, they were washed on a 550 μm mesh screen. The eggs were then transferred to a hatching jar where they remained until being transported from the Environmental Research Laboratory of the U.S Environmental Protection Agency, Narragansett, R.I., to Flax Pond Laboratory, Old Field, N.Y. To ensure maintenance of the spawning (acclimation) temperature during transport, the eggs were placed in plastic bags and maintained in an insulated container holding seawater. Aeration was continuous, using a battery-operated air pump.

At Flax Pond Laboratory, the eggs were placed in incubation baskets at the 5°C spawning temperature and acclimated to reduced salinity. The spawning salinity at Narragansett Bay was 31‰, while at Flax Pond the salinity was 27‰, a typical salinity for Long Island Sound in this region. The fertilized eggs remained in the incubation baskets until after hatching. Five-day-old larvae were then transported about 8 km to the Marine Sciences Research Center.

Larvae were pipetted in to 27 two-compartment hatching boxes, consisting of a polyvinyl chloride frame (7.5 × 6.0 × 16.0 cm) covered with monofilament bolting cloth, 243 μm mesh opening. In each compartment of a hatching box, 15 to 69 larvae were placed, providing 27 samples and their replicates. The hatching boxes were then placed in one of four partially filled 114 l aquaria, having a salinity of 27‰, and immersed in a constant temperature water bath system set at an acclimation temperature of 5°C. The constant temperature water bath system is a rectangular plywood box, measuring 2.4 m × 1.2 m × 0.45 m, filled with fresh water. Water temperature was controlled by thermostatically regulated refrigeration units and monitored with a continuous recording thermometer. The water was circulated by two submersible pumps.

For each test exposure, a hatching box with its larvae was placed in a polyethylene foam container holding 12 to 15 l of seawater for 4, 8, 16, 32, or 64 min. The excess temperature, ΔT, over the acclimation temperature of 5°C, in the initial trial was 22°C. For each subsequent trial, the ΔT was increased by an increment of 2°C until a final ΔT of 30°C was attained. Temperature in each container was monitored and maintained by the addition of hot or cold water of 27‰ salinity. Following each exposure period, the hatching boxes were returned to the acclimation aquaria (5°C) where they were held for 24 h after which survival/mortality counts were made. A larva was counted as living if it showed transparency or heart beat; otherwise, it was considered to be dead (Table 1). Of the 27 hatching boxes, two were chosen as controls. These controls received no thermal shock, but were handled in a manner similar to the experimental boxes.

Results

The larval survival/mortality counts (Table 1) for samples and their replicates were converted to square root transformations, $\sqrt{N + 0.5}$, and compared using the Chi-square test (Sokal and Rohlf 1969). Samples did not differ materially ($\chi^2 = 3.841$, $df = 1, P < 0.05$). It was therefore feasible to combine the samples to enlarge the sample size.

The data for each hatching box sample (Table 1) were converted to percentages of corrected mortality

(% surviving experimental/% surviving controls × 100). The values were then plotted as a function of mortality. Figure 1, a three-dimensional graph representing total temperature [acclimation + excess temperature (ΔT)] and excess temperature (ΔT), and exposure period (time) versus corrected mortality, shows relatively little or no mortality of 5-d-old winter flounder larvae exposed to a thermal shock of 22°C for exposures up to 32 min. Significant mortality occurred at Δ22 and at exposures between 32 and 64 min. These conclusions are substantiated by the Chi-square test (Table 2).

Mortality at lower excess temperatures, ΔT's of 22°, 24°, and 26°C, appears to be a function of time. This is shown in Figure 1 by sharp increases in mortality between Δ22-32 (ΔT-*t*) and Δ22-64. Sharper increases in mortality are found at Δ24 between exposures of 16 and 64 min, and Δ26 between 4 and 8 min. These increases in mortality are also represented in Table 2 by increases of Chi-square values of an order of magnitude. Total mortality was found in all samples when ΔT's exceeded 26°C and exposure times exceeded 8 min.

