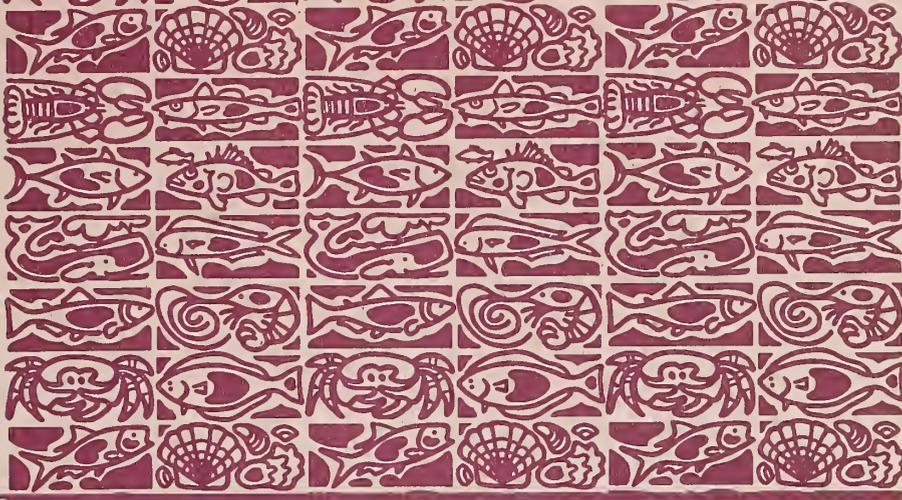


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Fishery Bulletin



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Abstract.—The fishery for blacklip abalone, *Haliotis rubra*, is one of the most valuable in New South Wales, Australia. An important part of the stock assessment process for this fishery is to quantify temporal changes in mean size and size structure of abalone in the landed catch. Variation in abalone growth over small spatial scales in this fishery and differences in harvest strategy among different divers result in large variations in sizes of abalone landed. Monte Carlo simulations were used to investigate the influence of these sources of variation on estimates of mean size and size structure. Different sampling scenarios were considered—from random sampling of all diver-days to a more realistic scheme where abalone were subsampled both within and among diver-days. For a given total number of abalone measured, error in estimated mean size and size structure declined asymptotically with increasing numbers of diver-days. By measuring at least 1,500 abalone from 100 diver-days, reliable estimates of size structure and mean size of abalone in the catch for the whole fishery were produced. This conclusion was robust with respect to the number of diver-days in the fishery. Estimated sampling intensity and probabilities of detecting differences based on simulated variances for the whole fishery are provided.

Optimal sampling for estimating the size structure and mean size of abalone caught in a New South Wales fishery

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Sample-size determination remains a crucial exercise in all aspects of ecology and fisheries biology, and the array of analytical tools available continues to grow (e.g. Gerrodette, 1987; Kimura, 1990; Peterman, 1990; Thompson, 1992). The great majority of these techniques are designed to optimize sampling for data derived from independent samples from a number of hierarchical sources of variation (e.g. Schweigert et al., 1985; Sen, 1986; Andrew and Mapstone, 1987; Kitada et al., 1992; Crone, 1995). Methods for determining sample sizes for describing size- or age-frequency distributions are less common (but see Smith and Sedransk, 1982; Schweigert and Sibert, 1983; Parkinson et al., 1988; Erzini, 1990).

Sample-size determination for the simultaneous estimation of different size classes is possible analytically only under limited circumstances in fisheries applications. If differences among individuals are the only source of variation to be contended with, then the proportion of individuals in each size class in a population may be estimated simultaneously by using the methods developed by Fitzpatrick and Scott (1987) and Thompson (1987), and the calculation of the variances of these estimates are simple.

In most situations facing fisheries biologists, however, there are

many sources of variation confounding simple random sampling and sample-size determination for estimating mean size at harvest and the underlying size structure. Typically, catches come from many boats, fishermen, and fishing grounds, and samplers are almost always faced with far more fish than they could possibly measure. Under these circumstances there are many sources of variation that may bias sampling. Not least of these is the likelihood of underlying spatial and temporal heterogeneity in the fished populations and changes in fishing behavior. Monte Carlo simulations provide a relatively straightforward, although computation-intensive, means of determining appropriate schemes in these instances. Sample-size determination for multistage survey designs relies on apportioning sampling effort to various levels on the basis of variance or cost (or both).

The fishery and the problem

The fishery for abalone *Haliotis rubra* in New South Wales (NSW) is managed by using a combination of size limits, closures, and output controls. In 1995, each of 37 divers had an annual quota of 9 metric tons (t). Since 1974, divers have

been required to provide details of daily catch weight and diving hours in each of 28 zones (Fig. 1). Divers may catch abalone in any of the zones, which range in length of coastline between 7 and 147 km. In 1994 there was a total of 3,129 diver-days in the fishery and an average of 104 diver-days per zone (Fig. 2A). Based on estimates of average weight per abalone, a catch of between 20 and 760 abalone was landed per diver-day (Fig. 2B). The mean size of abalone caught per diver-day ranged between 116 and 129 mm, although the majority were between 117 and 121 mm long (Fig. 2C). A minimum size limit of 115 mm has been applied to the fishery since 1987. Fishing pressure in this fishery is intense and the size structure of abalone in the landed catch in each zone may be

described by negative exponential distributions of varying instantaneous slope (see examples in Fig. 3).

Determining a sampling scheme to provide reliable estimates of the size structure and mean size of abalone in the landed catch is complicated by differences among diver-days. Worthington et al. (1995) and Worthington and Andrew (in press) have described large variations in demographic parameters, such as growth rate, maximum size, mortality, and fecundity, over a range of spatial scales. These studies report as much variation in the rates of growth and in the maximum sizes of abalone within sites separated by 2 km as there was among sites separated by hundreds of kilometers. Sizes of abalone in landed catches will therefore depend on how and where the diver worked as well as on the demographic attributes of the population being fished. For example, on any day, a diver may work areas where abalone are fast-growing and tend to be larger or areas where abalone are slow-growing and smaller (or both).

In this study we report the results of simulations in order to determine an appropriate allocation of sampling effort to estimate mean sizes and size structures of abalone in the landed catch in the New South Wales fishery. Sampling is considered for groups of zones and for the whole fishery. A simulation approach was adopted in preference to an analytical solution (e.g. Cochran, 1977) because we were interested in simultaneously optimizing sampling across a number of size classes—all of which were nonindependent. The simulation procedure allowed an estimation of the deviation of samples of different sizes from a known or true population. Parameters used in the simulations were based on preliminary sampling in 1993–94.

Materials and methods

Simulation study

A Monte Carlo simulation approach was used to estimate the relative efficiency of three strategies for sampling abalone:

- 1 Sample all abalone from randomly selected diver-days;
- 2 Sample a fixed number of abalone randomly from the catches of all diver-days; and

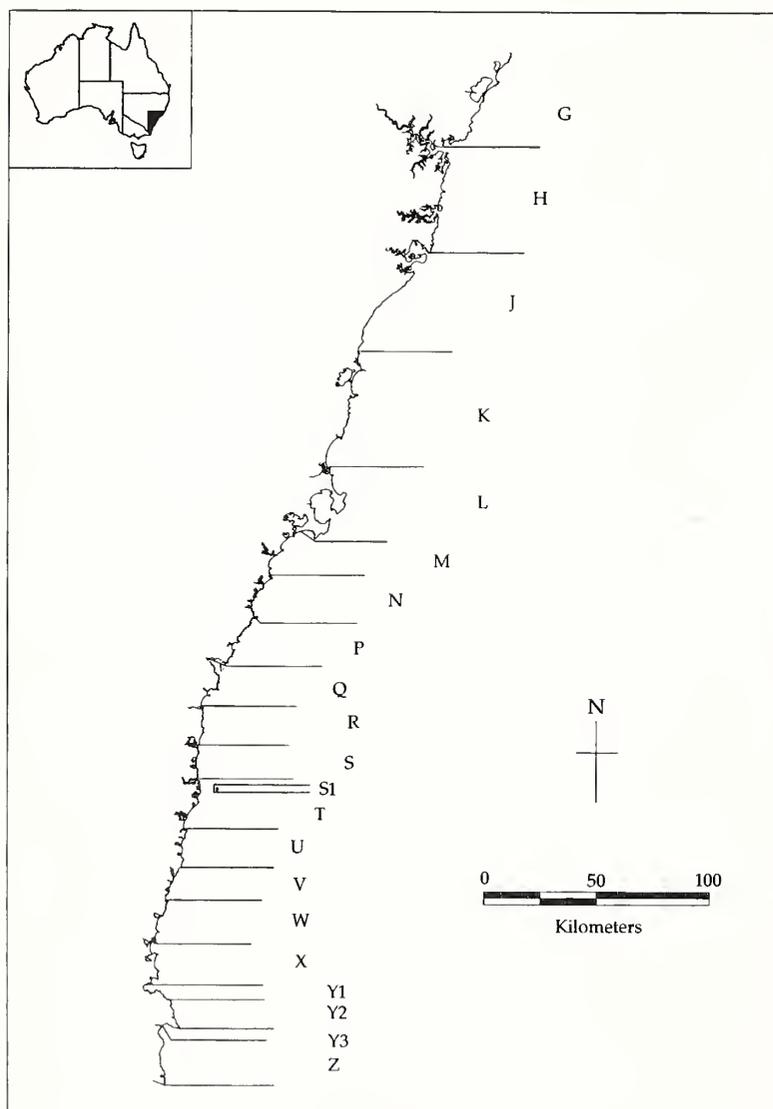


Figure 1

Map of the lower half of New South Wales showing zones in the abalone fishery. The zones are coded alphabetically from north to south.

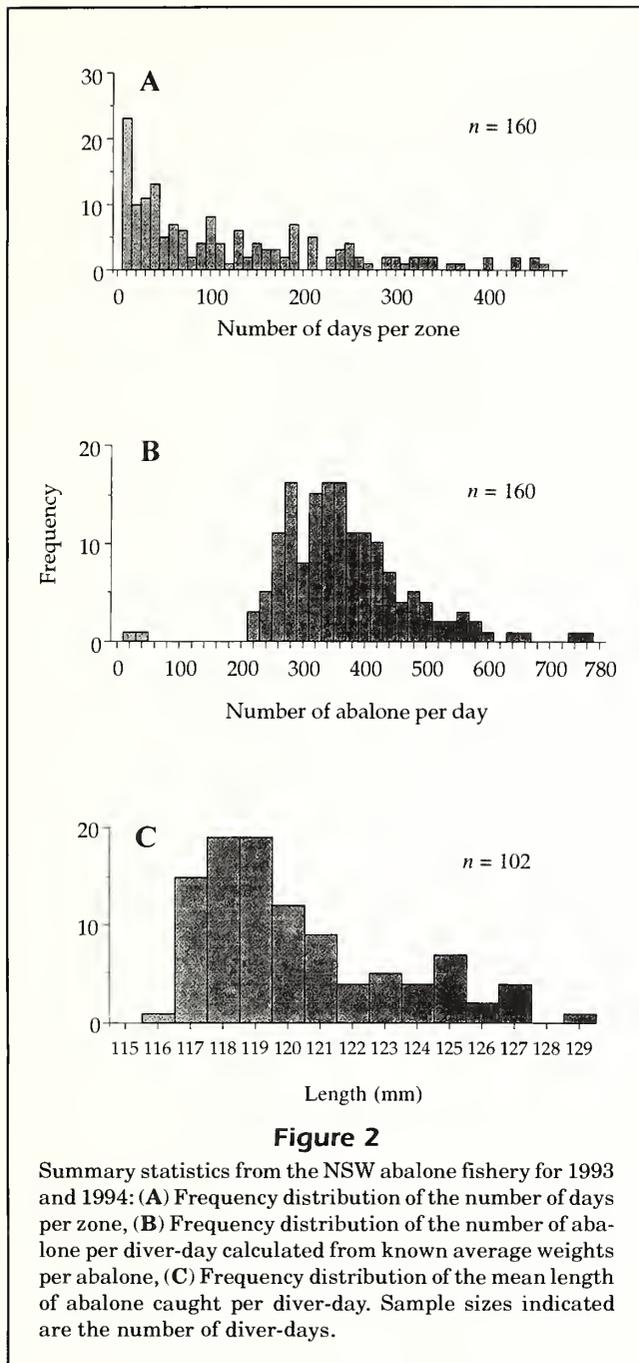


Figure 2

Summary statistics from the NSW abalone fishery for 1993 and 1994: (A) Frequency distribution of the number of days per zone, (B) Frequency distribution of the number of abalone per diver-day calculated from known average weights per abalone, (C) Frequency distribution of the mean length of abalone caught per diver-day. Sample sizes indicated are the number of diver-days.

3 Sample a fixed number of abalone randomly from diver-days selected randomly.

Of the three strategies, the third is the most logistically and financially reasonable. There is considerable unpredictability in where and when divers will work both because of weather conditions and a reluctance by divers to specify where they will work on a given day. These facts conspire to make it difficult to sample in a truly random manner. Nor is it practi-

cal to stratify appropriately across either divers or days because the population of diver-days to be sampled can be determined only in retrospect. For these reasons we have used a "diver-day" as the unit of stratification. Three sources of variation are confounded in "diver-day." Differences among divers, as a result of their fishing behavior (e.g. experience and ability) could not be separated from the variation inherent in where they fished, and therefore in the abalone caught. The third source of variation pooled into diver-day is the day itself (e.g. weather and sea conditions). Although these sources of variation were inseparable within the present study, the inferences drawn about a representative sampling scheme are not confounded. Strategy 1, although desirable, would limit the number of diver-days that could be sampled given a fixed total sampling effort. Strategy 2 represents the "ideal" sampling scheme and is used as a standard from which the remaining, more realistic, schemes are judged.

Parameters of the simulation

Parameters were determined for the simulations by using information collected during the 1993–94 fishing years. We assumed that there is as much variability in parameters among diver-days within a zone as among zones. Sampling schemes for zones or groups of zones and for the whole fishery were assessed by varying the total number of diver-days in the "fishery" per year. We therefore ran simulations by using up to 600 diver-days to determine sampling schemes for zones and groups of zones and simulated a 4,000-d fishery to determine a sampling scheme for the fishery as a whole.

Step 1 (determination of the number of abalone caught per diver-day) Based on previous sampling (Fig. 2B), the numbers of abalone caught in all diver-days were grouped into different catch groups ranging from the midpoint of 20 to 760 abalone, with the interval of the catch groups being 20. Thus, the total number of catch groups is 38 (i.e. $(760-20)/20 + 1 = 38$). The frequency of the number of abalone caught per diver-day was then estimated. Based on these frequencies, the total catch per diver-day was determined by multinomial sampling described as follows. Let P_J = probability of the number of abalone harvested in a diver-day in catch group J , where $J = 1, 2, \dots, 38$. The catch of diver-day i was determined by generating a random number R between 0 and 1 based on the uniform distribution and by assigning this number to one of the catch groups. The catch was assigned to catch group J if the random number followed

$$\sum_{k=1}^{J-1} P_k \leq R < \sum_{k=1}^J P_k.$$

After determining the catch group (i.e. J) for abalone harvested in diver-day i , the number of abalone harvested in diver-day i was determined as

$$C_i = (J - 0.5)20 + 20U,$$

where U is a random number between 0 and 1 generated from a uniform distribution. Because J in this equation has been determined from the previous

equation, we have omitted the subscript j from C_i for the sake of simplicity. This procedure was repeated for all diver-days in each simulation to determine the number of abalone harvested in each diver-day.

Step 2 (determination of the mean length of abalone caught per diver-day) The mean length of the catch for each diver-day was determined from the estimates derived from sampling 102 diver-days in 1993–94 (Fig. 2C). Lengths of abalone were measured to the nearest mm from catches from a range of zones and are assumed to be measured without error. The estimates of mean size ranged from 116 to 129 mm. Let P_I = probability of the mean length in length interval I ($I = 1, 2, \dots, 14$). The mean length for diver-day i was determined by generating a random number R between 0 and 1 based on a uniform distribution and by assigning this number to one of the length intervals. The length was assigned to length interval I if the random number followed

$$\sum_{k=1}^{I-1} P_k \leq R < \sum_{k=1}^I P_k.$$

After determining the length interval (I) for the mean length of abalone harvested in diver-day i , the mean length of diver-day i was determined as

$$L_i = I + 115(\text{mm}),$$

where 115 mm is the size limit. This procedure was repeated for all diver-days in each simulation to determine the mean length of abalone caught per diver-day.

Step 3 (determination of length composition of abalone caught per diver-day) The size distributions of abalone caught in a diver-day may be described by exponential distributions with varying slope, truncated at the lower limit by the legal size limit and at the upper limit by the value T , which was determined by random draws from the range of extreme values observed in preliminary sampling. The density function for such an exponential distribution can be written as

$$P(x) = Ae^{-\frac{(x-a)}{\sigma}},$$

where $a \leq x \leq T$, and A and σ are to be estimated. For an exponential distribution

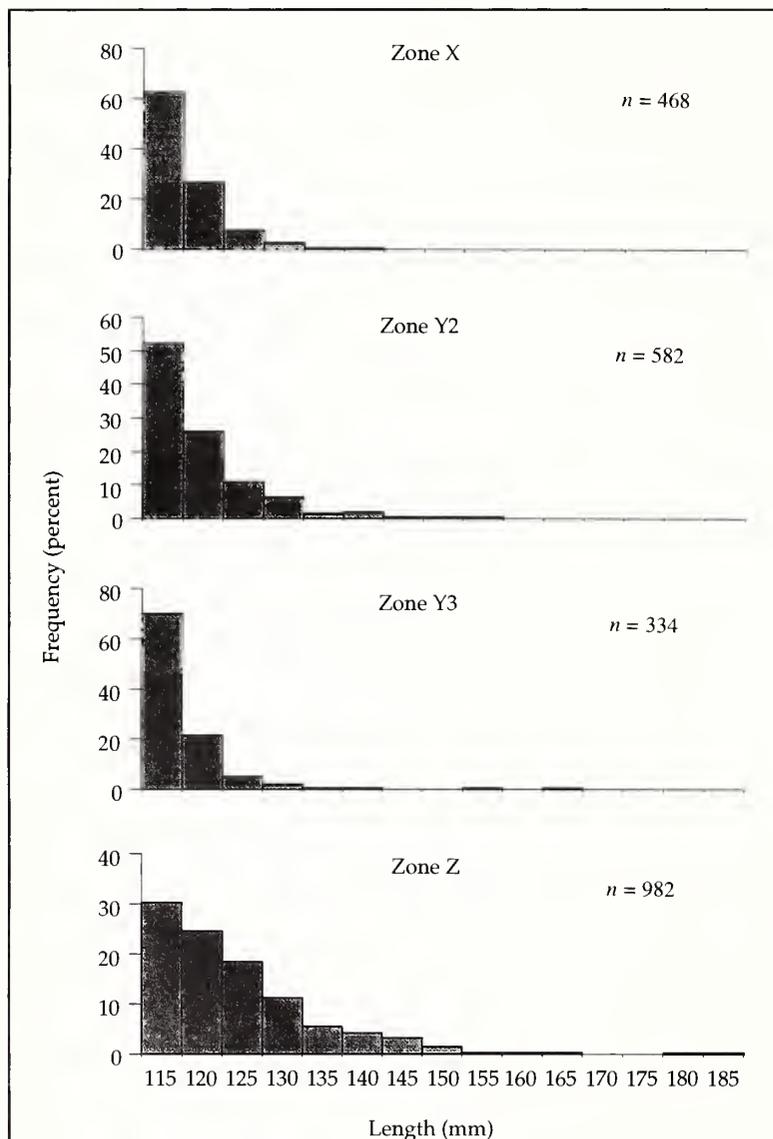


Figure 3

Examples of length-frequency distributions of abalone from four zones in the NSW abalone fishery. Data were pooled among diver-days from 1994.

with the above density function, $E(x) = a + \sigma$ and A is a constant defined by a , σ , and T . For a discrete variable X with the interval width d , constant A can be approximately estimated from

$$A \sum_{i=1}^N e^{-\frac{(x_i-a)}{\sigma}} = 1,$$

where
$$N = \frac{T-a}{d} + 1.$$

Solving this equation, we have

$$A = \frac{1}{\sum_{i=1}^N e^{-\frac{(x_i-a)}{\sigma}}}.$$

The lower bound (parameter a) is the size limit of 115 mm and is the same for all diver-days. Parameter T ranges from 117 to 150 mm among diver-days. For a diver-day i , parameter T_i was determined by randomly drawing an integer between 117 and 150 mm on the basis of the uniform distribution. For diver-day i , the mean size s_i was randomly selected from the frequency distribution of mean size estimated from data gathered in 1993–94 (Fig. 2C). The error σ for diver-day i is estimated as $\sigma_i = s_i - a$. Thus, the probability of abalone in length interval j being caught on diver-day i , $P_{i,j}^*$, was calculated. The number of abalone in length interval j caught in diver-day i , $C_{i,j}$, was then calculated as

$$C_{i,j} = C_i P_{i,j}^*.$$

Evaluation of the simulation

The size-frequency distribution and mean size of abalone at harvest calculated from the total catch of all diver-days were used as the “true” population of landed catch. Different sample sizes were used for each sampling scenario and compared to this known population. For each sampling scenario, 100 simulation runs were conducted. An error index, after measuring the difference between length-frequency distributions calculated from the catch of all diver-days in a year and from the sampled catch, was calculated as

$$\text{Error index} = \frac{\sum_{h=1}^{100} \sqrt{\sum_{k=1}^N (T_k - O_{h,k})^2}}{100},$$

where T_k is the frequency of abalone in length interval k calculated from the total catch of all diver-days.

This population was fixed among runs h calculated from the total catch of all diver-days, and $O_{h,k}$ is the frequency of abalone in length interval k in simulation run h calculated from the sampled catch. Thus the error index provides an index of the summed deviations from the true population across all size classes.

The difference between mean sizes of abalone estimated from the catch of all diver-days and from the sampled catch was evaluated by using an index defined as

$$\text{Average absolute difference in mean} = \frac{\sum_{h=1}^{100} |\hat{M}_h - M|}{100},$$

where \hat{M}_h is the estimated mean of the h^{th} simulation run for the sample catch and M is the mean of the total catch (i.e. the true mean size). The distribution of the calculated difference in means for 100 simulation runs was used to evaluate the variation in estimated average difference in mean size.

Results

We concentrated on results of simulations appropriate to estimating the size structure and mean size of abalone for the smaller spatial scale—that of zones or groups of zones. Results will be presented across a range of sample sizes for zones or groups of zones with up to 600 diver-days per year. We briefly discuss results for the whole fishery by sampling 100 diver-days in a fishery of 4,000 diver-days under scenario 3. Probabilities of detecting changes in mean size of abalone under this scheme are provided.

Under scenario 1, in which all abalone caught in a randomly selected diver-day are measured, there was a sharp decline in the error index of size composition as the number of diver-days sampled increased from 1 to 10 (Fig. 4). After 10 diver-days, the rate of decline in the error index slowed markedly. As expected, as the number of diver-days sampled approached the number of diver-days in the fishery, the error approached zero (Fig. 4). There was little variation in the error index among fisheries with 400 to 600 diver-days per year (Fig. 4). A similar pattern was observed in comparing differences in the mean size between the sampled catch and the total population for all sizes of the fishery (Fig. 4). For example, irrespective of the number of diver-days per year, when 10 diver-days were sampled, the average difference in mean size was 5 mm over 100 simulation runs.

Under scenario 2, diver-days were ignored as a source of variation and all abalone caught during the year had an equal probability of being sampled. This

is not a reasonable sampling scheme for most fisheries but provides a standard against which the others may be judged. Many more abalone must be measured under scenario 1 than scenario 2 to achieve comparable error indices (Figs. 4 and 5). For example, if under scenario 1 a total of 10 diver-days are sampled (approximately 3,400 abalone measured), then the error index is approximately 0.04. This level of error could be achieved by measuring only 400 abalone randomly distributed across all diver-days. As an example of variation in sampling under scenario 2, consider the differences in error index and difference in mean size when sampling 100 abalone and 1,000 abalone in a fishery of 400 diver-days (Fig. 5). Across the range considered (100–600 diver-days), the size of the fishery made little difference to estimates of error in the size composition or mean size of individuals (Fig. 5).

Under scenario 3, the most realistic of the sampling schemes, there were large differences in the error index, depending both on the number of abalone sampled in total and the number of diver-days sampled (Fig. 6). The magnitude of error was not, however, greatly influenced by the total number of diver-days per year (Fig. 6). The results suggest that, although the error in estimating the size-frequency composition depended on the total number of abalone sampled, the rate of decline in the error index was similar among all sample sizes (Fig. 6). In all cases, the rate of decline in the error index reached an asymptote at approximately 20 diver-days. For zones or groups of zones with up to 600 diver-days per year, there was an approximate two-fold reduction in the error index by increasing the total number of abalone measured from 100 to 1,000 abalone (Fig. 6). There was little further reduction in the error index by increasing replication from 1,000 to 1,500 abalone (Fig. 6).

The average error in estimated mean size of abalone declined rapidly with increasing number of diver-days between 1 and 15 diver-days (Fig. 7). Further increases in simulated sampling effort produced relatively modest gains without large increases in the number of diver-days sampled. For example, doubling the sampling effort from 15 to 30 diver-days caused only minor increases in precision (Fig. 7). In contrast to the patterns in errors in estimated size composition, increases in the total number of abalone measured from 100 to 1,500 produced little reduction in the average difference in mean size (Fig. 7).

The relative importance of diver-days as a source of variation is demonstrated by the difference between sampling a total of 100 abalone spread across five days and sampling 2 abalone on each of 50 diver-days (Fig. 7). In the latter case, the average difference in mean size between the true and estimated distributions and the sample was approximately 2 mm, in contrast to 6 mm when 100 abalone were sampled in 5 diver-days. The difference between observed and expected means was considerably smaller in comparing 200 abalone in each of 5 diver-days with the same total number of abalone spread over 50 diver-days irrespective of the size of the fishery (Fig. 7).

In considering the sampling scheme required for the whole fishery, scenario

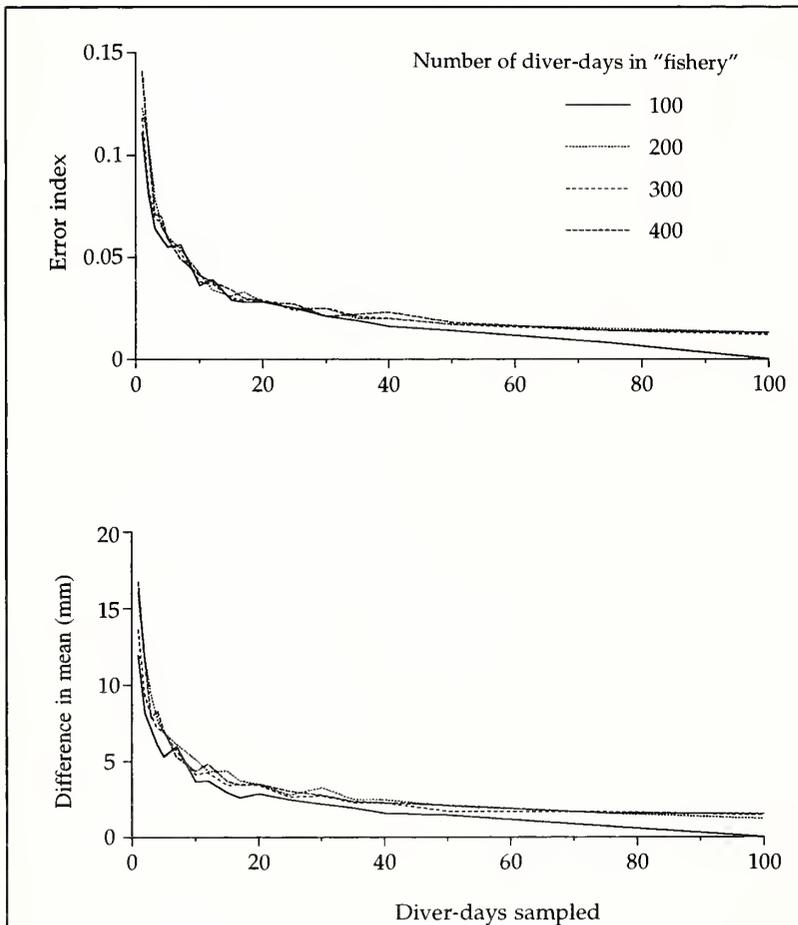


Figure 4

Errors in size composition and estimated mean size of abalone caught in different sizes of the "fishery" with sampling scenario 1. Calculation of the error index for the size composition and of the average difference in mean is described in the text.

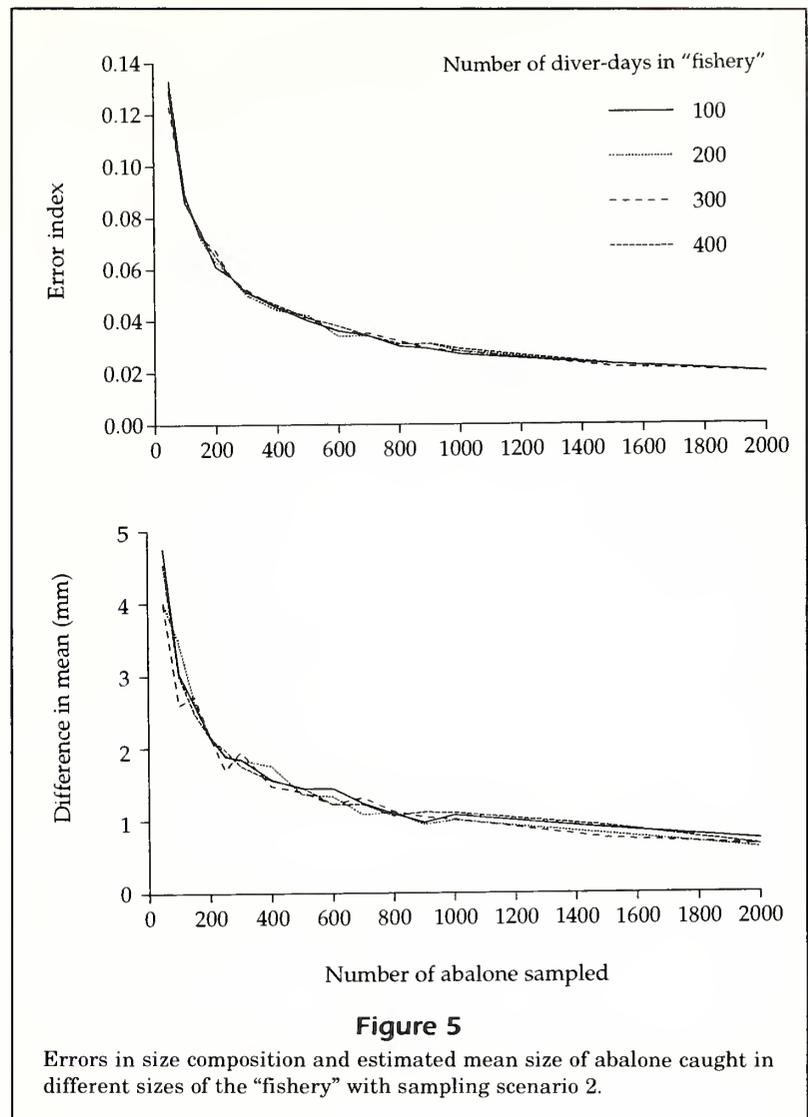
3 was scaled up to a larger number of diver-days per year. In 1994, there was a total of 3,129 diver-days in the fishery. We simulated the efficiency of measuring 50 abalone per day in 100 diver-days in a fishery of 4,000 diver-days. At this sampling intensity, the estimated error index for the size structure and average difference in estimated mean size of abalone were 0.018 and 1.5 mm respectively.