TABLE 1.—Survival/mortality counts for winter flounder larvae found in compartments of hatching box for ΔT-*t* levels (°C-min) from Δ22-4 to Δ30-64. Criteria for viability were transparency and heart beat.

	Left compartment		Right compartment	
ΔT-*t*	Alive	Dead	Alive	Dead
Control 1	45	0	—	—
Control 2	37	1	21	4
22-4	25	3	43	0
8	39	0	41	0
16	37	3	31	2
32	23	4	40	3
64	39	10	22	11
24-4	40	21	42	9
8	18	16	39	15
16	34	6	39	9
32	18	18	29	20
64	0	15	1	56
26-4	10	14	63	6
8	0	23	10	46
16	0	49	0	36
32	0	36	0	52
64	0	49	0	47
28-4	0	50	0	52
8	0	49	0	42
16	0	34	0	48
32	0	37	0	48
64	0	48	0	43
30-4	0	29	0	22
8	0	47	0	38
16	0	17	0	64
32	0	45	0	50
64	0	46	0	50

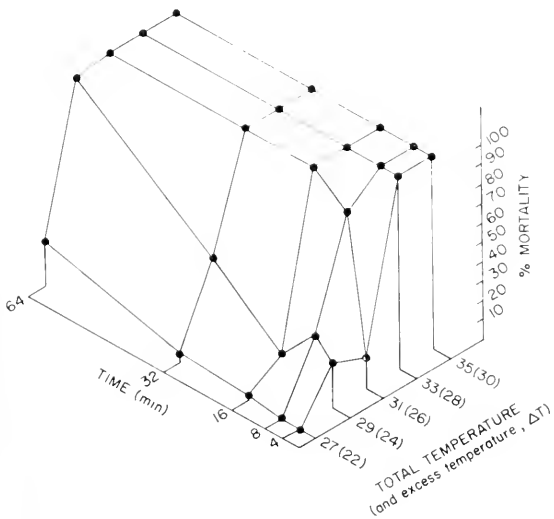

FIGURE 1.—Three-dimensional graph for 5-d-old winter flounder larvae representing total temperature [acclimation temperature + excess temperature (ΔT)] and excess temperature (ΔT), and exposure period (time) versus corrected mortality.

TABLE 2.—Chi-square probability values of counts of viable winter flounder larvae compared with dead larvae in treatments versus controls.

	Time (min)				
ΔT(°C)	4	8	16	32	64
22	0.016	3.805	0.411	1.948	17.370
24	20.175	30.277	8.158	44.118	156.411
26	13.067	130.533	173.893	176.876	184.924
28	190.919	179.902	170.790	173.893	179.902
30	138.100	173.839	169.770	183.922	184.924

*$P \leq 0.05$

Discussion

Flounder larvae appear to be resistant to acute thermal shock. This is substantiated by Barker et al. (1981), Valenti (1974), Carpenter (unpubl. data), and Hoss et al. (1974). Barker et al. (1981) acclimated smooth flounder, *Liopsetta putnami*, to 4°C and exposed them to ΔT's of 21.4°, 23.6°, 25.8°, 28.0°, and 30.2°C for periods of 5, 30, and 60 min. Significant differences in mortality were encountered at a ΔT of 23.6°C and at exposures between 30 and 60 min. Valenti (1974) simulated entrainment at the proposed Shoreham (New York) Nuclear Power Station, using winter flounder larvae similar in age to those used in the present study. Acclimation temperatures of 0°, 3°, 6°, 9°, and 12°C were used with ΔT's of 8°, 10°, 12°, and 14°C and exposures of 0, 5, and 13 min. Significant differences in mortality were detected only in those larvae acclimated to 3°C and exposed to a ΔT of 14°C for 13 min. Carpenter (unpubl. data), using older winter flounder larvae (18-22-d-old) in simulating entrainment at Millstone (Connecticut) Nuclear Generating Station, used an

[2]Permission was granted from the author to use the data.

acclimation temperature of 8°C, ΔT of 13°C, and exposures varying from 1 to 6 h. Depending on age, mortality ranged between 60 and 100%. The oldest larvae experienced total mortality. Hoss et al. (1974) compared the field-collected larvae of three species of flounder (*Paralichthys dentatus*, *P. lethostigma*, and *P. albigutta*) with the larvae of Atlantic menhaden, *Brevortia tyrannus*; spot, *Leiostomus xanthurus*; and pinfish, *Lagodon rhomboides*, and found the flounders most resistant. The flounders acclimated to 15°C withstood a thermal shock of 18°C for periods of 40 min with a survival rate of 30%.

The results of a number of studies (e.g., Schubel et al. 1978) indicate that resistance to thermal shock is age-dependent, with yolk-sac larvae being more tolerant than postyolk-sac larvae. Power plants should be designed and operated to sustain the most sensitive developmental stages of ichthyoplankton. Tests similar to the one described here should be made before site-specific tests are performed and before design and operating criteria are set. Sublethal effects, although not considered in this paper, should also be considered in the establishment of the excess temperature that will be utilized in a given season. Such sublethal effects reduce the chances of survival by entrained ichthyoplankton.

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MOVEMENTS OF ROCKFISH (*SEBASTES*) TAGGED IN NORTHERN PUGET SOUND, WASHINGTON

Recreational scuba divers and hook-and-line fishermen in northern Puget Sound (Fig. 1) have taken an annual catch of 150,000 bottomfish of all species; four species of Pacific rockfish (*Sebastes*) account for about 70% of the catch (Washington Department of Fisheries 1977-1980). These four species are copper rockfish, *S. caurinus*; quillback rockfish, *S. maliger*; black rockfish, *S. melanops*; and yellowtail rockfish,