The cumulative frequency distribution (Fig. 8) presents the probability of correctly rejecting the hypothesis of no difference under two scenarios. In the first, the probability of detecting a "real" difference between an estimated mean size and a nominated size is given. This nominated size may be a management benchmark, significant deviation from which will cause a change in management, such as a quota reduction. If, for example, the difference between a management threshold and an estimated mean size is 3 mm, there is an 85% chance that the observed difference is "real" and not sampling error (Fig. 8, line b). If the observed difference is greater than 3 mm, then the probability of this being due to sampling error is less than 15%.

In the second scenario, this logic is extended to situations in which differences among years are considered. In this instance, both estimates of mean size are measured with error. If, for example, there is a 3-mm difference in mean size between two years, the probability of incorrectly interpreting this as a real difference among years, i.e. more than sampling error, is $0.85 \times 0.85 = 0.72$ (Fig. 8, line a).

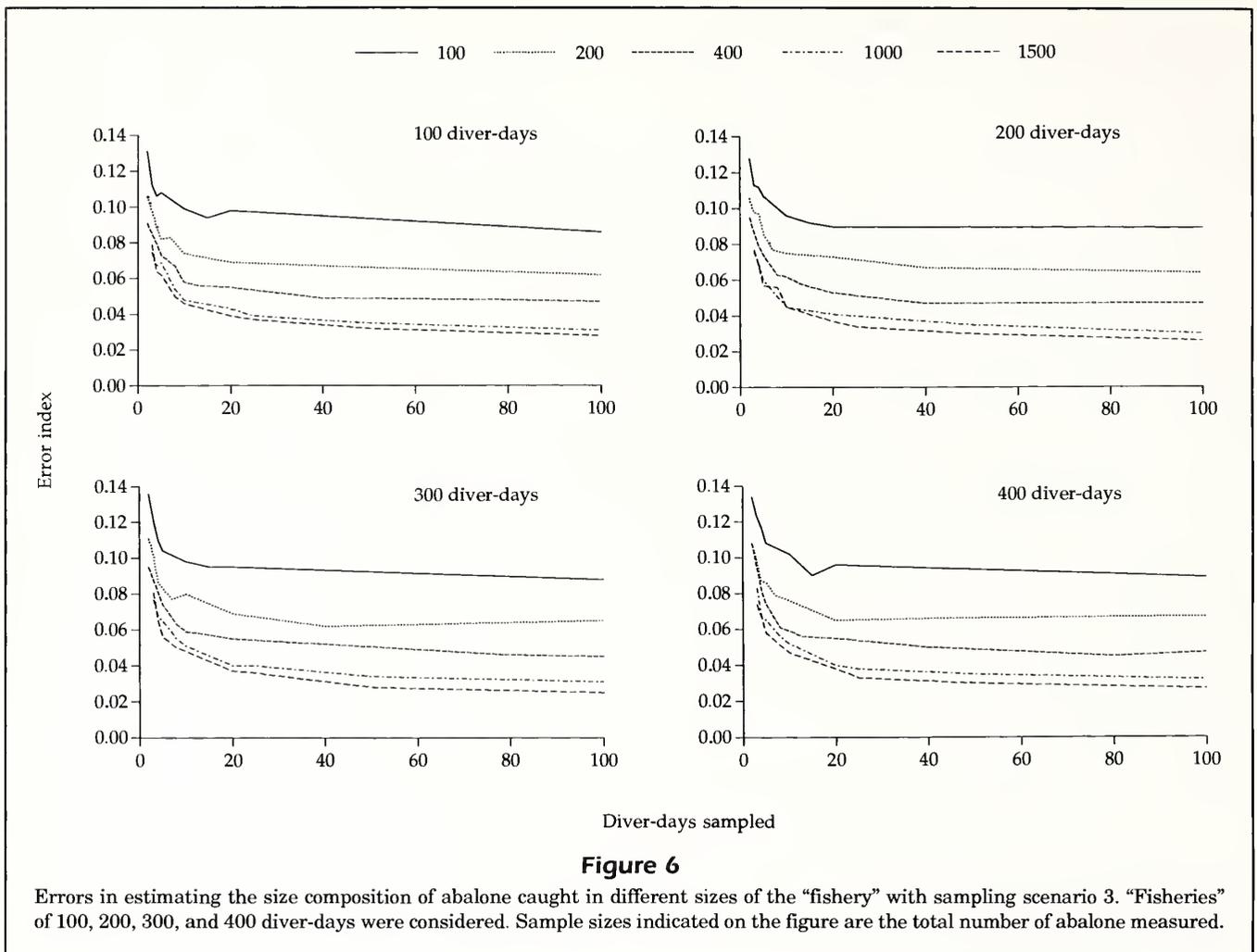
Discussion

Many stock assessment methods rely on reconstructions of the demography of exploited populations, using age-structured information (e.g. Fournier and Archibald, 1982; Deriso et al., 1985; Megrey, 1989; Kimura, 1990; Terceiro et al., 1992). Stock assessment methods available for species that cannot be aged are more limited, although recent development in size-based analogues of age-structured models have expanded the range of methods available (e.g. Sullivan et al., 1990). Size-based methods have tra-



ditionally relied on reducing size-frequency distributions into cohorts (e.g. Bhattacharya, 1967; Schnute and Fournier, 1980; Grant et al., 1987; Castro and Erzini, 1988). The reliability of these methods depends in large part on the representativeness of the sample distributions and the shape of the size-frequency distribution (e.g. Smith and Maguire, 1983; Chen, 1996).

The sampling scheme described in this study is essentially a stratified random design, with diver-day being the intermediate stratified factor (see also Sen, 1986; Kitada et al., 1992; Crone, 1995). An alternative approach used in sample-size determination for estimating age composition has been described by Schweigert and Sibert (1983). Their approach was to determine sample-size requirements for each size and age class separately and to develop an overall sampling scheme as a compromise solu-



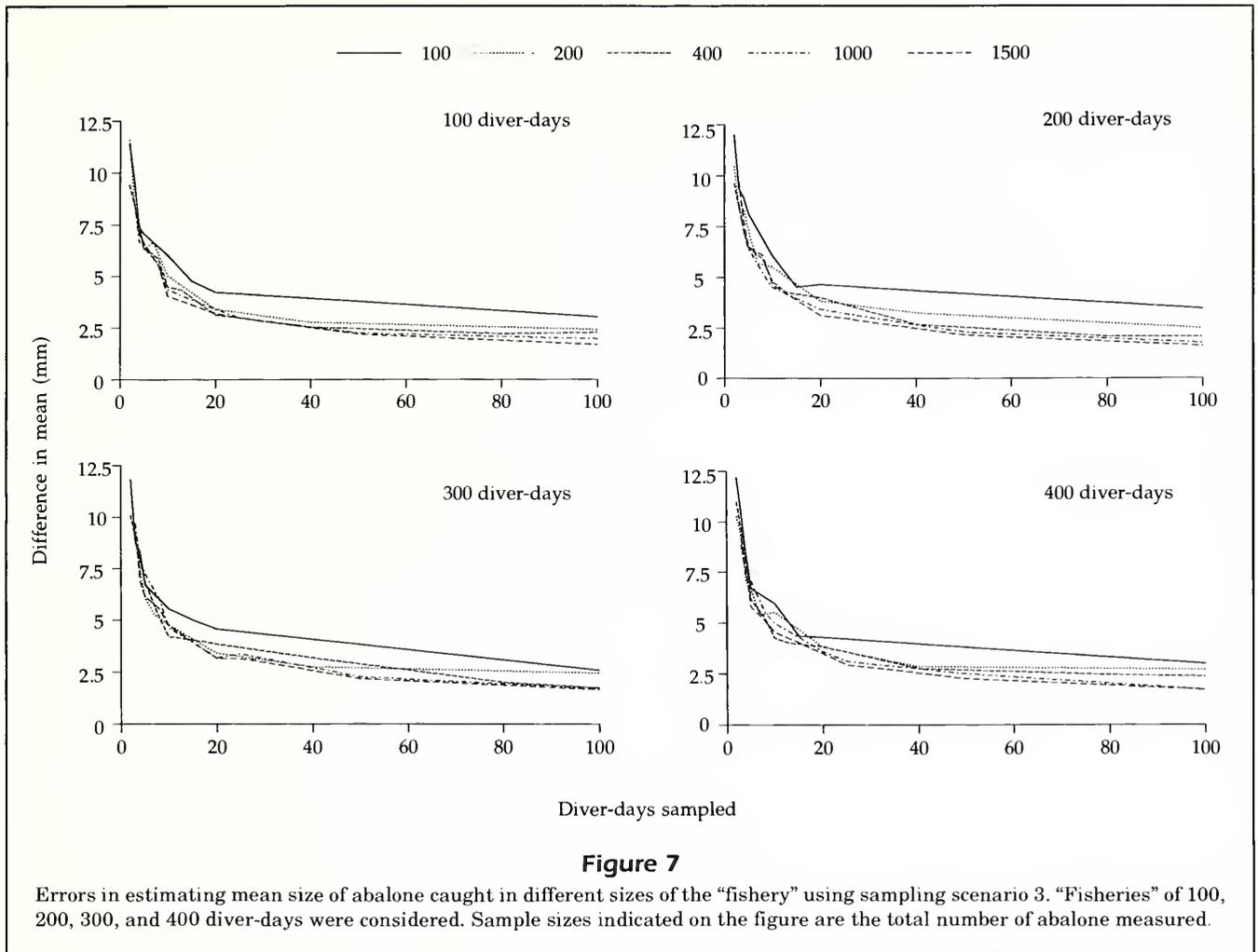
tion among those classes (see also Horppila and Peltonen, 1992). This approach was not appropriate for our situation because we were interested only in the size structure of landed abalone—*Haliotis rubra* can not be reliably aged by analysis of growth rings (McShane and Smith, 1992). The Monte Carlo approach that was adopted allowed us to simulate the simultaneous estimation of all size classes in the population.

The simulations described were based on the assumption that the size structures of abalone within a diver-day were distributed as a negative exponential function. If the fishery declined, the mean size of abalone would probably decline and the slope of the fitted exponential curve would increase. If this occurred, then the sampling scheme described would be conservative. If, however, the fishery improved and larger abalone were caught, then the size-frequency distribution might depart from the negative exponential distribution. If such a departure was significant, then the simulations would need to be reparameterized and each sampling scenario reex-

amined to determine an appropriate sample size for estimating the size structure of abalone in catches.

One of the objectives of this simulation study was to estimate the probability of detecting varying changes in mean size of abalone at harvest. Advice on trends in mean size at harvest may be given at two spatial scales: that of the whole fishery and that for individual zones or groups of adjacent zones. At present, the NSW abalone fishery is managed as one stock—size limit regulations and quota allocations are made on a statewide basis. Management measures, such as closures, are, however, possible at the smaller spatial scale if there are declines in indices of abundance (including mean size at harvest). Indeed, abalone stocks are increasingly being seen as comprising metapopulations of relatively discrete populations (see references in Shepherd et al., 1992), and thus such management measures are likely to be effective.

The simulations suggest that sampling more than 1,500 abalone spread across 100 diver-days would



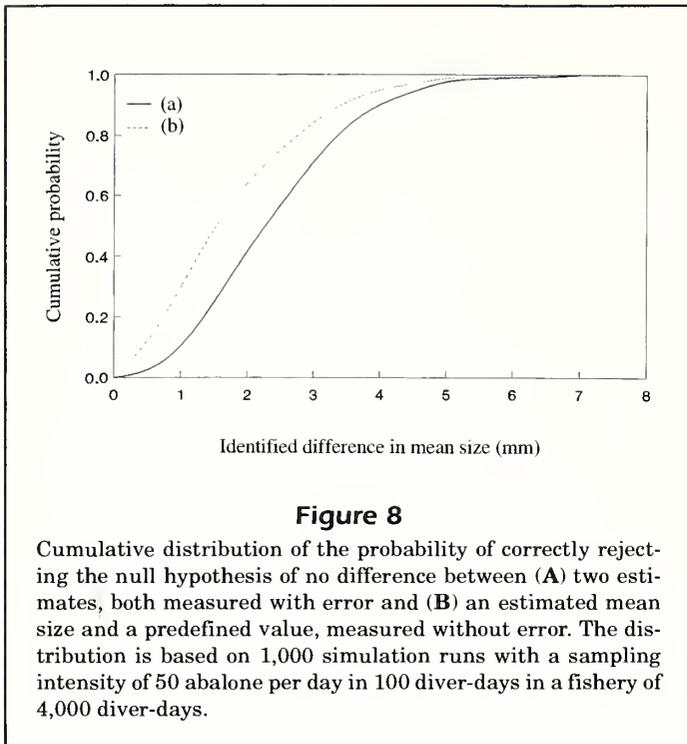
provide reliable estimates of the size structure of abalone in the landed catch and would detect relatively small changes in the mean size of abalone at harvest for the whole fishery. How small those changes are will be determined by how likely managers are prepared to accept the possibility of being wrong. At a smaller scale, 1,000 abalone from 20 diver-days would be needed to achieve a similar degree of discrimination. More intensive sampling did not greatly improve the reliability of these estimates over the range simulated. The simulations suggest that differences among diver-days were an important source of variation (see also Kitada et al., 1992; Crone, 1995).

Interpretation of trends in mean size of individuals among years requires some care. Divers may change their diving patterns among years, and fish populations may change with different demographic attributes. These patterns alone may produce changes in the composition of the landed catch independent of any underlying trend in the fishery. In essence, this problem is analogous to that in inter-

preting catch-rate information from heterogeneous fisheries, such as abalone. Several authors have claimed that apparent stability of catch rate is possible despite declining abundance of abalone as a result of changing diver behavior (e.g. Hilborn and Walters, 1987).

In these simulations we did not weight sampling effort in scenario 3 for the number of abalone caught in a diver-day. We, therefore, assume that there is no relation between the size and number of abalone caught. Using data from 1993–94, we found that there is no significant relation between the number of abalone caught in a diver-day and the size of those abalone. The impact of weighting is further diminished by the fact that the fraction sampled per day is relatively high, irrespective of the number caught (usually >25%). We assume that this sampling fraction provides a reliable estimate of mean size within diver-days.

The results of these simulations suggest that the large sample sizes possible in estimating mean size



of abalone at harvest may provide a false sense of reliability if higher level sources of variation are ignored. If variation above that found among abalone within a diver-day is not included, false conclusions may be drawn about the statistical significance of trends through time, both because of unrepresentative sampling and imprecise estimates of variability.

In the present study, the relatively large differences in sizes of abalone among diver-days meant that even relatively high sampling fractions (>10%) would have a relatively low probability of detecting changes in mean size less than 3 mm. This conclusion appeared to be robust over a realistic range in the number of diver-days sampled. Given the broad similarities between the sampling scheme described for this fishery and those in many commercial fisheries, concerns may be raised about the reliability of samples taken from processing plants in the absence of an understanding of the contributions of higher level sources of variation. The simulation framework described may be directly expanded to accommodate more complex situations.

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Abstract.—The distribution and abundance of two potentially competing flatfish species, smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, were examined along salinity and depth gradients in upper Great Bay Estuary, New Hampshire. Both species were abundant in the estuary but exhibited differential use of habitats along both gradients. Smooth flounder were most abundant at the mesohaline, riverine habitat, whereas winter flounder were most abundant at the polyhaline, open-bay habitat. Both species exhibited a generalized up-river movement as salinity increased with the seasons. Smooth flounder showed ontogenetic changes in distribution along the depth gradient, with smallest individuals occupying shallowest depths. Intertidal mudflats were an important nursery area for young-of-the-year smooth flounder. Winter flounder showed little separation by size along the depth gradient, and few were found in the intertidal mudflat habitat. The potential for competition between these two species is lessened by their partial segregation along the gradients examined.

Seasonal and ontogenetic changes in distribution and abundance of smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, along estuarine depth and salinity gradients

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Smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, are dominant members of fish communities in estuaries along the east coast of North America, co-occurring from Newfoundland, Canada, to Massachusetts Bay, USA. These morphologically similar species are sympatric over much of their geographic ranges. However, little is known of their spatial overlap within specific estuaries. Winter flounder use estuaries primarily as nursery grounds, whereas adults spend most of their lives in coastal waters (Bigelow and Schroeder, 1953; Percy, 1962; Scott and Scott, 1988). In contrast, smooth flounder complete their entire life cycle within estuaries.

Smooth flounder prefer softer bottom substrata than winter flounder (Bigelow and Schroeder, 1953), and Jackson (1922) noted they were most abundant in the low-salinity regions within Great Bay Estuary, New Hampshire. Little else is known of their intraestuarine habitat preferences. Several studies have examined movements and habitat use of juvenile winter flounder in estuaries south of Cape Cod

(e.g. Percy, 1962; Saucerman 1991). However, because many northern estuaries differ considerably from those south of Cape Cod, most obviously in their temperature regimes, it is possible that juvenile winter flounder use northern estuaries differently from ones to the south, as has been shown to be the case for adults (Hanson and Courtenay, 1996).

The purpose of this study was to provide a quantitative comparison of the occurrence of smooth and winter flounder in various habitats in upper Great Bay Estuary, New Hampshire. The habitats comprised gradients defined by depth or salinity. Comparative studies along habitat gradients can define which habitats are important to a species, especially in relation to different life history stages; such analyses can also be used to study the relative importance of physical and biotic factors in limiting species distributions (Connor and Bowers, 1987). Examination of the shape of species-abundance curves along a gradient can provide inferences into whether competition or physiological limitations are important in setting dis-

tributions (Terborgh, 1971) and can lead to the generation of testable hypotheses.

Methods

Study area

Great Bay Estuary (Fig. 1) is a complex embayment comprising the Piscataqua River, Little Bay, and Great Bay. It is a tidally dominated system and is at the confluence of seven major rivers and several small creeks, as well as the water from the Gulf of Maine (Short, 1992). Great Bay Estuary is a drowned river valley, with high tidal energy and deep channels with fringing mud flats. The main habitat types within the estuary are mudflat, eelgrass, salt marsh, channel bottom, and rocky intertidal. This study was conducted in the upper estuary, referred to as Great Bay, although preliminary sampling took place in the lower estuary also. Great Bay is a large, shallow embayment having an average depth of 2.7 m, with deeper channels extending to 17.7 m (Short, 1992) and a tidal range of about 2 m. The water surface of Great Bay covers 23 km² at mean high water and 11 km² at mean low water (Turgeon, 1976). Greater than 50% of the sediment surface of Great Bay is exposed mud or eelgrass flat at low tide. The Squamscott and

Lamprey Rivers are major sources of freshwater to Great Bay. River flow varies considerably on a seasonal basis but is generally highest during spring runoff. Vertical stratification of Great Bay is rare because of strong tide- and wind-induced currents, although partial stratification may occur during periods of high freshwater runoff, particularly at the upper tidal reaches of rivers (Short, 1992).

Smooth and winter flounder were sampled monthly, May 1989 through September 1991, at five sites in upper Great Bay Estuary (Fig. 1). Ice cover prevented sampling from December through March in all study years. A 4.8-m otter trawl of 38-mm stretch mesh, with a 25-mm stretch mesh codend and a 6-mm codend liner, was used for sampling. Preliminary studies indicated that the net retained flounder as small as 25-mm total length (TL). A sample consisted of all flounder collected in one 10-minute tow at approximately 2.5 knots. Four samples were taken at each site from April to November. Two samples were taken within two hours (\pm) of low slack tide, one tow with the tidal current and one tow against, and two samples were taken similarly around high slack tide. All flounder collected were measured to the nearest mm TL. Bottom temperature and salinity were measured after each tow with a Beckman Model 510 temperature, conductivity, and salinity meter.

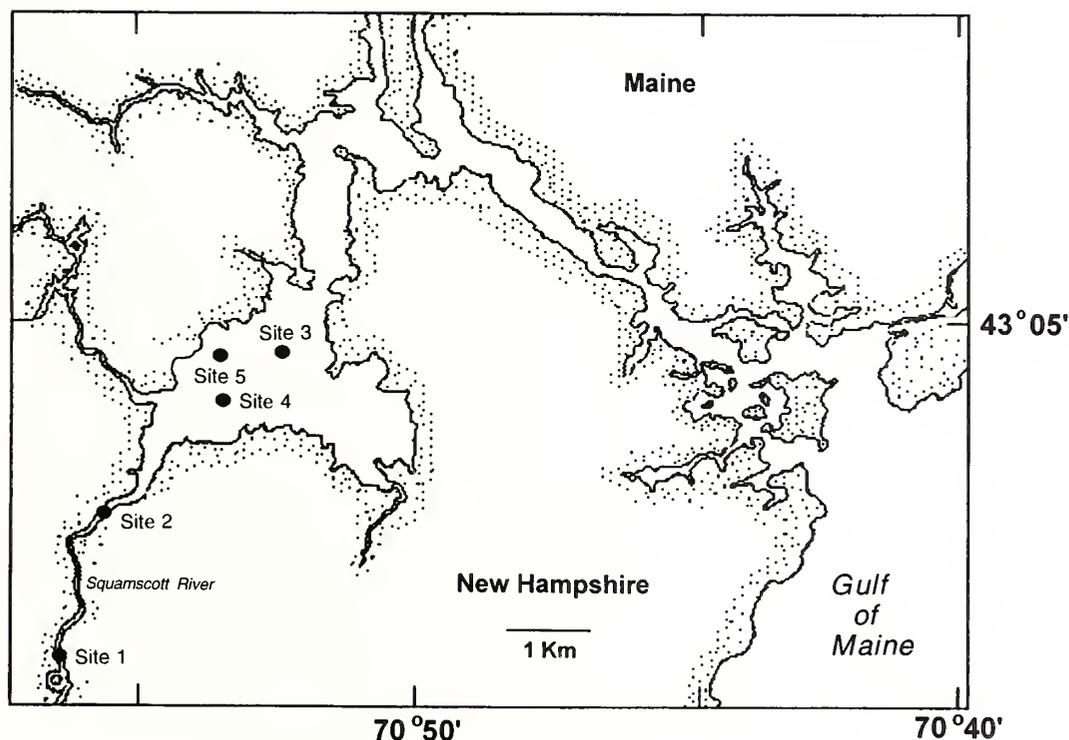


Figure 1

Study area. Survey sites were all located in Great Bay Estuary, New Hampshire, as indicated.

Site 1 (low salinity, Squamscott River at Route 51), site 2 (medium salinity, Squamscott River at Route 108), and site 3 (high salinity, middle of Great Bay) were located along a salinity gradient formed by Great Bay Estuary and one of its major tributaries (Fig. 1). The mean salinity value at each site varied considerably on a seasonal basis, but a salinity gradient always persisted along these sites. Table 1 summarizes some physical characteristics of these locations. Site 1 was located in the Squamscott River about 4 km above the mouth. Although the river is still tidal in this area, the water is often fresh or extremely low in salinity. Site 2 is also located in the Squamscott River but only 0.5 km above the mouth. Salinity at this site is highly variable but intermediate between the other two sites. Site 3, the site with greatest salinity, was located in the middle of Great Bay proper. The depth and bottom substratum were similar at all three stations (Table 1).

Sites 3 and 4 (high salinity, shallow Great Bay) and site 5 (high salinity, Great Bay intertidal flats) were located along a depth gradient in a contiguous area in the middle of Great Bay. Site 3 was the deepest site sampled along the depth gradient. Site 4 represented the intermediate depth, and site 5 was located on intertidal mudflats and therefore sampled only on high tides. All three sites had similar bottom substratum, silty mud, and owing to their proximity, experienced nearly identical salinities (Table 1).

Monthly length frequencies at each site were pooled over all study years. The Kolmogorov-Smirnov test was used to test for differences in length-frequency distributions among sites. One-way analysis of variance (ANOVA) was used to test for significant differences in catches among the three sites that made up each of the two gradients. To reduce the number of ANOVA's performed and to increase the power of the tests by increasing sample sizes, the monthly data were grouped into three seasons: spring, summer, and autumn. Months of April, May,

and June were considered spring; July and August were considered summer; and September, October, and November were considered autumn. Because many months contained zero catches and, in some cases, the variances were proportionate to the means, the data were transformed by using a square-root transformation ($\sqrt{X+1}$). The Kolmogorov-Smirnov test with the Lilliefors modification and probability plots of residuals indicated no significant deviations from normality, and Levene's test indicated homogeneity of variances after the transformation. Where a significant difference in catches was detected among sites, the sites were compared by using Tukey's HSD test (Zar, 1984).

Results

A total of 8,333 smooth flounder and 2,105 winter flounder were captured during the study period. Both juvenile and adult smooth flounder were abundant in the study area in contrast to winter flounder, which were abundant only as juveniles. However, length frequencies of the two flounders were similar because adult smooth flounder are about the same size as juvenile winter flounder. Smooth flounder were captured from many different year classes, whereas winter flounder were primarily age 0⁺, 1⁺, and 2⁺, based on length frequencies.

Salinity followed a typical boreal estuarine seasonal pattern (Figs. 2 and 3). The general trend at all stations was for salinity to be lowest in April, to increase over the late spring and summer months reaching the highest levels during August and September, and to decline during autumn. These seasonal patterns were especially pronounced at site 1 and site 2. Salinities in spring of 1991 were higher at all sites than in the other two years, a result of an uncharacteristically dry spring and limited spring runoff. Another salinity anomaly occurring in 1991

Table 1

Physical characteristics of the sampling sites. Sites 1, 2, and 3 make up the salinity gradient, whereas sites 4, 5, and 3 form the depth gradient.

Site number and habitat type	Salinity (ppt)		Temperature (°C)		Depth (m)		Bottom type
	Mean	Range	Mean	Range	Mean	Range	
1 (low salinity)	4.2	0.0–22.4	19.4	4.7–25.7	2.7	1.9–4.0	silty mud
2 (medium salinity)	10.9	0.4–24.0	17.1	0.0–27.8	3.7	1.8–4.3	silty mud
3 (high salinity, greatest depth)	20.3	6.5–29.9	15.4	1.8–23.9	6.2	4.9–7.9	silty mud
4 (intermediate depth)	20.9	6.5–29.5	16.4	2.3–24.9	2.1	1.5–4.4	silty mud
5 (intertidal flats)	19.8	11.0–28.5	15.2	0.2–24.2	1.5	1.1–2.2	silty mud

was a sudden decrease in salinity in September caused by dilution from the heavy rains with Hurricane Bob in late August of that year. Sites comprising the depth gradient had similar patterns of salinity in all years of the study.

Salinity gradient

Both species were unevenly distributed along the salinity gradient, and their distributions changed seasonally (Table 2). The timing of peak abundance

of smooth flounder at site 1 varied from year to year. In 1989 and 1990 smooth flounder were abundant in mid to late summer (Fig. 4). The influx of smooth flounder was associated with seasonal changes in the salinity regime from fresh to oligohaline (Fig. 2). In 1991, smooth flounder were present at site 1 in all months sampled. In this year, salinity was higher than that during the two previous years (Fig. 2). Length frequencies of smooth flounder at site 1 (Fig. 5) were significantly different ($P < 0.0001$ in all monthly K-S tests, May–October) from those at site 2 (Fig. 6), although the difference appears to be less in the autumn than in the spring. Larger fish (>100 mm) made up a higher proportion of the catch at site 1 in comparison with site 2, indicating differential migration among size classes. Winter flounder were rarely collected at site 1 (Fig. 7). They were found there only on a few occasions in September and October when salinity was at a seasonal high.

Smooth flounder were abundant at site 2 during all months, and their average abundance at this site exceeded that of all other sites. Their abundance was generally high in the spring, lower in late summer to early autumn, and high again in mid to late autumn (Fig. 4). This trend was opposite to that observed for site 1. Correlation analysis of catches of smooth flounder at sites 1 and 2 indicated a weak but significant negative relationship ($P = 0.032$, $r = -0.48$). When catches were large at site 1, they tended to be small at site 2. This finding suggests that the same population of smooth flounder was migrating between the stations, although the length frequencies show that a greater proportion of larger smooth flounder than smaller smooth flounder travel the 3 km between the sites.

Winter flounder were abundant at site 2 only during autumn (Fig. 7), although even during these periods of abundance, the catches of winter flounder were always lower than those for smooth flounder. The movement of winter flounder into site 2 from Great Bay proper was associated with relatively high salinities (Fig. 2) and with low abundances of smooth flounder (Fig. 4). The length frequencies of winter flounder collected from site 2 (Fig. 6) and site 3 (Fig. 8) were similar.

Smooth flounder occurred at site 3 in relative abundance only in April, May, and June (Fig. 4). Catches of smooth flounder decreased significantly after June in all years. Winter flounder were most abundant at this site than at the other two sites comprising the salinity

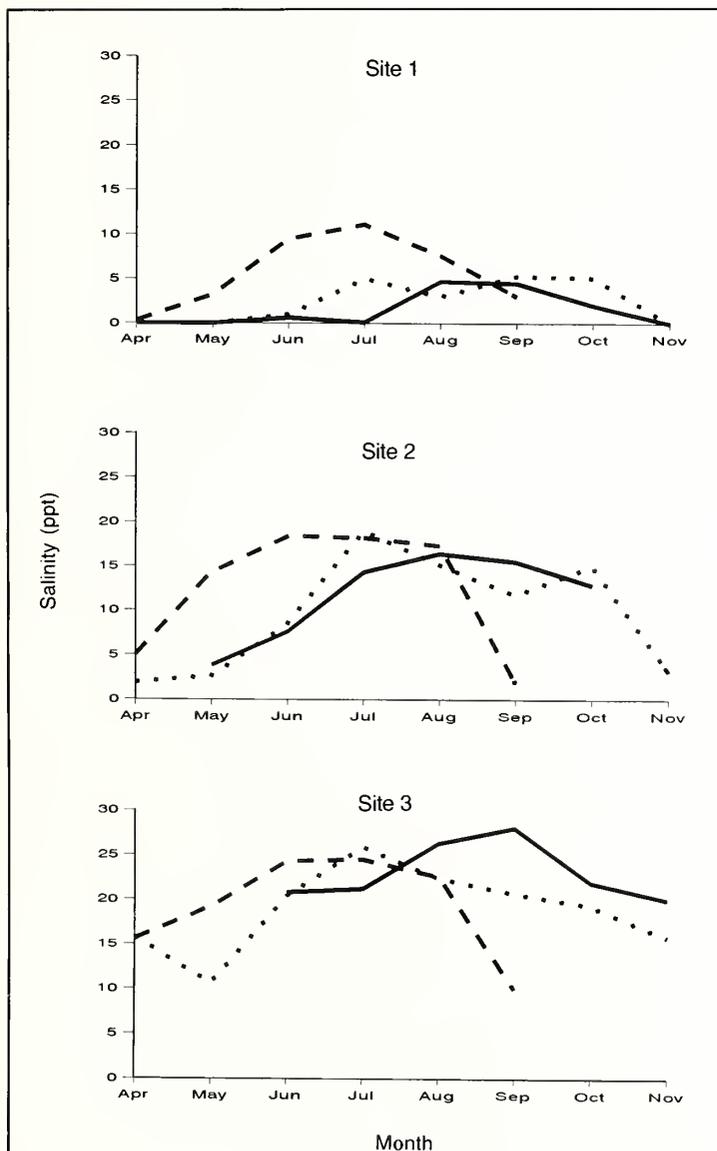


Figure 2

Salinity at three sites sampled along a salinity gradient in Great Bay Estuary, New Hampshire. Mean salinity was highest at site 3 (20.3 ppt) followed by site 2 (10.9 ppt) and then site 1 (4.2 ppt). Solid line = 1989; dotted line = 1990; dashed line = 1991.

gradient (Fig. 7). They were present in relatively large numbers during all months. There were no significant differences in catches of winter flounder among months for all study years.

Depth gradient

The two species of flounder showed a differential use of the three sites that comprised the depth gradient. There were also differences in the sizes of flounder that used the three sites. Seasonal changes in distri-

bution were less pronounced than those exhibited along the salinity gradient.

A broad size range of smooth flounder used site 3 (Fig. 8). However, their abundance dropped off sharply after June of each year, as previously discussed (Fig. 9). Winter flounder showed few seasonal trends in abundance at this station (Fig. 10). A broad size range of juvenile winter flounder was found here. A distinct influx of young-of-the-year winter flounder could be seen at site 3 from August through November of each year (Fig. 8).

At site 4, smooth flounder showed little seasonal change in abundance (Fig. 9), although there was a trend for catches to be lowest in late summer and early autumn. Length frequencies differed between site 3 and site 4. At site 4, few larger smooth flounder were present during any season (Fig. 11), whereas young-of-the-year, which were absent from site 3, were collected at most times. Abundance of winter flounder at site 4 was lowest in all years in early summer (Fig. 10), and catches were always smaller than those at site 3. Length frequencies indicated that smaller winter flounder made up a greater proportion of the catch at site 4 (Fig. 11) as compared to site 3 (Fig. 8).

Catches at site 5 were very variable for both species and showed no clear seasonal patterns (Figs. 9 and 10). Smooth flounder catches at site 5 were dominated by young-of-the-year. Few larger (>100 mm TL) individuals were ever caught at this site (Fig. 12), in contrast to site 3 (Fig. 8) but similar to site 4 (Fig. 11). Winter flounder occurred at site 5 sporadically and in very low numbers (Fig. 10). Catches of winter flounder were a mix of different sizes of juveniles.

Discussion

A variety of habitats are available to smooth and winter flounder in upper Great Bay Estuary. It was the purpose of this study to quantify the occurrence of these two species in various habitats. Although the species ranges of smooth and winter flounder overlap broadly, the evidence presented here indicates that they use habitats within the estuaries differently and that their habitat use is subject to seasonal variations.

Salinity gradient

In general, smooth flounder were most abundant at site 2, the mesohaline river mouth

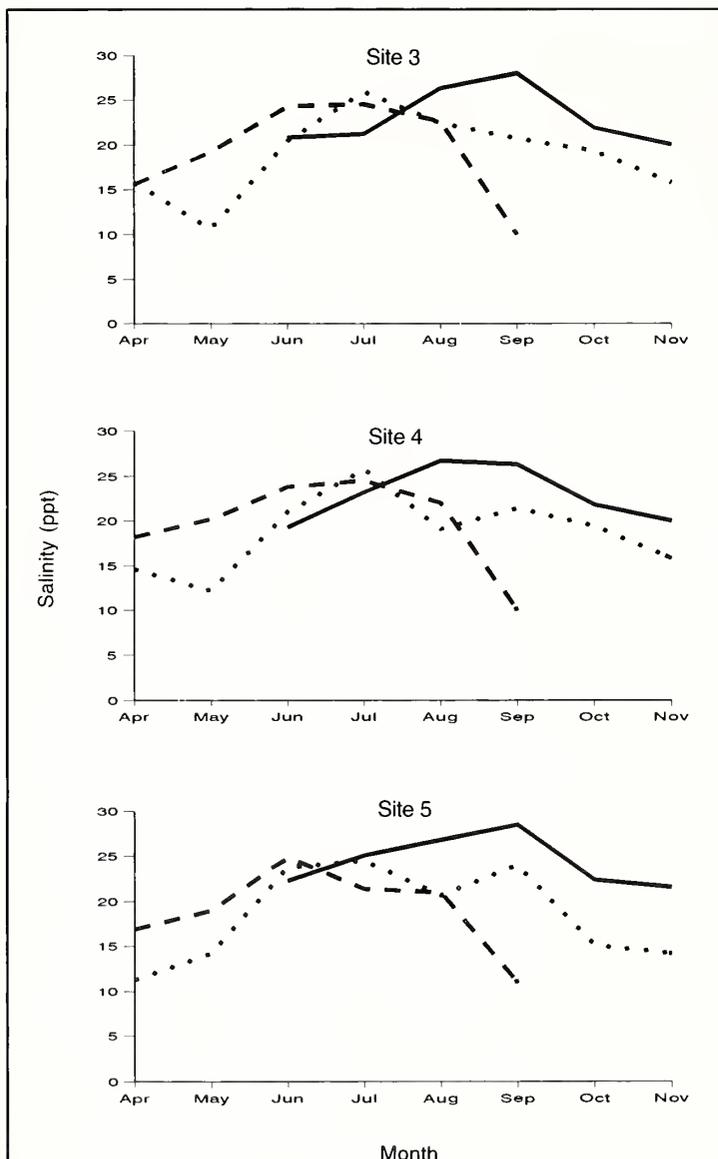


Figure 3

Salinity at three sites sampled along a depth gradient in Great Bay Estuary, New Hampshire. Mean depth was greatest at site 3 (mean = 6.2 m) followed by site 4 (2.1 m) and then site 5 (1.5 m). Solid line = 1989; dotted line = 1990; dashed line = 1991.

Table 2

Results of ANOVA's testing for differences in catches of smooth and winter flounder among three sites along the salinity gradient (sites 1, 2, and 3) and three sites along the depth gradient (5, 4, and 3). If there was a significant difference ($P < 0.05$) in catches among sites, the results of Tukey's HSD test are listed from lowest to highest. See Table 1 for a description of the sites. ns = not significant.

Year and season	Smooth flounder		Winter flounder	
	Salinity gradient	(<i>F</i> -value; df)	Salinity gradient	(<i>F</i> -value; df)
1989				
Spring	site 1 < site 3 < site 2	(25.80; 2,20)	site 1 = site 2 < site 3	(46.64; 2,20)
Summer	site 3 < site 1 = site 2	(6.13; 2,27)	site 1 = site 2 < site 3	(38.11; 2,27)
Autumn	site 3 < site 1 = site 2	(20.29; 2,23)	site 1 < site 3 < site 2	(12.62; 2,27)
1990				
Spring	site 3 = site 1 < site 2	(36.42; 2,22)	site 1 = site 2 < site 3	(8.24; 2,22)
Summer	site 3 < site 1 = site 2	(13.88; 2,20)	site 1 < site 2 = site 3	(12.99; 2,20)
Autumn	site 3 < site 2 = site 1	(9.69; 2,23)	ns	(0.56; 2,23)
1991				
Spring	site 3 < site 2 = site 1	(9.52; 2,29)	site 1 = site 2 < site 3	(11.56; 2,29)
Summer	site 3 < site 2 = site 1	(4.80; 2,21)	site 1 = site 2 < site 3	(7.07; 2,21)
Autumn	site 3 < site 1 < site 2	(121.79; 2,5)	site 1 < site 3 < site 2	(21.26; 2,5)
Year and season	Smooth flounder		Winter flounder	
	Depth gradient	(<i>F</i> -value; df)	Depth gradient	(<i>F</i> -value; df)
1989				
Spring	ns	(2.53; 2,11)	site 5 < site 4 < site 3	(17.15; 2,11)
Summer	ns	(0.28; 2,21)	site 4 = site 5 < site 3	(16.62; 2,21)
Autumn	site 3 = site 5 < site 4	(3.73; 2,23)	site 5 < site 4 = site 3	(7.02; 2,29)
1990				
Spring	ns	(0.13; 2,28)	site 5 < site 4 = site 3	(10.87; 2,28)
Summer	site 3 < site 5 = site 4	(4.41; 2,20)	site 5 = site 4 < site 3	(14.03; 2,20)
Autumn	site 3 = site 4 < site 5	(5.63; 2,29)	site 5 = site 4 < site 3	(7.96; 2,29)
1991				
Spring	ns	(1.08; 2,29)	site 5 = site 4 < site 3	(13.45; 2,29)
Summer	site 3 = site 4 < site 5	(14.19; 2,17)	site 5 = site 4 < site 3	(5.87; 2,17)
Autumn	site 3 = site 4 < site 5	(162.99; 2,5)	site 5 = site 4 < site 3	(5.82; 2,5)

habitat. Seasonal movements were seen into and out of the oligohaline riverine station (site 1) and the polyhaline station in Great Bay proper (site 3). In all years, there was an up-estuary movement of smooth flounder associated with increasing salinity in summer and early autumn. This movement was most pronounced for larger smooth flounder. Greater movement by larger individuals is probably related to their superior locomotive abilities due simply to their larger body size. This trend towards increasing range of movement with increasing body size has also been found in the hogchoker, *Trinectes maculatus*, a flatfish that is similar in general size to smooth flounders and that is also found in estuarine rivers (Dovel et al., 1969; Smith, 1986).

There is little information available on the distribution of smooth flounder along salinity gradients. Targett and McCleave (1974) found smooth flounder to be abundant in the Sheepscott River-Back Bay River estuary, Maine, in salinities of 17.3-24.7 ppt. Fried (1973), studying the same estuary, found that smooth flounder were not present above 28.5 ppt, whereas winter flounder occurred throughout the salinity range sampled (12.5 to 32.5 ppt). Gordon and Dadswell (1984) found the greatest abundance of smooth flounder in "warm, turbid, low-salinity water" in the upper reaches of the Bay of Fundy. Smooth flounder larvae were most abundant in the low-salinity portion of the St. Lawrence River estuary (Powles et al., 1984). The conclusion of the present

study, that the center of greatest abundance for smooth flounder is in the mesohaline part of the estuary, is in agreement with these previous studies.

Site 3 was the site of greatest abundance for winter flounder. Movements into site 2 were seen in late summer or early autumn in all years. Little information is available concerning the response of juvenile winter flounder to salinity gradients. Most studies on the distribution of winter flounder have con-

sidered only temperature or light as important abiotic factors that influence seasonal or short-term movements (McCracken, 1963; Oviatt and Nixon, 1973, Casterlin and Reynolds, 1982). Percy (1962) found a relatively homogeneous distribution of age-1 winter flounder throughout a salinity gradient in Mystic River Estuary, Connecticut, that was maintained through all seasons. However, his lowest salinity station was higher in salinity than both

site 1 and site 2; therefore he did not sample habitats that might be only seasonably available. Percy (1962) also documented movement of young-of-the-year winter flounder from the lower estuary to the upper estuary during the summer months. Indirect evidence for similar movement by young-of-the-year winter flounder in Great Bay Estuary is presented here. No young-of-the-year winter flounder were caught in upper Great Bay until late summer and early autumn (Figs. 8 and 11), indicating an influx from the lower estuary. The lack of small winter flounder during the early part of the year was not an artifact of gear selectivity because young-of-the-year smooth flounder as small as 25 mm TL were caught, indicating that small young-of-the-year winter flounder would have been caught also if they had been present. Winter flounder spawn in the middle and lower portions of Great Bay Estuary and adjacent to the estuary in shallow coastal waters. Young-of-the-year winter flounder show little movement for a few months after metamorphosis (Saucerman, 1991); therefore it is not until they reach a larger size (30–50 mm TL) that they begin to move into the upper estuary.

Salinity is considered one of the most important factors affecting habitat use by estuarine fishes. The distributions and movements of several flatfish species including *Solea solea* (Coggan and Dando, 1988; Dorel et al., 1991), *Pleuronectes platessa* (Poxton and Nasir, 1985), and *Platichthys flesus* (Riley et al., 1981; Kerstan, 1991) have been correlated with salinity. A natural estuarine salinity gradient, in which habitats are categorized from benign to harsh in relation to tolerance by species, may serve as part of a continuum of physiological stress (Peterson and Ross, 1991). Species seeking to maximize growth must

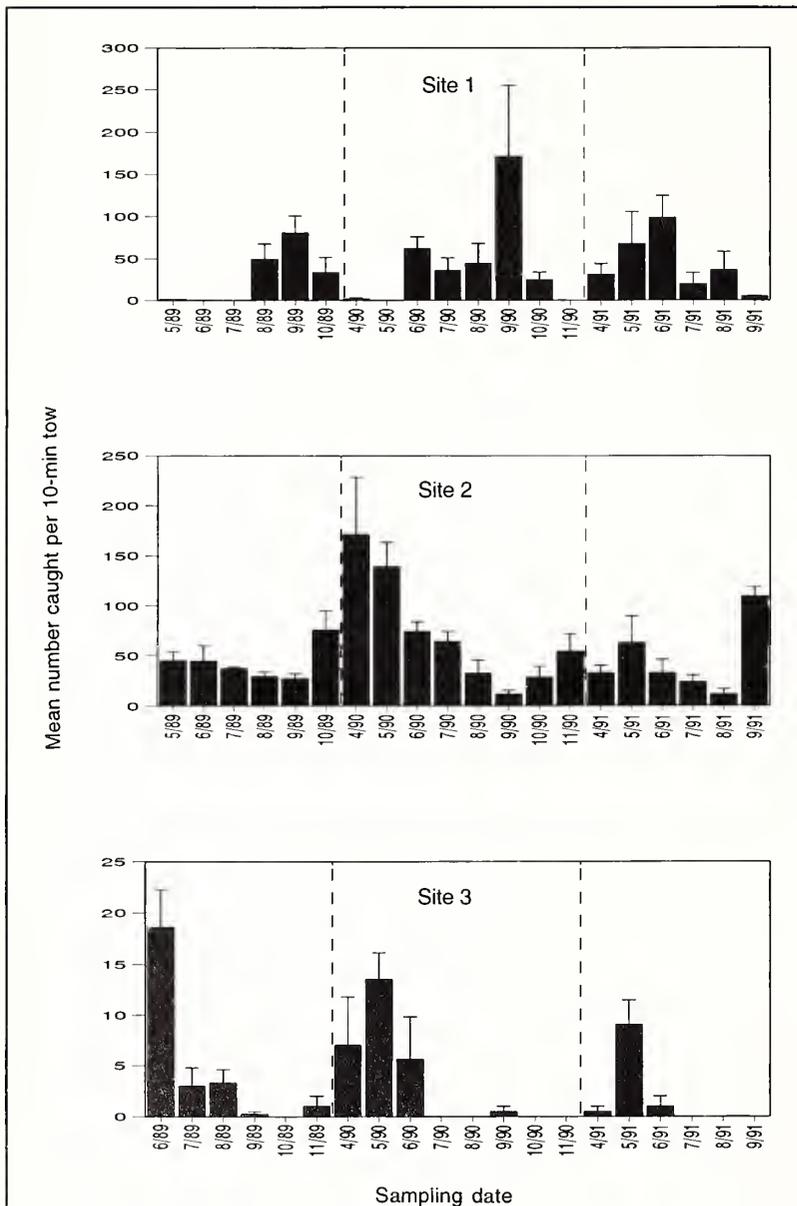
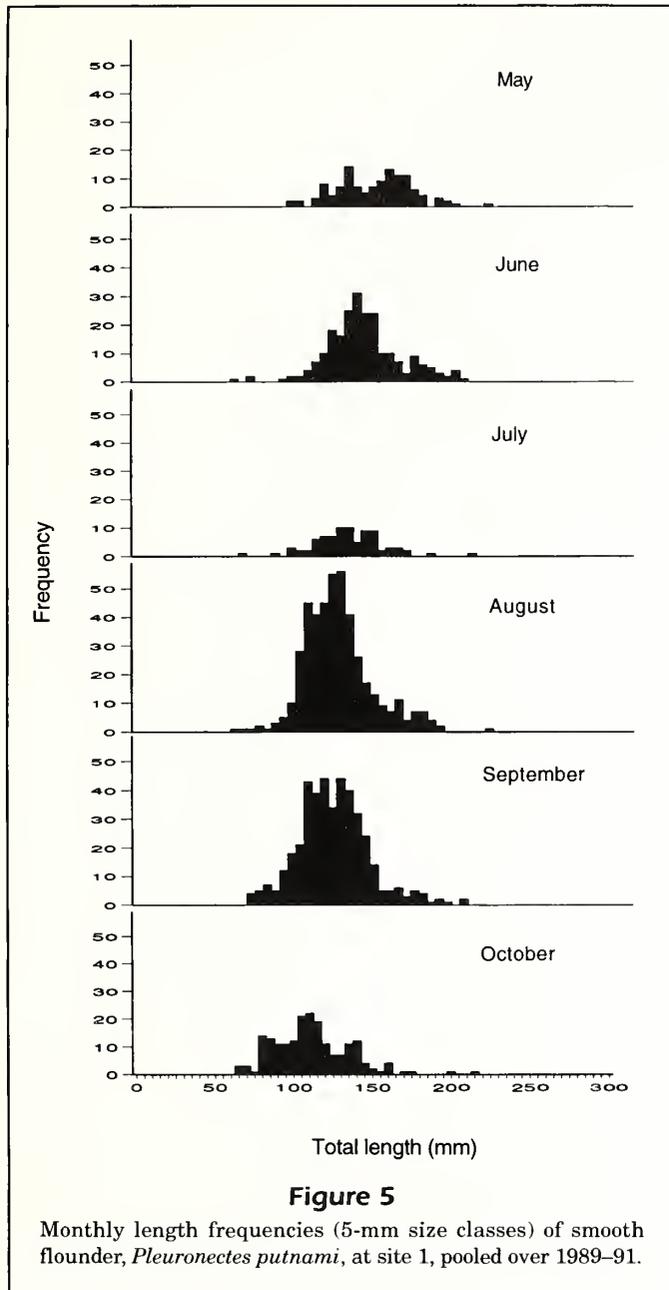


Figure 4

Mean number of smooth flounder, *Pleuronectes putnami*, caught per ten minute tow at three sites along a salinity gradient in Great Bay Estuary, New Hampshire, May 1989–September 1991. Site 1 = oligohaline; site 2 = mesohaline; site 3 = polyhaline. Error bars are one standard error of the mean.

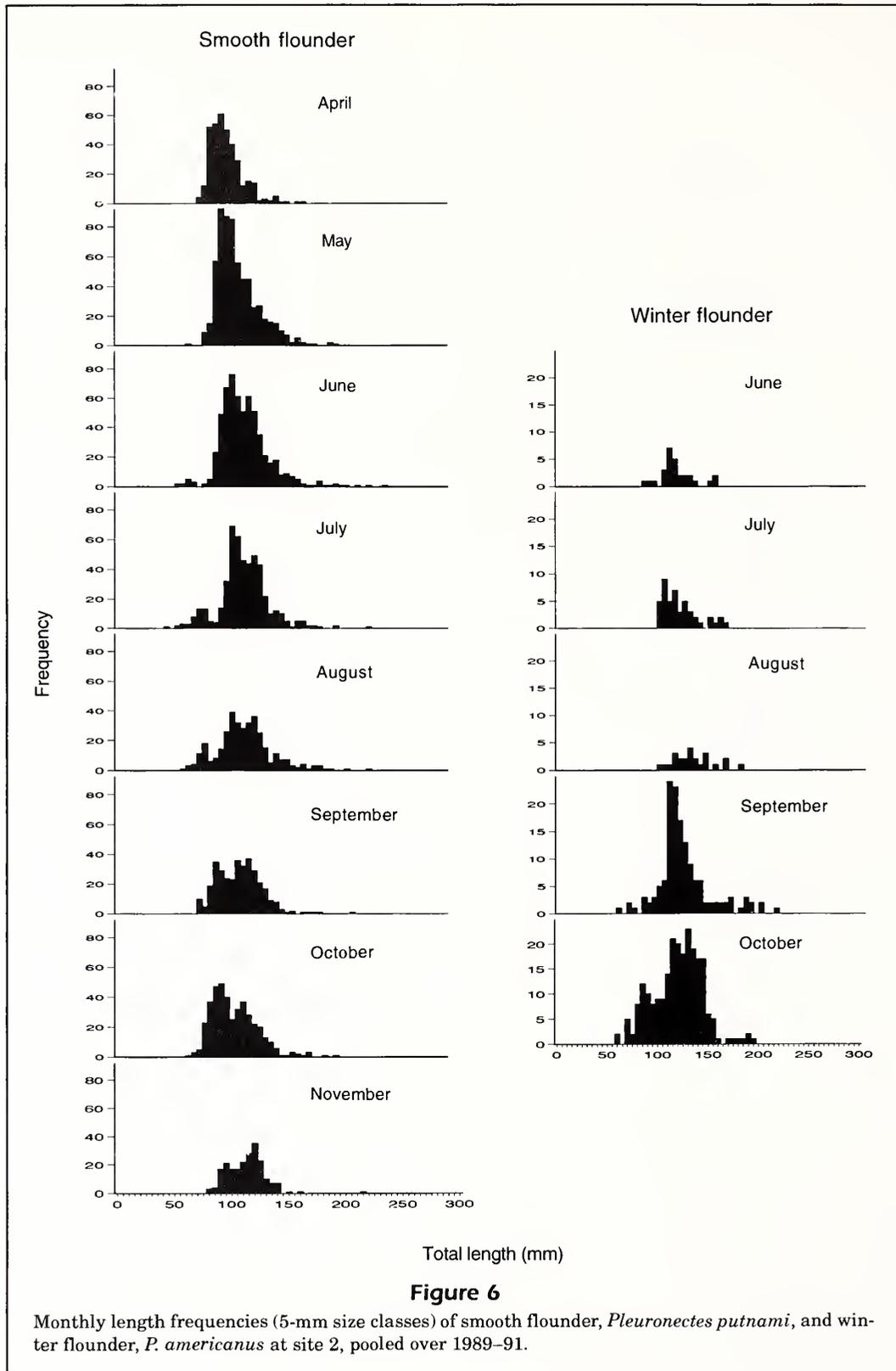


choose habitats that are of least cost bioenergetically. Several estuarine fish species have been found to be most abundant along a salinity gradient where their metabolic costs of osmoregulation were minimal, including *Ambassis* spp. (Martin, 1990), *Leiostomus xanthurus* and *Micropogonias undulatus* (Moser and Gerry, 1989), and *Paralichthys* spp. (Peters, 1971). Conversely, Peters and Boyd (1972) found that hogchokers, *Trinectes maculatus*, underwent movements that appeared physiologically disadvantageous. They concluded that other factors, in addition to salinity, must be considered. Salinity may

provide a broad abiotic framework (Menge and Olson, 1990) within which biotic interactions, such as competition, predation, and prey abundance, can act to modify distributions.

Depth gradient

Smooth flounder showed clear segregation by size along the depth gradient. Larger (>100 mm TL) smooth flounder occurred primarily at the deep-water station (site 3). They were abundant only during April-June, before migrating upriver as salinity increased. Small numbers remained at site 4 throughout the summer and autumn. The tidal flats (site 5) and shallow bay (site 4) were important nursery areas for smooth flounder. Young-of-the-year smooth flounder did not show a dramatic decrease in abundance during the summer, as seen in the larger individuals, and did not appear to make a pronounced seasonal up-estuary movement. Their inferior swimming ability, compared with that of larger individuals, or their inability to osmoregulate efficiently in lower salinity areas may underlie their relatively stationary habits. The tendency for smooth flounder to segregate by size, with the smaller individuals occurring in the intertidal and shallow subtidal areas, has been found in several other flatfish species including English sole, *Parophrys vetulus* (Toole, 1980), and European plaice, *Pleuronectes platessa* (Gibson, 1973; Kuipers, 1973). Segregation by size may reduce intraspecific competition. The intertidal zone may also function as a refuge from predators for small flatfish or as an abundant source of appropriate-size prey items (Toole, 1980). Ruiz et al. (1993) found that shallow water functioned as a refuge from size-selective predation on juveniles of several species of fish and crustaceans in Chesapeake Bay. Van der Veer and Bergmann (1986) found that young-of-the-year European plaice used tidal flats as a refuge from predators rather than for feeding purposes. Potential predators on smooth flounder in Great Bay Estuary include sand shrimp (*Crangon septemspinus*), grubbies (*Myoxocephalus aeneus*), bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), white perch (*Morone americanus*), great blue heron (*Ardea herodias*), and double-crested cormorants (*Phalacrocorax auritus*). Predation by large piscine predators is probably reduced in shallow water, and avian predation is likely increased. Sand shrimp were abundant in trawl samples from both channel and flats areas. The value of tidal flats as refugia from predation cannot be assessed without knowledge of the relative rates of predation by these different predatory groups.



Winter flounder showed little segregation by size along the depth gradient. This finding is in contrast with other studies, which have shown that juvenile

winter flounder segregate by size along depth gradients according to differential preferences to temperature and light intensity, with smallest individuals found

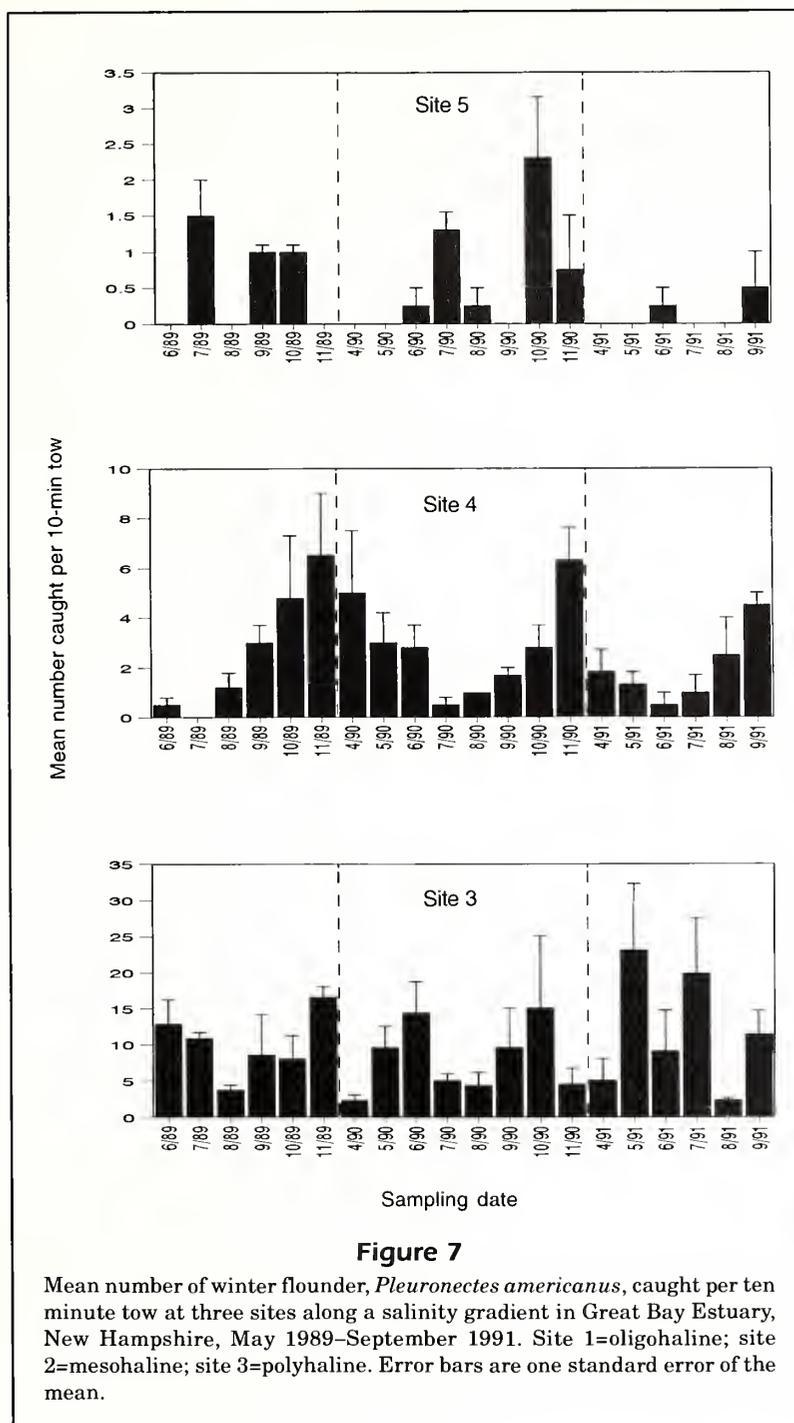


Figure 7

Mean number of winter flounder, *Pleuronectes americanus*, caught per ten minute tow at three sites along a salinity gradient in Great Bay Estuary, New Hampshire, May 1989–September 1991. Site 1=oligohaline; site 2=mesohaline; site 3=polyhaline. Error bars are one standard error of the mean.

at higher temperatures and light intensities (see reviews in Klein-MacPhee, 1978; Casterlin and Reynolds, 1982). It is especially interesting that winter flounder showed relatively little use of the intertidal flats. Tyler (1971), Wells et al. (1973), and Black and Miller (1991), however, found that winter flounder used intertidal flats extensively. Their studies took place in areas of higher salinity where no smooth flounder occurred. Their finding suggests that competition with smooth

flounder may be a possible reason for the near absence of winter flounder from the intertidal flats habitat in Great Bay. Targett and McCleave (1974) found that the tidal mudflats in Montsweag Bay, Maine, were dominated by smooth flounder, whereas Fried (1973) found that the channel areas in the same estuary were dominated by winter flounder. Fried (1973) felt that the tidal mudflats offered smooth flounders a refugium from competition with winter flounder and that winter floun-

der were unable to use this habitat type for reasons other than competition with smooth flounder.