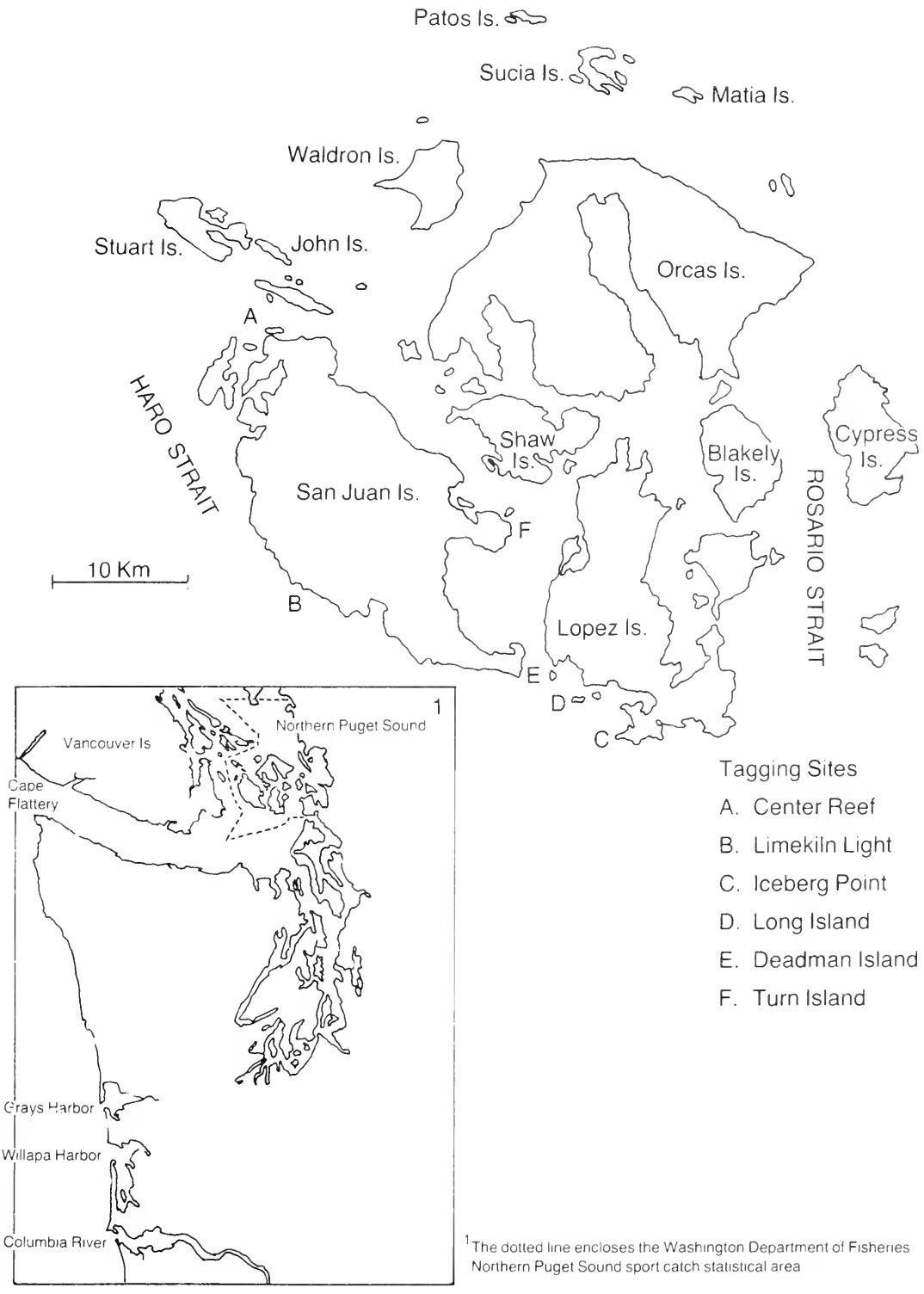

FIGURE 1.—San Juan Islands and rockfish tagging areas. Inset shows location of tagging area in relation to the Washington coast.

S. flavidus. There is also a commercial catch of these four species in northern Puget Sound by set net, longline, troll, and trawl gears, but the commercial catch of rockfish in northern Puget Sound is minor compared with the recreational catch (Petersen and DiDonato 1982).

All four species occur from California to Alaska (Hart 1973). In Washington, copper and quillback rockfish tend to be shallow-water, inlet inhabitants associated with nearshore reefs and rockpiles (Alverson et al. 1964; Patten 1973; Hart 1973). Black and yellowtail rockfish, although they are most abundant offshore in the ocean to depths of 400 m, are common in inlets such as Puget Sound where they are usually associated with shorelines or shallow rockpiles (Hart 1973). In northern Puget Sound, copper and quillback rockfish are usually caught on the bottom. Black and yellowtail rockfish tend to associate with the bottom, but are often caught well up in the water column, sometimes at the surface. Moulton (1977) observed the depth distribution of these four species in northern Puget Sound by scuba diving. All four species occurred in depths to 30 m, the deepest of Moulton's dives, although copper, black, and yellowtail rockfish were rarely seen below 22.5 m. The average depths of the individuals observed by Moulton during the months April-September were about 7.5 m for black and yellowtail rockfish, 12.5 m for copper rockfish, and 22.5 m for quillback rockfish. Moulton indicated that all four species may be distributed somewhat deeper in winter than in summer.

All Pacific rockfish are live-bearers (Phillips 1964). Those species most sought by commercial and sport fishermen are characterized by relatively long life and slow growth (Phillips 1964; Westrheim and Harling 1975; Beamish 1979; Boehlert 1980; Fraidenburg 1980). The maturation age (age by which 50% are mature) of yellowtail rockfish off California is 5 yr (Phillips 1964), whereas off Washington it is 8 and 10 yr for male and female yellowtail rockfish, respectively (Gunderson et al. 1980). Maturation age for both sexes of copper rockfish in Puget Sound is 4 yr (Patten 1973), 5 and 6 yr for black rockfish males and females, respectively, off central Oregon (McClure 1982), and 5 yr for both sexes of quillback rockfish in Puget Sound (Gowan 1983).