Temperature may be a factor in the winter flounder's avoidance of tidal mudflats. Hoff and Westman

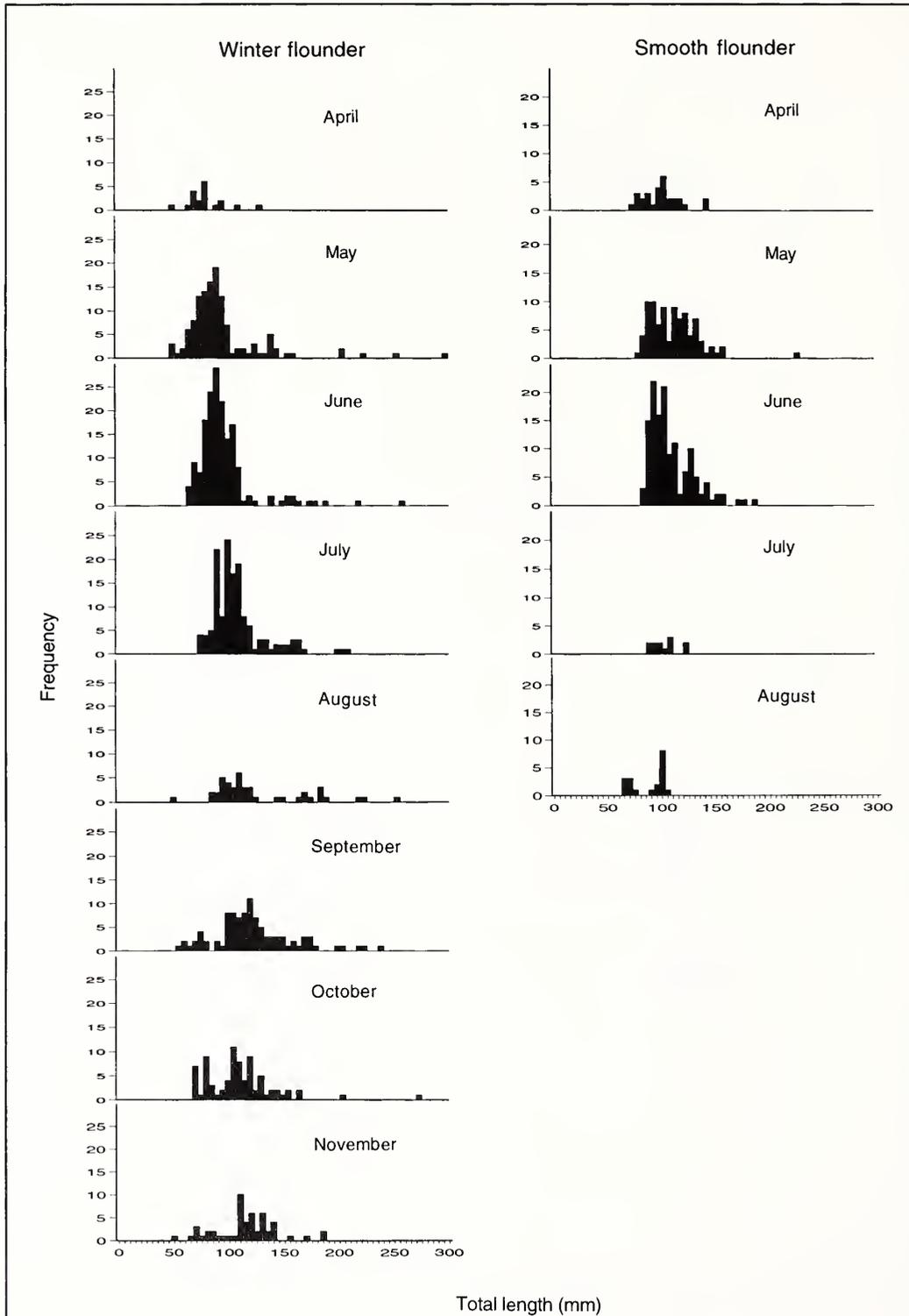


Figure 8

Monthly length frequencies (5-mm size classes) of smooth flounder, *Pleuronectes putnami*, and winter flounder, *P. americanus*, at site 3, pooled over 1989–91.

(1966) found that winter flounder, acclimated to 21°C, had an upper lethal temperature of 27°C. Pearcy (1962) found an upper lethal temperature of 30°C for flounder collected during the summer in Mystic River Estuary. Olla et al. (1969) observed that winter flounder exposed to temperatures above 22.2°C buried themselves in sediment and ceased to feed. Although comparable data do not exist for smooth flounder, Huntsman and Sparks (1924) reported that

upper lethal temperatures for smooth flounder were 2–4°C higher than those for winter flounder. In Great Bay Estuary, temperature may be a factor in determining the relative distribution of the two species in late summer when water temperatures at site 5 reached 22–24.2°C but would not be a factor during most of the year. The low abundance of winter flounder at site 5 persisted during times of the year when temperature would not seem to be limiting.

Substrate preference may play a role in excluding winter flounder from intertidal flats in Great Bay Estuary. Although the bottom type appeared similar (silty mud) at all three sites along the depth gradient (Table 1), this similarity was based on gross examination of core samples. No detailed sediment size analysis was conducted for this study (nor in Fried [1973] or Targett and McCleave [1974]), and therefore differences in sediment structure may have been present between sites but not noted on a gross scale. Sogard (1992) found that growth of winter flounder was negatively correlated with percent silt; faster growth occurred in sandier sediments. Bigelow and Schroeder (1953) found that winter flounder were more abundant on coarser sediments, in comparison with smooth flounder which were more abundant in muddier sediments. Thus, if the channel areas of Great Bay Estuary have coarser sediments than the intertidal flats, perhaps the coarser sediment may explain the difference in distribution along the depth gradient.

Summary

Smooth and winter flounder are partially segregated as species along salinity and depth gradients in upper Great Bay Estuary. It appears that this is due to differential responses to the physical and chemical regime, but the effects of seasonal changes in biotic interactions cannot be excluded. Smooth and winter flounder feed on similar prey items in Great Bay Estuary (Laszlo, 1972; Armstrong, 1995). Competition or movements related to prey abundance may influence their respective distributions. There are many instances where com-

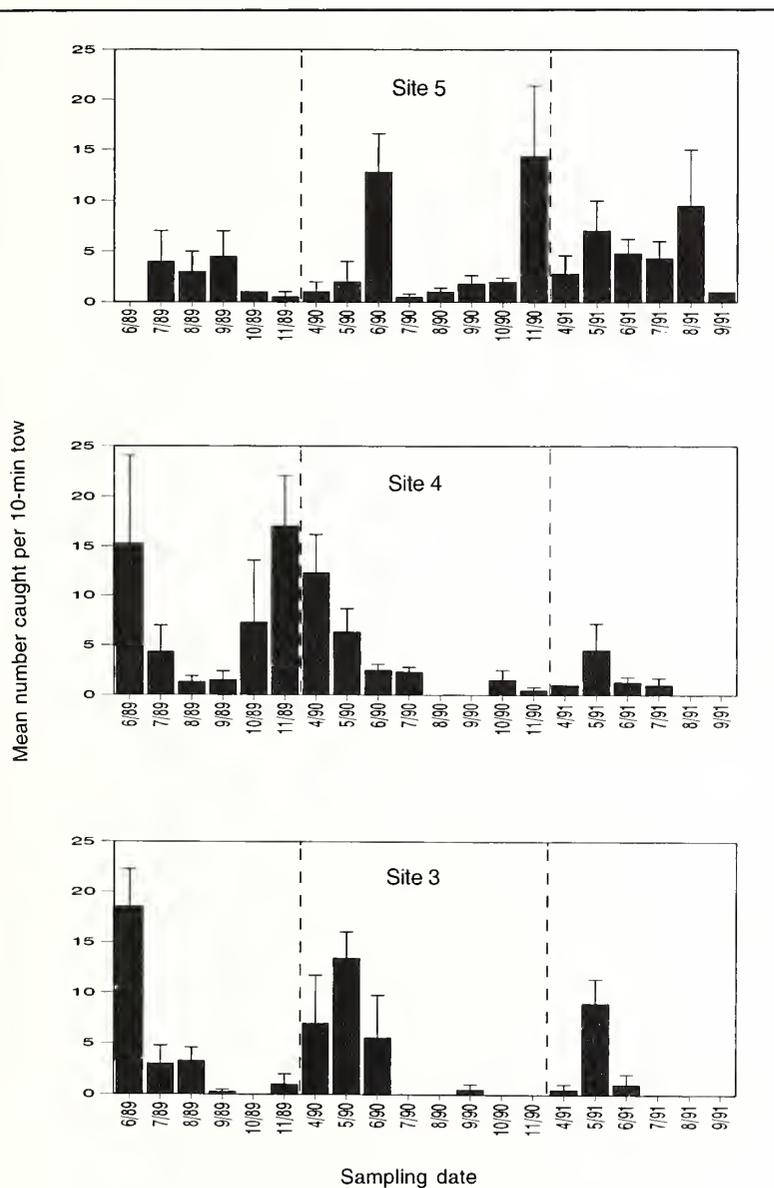
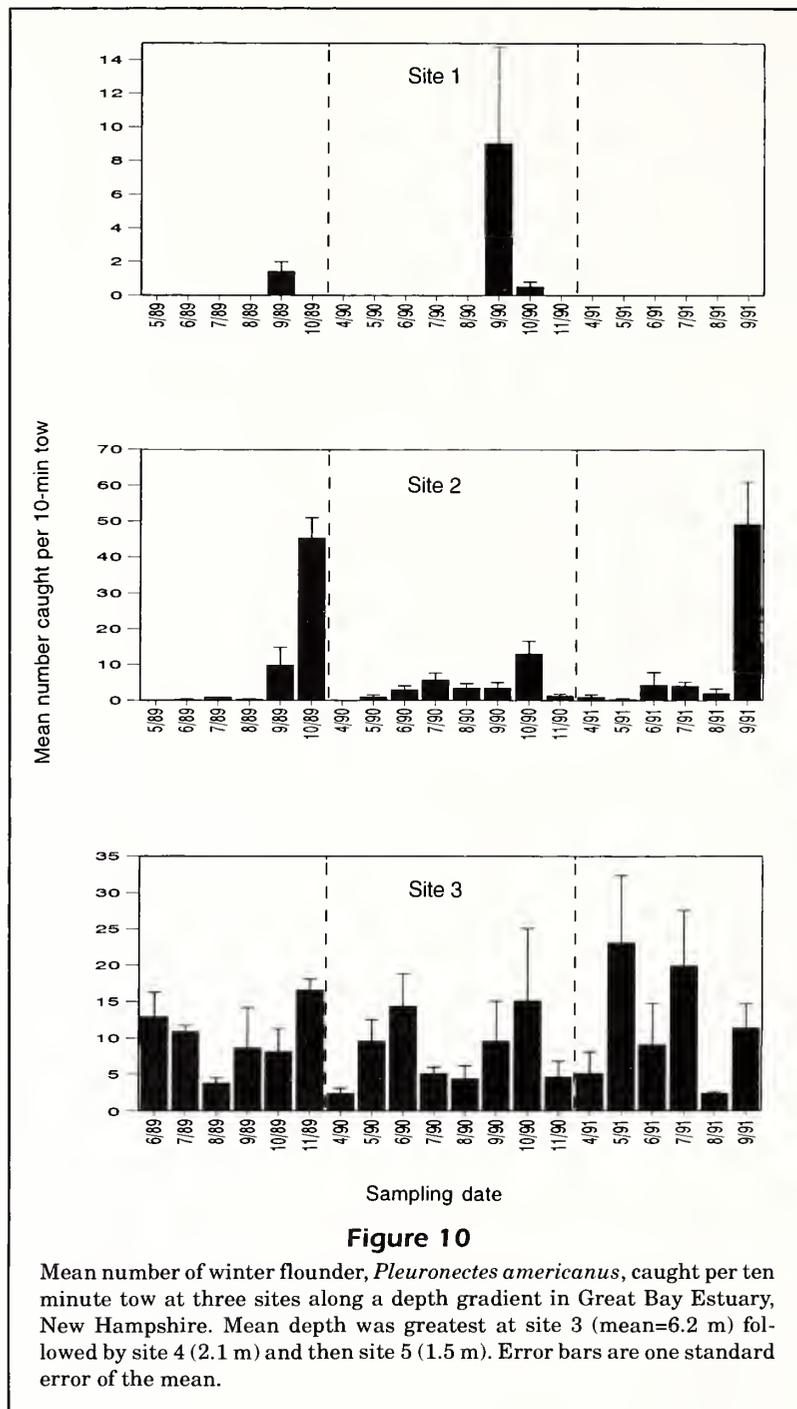


Figure 3

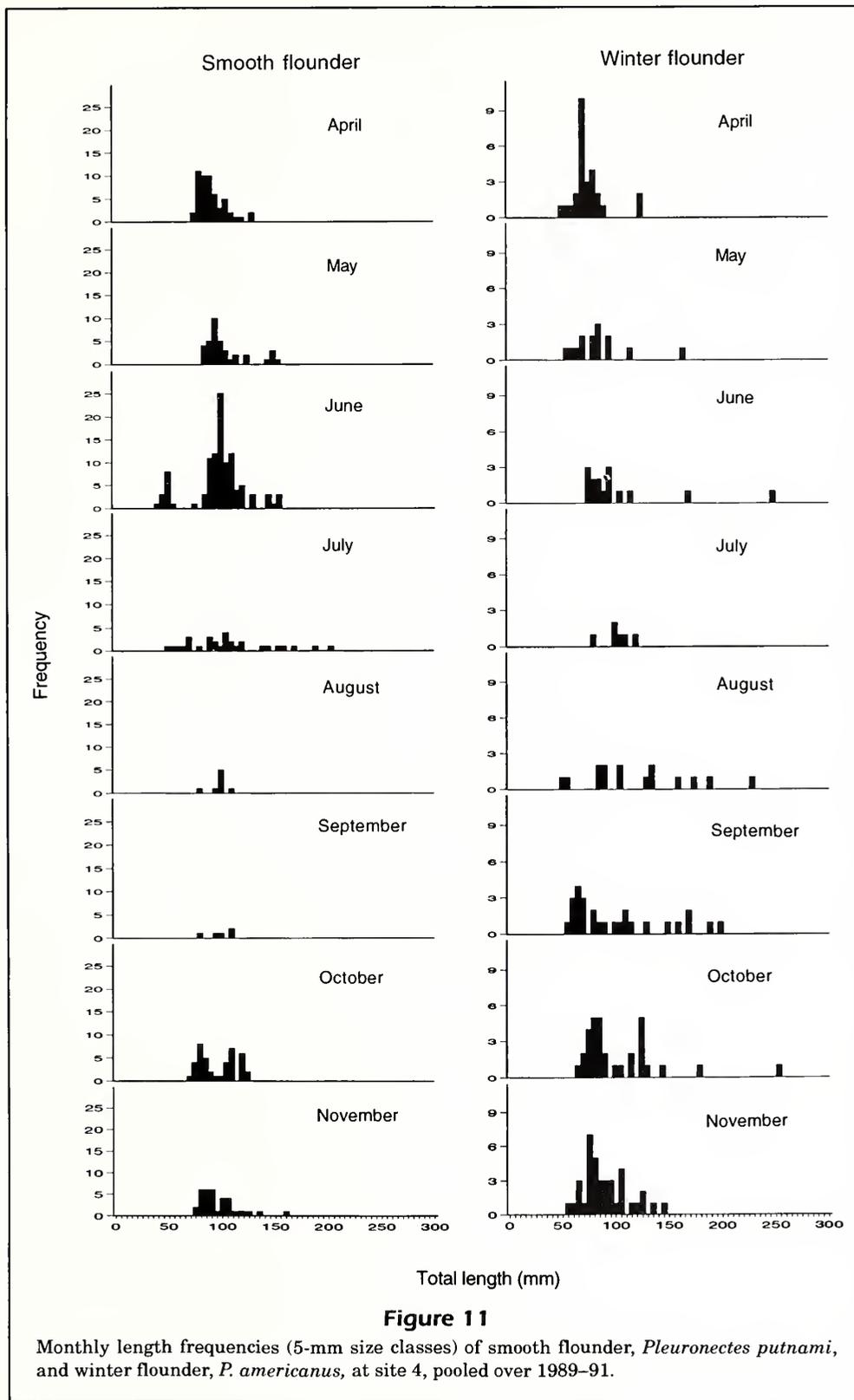
Mean number of smooth flounder, *Pleuronectes putnami*, caught per ten minute tow at three sites along a depth gradient in Great Bay Estuary, New Hampshire. Mean depth was greatest at site 3 (mean=6.2 m) followed by site 4 (2.1 m) and then site 5 (1.5 m). Error bars are one standard error of the mean.



petition appears to play a role in the distribution of ecologically similar species along environmental gradients (Connor and Bowers, 1987). In Great Bay Estuary, low salinity and intertidal flats appear to provide at least a partial refugium for smooth flounder from competition with winter flounder.

The relation between smooth and winter flounder changes on a seasonal basis. At times their segregation on a spatial scale is nearly complete, whereas at

other times, particularly April–June at site 3 and September–October at site 2, they overlap considerably. Competition theory predicts that niches should vary temporally as a function of resource abundance and of the population densities of potential competitors (Llewellyn and Jenkins, 1987). The predominant temporal pattern of niche overlap seen in studies is increased overlap during resource abundance (Schoener, 1982; Ross, 1986). The periods of great-



est overlap in habitat use seen for smooth and winter flounder may be associated with an abundance of some resource, for example, a shared prey item(s).

The upper Great Bay Estuary is an important area for both species. This study has shown the dynamic nature of habitat use by smooth and winter floun-

der. Further studies are needed to assess experimentally the relative importance of abiotic versus biotic factors in determining the patterns of smooth and winter flounder spatial distributions.

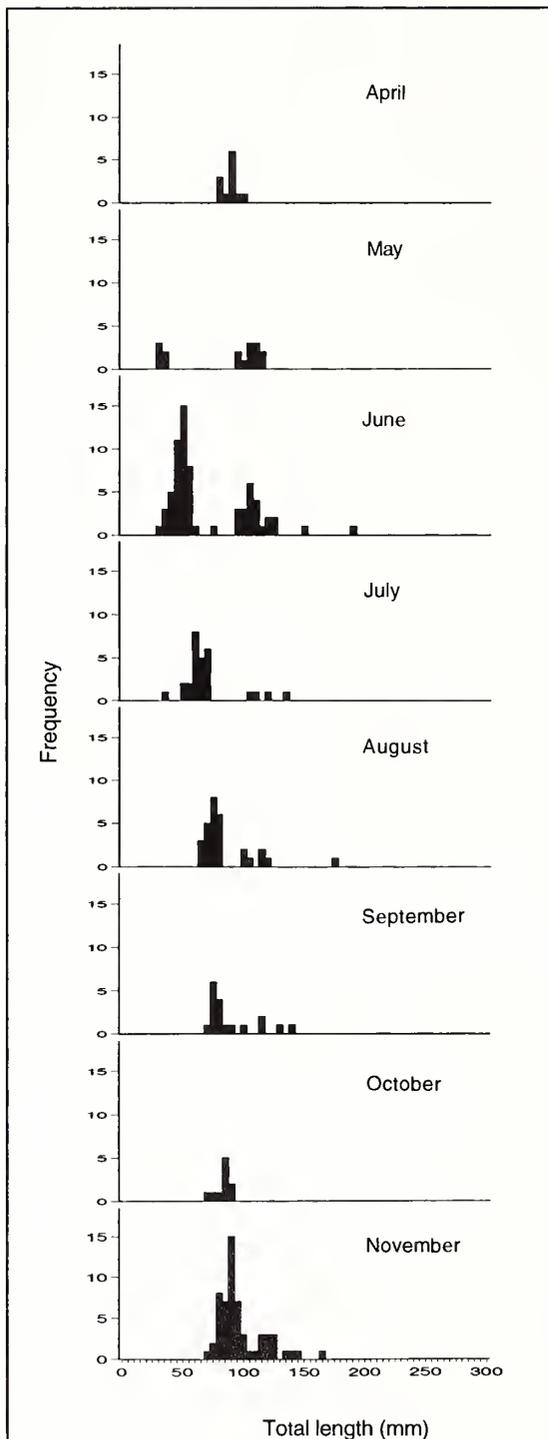


Figure 12

Monthly length frequencies (5-mm size classes) of smooth flounder, *Pleuronectes putnami*, at site 5, pooled over 1989-91.

Acknowledgments

I wish to thank the countless legions of work-study students, graduate students, and staff at the Zoology Department of the University of New Hampshire who assisted at various points in this work. S. Cadrin, D. Adams, H. Howell, J. Musick, L. Harris, P. Sale, J. Taylor, and three anonymous referees provided helpful reviews of the manuscript. The research formed part of a dissertation submitted in partial fulfillment of the Ph.D. degree, Department of Zoology, University of New Hampshire. This work was supported in part by a grant from the U. S. Fish and Wildlife Service Wallop-Breaux Fund and by a Central University Research Grant from the University of New Hampshire.

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Abstract.—The effects of ration level and temperature on growth were determined for larval red drum, *Sciaenops ocellatus*, during its first two weeks of life. Larvae were raised in the laboratory at 20°C at a ration level of 5.0 prey/mL, at 25°C at ration levels of 0, 0.1, 1.0, and 5.0 prey/mL, and in growout ponds at 25°C and 32°C and at ration levels of 4–6 prey/mL. Growth was measured as standard length, wet mass, and dry mass. Proximate (water, ash, protein, and lipid) and elemental (C, N) composition was determined at larval ages of 0, 2, 4, 6, 10, and 14 d to provide caloric values for the growing larvae and to examine the relative importance of protein and lipid during tissue deposition in the very early life history of these larvae. Biochemical indicators of growth, RNA-DNA ratio, and activity of the metabolic enzyme lactate dehydrogenase (LDH) were examined in larvae reared at all temperature and ration combinations. The effectiveness of the biochemical indicators as proxies for growth was assessed by comparing the directly measured growth rates with RNA:DNA levels and LDH activity. Larvae fed a ration of 1.0 prey/mL or less did not survive past the age of eight days. Growth rate increased with increasing temperature, reaching a maximum of 60% body mass/d in growout ponds at 32°C. Protein level (percent ash free dry mass: %AFDM) increased with increasing age in all treatments where individuals exhibited positive growth, whereas lipid (%AFDM) showed a concomitant decline. Nitrogen (%AFDM) and carbon (%AFDM) varied directly with protein and lipid contents, respectively. Biochemical indicators of growth showed a significant correlation with growth rate. However, the character of the correlation changed with temperature. RNA-DNA ratios and enzymic activities were lower at higher temperatures for equivalent growth rates. Introduction of a temperature term into multiple regression equations improved the relation between growth and the biochemical proxies. LDH activity scaled with the size of larvae, whereas RNA:DNA showed no significant relation with size.

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Energetics of larval red drum, *Sciaenops ocellatus*. Part II: Growth and biochemical indicators

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Red drum, *Sciaenops ocellatus*, is an important species in commercial and recreational fisheries in the southeastern United States, particularly in the Gulf of Mexico. Declines in red drum stocks (Swingle, 1990) have stimulated considerable interest in the early life history of this species, resulting in stock enhancement programs and larval monitoring programs designed both to improve and continually to assess the status of the fish in the field. Studies on red drum and other species indicate clearly that growth during the pretransformation period of development is particularly critical to survival (Buckley, 1980; Holt et al., 1981, a and b; Holt and Arnold, 1983; Holt, 1990). The increase in size and mobility that characterizes development during the early larval period results in an increase in the size range of prey items available to the larvae as forage and a decrease in the size range of potential predators on the larvae.

Two variables with great potential to influence rates of growth are

temperature and ration levels. As a subtropical species, red drum develop at temperatures greater than 20°C, grow rapidly, and have a greater energy demand for metabolic processes than do larvae developing in colder systems. For example, red drum eggs at 25°C hatch in 24 h, and larvae begin feeding in 48–72 h, whereas cold water species, such as Atlantic cod, *Gadus morhua*, and winter flounder, *Pleuronectes americanus*, developing at 4–8°C, spend 30 d as developing eggs.¹ High temperatures during early development stimulate rapid growth in red drum but leave them potentially more vulnerable to rapid starvation in absence of sufficient food. The interaction between temperature, ration level, and growth in size and calories, is an important part of the energetics of larval red drum, basic information which is unavailable for red drum and limited for other subtropical teleosts (Houde and Schekter, 1983).

¹ Hempel, G. 1979. Early life history of marine fishes; the egg stage. Univ. Washington Press, Seattle, WA, 70 p.

Objectives of the present study were four-fold. The first was to examine growth in size and energy in laboratory-reared red drum larvae, from egg to onset of transformation, at a single ration level (5 prey/mL) and at two temperatures (20 and 25°C). This examination was achieved by using direct measurements of standard length and mass with age; the biochemical composition and caloric value of the growing larvae were described by analyzing their proximate and elemental composition (water, ash, protein, lipid, carbon, and nitrogen). The second was to examine the relation of growth in size and energy as a function of ration level (0, 0.1, 1.0, and 5.0 prey/mL) at a single temperature (25°C). The third was to compare growth in size and energy in laboratory-reared larvae at 20 and 25°C and in the more heterogeneous conditions encountered by pond-reared larvae at 25 and 32°C. The fourth objective was to describe the relation between growth, temperature, and biochemical indicators of growth and condition: RNA:DNA ratios and activity of the key intermediate metabolic enzyme lactate dehydrogenase (LDH).

Methods and materials

Laboratory maintenance

Fertilized eggs were obtained from the Florida Department of Environmental Protection (FDEP) hatchery, Port Manatee, Florida. Broodstock were maintained at 25°C and 30 ppt. Eggs were obtained from five females and from separate spawnings, from November 1990 to November 1991, for all growth experiments described below. Broodstock females were similar in size, kept in highly controlled conditions, and fed well. Spawning was induced naturally by manipulation of photoperiod. As a consequence, eggs were very uniform in size, 0.9 to 1.0 mm in diameter.

Eggs were transported to the USF Marine Science Laboratory in St. Petersburg and sorted into 26-L experimental aquaria at a concentration of 2,500–3,000 individuals per aquarium. High mortality associated with first feeding resulted in a 30–40% reduction in initial numbers by day 3. Aquaria were placed in a photoperiod- and temperature-controlled incubator and maintained at either 20°C or 25°C and at a salinity of 30 ppt. Eggs were introduced to the 20°C temperature by slow exchange of water over a 60-minute period. A 13-h light and 11-h dark photoperiod was used throughout all experiments. Larvae were fed rotifers (*Brachionus plicatilis*) beginning at day 3 posthatch until flexion (approximately day 14), when experiments were terminated. Aquaria were aerated and a portion of the saltwater in each was changed daily.

Rotifers were obtained from Florida Aqua Farms, Dade City, Florida, and cultured according to the procedure of Hoff and Snell (1987). Rotifers were fed *Chlorella* once a day to avoid any loss in nutritional value. Seawater for culturing was obtained offshore in the Gulf of Mexico. The seawater was coarse-filtered, then treated with bleach (sodium hypochlorite, 5.25%) to remove any additional plankton, and neutralized with sodium thiosulphate. Seawater salinity was adjusted with distilled water and Tropic Marine Seasalt to achieve a final salinity of 30 ppt.

Pond maintenance

Pond-reared red drum larvae were obtained from the FDEP growout ponds, Port Manatee, Florida. Larvae from a single spawn were added to the plankton-rich ponds within 24 hours after hatching and allowed to grow. Two ponds, one at 25°C and another at 32°C, were sampled for the first 18 days of life of the red drum larvae. Temperature was monitored twice daily; the average temperature for the two-week sampling period was used to characterize the ponds.

Prey items in the ponds were monitored by sieving water samples into two size categories: 35–220 µm (copepod nauplii, rotifers, and small copepods) and larger than 220 µm (copepods); prey were then counted in 200-mL aliquots of each size range. The concentration of prey between 35 and 220 µm was 3–5 prey/mL, whereas that greater than 220 µm was 0.5–1 prey/mL in both the 25°C and 32°C ponds.

Growth versus prey density

Eggs from a single spawn were divided into four 26-L aquaria for experiments on growth versus prey density at 25°C. Prey were provided at four densities, 0, 0.1, 1.0, and 5.0 prey items per mL, from first feeding (day 3) through the start of flexion (day 14). Prey concentrations were monitored twice daily by removing a 25-mL sample from each aquarium, counting the number of prey in 5-mL aliquots, and taking the average. Prey concentrations were adjusted as necessary. Larvae reared at 20°C were fed prey at a ration level of 5.0 prey items per mL.

Standard length measurements Growth in standard length was monitored according to prey concentration. Aquaria with 0, 0.1, and 1.0 prey/mL were sampled daily. Aquaria with 5.0 prey/mL were sampled every other day, and ponds were sampled every third day. The samples were taken each morning before the larvae began to feed. Standard length

of five individual larvae that had been anesthetized with MS-222 was measured with the aid of a dissecting microscope. Standard length was considered to be the distance from the snout to the tip of the tail in preflexion larvae and from the snout to the tip of the notochord in post-flexion larvae.

Mass measurements Growth in mass was monitored at the same intervals as those used for standard length. At each monitoring interval, 30 individuals were removed for wet, dry, and ash-free dry mass analysis. To determine mass, larvae were first separated into three groups of ten. Each group of larvae was filtered onto a preweighed 0.5-cm Whatman glass fiber filter (made with an office hole-punch) that was placed in a custom-made miniaturized vacuum funnel. Larvae were then rinsed very briefly by introducing distilled water into the funnel with a pasteur pipette and by removing the water immediately with the vacuum filter. To minimize evaporation, samples were immediately placed in preweighed microcentrifuge tubes which were then weighed to the nearest μg on a Mettler electrobalance to determine wet mass. Specimens were dried at 60°C to a constant mass (about 24 h) to determine dry mass.

Average proximate and elemental composition of prey items

Rotifers were collected in bulk from two 28-L culture bags (approximately 50 mg dry mass/bag) for determination of proximate and elemental composition. Proximate composition (water, ash, protein, and lipid content) was determined by using the methods of Stickney and Torres (1989) and Donnelly et al. (1990). Elemental composition was determined by using a C:H:N analyzer.

Average proximate and elemental composition of fish larvae

Methods used to estimate the proximate and elemental composition of fish larvae were the same as those used for prey. Larvae were obtained in bulk (50 mg dry mass) for each day sampled. Each pond was sampled from the hatchery at 0, 2, 6, 10, and 14 days. Laboratory-raised larvae were sampled at prey concentrations of 0, 0.1, 1.0, and 5.0 prey/mL at 0, 2, 6, 10, and 14 days for each of four spawns. Protein and lipid values as percent ash-free dry mass (%AFDM) were multiplied by individual ash-free dry mass to obtain concentrations as mg/individual. The instantaneous protein growth rate (G_{pi}) was calculated by using the formula from Buckley (1982):

$$G_{pi} = \frac{\ln M_{t_2} - \ln M_{t_1}}{t_2 - t_1} \times 100,$$

where M = mass in mg; and
 t = age in d.

Caloric content of prey and larvae

Caloric content was calculated from proximate compositional data of the rotifers and larvae by using a value of 0.0048 cal/ μg for protein and 0.0095 cal/ μg for lipid (Brett and Groves, 1979).

RNA-DNA ratio

Ten to 20 individuals were removed for analysis of RNA:DNA content each time sampling occurred for measurements of mass. Larvae were filtered onto preweighed Whatman glass-fiber filters, rinsed with distilled water, weighed, placed in microcentrifuge tubes, and frozen at -80°C until analysis. RNA:DNA was analyzed by first homogenizing the freshly thawed groups of larvae in 1.2 M NaCl, then by using the sequential enzymatic method of Bentle et al. (1981) to determine RNA:DNA.