Relatively few studies on the movements of tagged Pacific rockfish were done. Carlson and Haight (1972) tagged yellowtail rockfish in southeast Alaska to study homing behavior. Coombs (1979) tagged blue rockfish, *S. mystinus*; yelloweye rockfish, *S. ruberrimus*; and black rockfish on a reef near Depoe Bay, Oreg., to determine if these species were resident or transient on the reef. Gowan (1983) tagged copper, yellowtail, black, and brown, *S. auriculatus*, rockfish in central Puget Sound (near Seattle) to learn about their movements and harvest rates. The Washington Department of Fisheries tagged black rockfish off the central Washington coast near Westport in 1981 and 1982 to study their movements (B. Culver[1]).

Our tagging study, supported by the University of Washington Sea Grant program, was initiated in response to public concern expressed to the Washington Department of Fisheries that certain heavily fished reefs in northern Puget Sound were becoming depleted of rockfish. Our intent was to determine the extent of the differences in migratory behavior among rockfish species most commonly caught. A species for which there is little migration of individuals once they reach a fishable size could be depleted more easily on popular fishing reefs by overfishing than a species in which the fishable-sized individuals are migratory; therefore, a sedentary species might need more restrictive fishing regulations than a migratory one.

Methods

Between July 1975 and June 1977, a total of 700 rockfish were tagged and released at six popular fishing sites in the San Juan Islands (Fig. 1). The tag used is the Floy[2] anchor tag with orange colored vinyl tubing (Floy FD67 "spaghetti" tag with #20 tubing). This tag is inserted below the dorsal fin, following the method of Dell (1968). In addition to releasing tagged fish, we also held a lot of rockfish in an aquarium for 2 yr to observe tag retention and behavior of tagged fish. This lot consisted of 10 fish that were caught, handled, and tagged similarly to the fish tagged and released.

Numbers tagged (by species) were 82 copper rockfish, 342 quillback rockfish, 123 black rockfish, and 153 yellowtail rockfish. The method of capture for tagging was by hook-and-line with conventional angling techniques. The fish were brought aboard singly and placed in a cradle for hook removal, measuring, and tagging. These activities were completed as quickly and gently as possible, and the fish were released within about 2 min from time of capture. Only fish that appeared lively, were relatively uninjured by the hook, and had no external indications of decompression stress were tagged. We restricted

[1]B. Culver, Washington Department of Fisheries, Montesano, WA 98563, pers. commun. October 1982.

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

the depths of capture for tagging to 30 m or less. Rockfish caught from depths >30 m usually showed signs of decompression stress, such as loss of equilibrium and eversion of the stomach from swim bladder expansion.

Rockfish suffering from decompression stress can be successfully treated by releasing gases from the swim bladder or behind the eye with a hypodermic needle (Gotshall 1964). Before doing any tagging, we deflated swim bladders of 10 quillback rockfish using Gotshall's technique and held them in an aquarium. All died within 3 mo. Although we are uncertain if all deaths were from decompression stress, we decided to tag fish only from relatively shallow depths, avoiding deflation of the swim bladder.

For tag recoveries, we relied upon voluntary returns from anglers, scuba divers, and commercial fishermen. To encourage the returns a $2.00 reward was paid for each return, posters advertising the program and the rewards were placed at appropriate locations, and informational reply letters were sent to those who returned the tags. If incomplete recapture information accompanied a returned tag, we would attempt to contact the individual who had caught the fish in order to complete the record.

During the tagging period we sacrificed a total of 389 rockfish specimens to determine sex and state of maturity from external gonadal inspection and age from surface reading of otoliths. It was our intent that the sacrificed fish be representative of the tagged lots. We fullfilled this intent by systematically allocating our field effort between tagging and collection of samples for sacrifice. At each tagging site we would alternate between days for tagging and days for sacrificing. On one day, all fish caught would be tagged; the next day at this site all would be sacrificed—this procedure was followed for the duration of the study.