Activity of lactate dehydrogenase

Larvae were sampled in bulk (minimum 10–20 mg wet tissue mass) every day at a prey concentration of 0 prey/mL. Samples were taken at 0, 2, 6, 10, and 14 days for larvae fed 5 prey/mL and for those collected in the growout ponds. Tissue was introduced frozen into the homogenizing medium, ice-cold Tris/HCL buffer (10 mM, pH 7.5 at 10°C), and homogenized by hand at 0 to 4°C with conical glass homogenizers having ground-glass contact surfaces (Kontes Glass Co., "Dual" models). Homogenates were centrifuged at $4,500 \times g$ for 10 minutes and the supernatants saved for enzyme analysis.

L-Lactate dehydrogenase (LDH, EC 1.1.1.27; Lactate: NAD⁺ Oxidoreductase) activity was assayed in the pyruvate reductase direction by using methods described in Torres and Somero (1988) at a temperature of 25°C . Enzyme activity was expressed as units/gWM (wet mass), where a unit was 1 μmole of substrate converted to product per minute.

Statistical analyses

Simple regressions for each relationship were fitted by using the least-squares method (Statgraphics Plus, Manugistics Corporation). Data from treatment groups were compared by using one-way analysis of variance (ANOVA). Differences between the means

were determined by using the least-significant-differences multiple range test. Multiple regression analysis (Statgraphics Plus, Manugistics Corporation) was used to examine the relation between the observed protein growth rates and the following combinations of factors: the three experimental temperatures (20°C laboratory, 25°C laboratory, 25°C pond, 32°C pond), the three ration levels at 25°C (0, 5 prey/mL, and pond), RNA:DNA, and LDH activity.

Results

Growth rate versus prey density

Standard length Starved red drum larvae (0 prey/mL) kept at 25°C increased in standard length even as they were declining in dry mass (Figs. 1 and 2; Table 1). The average size at death on day 6 was 2.89 mm, which corresponds to a daily increase of 0.075 mm/day for days 2–6. Surprisingly, these values were similar to those for larvae fed at 5.0 prey/mL at 25°C, which attained an average length of 2.90 mm by day 6.

Growth in larvae fed ad libitum increased with increasing temperature in both the laboratory and ponds. At 20°C, day-14 larvae averaged 4.13 mm, and very few of the larvae exhibited flexion of the notochord (Fig 1; Table 1). Laboratory-reared individuals at 25°C grew to an average of 4.45 mm by day 14. Mean masses at day 14 were significantly different between the two temperatures (ANOVA: $df=1$, $F=60.3$, $P<0.001$). Flexion of the notochord within the tail region had begun by day 14 at 25°C, indicating the onset of transformation. Larvae raised in ponds at 25°C averaged 6.45 mm at day 14. Notochord flexion in these larvae began on day 9 or 10, when the

larvae were at a size between 4.11 and 4.50 mm. Pond-reared larvae at 32°C had reached an average standard length of 7.48 mm at day 14. Notochord flexion occurred on day 7 or 8, when larvae were at a length of 4.53 mm (similar to the size at flexion of the laboratory-raised larvae) and at an earlier chronological age than that of the laboratory-raised individuals.

Mass measurements Growth in mass of laboratory-reared larvae at ration levels less than 5.0 prey/mL (0, 0.1, and 1.0 prey/mL) at 25°C was negative, and no larvae survived more than 8 days (Fig. 2). Slopes

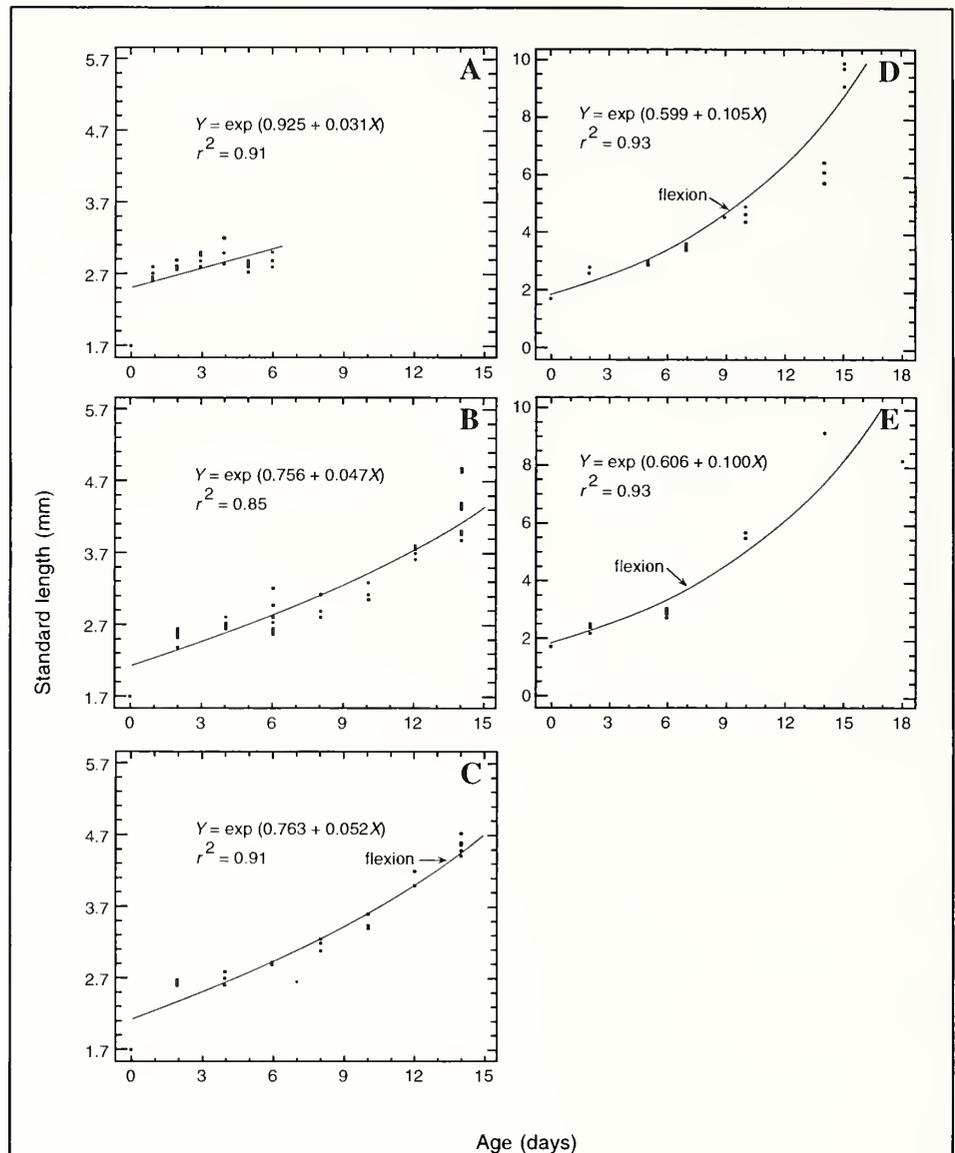
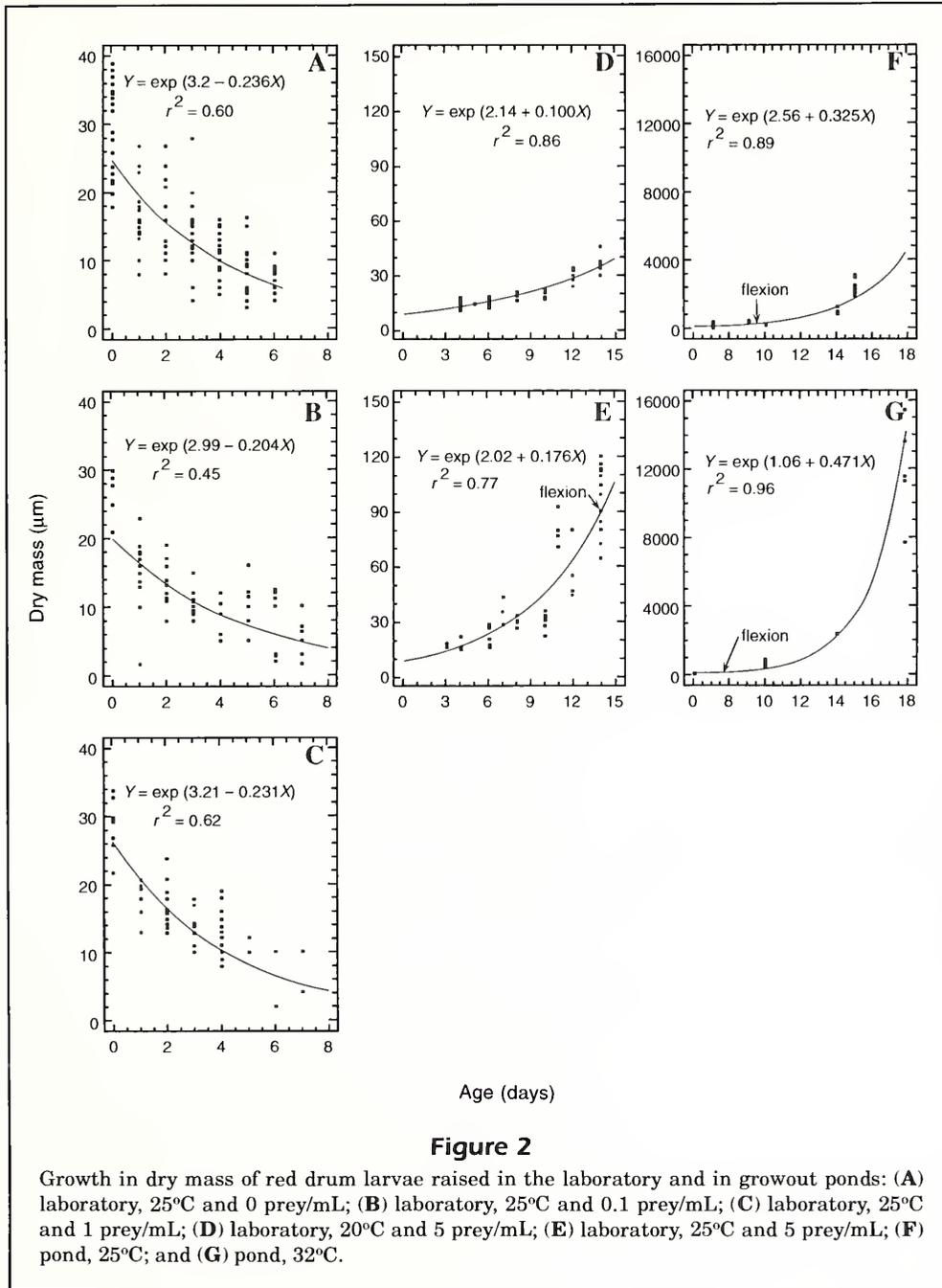


Figure 1

Growth in standard length of red drum larvae raised in the laboratory and in growout ponds: (A) laboratory, 25°C and 0 prey/mL; (B) laboratory, 20°C and 5 prey/mL; (C) laboratory, 25°C and 5 prey/mL; (D) pond, 25°C; and (E) pond, 32°C.



of the three curves describing the time-dependent decline in individual dry biomass at the three ration levels were not significantly different (Student's *t*-test: $P > 0.05$). Growth in dry mass at a ration level of 5.0 prey/mL was significantly higher than at the three lower ration levels (0, 0.1, and 1.0 prey/mL).

In contrast, wet masses in 2–6 day-old larvae were slightly lower at ration levels of 0, 0.1, and 1.0 prey/mL than at 5.0 prey/mL but were not significantly different. This finding indicated that body water con-

tent was increasing in larvae maintained at the three lower ration levels.

Larvae held at 25°C and fed 5.0 prey/mL had higher growth rates than those raised at 20°C at the same ration level (Fig. 2; Table 1). Growth averaged 2.86 $\mu\text{g}/\text{day}$ for the first two weeks of life in larvae raised at 20°C and 10.09 $\mu\text{g}/\text{day}$ for larvae reared at 25°C. Expressed as a percent increase in mass, larvae reared at 20°C increased 10.5 %BM/d and those reared at 25°C increased 19.3 %BM/d.

Table 1

Proximate and elemental composition and energetic density of red drum larvae determined at different levels of ration, temperature, and age. (nd = no data; DM=dry mass; WM = wet mass; AFDM = ash-free dry mass). Parenthetical values (SD, n) represent standard deviations and sample sizes below each of the mean values in the table.

Ration (prey/mL)	Temp C°	Day	Standard length (mm)	Wet mass (µg)	Dry mass (µg)	Calories per ind.	% Water	Protein			Lipid			Carbon % AFDM	Nitrogen % AFDM	Calories/mg DM
								AFDM as %DM	% WM	% AFDM	% WM	% AFDM	% WM			
0	25	0	1.70 (0.05, 5)	447.00 (86.10, 18)	29.28 (7.08, 18)	0.1063	94.4 (1.4, 15)	91.3 (4.5, 15)	2.58 (0.80, 15)	43.84 (4.47, 15)	1.22 (0.50, 15)	19.72 (4.16, 15)	51.83 (3.98, 3)	10.31 (0.55, 3)	3.631	
0	25	1	2.69 (0.09, 5)	274.80 (176.00, 15)	16.36 (4.52, 15)	0.0698	92.8 (1.2, 5)	94.5 (0.2, 5)	4.01 (0.81, 5)	57.33 (5.53, 5)	1.23 (0.01, 5)	18.45 (2.08, 5)	48.93 (0.93, 3)	10.41 (0.52, 3)	4.266	
0	25	2	2.83 (0.06, 5)	140.40 (24.30, 15)	6.64 (1.54, 15)	0.0725	90.8 (0.7, 10)	90.7 (1.8, 10)	4.71 (0.56, 10)	55.68 (3.79, 10)	1.74 (0.47, 10)	22.39 (6.02, 10)	53.99 (1.10, 4)	9.70 (0.48, 4)	4.353	
0	25	3	2.91 (0.09, 5)	126.20 (26.30, 15)	13.48 (4.93, 15)	0.0596	92.8 (1.0, 10)	90.6 (0.9, 10)	3.90 (0.47, 10)	59.68 (5.41, 10)	1.34 (0.29, 10)	21.24 (6.06, 10)	49.79 (4.84, 3)	9.80 (0.50, 3)	4.423	
0	25	4	3.01 (0.15, 5)	120.60 (21.70, 15)	10.99 (3.31, 15)	0.0438	91.1 (0.8, 10)	90.1 (1.2, 10)	4.69 (0.43, 10)	58.74 (2.48, 10)	1.32 (0.26, 10)	16.86 (4.35, 10)	49.79 (1.92, 3)	10.05 (0.13, 3)	3.983	
0	25	5	2.81 (0.07, 5)	103.30 (26.00, 15)	8.13 (3.86, 15)	0.0308	91.8 (0.6, 5)	89.6 (0.7, 5)	4.33 (0.36, 5)	62.89 (1.20, 5)	0.83 (0.17, 5)	12.67 (1.72, 5)	46.06 (5.81, 3)	10.60 (0.23, 3)	3.783	
0	25	6	2.89 (0.08, 5)	91.50 (20.90, 15)	7.00 (1.80, 15)	0.0278	91.0 (1.0, 5)	93.1 (1.6, 5)	5.21 (0.26, 5)	62.47 (3.28, 5)	1.14 (0.01, 5)	13.29 (1.28, 5)	nd	nd	3.967	
5	20	0	1.70 (0.05, 5)	363.30 (109.90, 0)	29.40 (4.26, 0)	0.1230	95.4 (0.5, 5)	94.8 (7.4, 5)	2.35 (0.44, 5)	43.74 (4.27, 5)	0.89 (0.18, 5)	24.34 (1.28, 5)	nd	nd	4.182	
5	20	2	2.54 (0.10, 5)	156.80 (22.30, 10)	15.52 (3.78, 10)	0.0651	90.3 (1.1, 5)	93.2 (2.3, 5)	4.20 (0.49, 5)	53.08 (4.86, 5)	1.70 (0.31, 5)	20.54 (3.12, 5)	nd	nd	4.194	
5	20	6	2.79 (0.21, 5)	192.00 (106.50, 10)	15.64 (1.87, 10)	0.0509	90.3 (nd)	91.0 (nd)	4.71 (nd)	53.19 (nd)	0.95 (nd)	10.78 (nd)	nd	nd	3.255	
5	20	10	3.14 (0.10, 5)	233.80 (20.30, 10)	20.43 (2.15, 10)	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	
5	20	14	4.33 (0.12, 5)	384.40 (47.30, 10)	35.91 (4.57, 10)	0.1056	85.7 (0.7, 5)	87.7 (2.4, 5)	6.50 (0.01, 5)	51.73 (0.67, 5)	1.15 (0.01, 5)	9.17 (2.16, 5)	nd	nd	2.943	
5	25	0	1.70 (0.09, 5)	385.80 (17.40, 5)	35.25 (1.26, 3)	0.1373	95.7 (0.7, 5)	97.4 (2.4, 5)	1.81 (0.01, 5)	43.39 (0.67, 5)	0.84 (0.01, 5)	20.18 (2.16, 5)	46.66 (49.88)	10.46 (10.29)	3.896	
5	25	2	2.64 (0.03, 5)	206.30 (85.20, 5)	18.67 (0.58, 5)	0.0849	93.5 (2.1, 5)	91.8 (1.3, 5)	3.27 (0.01, 5)	54.64 (1.24, 5)	1.49 (0.01, 5)	24.54 (17.23)	49.88 (45.77)	12.03 (0.41, 3)	4.548	
5	25	6	2.90 (0.02, 5)	207.80 (74.50, 5)	20.33 (5.47, 5)	0.0775	88.0 (0.7, 5)	91.3 (89.4)	5.79 (7.07)	52.91 (55.59)	1.89 (1.49)	17.23 (11.74)	45.77 (0.41, 3)	12.03 (11.91)	3.813	
5	25	10	3.46 (0.10, 5)	273.50 (121.00, 6)	29.71 (4.23, 6)	0.1005	85.8 (0.1, 3)	89.4 (0.7, 8)	7.07 (0.08, 8)	55.59 (55.13)	1.49 (1.22)	11.74 (11.64)	42.92 (1.17, 3)	11.91 (0.50, 3)	3.382	
5	25	14	4.53 (0.12, 5)	682.80 (181.40, 15)	98.92 (18.43, 15)	0.3120	87.8 (0.1, 3)	86.7 (0.7, 8)	5.59 (0.08, 8)	55.13 (42.70)	1.22 (0.72)	11.64 (18.08)	45.73 (nd)	12.27 (nd)	3.253	
Pond	25	0	1.72 (0.04, 5)	352.30 (71.00, 5)	28.91 (4.43, 5)	0.1008	95.0 (nd)	92.56 (93.1)	1.74 (4.42)	42.70 (56.21)	0.72 (1.72)	18.08 (24.82)	nd	nd	3.450	
Pond	25	2	2.70 (0.12, 5)	179.00 (62.60, 5)	15.67 (2.71, 5)	0.0738	91.4 (nd)	93.1 (nd)	4.42 (nd)	56.21 (nd)	1.72 (nd)	24.82 (nd)	nd	nd	4.707	
Pond	25	7	2.93 (0.06, 5)	334.05 (84.80, 5)	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	
Pond	25	10	4.70 (0.03, 5)	2833.80 (381.50, 5)	137.30 (23.20, 5)	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	
Pond	25	14	6.30 (0.31, 5)	6010.00 (542.50, 5)	983.30 (167.60, 3)	3.1318	91.7 (nd)	87.6 (97.2)	10.18 (3.60)	56.22 (45.62)	1.99 (1.76)	9.87 (24.98)	nd	nd	3.185	
Pond	32	0	1.75 (0.04, 5)	nd	nd	nd	93.9 (92.7)	97.2 (91.3)	nd (3.60)	45.62 (54.00)	nd (1.76)	24.98 (26.36)	47.70 (51.53)	9.10 (10.51)	nd (4.652)	
Pond	32	2	2.37 (0.14, 5)	187.80 (72.40, 5)	17.32 (4.78, 5)	0.0806	92.7 (88.5)	91.3 (91.6)	3.60 (6.92)	54.00 (65.61)	1.76 (1.38)	26.36 (13.05)	51.53 (nd)	10.51 (nd)	4.652	
Pond	32	6	2.89 (0.12, 5)	374.30 (83.50, 5)	36.20 (35.30, 5)	0.5476	88.5 (88.0)	91.6 (87.1)	6.92 (6.71)	65.61 (64.16)	1.38 (1.23)	13.05 (11.70)	nd (44.35)	nd (11.86)	4.021	
Pond	32	10	5.65 (0.10, 5)	5491.00 (1802.00, 5)	583.00 (168.40, 5)	2.1330	88.0 (89.3)	87.1 (81.7)	6.71 (5.00)	64.16 (64.16)	1.23 (nd)	11.70 (9.87)	44.35 (46.79)	11.86 (13.14)	3.658	
Pond	32	14	7.48 (0.27, 3)	nd	2127.80 (293.00, 3)	6.9808	89.3 (81.7)	81.7 (81.7)	5.00 (81.7)	64.16 (64.16)	nd (nd)	9.87 (9.87)	46.79 (46.79)	13.14 (13.14)	3.282	

Growth rates for pond-raised red drum larvae (Fig. 2) were far greater than those for larvae fed rotifers in the laboratory, owing almost certainly to the greater prey diversity in the ponds. Larvae raised at 25°C in the ponds increased in size an average of 81.9 µg/day over 14 days: a 47.2 %BM/d increase. Larvae raised at 32°C in the ponds increased an average of 799.22 mg/day: a 60.2 %BM/d increase; an increase of 10°C in the pond environment resulted in a two- to three-fold increase in absolute daily mass gain.

Proximate and elemental composition of prey

Brachionus plicatilis raised on *Chlorella* exhibited a protein level of 32.71% and a lipid level of 9.37% of its ash-free dry mass (AFDM). Carbohydrate level was low, averaging 2.84% (AFDM). The unrecovered mass was assumed to be due to refractory structural molecules that were not assayed for, e.g. chitin. Using a figure of 0.24 µg for average individual biomass (Hoff and Snell, 1987) and the caloric values for protein, lipid, and carbohydrate of Brett and Groves (1979, see methods section), we suggest that each rotifer has an average energetic value of 0.000526 calories.

Elemental composition of the rotifers showed that the percent carbon was 42.02 %AFDM and the percent nitrogen was 10.41 %AFDM. The carbon-nitrogen ratio was 3.56:1.

Proximate and elemental composition of larvae

Proximate composition can be expressed in three ways: as a percent of wet mass (%WM), a percent of ash-free dry mass (%AFDM), and as the total content per larva (mg/individual). Table 1 shows the changes in proximate composition (%WM and %AFDM) as a function of ration level and age of the larvae; total content (mg/individual) is reported below in the text.

Red drum eggs exhibited large water content (94.65 %WM), a high protein content (42.17 %AFDM) and an intermediate lipid content (19.35 %AFDM) (Table 1). Carbohydrate, generally an extremely small fraction of the overall proximate composition of marine species, proved to be so in this case as well (0.47 %AFDM).

Viewed as a fraction of the total body mass of each larva, the protein level (%AFDM) shows an increase through time at zero ration (43.84% to 62.47%) accompanied by a reduction in lipid (19.72% to 13.29%), which indicates that, in starving larvae, lipid was used in preference to protein for energy production. On a µg/individual basis, protein actually decreased in starved larvae from 8.44 µg/individual in newly hatched larvae to 4.07 µg/individual for 6-day-old starved larvae (Table 2). Lipid values declined from 2.59 µg/individual on day 3 to 0.87 µg/individual on day 6. Percent water remained high until death at day 6, averaging 91.0% throughout the survival period.

Table 2

Protein content, protein growth, RNA:DNA, and LDH in red drum larvae. Protein content was calculated from values reported in Table 1. Where values for % protein or % ash-free dry mass were missing, nearest neighbor values were used. Protein growth was calculated as described in text. RNA:DNA values are the mean for all RNA:DNA measurements within the last 2 d of the age interval shown in the table. They are reported as mean ±SD (n). Values for the 25°C pond were taken at day 7 instead of day 6 and calculated accordingly. All (6–14) day RNA:DNA values are significantly different ($P < 0.05$, Student's t). nd = no data

	Day															
	2	6	10	14	2-6	6-10	10-14	2-14	6-14	6	10	14	6-14	6	10	14
	Protein (µg/indiv)				Protein growth (%/d)					RNA:DNA				LDH (units/gWM)		
Starved	8.44	4.07	nd	nd	-18.20	nd	nd	nd	nd	0.68±0.35 (14)	nd	nd	nd	7.48	nd	nd
5/mL at 2°C	7.66	7.55	9.29	16.34	-0.40	5.20	14.10	63.00	9.50	1.51±0.43 (6)	1.45±0.24 (4)	1.49±0.14 (4)	1.50±0.30 (14)	9.19	14.44	19.69
5/mL at 25°C	9.36	9.77	14.80	47.33	1.10	10.40	29.10	13.50	19.70	1.15±0.20 (2)	1.19±0.32 (3)	1.26±0.19 (7)	1.25±0.21 (12)	15.06	24.33	33.60
Pond 25°C	8.16	15.00	67.70	484.30	12.10	50.20	49.20	34.00	49.60	2.89±0.51 (4)	3.06±0.81 (4)	3.56±0.27 (2)	3.09±0.62 (10)	18.94	30.86	42.78
Pond 32°C	8.51	82.20	324.60	1,116.20	56.70	34.30	30.90	46.00	32.60	1.19	2.21	1.39	1.60±0.54	12.69	19.44	26.19

The counterpoint to 0-ration data is provided by the data at 5.0 prey/mL at 20°C and 25°C (Table 1). The data clearly demonstrate accumulation of energy as protein and little storage of lipids. Larvae raised at 20°C increased in protein level (%AFDM) from 43.74% as eggs to 51.73% as day-14 larvae. Lipid levels decreased (%AFDM) from 24.34% in eggs to 9.17% in day-14 larvae. Protein concentrations increased from 7.66 µg/individual at day 2 to 16.34 µg/individual at day 14. Lipid concentrations increased from 1.53 µg/individual at day 6 to 2.89 µg/individual at day 14. An identical pattern was observed in larvae reared at 25°C (Table 1).

The data set for proximate composition values collected on pond-raised larvae was smaller than ideal owing to problems in obtaining adequate sample sizes from the ponds. However, the data on accumulated protein and lipid concentrations give an excellent indication of maximum growth. Pond-raised larvae at 25°C and 32°C showed faster accumulation of total protein and lipid than larvae raised in the laboratory (Table 1). Protein levels of larvae increased in %AFDM from 42.70% and 45.62%, in eggs, to 56.22% and 64.16% in day-14 larvae, at 25°C and 32°C, respectively. Lipid levels (%AFDM) decreased from 24.98% to 9.87% at 32°C; decreases in lipid percentages were also observed in the 25°C pond and in the laboratory-raised larvae.

Pond-reared larvae at 25°C increased in total protein content from 8.16 µg/individual at day 2 to 484.30 µg/individual at day 14, whereas those kept at 32°C increased from 82.20 µg/individual at day 7 to 1,116.20 µg at day 14 (Table 2). Thus, an increase in 10°C resulted in a three-fold increase in protein (µg/individual) in 2-week-old larvae raised in the ponds. Lipid values for larvae raised at 25°C and 32°C were also much higher than those for larvae raised in the laboratory; day-14 pond larvae on average had lipid contents of 85.06 µg/individual and 171.44 µg/individual, respectively.

Carbon (%AFDM) remained about the same with age in all rearing conditions (Table 1), whereas nitrogen (%AFDM) remained fairly constant or increased with age at all ration levels. Carbon-nitrogen (C:N) ratios were higher in larvae kept at a ration level of 0 prey/mL than in larvae raised either at 5.0 prey/mL or in the ponds, indicating that protein commanded the largest fraction of the starved larva's mass. Values for C:N remained high in starved larvae until death at day 5 (4.35 ± 0.46). Pond-raised larvae had values similar to those observed in larvae reared on 5.0 prey/mL in the laboratory but were slightly lower at day 14 (3.56 vs. 3.73). Caloric contents of the larvae were calculated from protein and lipid content by using the conversion factors in Brett and Groves (1979) and are reported in Table 1.

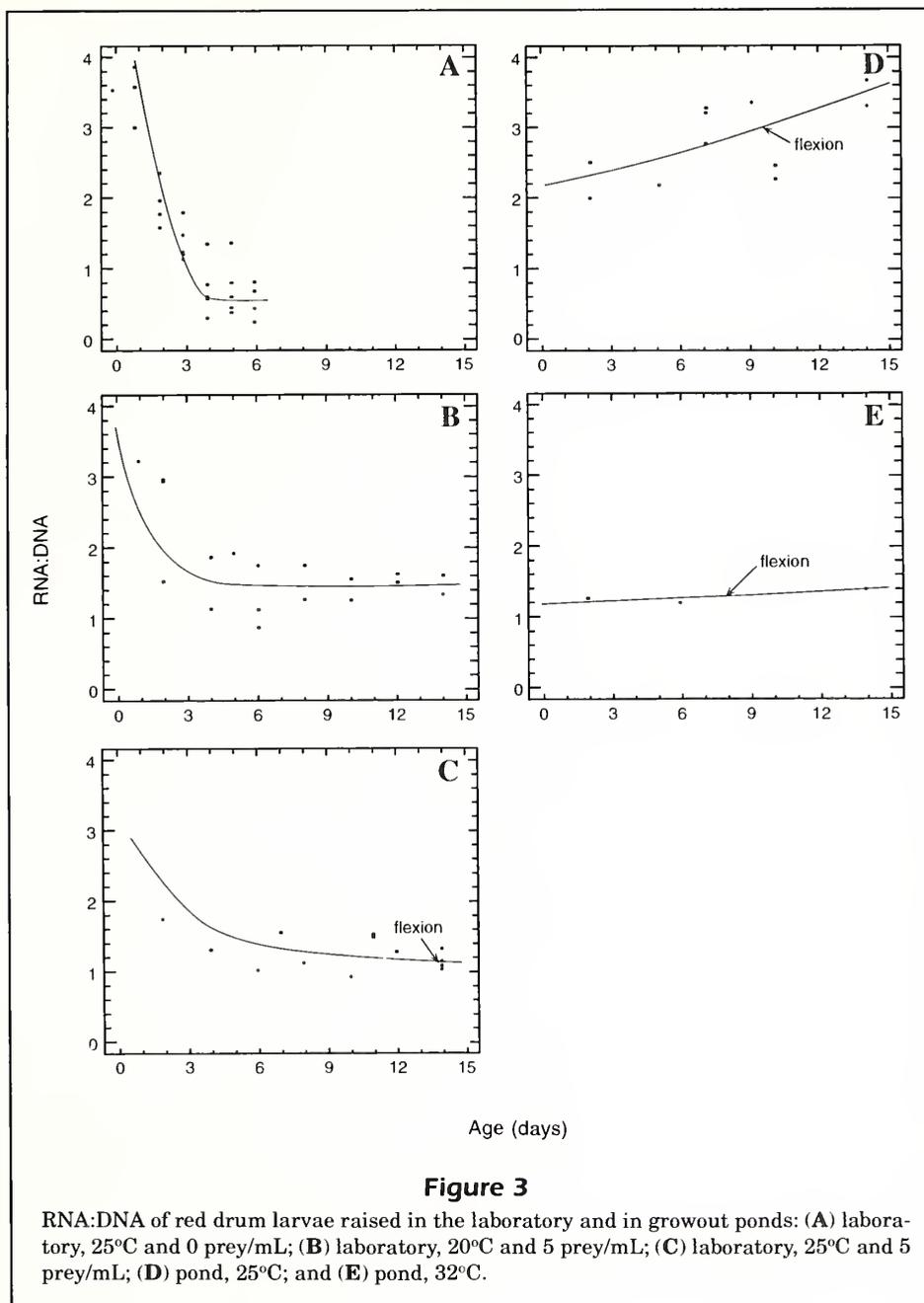
Protein-specific growth and biochemical indicators

Table 2 summarizes results for growth in protein (absolute and instantaneous) and the two biochemical indicators, RNA:DNA and LDH activity, for easy comparison. Instantaneous growth shows an interesting trend with the age interval chosen for calculation. If growth in protein was calculated from day 2 to day 14, larvae exhibit the trends discussed previously for growth in dry mass (see results) where lowest growth was observed in the 20°C laboratory treatment and highest in the 32°C ponds. If instantaneous growth was calculated instead for the interval from day 6 to day 14, the highest growth was observed in the 25°C ponds (Table 2) and would suggest that the growth spurt during the first 4 d of feeding in the 32°C pond was important in determining growth during the larvae's first 14 d of life.

RNA-DNA ratio RNA:DNA in each treatment showed a decline from a high value typical of the yolk-sac stage (day 1: grand mean for all treatments 4.27 ± 0.83 ; $\bar{x} \pm SD$) to a plateau at day 4 that characterized the treatment and showed no significant change over the remaining 10 days (Fig 3; Table 2). In starved larvae RNA:DNA reached a plateau at a value of 0.7, indicating that protein synthetic capacity was severely diminished after that time. RNA:DNA in larvae raised at 5.0 prey/mL in the laboratory showed a gradual decline to a plateau of 1.5 at 20°C and 1.3 at 25°C (Fig 3; Table 2); values at the plateau were significantly different between the two temperatures (ANOVA: $df=25$, $F=6.31$, $P=0.019$).

Pond-raised larvae had higher growth rates than laboratory-reared individuals (Figs. 1 and 2; Tables 1 and 2), and values for RNA:DNA were much greater in the 25°C pond than in any of the laboratory treatments (Fig. 3). Larvae raised in the ponds at 25°C had a value of 3.6 at 2 weeks of age, whereas those reared at 32°C averaged 1.5 at day 14. RNA:DNA values were significantly different between the two pond treatments (ANOVA: $df=12$, $F=14.19$, $P=0.003$).

Three treatments took place at a temperature of 25°C: starved, 5 prey/mL, and pond. If protein growth rates and RNA:DNA are compared between laboratory and ponds at 25°C (Table 2), there is an excellent correlation between protein growth and RNA:DNA. Instantaneous protein growth rate in the laboratory was 13.5%/d from day 2 to day 14; in the pond it was 34%/d over the same interval: an increase of 2.5 fold. RNA:DNA showed an increase of 1.3 to 3.0 in laboratory- versus pond-reared larvae over the same interval with a similar 2.3-fold increase. The negative growth observed in starved larvae at 25°C

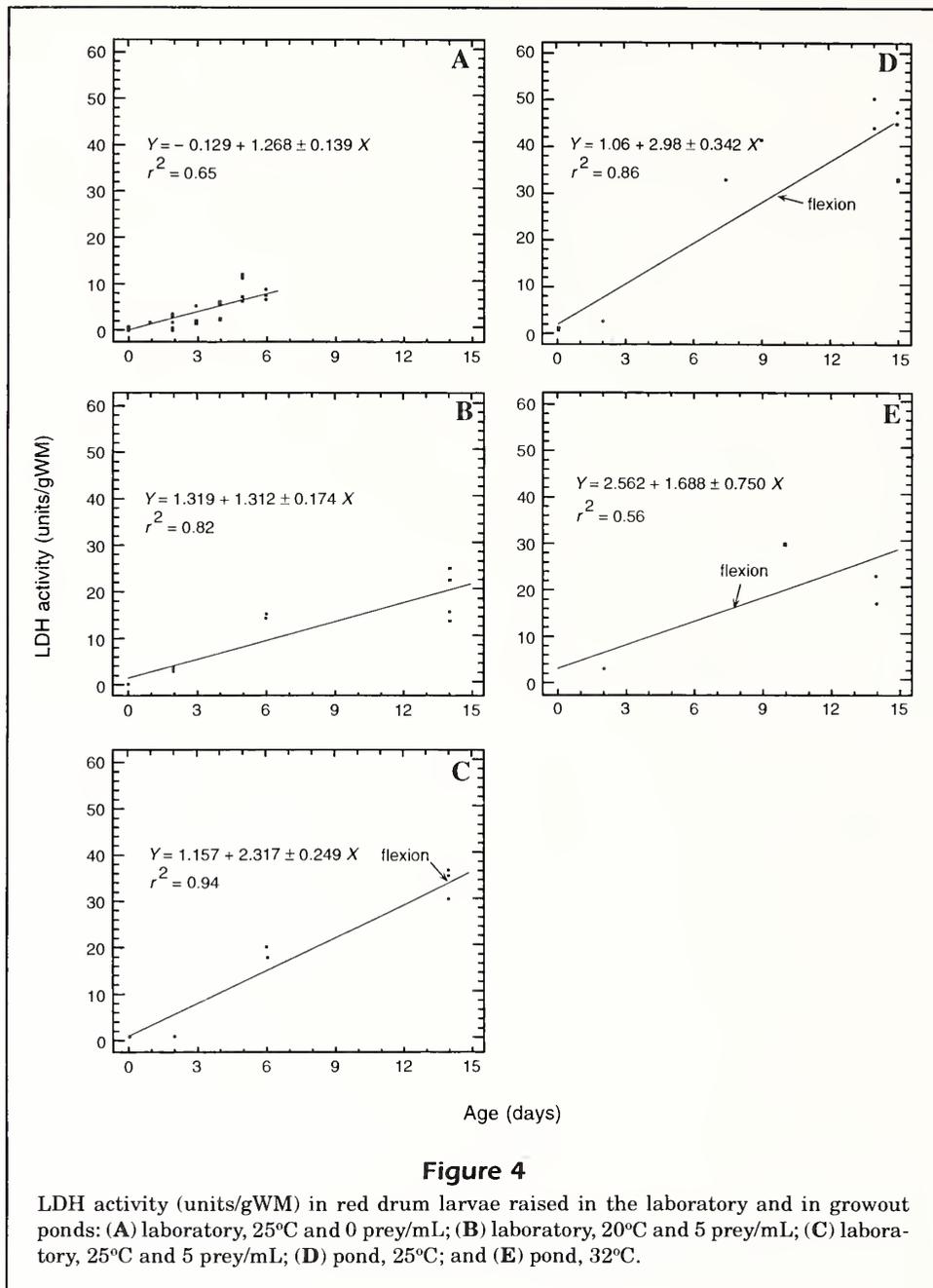


(-18%/d) also showed a much lower value for RNA:DNA ratio : 0.7:1. Differences in RNA:DNA between the three treatments were highly significant (ANOVA: $df=35$, $F=107.6$, $P=0.000$).

Overall, RNA:DNA was only a modest predictor of protein growth. Regression analysis of protein growth (y , % per d) versus RNA:DNA (x), by using all the values in Table 2, showed a marginal fit ($y = -3.64 + 14.76x$; $P=0.01$; $r^2=0.34$). However, as discussed above, within a temperature, RNA:DNA was an excellent predictor of instantaneous protein growth,

and this was borne out in a regression using only the data collected at 25°C: y (% per d) = $-12.43 + 17.39$ (RNA:DNA); $P=0.01$; $r^2=0.64$. The performance of RNA:DNA as an overall predictor was improved significantly by using a multiple regression equation with a temperature term (Table 3).

LDH Activity LDH activities of laboratory-raised larvae increased with age at ration levels of 0 and 5.0 prey/mL and with temperatures of 20°C and 25°C (Fig 4). Larvae that were starved continued to pro-



duce LDH, although at lower concentrations than those for fed individuals, until death at day 6. Larvae reared at 20°C had LDH values of 20–25 units/gWM at day 14. These LDH activities were slightly lower than those for larvae raised at 25°C, which had LDH values of between 30 and 35 units/gWM at day 14. Larvae reared at 25°C in the ponds averaged LDH activities of 40–50 units/gWM, higher than the values for larvae raised at 32°C, which averaged 25–30 units/gWM, and higher than the values for larvae reared in the laboratory.

Like RNA:DNA, LDH activity taken overall was only a modest predictor of protein growth rate: y (% per d) = $-8.17 + 1.39$ (LDH); $P=0.02$; $r^2=0.39$. However, within a temperature, its performance as a predictor was much improved. A regression using only the 25°C data yielded an excellent coefficient of determination: y (% per d) = $-28.74 + 1.94$ (LDH); $P=0.003$; $r^2=0.86$. A multiple regression with a temperature term improved its use as an overall predictor (Table 3).

Table 3

Multiple regressions describing instantaneous protein-specific growth (Y ; %/d) in red drum larvae versus temperature (T), ration (0/ml, 5/mL, and pond), RNA:DNA, and LDH activity (units/gWM). Only significant regressions are presented ($P < 0.05$).

Equation	X_i	X_{ii}	Y	n	r^2	P
1	T		$Y = 2.71X_i - 49.52$	20	0.21	0.023
2	Ration		$Y = 6.35X_i - 8.53$	20	0.45	0.001
3	T	Ration	$Y = 2.07X_i + 5.67X_{ii} - 58.34$	20	0.57	0.022
4	RNA:DNA		$Y = 14.76X_i - 3.64$	17	0.30	0.013
5	T	RNA:DNA	$Y = 2.59X_i + 14.61X_{ii} - 69.41$	17	0.56	0.007
6	LDH		$Y = 1.39X_i - 8.17$	13	0.34	0.022
7	T	LDH	$Y = 2.55X_i + 1.26X_{ii} - 70.35$	13	0.57	0.034

Discussion

Growth versus prey density

Standard length and mass measurements The basic pattern of growth and development in red drum larvae, e.g. in size at flexion, was similar for larvae under a wide variety of rearing conditions. Within the basic blueprint, growth and development of red drum larvae fed to satiation could be accelerated or retarded according to the rearing temperature.

Thus, larvae raised in the laboratory and the ponds underwent metamorphosis at roughly the same size, independent of the age of the larvae. In the case of the 32°C pond, day-7 larvae were already the size of day-14 larvae reared at 25°C in the laboratory, and were at the same stage of development. Similarly, dry mass at transformation was approximately the same in the laboratory and ponds, despite the differences in chronological age.

Proximate and elemental composition of larvae

Red drum larvae, whether fed to satiation or starved, depleted their lipid level from 40% to 50% by day 6. The increase in protein (%AFDM) reflected the decline in lipid and was most evident in the starved red drum larvae. Larvae that have been starved conserve protein as musculature until the time of death. Conservation of muscular proteins allows the animal to swim as long as possible before complete muscle atrophy, or "point of no return," allowing the larvae to search out prey in other, possibly more productive, areas.

The loss of dry mass in starving larvae, compared to fed larvae of equal age, reflected the catabolism of lipid and protein (Wallace, 1986). A similar, but less severe, drop in lipid was observed in all rearing conditions and has been observed in other species of fish.

For example, Fraser et al. (1987) found that larval Atlantic herring had a lipid level of 23% dry mass (176 μg) one day after hatching decreasing to 11% (221 μg) by day 16. Those percentages were similar to those found for red drum larvae in the present study (20.18% to 11.74%) over the first two weeks of life. It is likely that lipid serves as a buffer fuel during the early life history of red drum. It is not accumulated. When high-quality food energy is available in excess, larval red drum larvae grow faster rather than accumulate an energy reserve. This is best exemplified by the differences in larvae growing at 25°C in the laboratory and 25°C in the ponds.

Elemental composition agreed well with other published values for red drum (Lee et al., 1988) and larval herring of similar size (Ehrlich, 1974, a and b; 1975) as well as with our own results on proximate composition (Table 1). Larvae that are growing normally, as in the 5.0 prey/mL experiments and the ponds, show greater increases in protein than in lipid. The increase in %N with age, and the declining %C, mirrored the changes (protein increase, lipid decrease) in proximate composition. This changing elemental composition resulted in a declining C:N in normally growing larvae. Starving individuals had slightly higher C:N than fed individuals as a result of their diminished protein synthesis. Larvae raised in the ponds have the lowest C:N as a result of the high protein levels relative to lipid. Thus, the C:N can be used as an indicator of physiological status in developing fish. It should be noted, however, that this ratio applies in the opposite fashion to adult fish. A declining C:N in older fish indicates starvation where lipid is laid down as an energy reserve and is combusted before protein. The rapidly accumulating musculature of a healthy, growing fish larva results in a declining C:N, giving the appearance of starvation when, instead, this ratio indicates that protein is accumulating at a faster rate than lipid.

Protein-specific growth and biochemical indicators

RNA-DNA ratio Our values for RNA:DNA fall at the low end of the range of ratios reported in the literature for larvae reared under a variety of different conditions (Ferron and Legget, 1994). Wright and Martin (1985) found similar RNA-DNA ratios (1 to 2 at 19–21°C) for starved striped bass, whereas fed striped bass larvae had ratios of 3–3.4 during the first two weeks after hatching. Robinson and Ware (1988) observed a similar trend in RNA-DNA ratios with starvation in the early life of larval Pacific herrings, as we did with red drum; ratios declined up to yolk-sac absorption, where the ratios leveled off. Values for RNA:DNA obtained in the laboratory in this study (1 to 2) were lower than previously reported values (2 to 4) for red drum larvae (Westerman and Holt, 1994).

As has been reported previously (Buckley, 1982; Ferron and Legget, 1994), the relation of growth rate and RNA:DNA changed with temperature. The higher mass-specific and protein-specific growth rates observed in the laboratory at 25°C, in comparison with those at 20°C and in the ponds at 32°C, as well as in comparison with those at 25°C, were accompanied by lower RNA:DNA values (Tables 1 and 2). The inverse relation between RNA:DNA and temperature holds true in field-caught larvae as well. It was observed by Setzler-Hamilton et al. (1987), who found that in late spring, values for RNA-DNA ratios in striped bass larvae were higher than values measured in hotter, early summer months (spring values were about 3 and summer values were 2 to 2.5).

A high growth rate accompanied by a low RNA-DNA ratio, such as we observed in the 32°C ponds, is probably due to an increase in the efficiency of ribosomes in initiating protein synthesis and to an increase in the rate of chain elongation due to a direct effect of temperature, i.e., an increase in the production of protein per unit of ribosomal RNA due to a Q_{10} effect (cf. Westerman and Holt, 1988). Despite the effect of temperature on the relation of RNA:DNA and growth rate, RNA:DNA is a useful tool for determining nutritional status of fish larvae, particularly if it is understood that temperature contributes substantially to the relationship between RNA:DNA and growth (Buckley, 1982; Buckley et al., 1984; Ferron and Legget, 1994).

LDH Activity LDH, the terminal enzyme in vertebrate anaerobic glycolysis, is an important factor in the ability of some fish to produce sudden bursts of swimming and is found in large quantities in white

muscle (Somero and Childress, 1980). The observed increase in LDH activity with age until death of starved larvae seems at first glance to conflict with priorities expected of an energy-deprived individual, in which metabolic processes would be expected to be declining. However, it is to be expected that LDH activity would be conserved, even in starving larvae, so that the muscle would remain functional as long as possible. A larva with no capability for movement would be doomed; thus, a metabolic investment in locomotory capability makes good adaptive sense.

Unlike in RNA:DNA, LDH activity showed a direct correlation with both mass- and protein-specific growth rate in the two fed laboratory treatments despite the increase in temperature from 20°C to 25°C. In the ponds, LDH activities showed an interaction with temperature similar to that seen in RNA:DNA, i.e. a lower specific activity at 32°C despite a higher growth rate. In the case of LDH, the declining activities observed in larvae from the higher temperature pond probably indicate that a lower concentration of enzyme is sufficient to maintain the catalytic efficiency needed by the tissues at the higher temperature (cf. Hochachka and Somero, 1984). The fact that a similar drop was not noted in the laboratory suggests a threshold for the drop in activity between 25°C and 32°C that was not present in the transition between 20°C and 25°C.

Clarke et al. (1992) found similar values for LDH in red drum larvae raised on wild zooplankton. Values for LDH activity in Clarke's study, assuming 87% water content, averaged 19–26 units/gWM for two-week-old larvae, slightly lower than the values we observed in the larvae raised in the laboratory and ponds.

Biochemical parameters as predictive tools

Although similar in their use as biochemical proxies for growth, LDH activity and RNA:DNA are fundamentally different in many other respects. RNA:DNA is a ratio of measured quantities, whereas LDH activity is a determination of a rate: a kinetic measurement. Inherent in the measurement of RNA:DNA is the assumption that the methods for determining the quantities of RNA and DNA are accurate, but there is no direct effect of temperature on the assay itself. For LDH, activities are measured in saturating conditions of substrate, which means that the activities are maximal activities (V_{max} from Michaelis-Menten kinetics; Lehninger, 1982) for each treatment. It is tacitly assumed that if assays are performed in saturating conditions at the same temperature, the differences in activity, or V_{max} , are due to differences in concentration of the enzyme. This assumption is

a reasonable one. It is important, however, to be aware of other potential causes of variability in the relation of both RNA:DNA and LDH activity to growth or condition in fish larvae. It has been demonstrated here and elsewhere (Ferron and Leggett, 1994) that rearing temperature alters the relation of growth and biochemical proxies for growth. Another potential source of variability in the relation is the scaling of each of the proxies with individual size.

RNA:DNA increases slightly with individual size (Buckley, 1982) but overall is insensitive to the changes in individual mass that would be expected in a study of larval fish growth within a single field sample. This is not the case for LDH activity which scales strongly with mass in fishes (e.g. Somero and Childress, 1980; Torres and Somero, 1988). In this study, a significant relation was observed between LDH activity (y , units/gWM) and protein mass (x , μg protein): $y = 2.25x^{0.187}$; $P=0.02$; $r^2=0.43$. RNA:DNA showed no significant change with size. Our study suggests that, for maximum accuracy, direct comparisons of field-caught larvae for LDH activity are best confined to narrow size ranges or the relation between LDH and size is described empirically. On the other hand, it could be argued that since mass-specific LDH activity increases with increasing mass, it is actually incorporating a growth-specific change within its scaling behavior, making it a better proxy. Either way, it shows considerable potential.

Acknowledgments

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Abstract—Historical and retrospective comparisons of Atlantic menhaden virtual population analyses (VPA) from 1955 to 1995 revealed substantial inconsistency in estimates of management variables in the last year of stock assessments. Estimates of management variables from several historical stock assessments were generally consistent throughout most of the time series. In the last two years, however, historical estimates have deviated from revised estimates. Relative performance of alternative ad hoc methods for estimating fully recruited fishing mortality (F) in terminal years showed that all methods were imprecise, but conventional catch-curve estimates were unbiased and had the least retrospective inconsistency. Retrospective differences in terminal estimates of age-1 F by separable VPA ranged widely for eight alternative settings but were clearly minimized by using seven years of catch data. The general magnitude of retrospective difference was ± 1.2 billion recruits (46% relative difference), $\pm 9,000$ metric tons of spawning stock biomass (33% relative difference), and ± 4.7 percent maximum spawning potential (106% relative difference). Retrospective differences in recruitment, spawning stock biomass, and spawning potential were positively skewed but not biased, indicating that the frequency of positive and negative inconsistencies are equal but that the positive differences are much greater in magnitude. The skewed distribution of retrospective inconsistency should be considered for managing the Atlantic menhaden fishery.

Retrospective analysis of virtual population estimates for Atlantic menhaden stock assessment

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The Atlantic menhaden, *Brevoortia tyrannus*, is a planktivorous clupeid that schools in coastal waters off the east coast of the United States. Atlantic menhaden dominated total U.S. fishery landings from 1946 to 1962 (Ahrenholz et al., 1987), yielding approximately 600,000 metric tons (t) per year 1953–62 (Henry, 1971), after which landings steadily declined to 162,000 t in 1969 owing to recruitment failure and subsequent overfishing. Since then, catch has increased to an average of 330,000 t per year 1970–95 (AMAC, 1992).¹ The Atlantic menhaden fishery is currently managed according to six fishery and population thresholds that indicate overfishing in relation to historic production (AMAC, 1992). Three of the minimum population thresholds (2 billion recruits, 17,000-t spawning stock biomass, and 3% maximum spawning potential) are derived from virtual population analysis (VPA) (Megrey, 1989).

Atlantic menhaden landings have been reported from processing plants since 1940 and have been sampled for length, weight, and age since 1955 according to a two-stage cluster sampling design in which fish were sampled weekly from each port where menhaden were pro-

cessed (Nicholson, 1975; Chester, 1984; Smith et al., 1987). The frequency of fishery samples and the consolidated nature of the fishery provide an extremely reliable 41-year series of catch at age, ages 0–6+, for estimation of abundance and mortality through VPA (Table 1). Unfortunately, no independent indices of relative abundance are available to calibrate abundance estimates for the last year of catch: commercial catch per unit of effort is a biased index because commercial catchability is inversely related to abundance (Schaaf, 1975; Ahrenholz et al., 1987; Vaughan and Smith, 1988; Atran and Loesch, 1995) and fishery-independent survey indices are not correlated with abundance (Ahrenholz et al., 1989). In the absence of reliable abundance indices, and therefore of a formal statistical estimator for year-class abundance in the last year of the VPA, ad hoc estimation rules have been used to approximate abundance.

The error in estimates of abundance is progressively less in previous years than in the last year of

¹ 1992–95 landings from Joseph Smith, Beaufort Laboratory, National Marine Fisheries Service, Beaufort, NC. Personal commun.

Table 1

Age-based stock assessments of Atlantic menhaden. Y_t indicates the terminal year the VPA.

Y_t	Source
1976	AMMB, 1981; Powers, 1983
1981	Vaughan et al., 1986; Ahrenholz et al., 1987
1984	AMMB, 1986; Vaughan and Smith, 1988
1988	Vaughan, 1990; Vaughan and Merriner, 1991
1990	AMAC, 1992 (p. 40-50); Vaughan, 1993
1992	AMAC, 1992 (p. 17-30)
1993	Vaughan, 1994 ¹
1994	Vaughan, 1995 ¹
1995	Vaughan, 1996 ¹

¹ Vaughan, D. S. Trigger variables for Atlantic menhaden. Natl. Mar. Fish. Serv., NOAA, Unpubl. AMAC reports.

Methods

Historical comparisons

Three Atlantic menhaden management variables derived from VPA (age-1 abundance [R], spawning stock biomass [SSB], and percent maximum spawning potential [%MSP]) were compared among ten reported stock assessments (Table 1). The number of historical estimates of each variable differed because some reports did not document all three population estimates.

Consistency of successive stock assessments was measured by comparing historical estimates with revised estimates (from the 1995 VPA), which are more reliable. Inconsistency may result from historical estimation error or inaccurate estimates for prior years in the current VPA (Sinclair et al., 1990). The population thresholds used to define overfishing are subject to some uncertainty because they are also VPA estimates; but they are converged estimates, which are much more certain than current estimates. In comparing current VPA estimates with these overfishing thresholds for an annual assessment of stock status, converged and current estimates are assumed to be consistent. Estimates in the last year (Y_t), and back-calculated years (Y_{t-1} , Y_{t-2} , etc.) were compared with the time series of estimates derived in 1995. Differences between historical estimates and revised estimates were calculated as follows:

$$\Delta R_{t,t+k} = R_{t,t+k} - R_{t,1995}$$

where $R_{t,1995}$ = the most recent estimate of recruitment in year t ;

$R_{t,t+k}$ = recruitment in year t as estimated when $t+k$ was the last year in the assessment; and

k = is the retrospective lag between year t and the last year of the historical VPA.

For example, $R_{1990,1993}$ is the 1993 estimate of 1990 recruitment, which has a three-year retrospective lag (i.e. $k=3$). When $k=0$, $R_{t,t}$ is an estimate of recruitment for the last year in an assessment and is referred to as a terminal estimate. Historical differences in SSB and %MSP were similarly calculated:

$$\begin{aligned} SSB_{t,t+k} &= SSB_{t,t+k} - SSB_{t,1995} \\ \Delta \%MSP_{t,t+k} &= \%MSP_{t,t+k} - \%MSP_{t,1995} \end{aligned}$$

Root mean square (RMS) difference was used as a measure of dispersion of historical estimates from

the VPA, provided that catch at age and natural mortality (M) are well estimated and fishing mortality (F) is at least moderate (Jones, 1961; Tomlinson, 1970; Pope, 1972; Ulltang, 1977; Megrey, 1989). As stated in the Atlantic menhaden fishery management plan, "Trigger estimates for recent years from VPA are subject to large uncertainty, while estimates 2 to 3 years old are more reliable" (AMAC, 1992). Consistency in successive stock assessments can be evaluated by using "historical analysis," which compares estimates from the most recent assessment with contemporary estimates from prior stock assessments (Sinclair et al., 1985),² but historical assessments of the menhaden stock were not conducted with a common estimation rule. Consistency of the current estimation rule can be evaluated by using "retrospective analysis," which recreates a historical series of VPA's with a single estimation rule (Sinclair et al., 1990).²

The first objective of the current investigation was to report the general magnitude and potential bias of retrospective differences for guidance on interpreting current estimates and for providing fishery management advice. The second objective was to attempt alternative estimation rules to improve consistency of estimates.

² Examples of historical and retrospective analyses, interpretation, and discussion can also be found in the following two references:

Int. Counc. Explor. Sea. 1991. Report of the working group on methods of fish stock assessments. ICES Council Meeting Assess., p. 25.

Northeast Fisheries Science Center. 1994. Report of the 18th Northeast Regional Stock Assessment Workshop (18th SAW). NEFSC Ref. Doc. 94-22.

converged estimates for the additive properties of mean square difference. Sample sizes for historical differences were low, because of the limited number of historical stock assessments, but the following retrospective analyses have greater sample size for estimating RMS difference ($n > 30$).

Retrospective comparisons

Retrospective analysis was performed in two stages to investigate consistency of both elements of the estimation rule: 1) estimation of fully recruited F by ad hoc methods and 2) estimation of partial recruitment to the fishery at ages 0 and 1 by separable VPA (SVPA; Pope and Shepherd, 1982). Both analytical stages assumed that menhaden were fully recruited to the fishery at age 2 and that M was 0.45 for all ages, over the entire time period.

Fully recruited F was approximated by using three alternative ad hoc methods for the first element of the analysis. Conventional catch curves (Beverton and Holt, 1957; Ricker, 1975; Gulland, 1983) and modified catch curves (Chapman and Robson, 1960; Robson and Chapman, 1961) were used to estimate mortality of the age-5 cohort over the four terminal years of the catch record (i.e. ages 2–5). These two catch-curve methods assumed that F in the current year was similar to F experienced by that cohort over the previous three years. The third ad hoc method, log catch ratios (Ricker, 1975; Gulland, 1983), derived fully recruited F from the negative log ratio of age-3+ abundance in the terminal year to age-2+ abundance in the previous year and assumed that F in the last year was similar to F in the previous year. All three ad hoc methods assume that menhaden are fully recruited and equally available to the fishery at age-2+, which was confirmed through inspection of back-calculated F from the 1995 VPA.

The second element of the assessment, estimation of partial recruitment, was performed by using SVPA on a fixed number of years. For example, a retrospective series of 5-year SVPA's was produced with the following algorithm.

- Step 1 SVPA was run on an initial time series of catch-at-age data (e.g. 1955–60) with the appropriate estimate of fully recruited F in the terminal year.
- Step 2 Catch data in the starting year (e.g. 1955) were deleted, and catch data from a new terminal year (e.g. 1961) were appended.
- Step 3 SVPA was rerun on the revised time series with the appropriate estimate of fully recruited F in the new terminal year.

Steps 2 and 3 were repeated until 1995 was the terminal year.

Significance of retrospective bias was tested with a conventional t -ratio test (H_0 : mean difference=0). Normality was tested by using the Shapiro and Wilk (1965) method. Results of t -ratio tests were confirmed by using nonparametric chi-square and sign tests. Dispersion of retrospective estimates from converged estimates was compared among alternative assessment rules by using RMS of retrospective differences. Retrospective estimates of fully recruited F in terminal years were compared with back-calculated estimates of fully recruited F from the 1995 VPA, as the average of ages 2–5 (weighted by abundance), to derive retrospective differences:

$$\Delta F_{t,t} = F_{t,t} - F_{t,1995}$$

Note that there is no k subscript, as there were in the formulae for historical comparisons, because all retrospective estimates of fully recruited F were for terminal years (i.e. $k=0$). The relative retrospective difference ($\Delta F_{t,t}/F_{t,1995}$) was also calculated to remove the magnitude of the estimate from estimates of general inconsistency.

Back-calculated estimates of fully recruited F from the 1995 VPA were used in terminal years to compare retrospective inconsistency of SVPA settings without including retrospective inconsistency from ad hoc estimates of terminal F . The fixed number of years in each series of retrospective SVPA's was varied from three to ten years by using the algorithm described for the five-year example above. Retrospective consistency was compared among the eight series of retrospective SVPA's according to RMS difference of age-1 F estimates. Full recruitment of age-2 and oldest age (6+) menhaden was confirmed through inspection of back-calculated F at age from the 1995 VPA and was not adjusted for retrospective comparison.

Final SVPA runs were performed with seven years of catch-at-age and catch-curve estimates of terminal F to emulate more realistic inconsistency and describe the general magnitude and direction of retrospective differences. Retrospective estimates of R were derived directly from SVPA terminal estimates of age-1 abundance. SSB was estimated from terminal SVPA estimates of age-3+ abundance and estimated weight at age of spawners. Percent MSP was calculated according to egg production per recruit (Vaughan, 1990; AMAC, 1992). Retrospective differences and relative differences of management variable estimates were log transformed [e.g. $\log_e (R + \text{constant})$] to test bias, and geometric mean square was used to estimate mean square difference because differences had skewed distributions.