Results and Discussion

Tag Retention

The lot held to observe tag retention consisted of 6 copper, 3 quillback, and 1 black rockfish. After 4 mo, no fish had died or lost tags, and the tag insertion points on the body looked well healed. During the following 20 mo, 1 copper and 3 quillback rockfish died, but this was not, in any way apparent, due to tagging. None of the dead fish showed any necrosis around the tag insertion point, and the tags on all dead fish were well imbedded, intact, and readable. When the retention experiment was terminated after 24 mo, the 6 rockfish that were still alive showed no ill effects from the tags, and the tags were well imbedded, intact, and readable.

Composition of Sacrificed Lots

Copper and quillback rockfish tended to be mature and relatively old individuals (Table 1). Sex ratios of these two species were not significantly different from 50:50. On the average, black rockfish were younger than the previous two species, but all the sacrificed fish were mature. There was a significant predominance of male black rockfish over females ($\chi^2 = 5.4$, 1 df, $P < 0.05$). Yellowtail rockfish tended to be younger than any of the previous species ($\bar{x} = 5.3$ yr) and all were immature. The sexes of the yellowtail rockfish were indistinguishable based on external inspection of gonads.

TABLE 1.—Age, length, sex, and maturity composition of samples of four species of rockfish collected by hook-and-line concurrently with tagging efforts in the San Juan Islands, Wash., during the period July 1975-June 1977. Also shown are means and standard deviations of lengths of samples of these species from the recreational scuba diver and boat angler catch in the San Juan Islands, 1979-80.

	Copper rockfish	Quillback rockfish	Black rockfish	Yellowtail rockfish
n	199	155	60	115
Total length (cm)				
$\bar{x}$	35.5	34.3	41.0	34.2
range	24-57	22-45	23-54	25-42
SD	9.2	5.5	6.0	3.8
Age, yr[1]				
$\bar{x}$	11.7	14.2	7.4	5.3
range	5-34	5-37	3-14	3-7
% male: % female	54:44	46:54	65:35	unknown
% mature	100.0	98.3	100.0	00.0
Total lengths from 1979-80 recreational catch (cm[2])				
n	233	354	62	56
$\bar{x}$	34.4	37.2	37.0	33.9
SD	6.8	5.6	6.7	3.0

[1]For copper and quillback rockfish ages, the means and upper limits may be too low. Surface readings of otoliths were used for aging which may underestimate ages of rockfish older than about 22 yr according to Beamish (1979).

[2]Source: LaRiviere, M. G., and G. G. Bargmann. 1982. The fisheries for bottomfish by scuba divers and recreational anglers in the San Juan Islands during 1979 and 1980. Prog. Rep. Wash., Dep. Fish., Mar. Fish. Sect. (Draft).

Composition of Tagged Lots

The mean lengths of the tagged lots of copper, quillback, and yellowtail rockfish (Table 2) conformed closely to those of the respective sacrificed lots. It is therefore reasonable to assume that virtually all the tagged copper and quillback rockfish were mature and that all the tagged yellowtail rockfish were immature. The tagged black rockfish lot averaged less in length than the sacrificed lot for no apparent reason other than random sampling effects (36.0 cm vs. 41.0 cm), and may therefore have included some immature individuals. McClure (1982) indicated that 5-yr-old male and 6-yr-old

TABLE 2.—Tag and recapture data for four species of rockfish tagged in the San Juan Islands, Wash., during the period July 1975-June 1977.