Results

Historical comparisons

Management variable estimates from past stock assessments were generally consistent throughout most of the time series, except for the last two years

of each assessment, when some historical estimates deviated from revised estimates from the 1995 VPA (Fig. 1). Terminal estimates of age-1 abundance were greater than revised estimates for five assessments and less than revised estimates for three assessments, but positive historical differences (i.e. historical estimate > revised estimate) were greater. For ex-

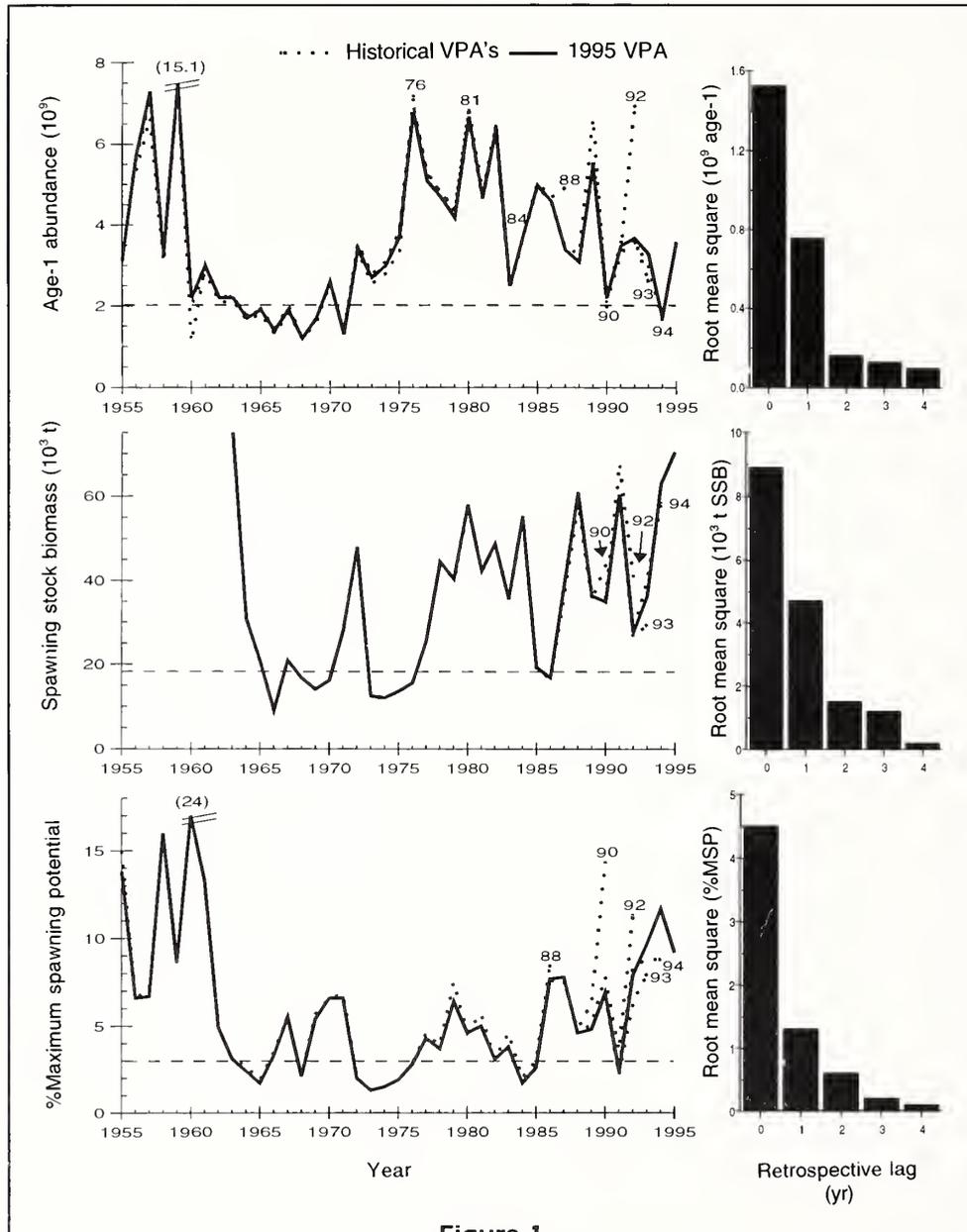


Figure 1

Comparison of historical estimates of Atlantic menhaden recruitment, spawning stock biomass, and percent maximum spawning potential. In the left charts, terminal years of historical stock assessments are labeled at the end of each series, overfishing thresholds are indicated by broken horizontal lines, and values in parentheses are not plotted. Convergence of estimates is illustrated by reduction in root mean square of historical differences over time in the charts on the right.

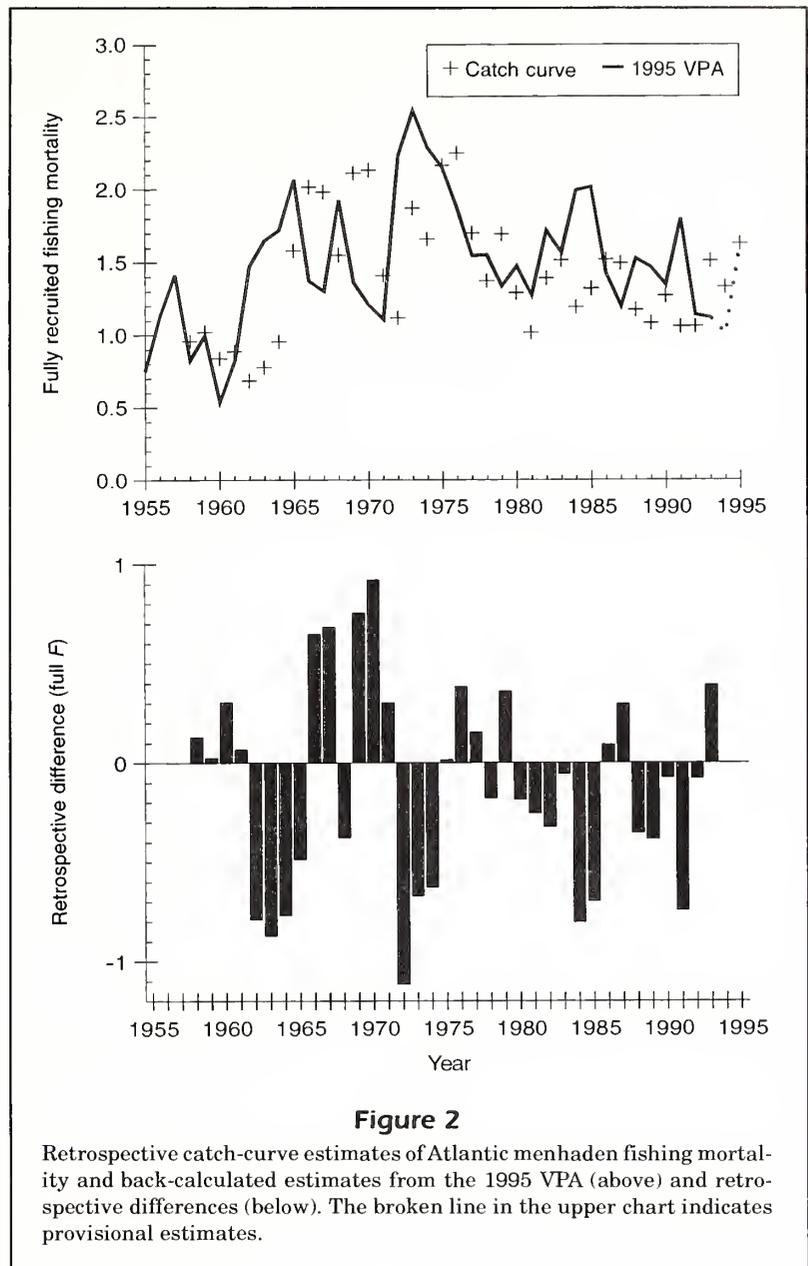
ample, in 1992, recruitment was estimated to be 3.4 billion greater than the 1995 estimate of 1992 recruitment. Estimates converged to within 160 million recruits of 1995 VPA estimates, when the retrospective lag (k) was greater than one year.

Only five terminal estimates of SSB and %MSP were available, including 1995 estimates. Two historical estimates of SSB were greater than revised estimates and two were less than revised estimates. Historical estimates of SSB converged to within 1,500 t of 1995 VPA estimates when $k > 1$ year.

Historical estimates of %MSP were greater than revised estimates for three assessments and less than revised estimates for two assessments. The 1992 estimate of 1991 %MSP (i.e. backcalculated one year) was 3.6, but subsequent estimates of 1991 %MSP were below the overfishing threshold of 3 %MSP. Therefore, an overfishing trigger fired, but it was not detected until two years later. Estimates of %MSP converged to within 0.6 of 1995 VPA estimates when $k > 1$ year.

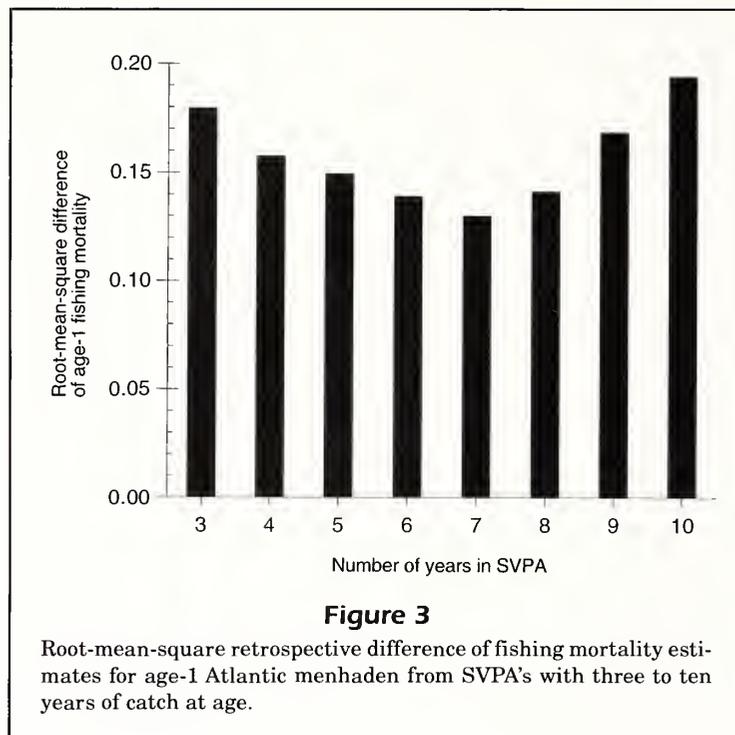
Retrospective comparisons

Conventional catch curves produced the most consistent estimates of fully recruited F among the three ad hoc methods used. Retrospective differences from catch-curve estimates in terminal years ranged from -1.12 to 0.92 (Fig. 2). The RMS difference was 0.51 and the RMS relative difference was 33% ($n=36$). The mean retrospective difference in fully recruited F was not significantly different from zero. Therefore, although terminal estimates were imprecise, they were not biased. Retrospective differences in catch-curve estimates were negatively correlated with back-calculated F from the 1995 VPA ($r=-0.62$) (i.e. when F was low, catch-curve estimates were generally greater than revised estimates; when F was high, catch-curve F was generally less than the revised estimate). Retrospective differences in fully recruited F produced opposite inconsistencies in SSB and %MSP. For example, in 1993, catch-curve F was greater than the revised F (Fig. 2), and initial VPA estimates of SSB and %MSP were less than revised estimates (Fig. 1). Alternative methods of estimating fully recruited F produced even greater incon-



sistency. The RMS retrospective difference from modified catch curves was 0.60 (49% relative difference), and log catch ratios produced a RMS difference of 0.61 (52% relative difference) ($n=36$ for both methods).

Retrospective differences in estimates of age-1 F from SVPA ranged from -0.59 to 0.45 for all retrospective SVPA's and were not significantly different from zero ($n=31$ for each series). RMS difference was minimized when seven years of catch-at-age data were used and increased regularly as the number of years deviated from seven (Fig. 3). The RMS retrospective difference for estimates of age-1 F was



0.13 (33% relative difference) with back-calculated values of fully recruited F and increased to 0.18 (45% relative difference) with catch-curve estimates (Fig. 4).

Retrospective differences in age-1 abundance ranged from -2.4 billion to 11.5 billion individuals in terminal years (Fig. 5). There was no significant bias in log-transformed differences, and the RMS difference was 1.2 billion recruits ($n=34$). The RMS relative difference for estimates of age-1 abundance was 46%.

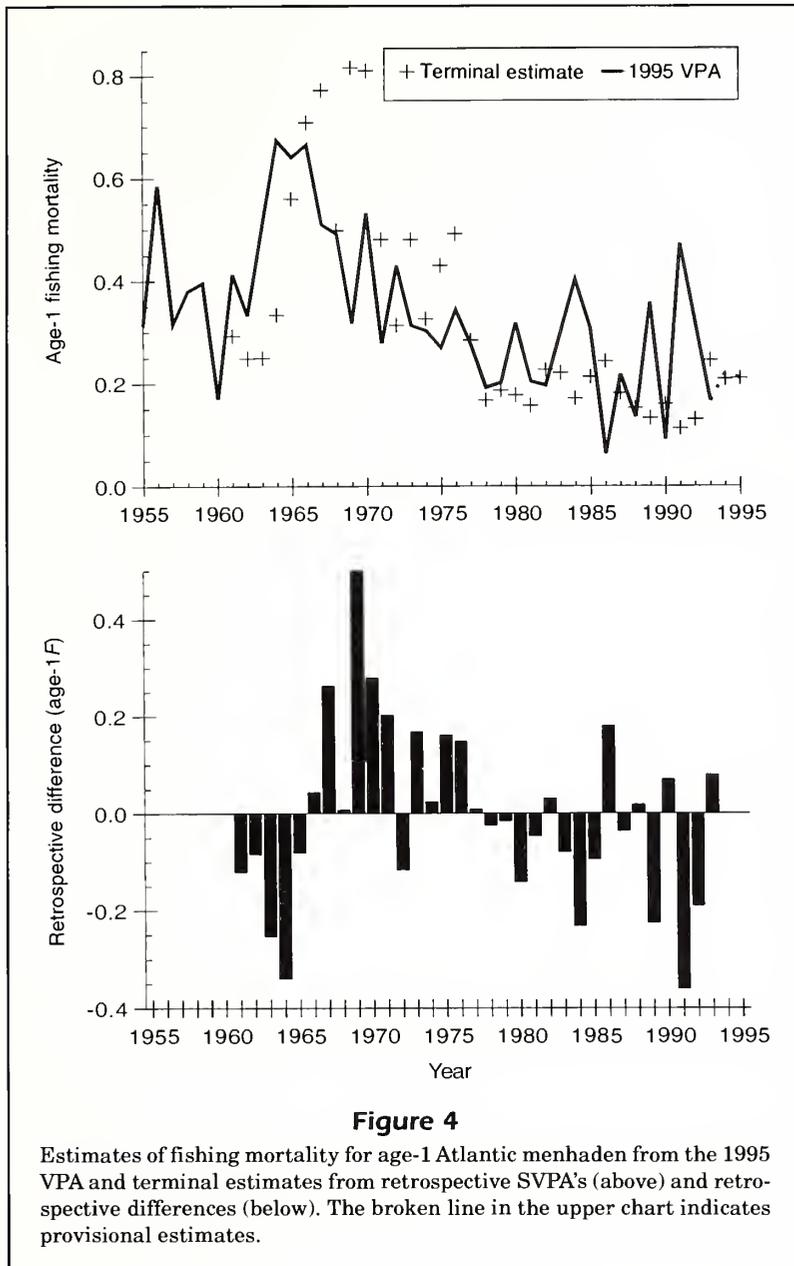
Retrospective differences in terminal SSB estimates ranged from $-72,000$ t to 448,000 t (Fig. 6). The large positive differences in 1962 and 1963 SSB were primarily due to large negative differences in fully recruited F (Fig. 2). Log-transformed retrospective differences were not significantly biased, and the RMS difference was 9,000 t SSB ($n=34$). The RMS relative difference for estimates of SSB was 33%. Retrospective differences in %MSP ranged from -5.5 to 19.5 in terminal years (Fig. 7).

The RMS difference was 4.7 %MSP, and there was no significant bias in log-transformed differences ($n=34$). The RMS relative difference for estimates of %MSP was 106%, because inconsistencies were larger than the estimated level of %MSP. Retrospective differences in %MSP were negatively correlated with retrospective differences in fully recruited F ($r=-0.79$).

Discussion

This case study illustrates how retrospective comparisons can provide useful data for analytical decisions and reveal important insights for management advice, especially in situations where statistical estimates of uncertainty are not available. For example, SVPA with seven years of catch data clearly provided more consistent results than SVPA of longer or shorter time series (Fig. 3). A time period of seven years appears to be long enough to smooth annual variation in partial recruitment, while including only years which represent the current schedule of F at age. By including more years in the analysis, there is a likelihood that catches from substantially different exploitation patterns will be incorporated. Performance of alternative intervals of catch data was judged according to general conditions over three decades. Although such guidance is valuable, specific SVPA runs should be examined to confirm the assumption of separability. For example, targeting specific cohorts, such as the superabundant 1958 year class, may change fishing patterns. Abrupt changes should be reflected in patterns of log catch-ratio residuals (Pope and Shepherd, 1982) and may necessitate a longer or shorter time series of catch at age for SVPA.

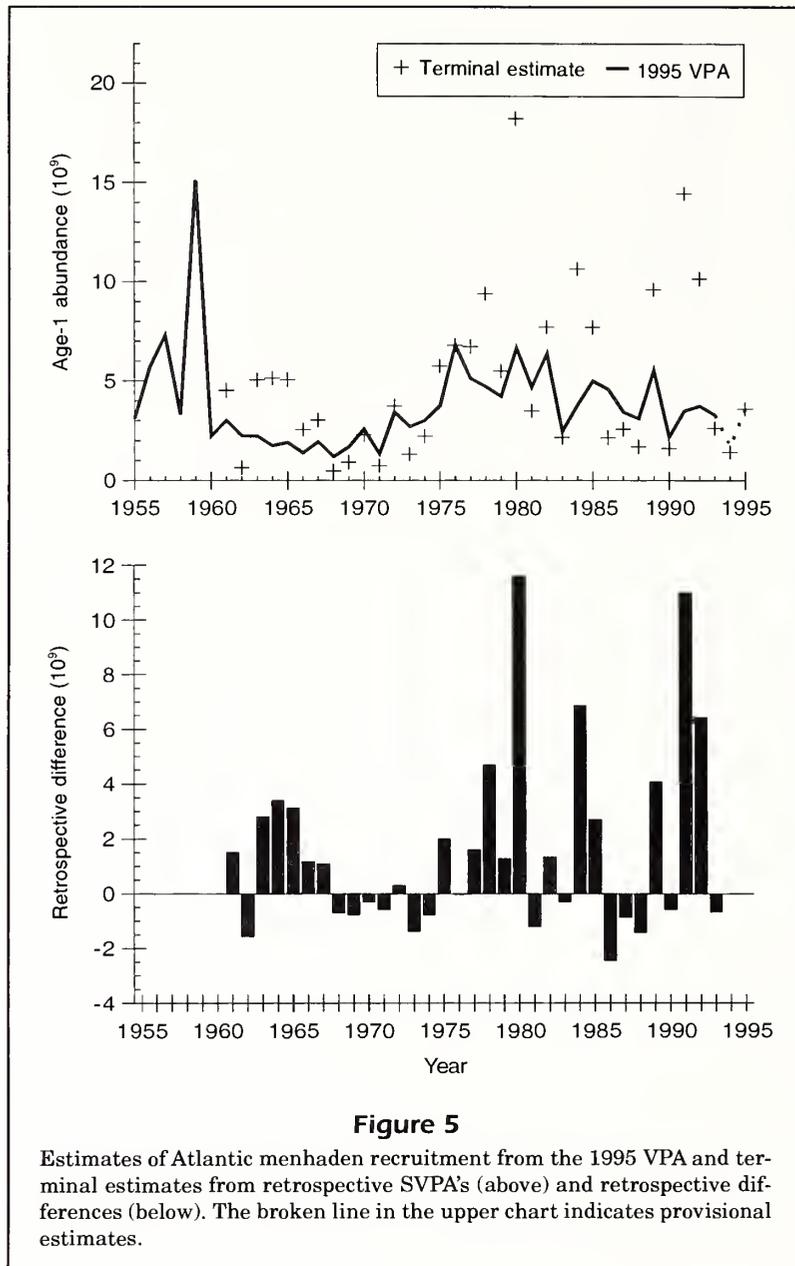
Retrospective inconsistency can result from a host of systematic problems, including errors in the cur-



rent VPA (Sinclair et al., 1990). For example, Lapointe et al. (1989) simulated Atlantic menhaden catch for VPA's to show that 50% underestimates of M produced 12% overestimation of recruitment and 6% overestimation of biomass and that overestimation of M produced similar underestimates of recruitment and biomass. Therefore, the assumption that M is constant when M varies among years and ages may cause VPA inconsistency. It appears that the inability to estimate fully recruited F accurately in terminal years accounts for a substantial portion of the retrospective differences in management variables reported here. Inaccurate estimates of terminal

F may result from abrupt changes in F or M . Catch-curve estimates of terminal F are not sensitive to changes in current mortality because they reflect the average mortality over the last three years more than mortality in the terminal year.

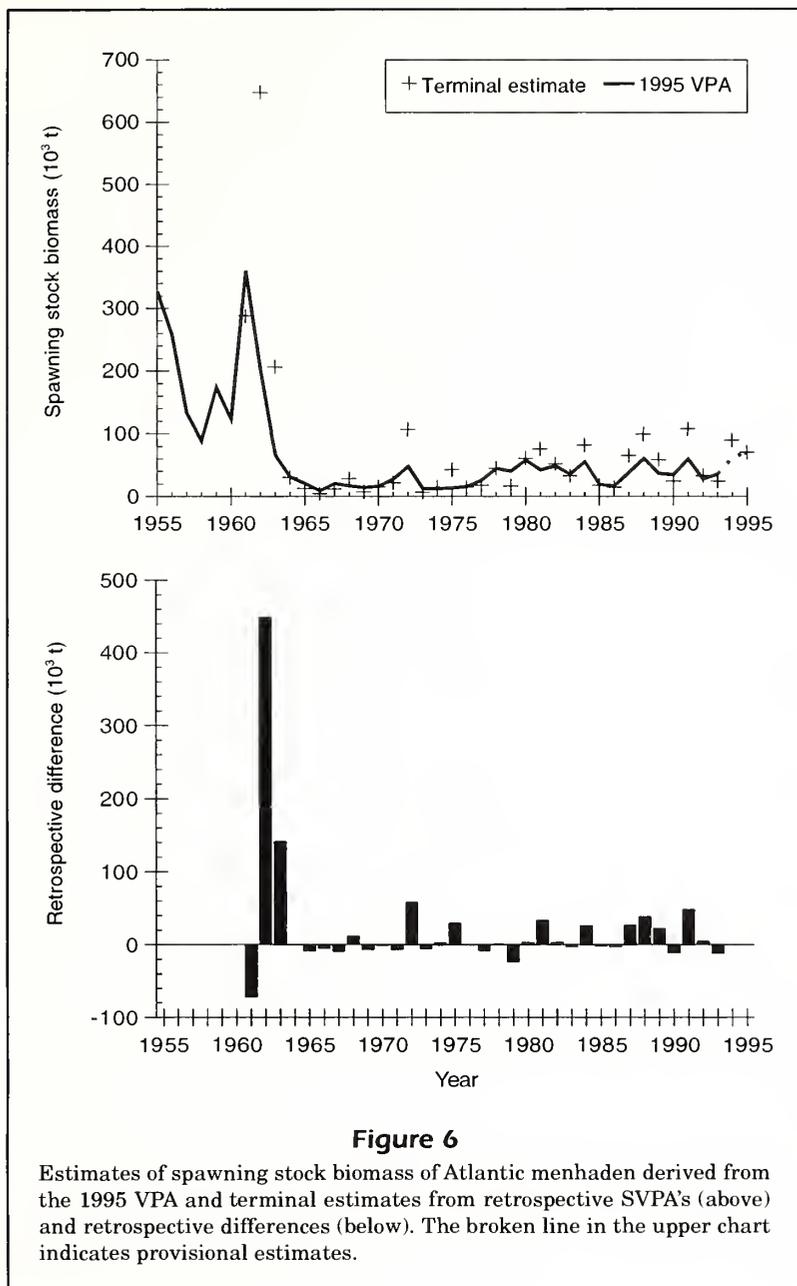
Retrospective differences in management variables were positively skewed, and log transformation was necessary to test for bias. Skewed retrospective differences with no bias imply that positive and negative differences occur with equal frequency, but positive differences are generally greater in magnitude. Theoretically, normally distributed errors in F will produce lognormally distributed errors in R ,



SSB, and %MSP because they are based on estimated abundance, biomass, and egg production, respectively, which have a negative exponential relation with fishing mortality. Therefore, small underestimates in F can produce large overestimates of abundance. Retrospective differences may also be skewed because negative values of R , SSB, and %MSP are not possible. Despite the conclusion that log-transformed retrospective differences were not biased, the positive skewness of retrospective differences and relative differences has important implications for management of the fishery. A skewed distribution of

inconsistency from converged estimates may be considered a characteristic feature of terminal estimates from future menhaden VPA's. Therefore, management advice should account for the equal likelihood of moderate underestimation and substantial overestimation of R , SSB, and %MSP.

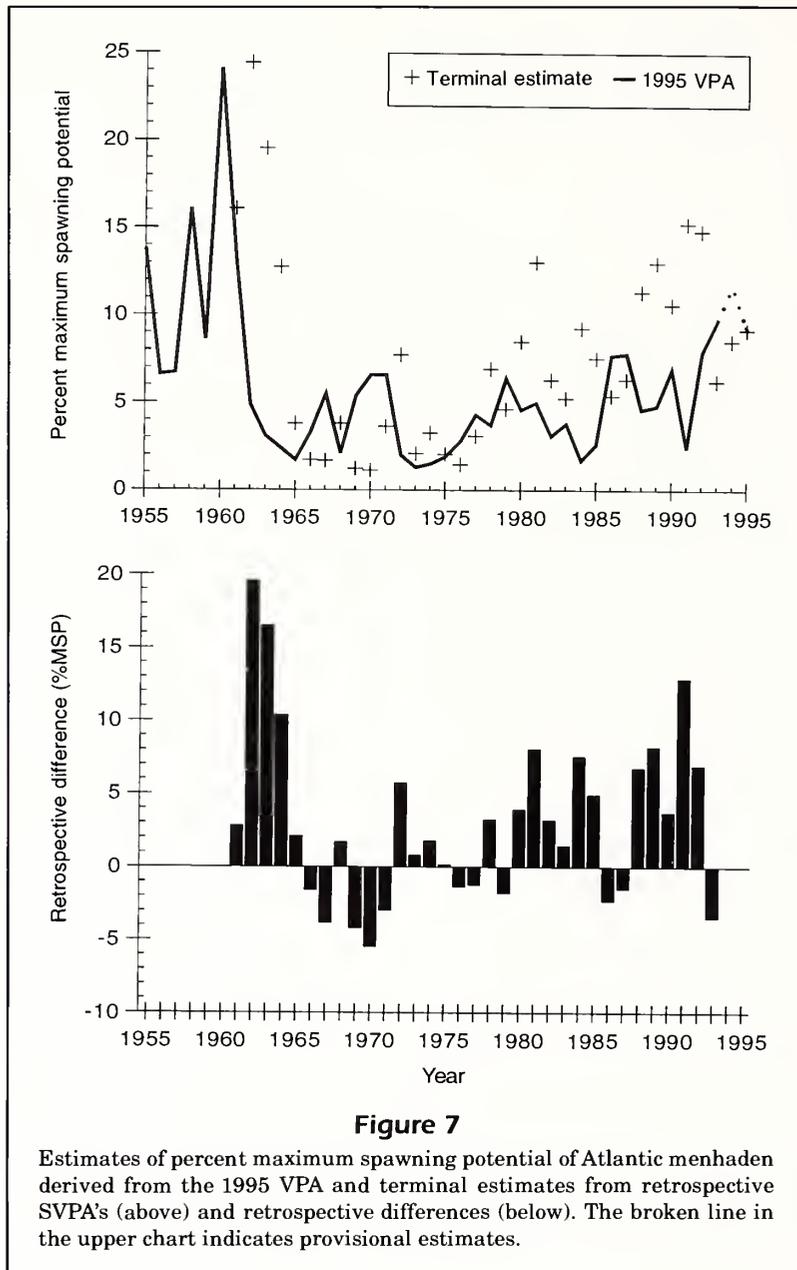
Management decisions must consider the difference between converged estimates, which are used to define overfishing thresholds, and terminal estimates, which are used to determine current status. Although inconsistency does not quantify uncertainty of estimates, the large retrospective differences re-



ported here suggest large uncertainty in terminal estimates. Fredrick and Peterman (1995) simulated uncertainty in Atlantic menhaden VPA's to show that much more conservative overfishing thresholds would be needed to incorporate high levels of uncertainty into risk-averse management decisions. An alternative to incorporating uncertainty adjustments is to make management decisions based on converged estimates that indicate conditions of two years earlier (AMAC, 1992). If more timely management is desirable, methods to calibrate terminal estimates of abundance are necessary.

Acknowledgments

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Abstract.—We examined 528 bonefish to estimate length and age at sexual maturity and to describe seasonal patterns in gonadal development. These fish ranged from 21 to 702 mm fork length (FL) and were collected in South Florida waters from 1989 to 1995. Gonads of 437 bonefish were examined histologically, and gonadosomatic indices (GSI) were calculated for 449 bonefish. Male bonefish reached 50% sexual maturity (the predicted size and age at which half the individuals are expected to be sexually mature) at 418 mm FL (95% confidence interval 393–443 mm) and an age of 3.6 years (95% confidence interval 3.3–3.9 years). Females reached 50% sexual maturity at 488 mm FL (95% confidence interval 472–504 mm) and 4.2 years (95% confidence interval 3.9–4.6 years). Lengths and ages at 50% maturity for males and females were significantly different. The smallest sexually mature male was 425 mm FL, and the smallest sexually mature female was 358 mm FL. The youngest sexually mature male was 3 years old, and the youngest sexually mature female was 2 years old. Gonadal activity was seasonal and peaked during November–May. Vitellogenic oocytes were present in ovaries in every month except August and September and were most abundant during November–May. Median GSI's were greatest during November–May and least during July–September for both males and females. No fully hydrated ovaries or postovulatory follicles were found, therefore we could not estimate spawning periodicity or batch fecundities. Total fecundity ranged from 0.4 to 1.7 million oocytes and had a significant positive relation to fish weight. The absence of fully hydrated ovaries and postovulatory follicles in the bonefish we sampled suggests that bonefish spawn outside the traditional shallow-water (<2 m) fishing grounds in the Florida Keys.

Maturation and reproductive seasonality in bonefish, *Albula vulpes*, from the waters of the Florida Keys

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Bonefish, *Albula* spp., frequent coastal and inshore waters of tropical seas worldwide and are the basis of economically important recreational fisheries in many areas of their range. Although 23 nominal *Albula* species have been described (Whitehead, 1986), only two Atlantic species, *A. vulpes* and *A. nemoptera*, are recognized (Rivas and Warlen, 1967). In the western Atlantic, *A. vulpes* is common in the Florida Keys, the Bahama Islands, and throughout the Caribbean Sea (Hildebrand, 1963). *Albula nemoptera* appears to have a more restricted distribution than *A. vulpes* and has been reported from the Guianas, Venezuela, Columbia, Panama, Jamaica, and Hispaniola (Rivas and Warlen, 1967; Uyeno et al., 1983). The single record of *A. nemoptera* from Florida waters is considered questionable (Robins and Ray, 1986), and the species has not been reported from the Bahama Islands (Böhlke and Chaplin, 1993).