	Copper rockfish	Quillback rockfish	Black rockfish	Yellowtail rockfish
No. tagged and released	82	342	123	153
Total lengths at tagging (cm)				
$\bar{x}$	33.4	32.5	36.0	34.7
range	24-49	20-46	23-55	21-44
SD	4.5	5.7	6.4	4.5
Number recaptured at				
release site	11	11	5	2
near release site	0	1	0	0
open ocean	0	0	3	8
total	11	12	8	10
% of tagged fish recaptured	13.4	3.2	6.5	6.5
Number of days between date tagged and date recaptured				
$\bar{x}$	614	457	908	982
range	2-1,844	31-1,913	8-2,207	18-2,214
Mean lengths of recaptured fish at time of tagging (cm)	31.4	31.8	36.1	34.7

female black rockfish off central Oregon (the respective ages by which 50% are mature) averaged about 34 and 36 cm, respectively.

The means and standard deviations of the sacrificed lots were similar to those in the 1979-80 recreational catch, species by species (Table 1). Accordingly, we would conclude that the recreational catch of copper, quillback, and black rockfish consists mostly of mature individuals, whereas the yellowtail rockfish catch tends to be immature individuals.

Tag Recoveries

Numbers of recoveries by general area of recapture are listed in Table 2. Each of the 11 copper rockfish recoveries was recaptured at its release site, which we define as the area within 300 m of the exact point of release, according to our knowledge of the extent of each fishing reef and judgment of the accuracy of geographical specificity by fishermen who returned tags. All tagging sites are well-known fishing areas with ready geographic reference points. Length of time between date of tagging and date of recapture for copper rockfish varied from 2 to 1,844 d, averaging 614 d.

Ten of 11 quillback rockfish recoveries were at the release sites; the other recovery was caught about 2.8 km from the release point. The latter fish was initially caught over a shallow reef, but released into much deeper water as the boat drifted off the reef. A fish so released may find it difficult to navigate back to its "homesite" as was postulated similarly for yellowtail rockfish in Carlson and Haight's (1972) homesite study. Length of time between tagging and recapture of quillback rockfish ranged from 31 to 1,913 d, averaging 457 d.

Our findings indicate that mature copper and quillback rockfish roam very little. It is possible that they migrate seasonably from the homesites, but this seems unlikely since times of year of recoveries appeared to be random relative to times of year of tagging. Four copper rockfish tagged in the summer (August and September) were recaptured during winter months (January-March); four quillback rockfish tagged in the summer were recaptured during February and March.

Mature-sized copper rockfish were tagged near Bainbridge Island (central Puget Sound) by the National Marine Fisheries Service from 1975 to 1979. All recoveries, 75 of 554 tagged fish, indicated, as did ours, that there was no roaming from the tagging site (Gowan 1983).

An explanation for our higher recapture rate for copper rockfish, 13.4%, compared with that of quillback rockfish, 3.2% ($\chi^2 = 15.9$, 1 df, $P < 0.01$), is that copper rockfish tend to occupy shallower waters than quillback rockfish and are therefore more susceptible to scuba divers and anglers, who fish in depths of 20 m or less primarily for rockfish.

Of 8 recoveries from 123 black rockfish tagged, 5 were recaptured at their release sites and 3 were recaptured off the Washington coast between Willapa Harbor (360 km from the release site) and the Columbia River mouth (400 km). The time between release and recapture ranged from 8 to 829 d for black rockfish recaptured at their release sites and from 703 to 2,207 d for those recaptured offshore.

The Washington Department of Fisheries tagged a total of 6,913 adult black rockfish near Westport, Wash., in the summer of 1981 and spring of 1982. Of 77 recoveries to date, 53 were caught near release site, but the remainder migrated southward as far as

the Columbia River mouth, 40 km from the release site (B. Culver footnote 1). Coombs (1979) reported that a tagged black rockfish migrated 619 km, from the central Oregon coast northward to Puget Sound.

Eight out of 10 recoveries from 153 tagged yellowtail rockfish indicated that there is a pattern of inshore to offshore migration. Seven recoveries were off the Washington coast, from Cape Flattery (144 km from the release site) to Willapa Harbor, and one was recaptured from Queen Charlotte Sound, B.C. The latter recovery, however, could have been caught near Cape Flattery, since it was recovered by a U.S. trawler that fished both the Cape Flattery and Queen Charlotte grounds on the same trip. The time between release and recapture ranged from 58 to 2,214 d for the 8 yellowtail rockfish recaptured offshore. The other two recoveries of tagged yellowtail rockfish were at the tagging site, one 18 d and the other 1,194 d after tagging.

The movement of yellowtail rockfish from Puget Sound to the open coast may concur with time of maturation. According to our observations, the population of this species in northern Puget Sound apparently consists of immature individuals of 7 yr or younger in contrast to the other three species tagged for which the individuals recruited to the fisheries are apparently mostly mature. Moulton (1977) and Gowan (1983) found only immature yellowtail rockfish in Puget Sound. Commercial trawl catches of yellowtail rockfish off the Washington coast contain mostly older (>7 yr) individuals than those found in Puget Sound, and the coastal catch is mostly adults according to length-maturity relationships (Gunderson et al. 1980), length-at-age relationships (Fraidenburg 1980), and age composition of offshore catches (Fraidenburg 1981).

Tagged yellowtail rockfish in inside waters of southeast Alaska showed strong homing tendencies, returning to site of first capture when experimentally displaced as far as 22.5 km (Carlson and Haight 1972). The reported ages of fish tagged in this homesite study were 7-16 yr, and many or all could have been mature. Carlson and Haight labeled them as adults in the title of their paper.

Our evidence supports the contention that yellowtail rockfish in Puget Sound are immature and migratory, heading for the ocean before maturation. Traits of adopting, adhering to, or returning to homesites may become firmly developed only after maturation. The probable mechanism maintaining Puget Sound populations is drift or migration from the ocean of juveniles spawned offshore. W. Lenarz[3] believed there is a similar pattern for brown rockfish in San Francisco Bay; there they are virtually all juveniles, ages 5 or younger, leaving inshore waters before onset of maturity (age 6 or 7).

Acknowledgments

Financial support was by the Washington Sea Grant Program (Grant Contract 04-7-158-4421-RF-8). Several individuals with the Washington Department of Fisheries helped with tag processing, including J. Beam, K. Swenson, and G. Bargmann. R. Trumble and R. Buckley, with the Washington Department of Fisheries, reviewed the manuscript and their suggestions were helpful. One of the referees gave a very detailed review and thanks are given for the resulting improvements in the paper.

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449. Synopsis of biological data on the pigfish, *Orthopristis chrysoptera* (Pisces: Haemulidae). By George H. Darcy. March 1983, iv + 23 p., 22 figs., 15 tables.
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ERRATA

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Durbin, Edward G., and Ann G. Durbin, "Energy and nitrogen budgets for the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupidae), a filter-feeding planktivore," pages 177-199. Correct to read as follows:

Page 182, column 1, line 34:

stants by A, B, D, E, E, J, and M,

Page 182, Equation (35):

where $K = \dfrac{A}{B\,(\log_e 10)D}$

Page 182, Equation (37):

$$= \frac{h\,[Asc - B(10^{(D_S - E)} + J] - M}{Psch}$$

Page 182, Equation (43):

$$K_1 = A' - \frac{B'\,10^{(D_S - E)} - J'}{sc} - \frac{M'}{sch}$$

Page 183, column 1, line 41:

and $K_{1,K}$, respectively, we are able to eliminate s as

Page 183, Equation (50):

$R_N = 0.079574\ s\ n\ h$ (mg N/g dry weight per d)

Page 195, column 2, line 35:

most strongly regulate their foraging speed. s_{GOPT}

Brown, Robin F., and Bruce R. Mate, "Abundance, movements, and feeding habits of harbor seals, *Phoco vitulina*, at Netarts and Tillamook Bays, Oregon," pages 291-301.

Page 294, first column, second line, correct line to read:

(20.0%), by Everitt et al.[6]

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