Bonefish are esteemed for their wariness and fighting abilities, and fishing for them provides an important source of income to Florida Keys and Bahamian fishing guides. Commercial sale of bonefish in Florida is prohibited, and regulations on the recreational fishery restrict catches to one fish per angler per day and the length of captured fish to a minimum total length of

457 mm (390 mm fork length). Most bonefish caught in Florida waters are released.

The life history of bonefish has not been adequately described. Crabtree et al. (1996) described the age and growth of bonefish from South Florida and found that bonefish can attain ages of 19 years. Female and male growth models were significantly different; females were slightly longer than males of the same age. Although the age and growth of Florida Keys bonefish have been studied, important questions remain regarding bonefish reproduction. Bruger (1974) reported sexually mature females as small as 210 mm standard length (221 mm fork length) and as young as 1 year from waters off the Florida Keys, but his sample size was inadequate to determine the age or length at 50% maturity (the predicted size and age at which half the individuals are expected to be sexually mature). Bruger found ripe female bonefish throughout the year in waters off the Florida Keys and concluded that reproduction was not seasonal, but his sample size was small ($n=148$) and his conclusions equivocal. In other areas, bonefish reproduction appears to be seasonal according to patterns of larval and juvenile abundance (Alexander, 1961; Pfeiler, 1984; Pfeiler et al., 1988; Mojica et al., 1995). There

is also no published information on bonefish fecundity. In this article, we estimate the age and length at which sexual maturity is attained and describe the seasonal cycle of gonadal development in bonefish from waters off the Florida Keys. We also estimate the total fecundity of 33 bonefish collected from these waters.

Methods

Sampling

We examined 528 bonefish collected from South Florida waters from February 1989 to April 1995. Most of these bonefish were caught with hook-and-line gear either by biologists or by a single professional bonefish guide and his anglers from waters off the Florida Keys and in Florida and Biscayne Bays. Five bonefish caught with hook-and-line gear were obtained from taxidermists in Fort Lauderdale and five others from tournaments in the Keys. Supplemental collections of small bonefish (<425 mm) were made with various-size seines and gill nets in waters off the Keys. Ages, based on validated sectioned otoliths and growth rates of these bonefish, were described by Crabtree et al. (1996).

Fork length (FL) was measured to the nearest millimeter (mm), and fish were weighed to the nearest gram. Sex, gonad condition, and gonad weight (g) were recorded. Gonad samples for histology and for estimation of fecundity were removed from the fish and preserved in 10% buffered formalin; they were later soaked in water for one hour and then stored in 70% ethanol. Histological sections of gonads from 437 bonefish ranging from 228 to 702 mm were prepared and assessed for reproductive state. Gonad samples were processed histologically with a modification of the periodic acid Schiff's (PAS) stain for glycol-methacrylate sections, with Weigert's iron-hematoxylin as a nuclear stain and metanil yellow as a counterstain (Quintero-Hunter et al., 1991).

Oocyte staging

Oocytes were staged and counted from histological preparations at 100 \times with a compound microscope attached to a digital image-processing system. Three oocyte stages were recognized in bonefish ovaries: primary growth, cortical alveolar, and vitellogenic (Wallace and Selman, 1981; Fig. 1A). In addition, we counted PAS-positive melanomacrophage centers (Ravaglia and Maggese, 1995), which were present in many ovaries (Fig. 1B). When stained with the

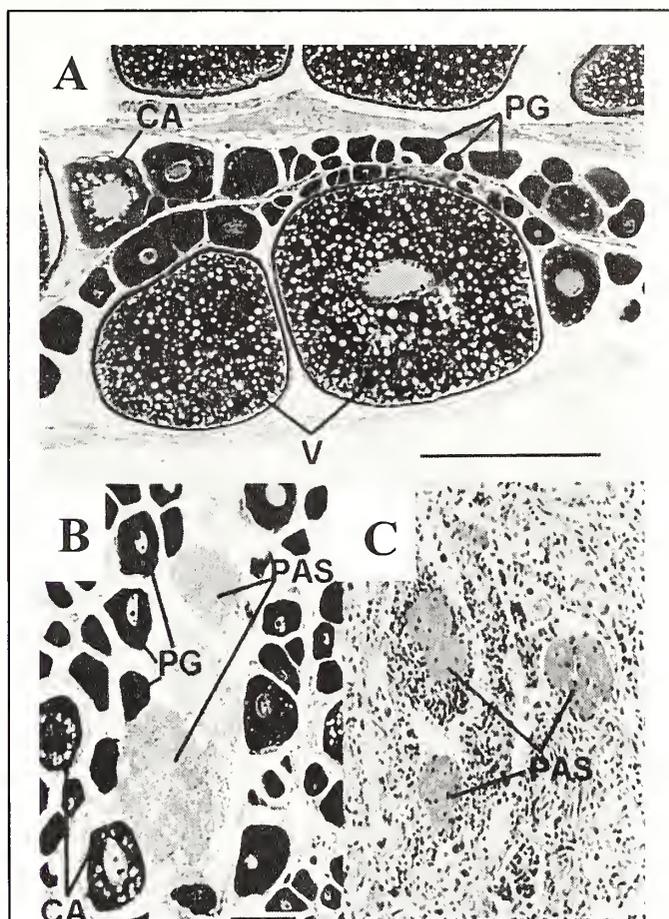


Figure 1

(A) A histological section from an ovary of a 677-mm-FL bonefish, *Albula vulpes*, showing oocyte stages. PG = primary growth oocytes, CA = cortical alveolar oocytes, and V = vitellogenic oocytes. Scale bar = 400 microns. (B) A histological section showing PAS-positive melanomacrophage centers (PAS), cortical alveolar oocytes, and primary growth stage oocytes in a regressed ovary from a 692-mm-FL bonefish. When stained with periodic acid Schiff's stain, melanomacrophage centers are brilliant purple. Scale bar = 100 microns. (C) A histological section showing PAS-positive melanomacrophage centers in a regressed testis from a 586-mm-FL bonefish. Scale bar = 50 microns.

PAS stain, these structures are brilliant purple. Melanomacrophage centers are thought to be active in degrading atretic oocytes, postovulatory follicles, and residual cells of the spermatogenic cycle (Chan et al., 1967; Ravaglia and Maggese, 1995). At least 300 combined oocytes and melanomacrophage centers per slide were staged and counted in arbitrarily chosen fields, and frequencies were expressed as a percentage of the total count. We counted all structures that had at least 50% of their area visible in a field before moving to the next field. The presence of atretic hydrated oocytes was also noted.

Length and age at sexual maturity

Females were considered sexually mature if vitellogenic oocytes were present or if the histological sections appeared disorganized, highly vascularized, and contained widespread evidence of atresia. Documentation of atresia followed the classification of Hunter and Macewicz (1985). Immature females had small (gonadosomatic index <0.35), well-organized gonads that contained little evidence of atresia. We interpreted the widespread occurrence of PAS-positive melanomacrophage centers in inactive ovaries as evidence of past gonadal development, and we considered bonefish that had regressed (no vitellogenic oocytes present) ovaries containing many of these structures to be sexually mature (Fig. 1B). Males were considered sexually mature if the testes contained evidence of ongoing spermatogenesis, residual sperm, or widespread PAS-positive melanomacrophage centers associated with gonadal recrudescence (Fig. 1C).

Sometimes distinguishing between the gonads of sexually immature bonefish and the regressed gonads of mature fish was difficult. We reduced the probability of misclassifying regressed and immature fish by eliminating all bonefish collected during June–October from our analyses of age and length at sexual maturity. June–October was the season of minimal gonad development in bonefish, and most of the regressed bonefish in our sample were captured during this period. By excluding the postreproductive months from our analysis, we eliminated

84% of the regressed females and 63% of the regressed males in our sample. Hunter et al. (1992) recommended that only fish collected early in the spawning season be used to estimate the length at 50% maturity, but our sample size was not large enough to allow us to restrict our analysis to this extent.

To describe age and length at sexual maturity, we used nonlinear regression procedures to determine the inflection point of a logistic function fitted to the percentage of males and females that were sexually mature and to their respective lengths and ages. Parameter *b* in Table 1 is the inflection point and is the estimate of length or age at 50% maturity. Likelihood-ratio tests were used to compare the overall regression models and parameter estimates for males and females (Kimura, 1980).

Seasonality of gonad development

Monthly median gonadosomatic indices (GSI) of sexually mature males and females were plotted to show seasonal reproductive patterns. GSI's were calculated for 449 bonefish ranging from 228 to 702 mm as

$$GSI = (GW/(TW - GW)) \times 100,$$

where *GW* = total gonad weight (g); and
TW = total fish weight (g).

We also plotted the monthly frequency of occurrence of the various oocytes stages that we counted for fish

Table 1

Percentage mature-age, percentage mature fork length, and weight-fecundity regressions for bonefish, *Albula vulpes*, from the waters of the Florida Keys. Wt = weight (g), FL = fork length (mm), AGE = age in years, FEC = fecundity. Values in parentheses are standard errors.

Y	X	n	a (1 SE)	b (1 SE)	r ²	Range of X for regressions
$Y = \left(1 / (1 + e^{-a(X-b)})\right) \times 100$						
% Mature (Females)	FL	150	0.028 (0.0064)	487.6 (8.14)	0.632	228–702
% Mature (Females)	AGE	143	1.122 (0.2345)	4.24 (0.192)	0.445	1–19
% Mature (Males)	FL	116	0.545 (2.8227)	417.5 (12.59)	0.735	322–687
% Mature (Males)	AGE	109	1.618 (0.3674)	3.60 (0.156)	0.464	2–19
$Y = a + bX$						
log ₁₀ FEC	log ₁₀ Wt	33	1.936 (0.4708)	1.131 (0.1312)	0.706	1,790–5,790

collected in the years during which we had regular monthly collections.

Fecundity

The total fecundity (the standing stock of advanced yolked oocytes) of 33 bonefish was estimated gravimetrically. Ovaries were subsampled from anterior, middle, and posterior portions of each ovary to evaluate spatial variations in oocyte size within the ovary and between ovaries. Subsamples of ovary containing 1,000–1,500 vitellogenic oocytes were weighed to the nearest 0.01 mg, and total fecundity was calculated on the basis of the mean number of oocytes per gram of ovary. Ovaries that contained widespread atresia, which suggested that partial spawning might have occurred, were not used for fecundity estimation.

Results

Two of the bonefish that we examined were statistically significant outliers (Crabtree et al., 1996); both were exceptionally small for their estimated ages and the weights of their otoliths were exceptionally light. Crabtree et al. excluded both fish from growth models, age-frequency distributions, and otolith weight-age regressions, and we also excluded them from our analyses. One was a 351-mm female that was 7 years old and the other was a 458-mm female that was 18 years old. Both fish were caught with hook-and-line gear on the ocean (Florida Straits) side of North Key Largo, and they were the smallest females examined whose ovaries contained vitellogenic oocytes. The 458-mm female had oocytes that were in the nuclear migratory stage, and these were the most advanced oocytes we found in any bonefish.

Length and age at sexual maturity

Male bonefish reached 50% sexual maturity at a length of 418 mm (95% confidence interval 393–443 mm) and an age of 3.6 years (95% confidence interval 3.3–3.9 years); females reached 50% sexual maturity at a length of 488 mm (95% confidence interval 472–504 mm) and an age of 4.2 years (95% confidence interval 3.9–4.6 years; Fig. 2; Table 1). The lengths at 50% maturity ($\chi^2=124.43$, $df=1$, $P<0.001$) and the ages at 50% maturity ($\chi^2=5.59$, $df=1$, $P=0.018$) for males and females were significantly different. In addition, the overall logistic equations for length at 50% maturity ($\chi^2=51.18$, $df=2$, $P<0.001$) and for age at 50% maturity ($\chi^2=11.55$, $df=2$, $P=0.003$) for males and females were significantly different. The smallest sexually mature male was 425 mm long, and the smallest sexually mature female was 358

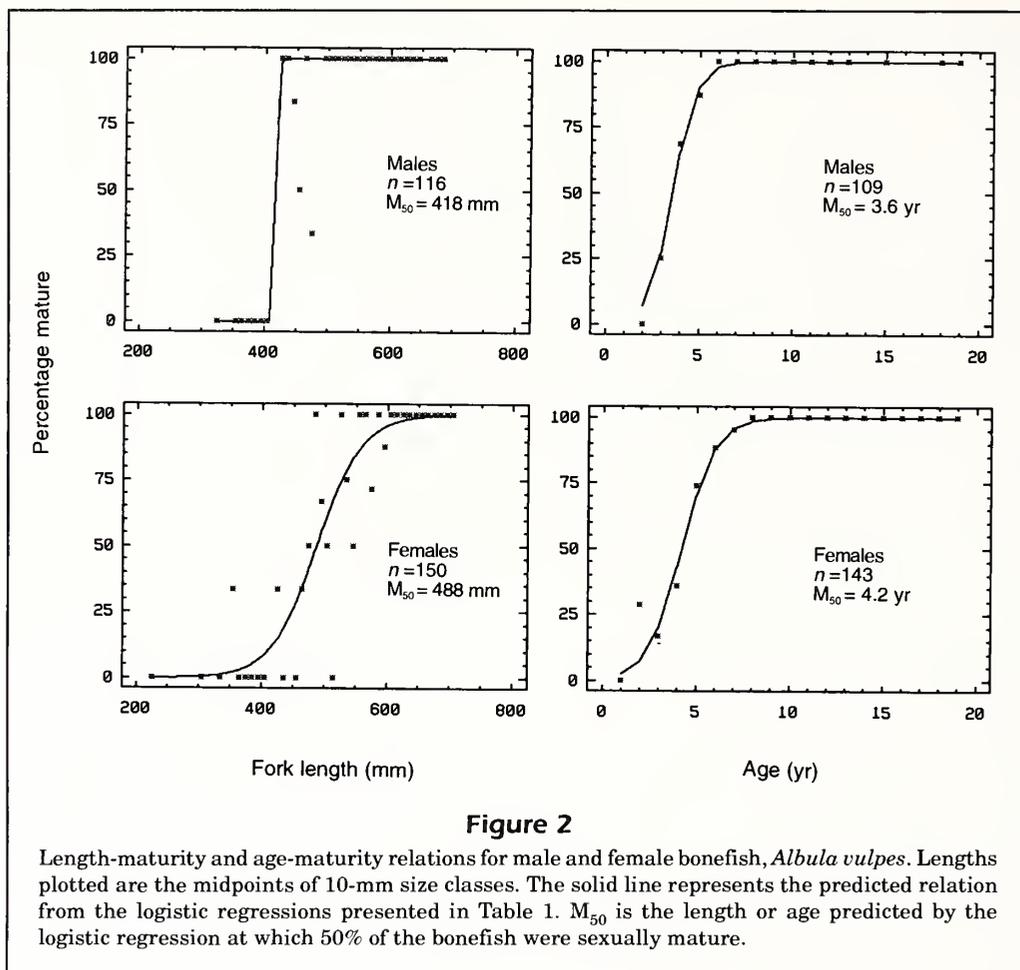
mm long. The youngest sexually mature male was 3 years old, and the youngest sexually mature female was 2 years old. All males longer than 477 mm and all females longer than 594 mm were sexually mature. All males older than 5 years and all females older than 7 years were sexually mature.

Primary growth stage oocytes were present in all ovaries in which we counted oocytes (Fig. 3A). Cortical alveolar oocytes were present only in ovaries from fish longer than about 400 mm and older than 2 years and were common only in fish longer than about 475 mm and older than 4 years (Fig. 3B). Vitellogenic oocytes were found only in fish longer than 450 mm and were common only in fish longer than 550 mm and older than 5 years (Fig. 3C). PAS-positive melanomacrophage centers were common only in females longer than about 550 mm and older than 5 years (Fig. 3D): the same length and age as those for females that contained vitellogenic oocytes.

Seasonality of gonad development

Bonefish gonadal activity was seasonal. Vitellogenic oocytes were present in greatest numbers during November–May, and their numbers declined during May–June (Fig. 4). There were no vitellogenic oocytes in any ovaries from females collected during August–September of any of the three summers during which we sampled. Cortical alveolar oocytes were present during all months but were least abundant during July–October. Primary growth stage oocytes were present in all females examined and made up at least 20% of the total number of oocytes present. PAS-positive melanomacrophage centers were most abundant in the gonads of spent and regressed males and females and were most abundant in ovaries at the end of the spawning season in June–August (Fig. 5). They were least abundant in ovaries immediately before the initiation of spawning in November, when recrudescence was complete and most ovaries were ripening to spawn during winter–spring. We saw no evidence of recent or imminent spawning, such as postovulatory follicles or fully hydrated females. Only six ovaries contained atretic hydrated oocytes, and no single histological preparation contained more than a few hydrated oocytes.

Seasonal GSI patterns suggest that bonefish spawned during a prolonged period from November to June (Fig. 6). Median GSI's were greatest during November–May and were least during July–September. The decrease in female GSI's during July–September corresponded with the decrease in the number of vitellogenic oocytes present in ovaries and with the increased abundance of spent and regressed fish during late summer.



Fecundity

Bonefish total fecundity estimates ranged from 0.4 to 1.7 million oocytes and had a significant positive relation to fish weight (Table 1; Fig. 7). Relative fecundity (the number of oocytes per gram fish weight) ranged from 159 to 385 oocytes/g (mean=259 oocytes/g, $SD=47.1$, $n=33$) for fish ranging in length from 485 to 702 mm. There was no significant relation between relative fecundity and fish length ($n=33$, $r^2=0.014$, $P=0.514$) or weight ($n=33$, $r^2=0.043$, $P=0.247$), but there was a significant positive relation between relative fecundity and age ($n=32$, $r^2=0.248$, $P=0.003$).

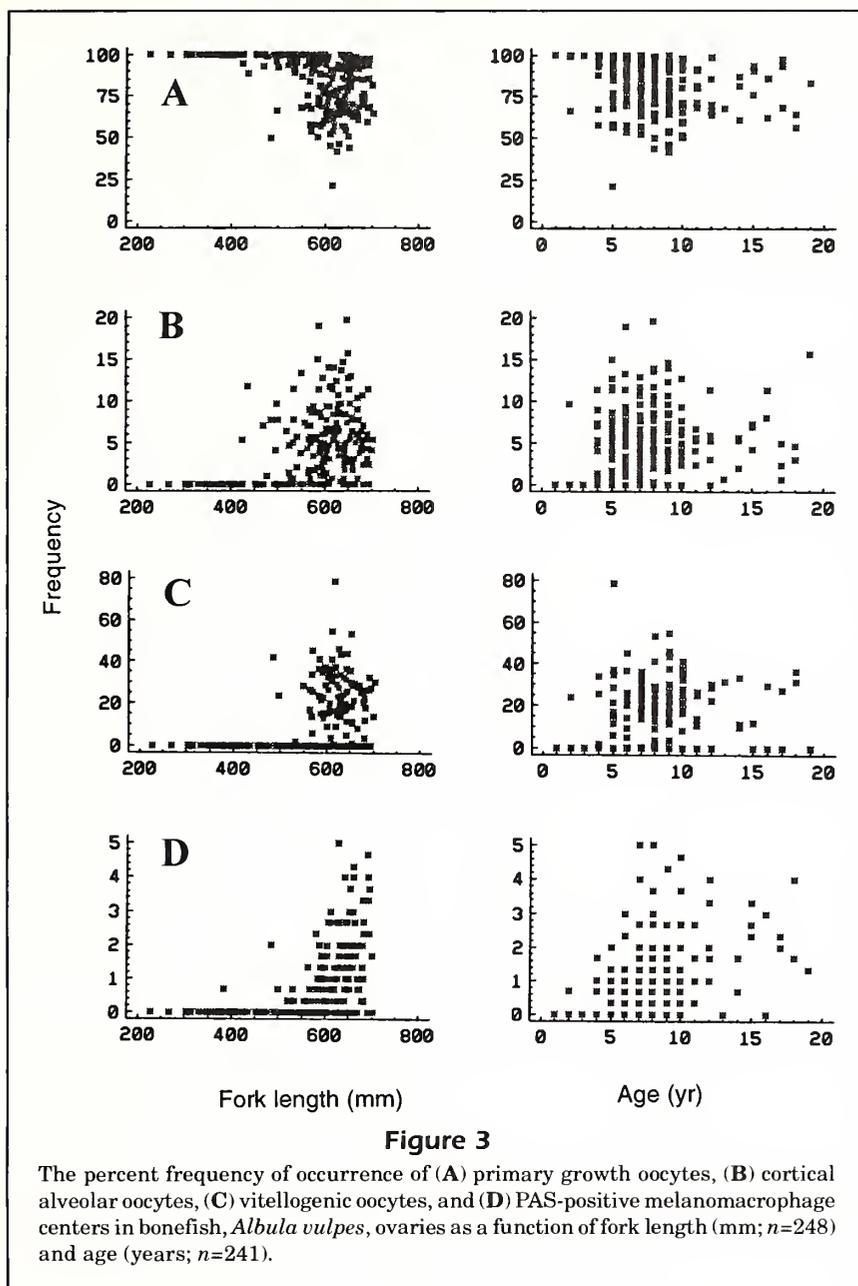
Oocyte development among areas within the ovary was homogeneous. We used a two-factor analysis of variance to compare oocyte densities with side (right or left) and position (anterior, middle, or posterior section of the ovary) as the effects. The number of late vitellogenic oocytes per gram of wet ovary weight was not significantly different between left and right ovaries (ANOVA, $df=1$, $P=0.648$) or among subsamples from anterior, middle, or posterior sections of the ovary (ANOVA, $df=2$, $P=0.709$). Furthermore,

we found no significant interaction between side and position from which subsamples were taken (ANOVA, $df=2$, $P=0.702$). Weights of left and right ovaries from sexually mature females were not significantly different (paired t -test, $n=112$, $t=0.480$, $P=0.632$), but right testes from sexually mature males were significantly larger than left testes (mean difference=9.1 g, $SD=18.62$; paired t -test, $n=98$, $t=4.826$, $P<0.001$).

Discussion

Length and age at sexual maturity

The bonefish we examined reached sexual maturity at an older age and larger size than reported by Bruger (1974). He reported sexually mature females that were 1 year old and ranged from 221 to 352 mm FL (reported as 210 to 338 mm standard length). Bruger considered these small bonefish to be sexually mature on the basis of the presence of vitellogenic oocytes, one of the criteria that we used. He did not report how many of these small sexually mature fe-



males were captured or the typical length and age at sexual maturity. Some of the sexually mature females he collected were smaller than the 351-mm sexually mature female that we considered an outlier and excluded from our analysis. Furthermore, the lengths of Bruger's fish were substantially shorter than our estimated length at 50% maturity for females (488 mm). We also did not find any 1-year-old bonfish that were sexually mature; the youngest sexually mature fish we examined was 2 years old. All of the small mature females reported by Bruger were caught in deeper water (9.1–12.2 m) than that surveyed for bonfish in our sample; most of our fish

were caught in water less than 2 m deep. Both Bruger (1974) and Crabtree et al. (1996) considered the possible existence of a cryptic bonfish species in waters off the Florida Keys as a potential explanation for the presence of exceptionally small and sexually mature bonfish, but additional study is needed to resolve this question.

Little is known regarding bonfish maturation in other areas. Pfeiler et al. (1988) reported 12 *Albula* sp., ranging in length from 205 to 264 mm (SL) from the Gulf of California, that had ripe or ripening gonads; this finding suggests a smaller length at sexual maturity there than we found in the Keys. The *Albula*

species in the Gulf of California is distinct from the Caribbean *A. vulpes* (Pfeiler, 1996).

Most of the bonefish in our sample that were caught with hook-and-line gear were 500–700 mm long (80%) and 3–10 years old (86%; Crabtree et al., 1996). If the length and age composition of our hook-

and-line sample reflects that of the fishery, as suggested by Crabtree et al. (1996), then most of the fish caught in the fishery are longer than our estimate of length at 50% maturity and older than our estimate of age at 50% maturity. The current 390-mm-FL (457-mm-TL) legal minimum fish length imposed upon the fishery is less than our estimate of the length at 50% maturity for males (418 mm FL) and females (488 mm FL). Crabtree et al. (1996) found little evidence of fishing mortality in the Florida Keys because most bonefish caught by recreational anglers are released; thus, the population would probably be insensitive to changes in the legal minimum fish length.

The presence of PAS-positive melanomacrophage centers was related to gonadal activity. They appeared to be associated with the resorption of postovulatory follicles and atretic vitellogenic oocytes, as has been suggested by Ravaglia and Muggese (1995). The presence of vitellogenic oocytes is an unambiguous indication of sexual maturity, and the length and age at which vitellogenic oocytes first developed in bonefish corresponded to the length and age at which PAS-positive melanomacrophage centers first appeared (Fig. 3). Melanomacrophage centers were most abundant at the end of the spawning season, when spent fish were most common, and decreased in abundance during

the postreproductive period (July–November), when recrudescence occurred (Fig. 5). Ravaglia and Muggese (1995) found that the abundance of melanomacrophage centers was also seasonal in *Synbranchus marmoratus* and peaked during the postreproductive season.

Seasonality of gonad development

Bonefish gonadal activity in the Florida Keys was seasonal, and development occurred over about eight months, from November to June. Bonefish were reproductively inactive for only a few months during summer. This period of inactivity roughly corresponds with the period of maximum water temperatures in the Keys (Crabtree et al., 1996). Bruger (1974) reported no evidence of a seasonal pattern of gonadal development for bonefish off the Florida Keys, but his small sample size during July–September ($n=7$ females, $n=4$ males) may have obscured seasonal patterns. Alexander (1961)

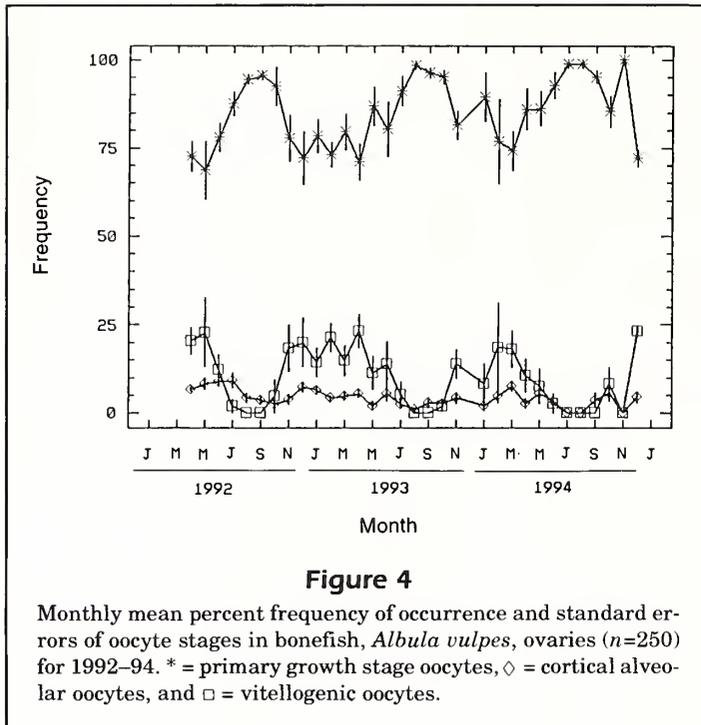


Figure 4

Monthly mean percent frequency of occurrence and standard errors of oocyte stages in bonefish, *Albula vulpes*, ovaries ($n=250$) for 1992–94. * = primary growth stage oocytes, \diamond = cortical alveolar oocytes, and \square = vitellogenic oocytes.

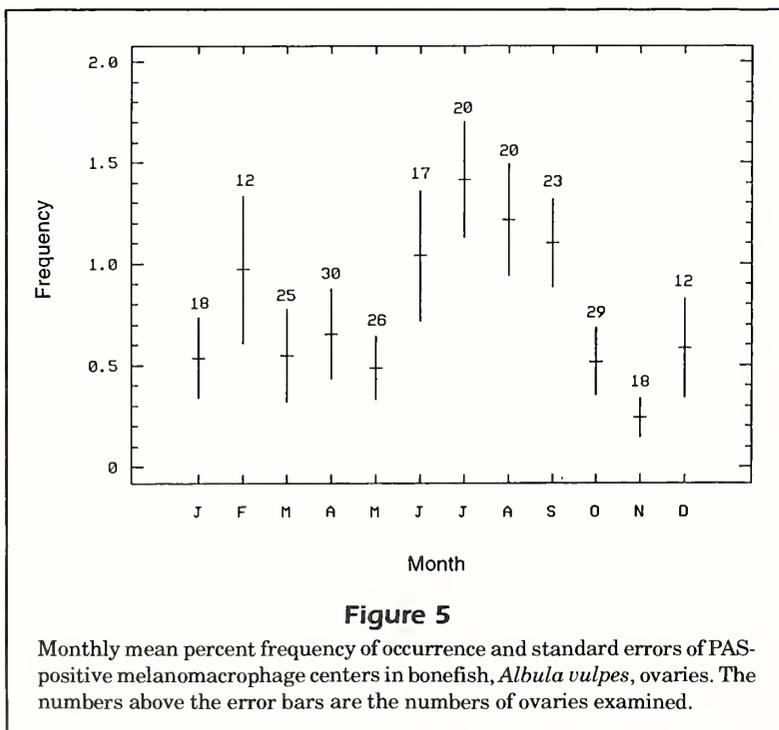


Figure 5

Monthly mean percent frequency of occurrence and standard errors of PAS-positive melanomacrophage centers in bonefish, *Albula vulpes*, ovaries. The numbers above the error bars are the numbers of ovaries examined.

found that the abundance of pre-metamorphic bonefish larvae in the West Indies was seasonal and that most larvae (96% of a total collection of 417 premetamorphic larvae) were caught during November–April. She concluded, from the capture of 17 premetamorphic larvae during August, that bonefish spawn throughout the year in the West Indies, but she suggested that bonefish spawn at reduced levels during the hot summer months. The 17 larvae that she reported were captured in August and were caught far south of the Florida Keys—at 13°11'N latitude, where spawning may follow a different seasonal pattern than it does in the Keys.

Studies from other areas also suggest seasonal reproduction in bonefish. Recruitment studies off the Bahama Islands suggest that spawning there has a seasonal pattern that is similar to that of spawning in the Florida Keys. Mojica et al. (1995) backcalculated hatching dates from the analysis of otolith microstructure of field-collected larvae and found that bonefish spawned continuously from mid-October through early January. Recruitment patterns suggest that spawning probably continues until spring, because Mojica et al. (1995) observed recruitment pulses of bonefish larvae as late as June—presumably resulting from April and May spawning. Bonefish spawning in the Gulf of California also appears to be seasonal. Pfeiler et al. (1988) examined gonads from 33 bonefish ranging from 202 to 279 mm (SL) and suggested that *Albula* sp. in the Gulf of California spawn during late spring and early summer. Metamorphic leptocephali are abundant in coastal regions and hypersaline lagoons throughout the Gulf of California during winter and spring (Pfeiler, 1984; Pfeiler et al., 1988). Pfeiler et al. (1988) suggested that the premetamorphic larval phase lasts 6 or 7 months.

The location of bonefish spawning grounds remains unknown, but the absence of females with post-ovulatory follicles or many hydrated oocytes in our samples suggests that bonefish do not spawn in the

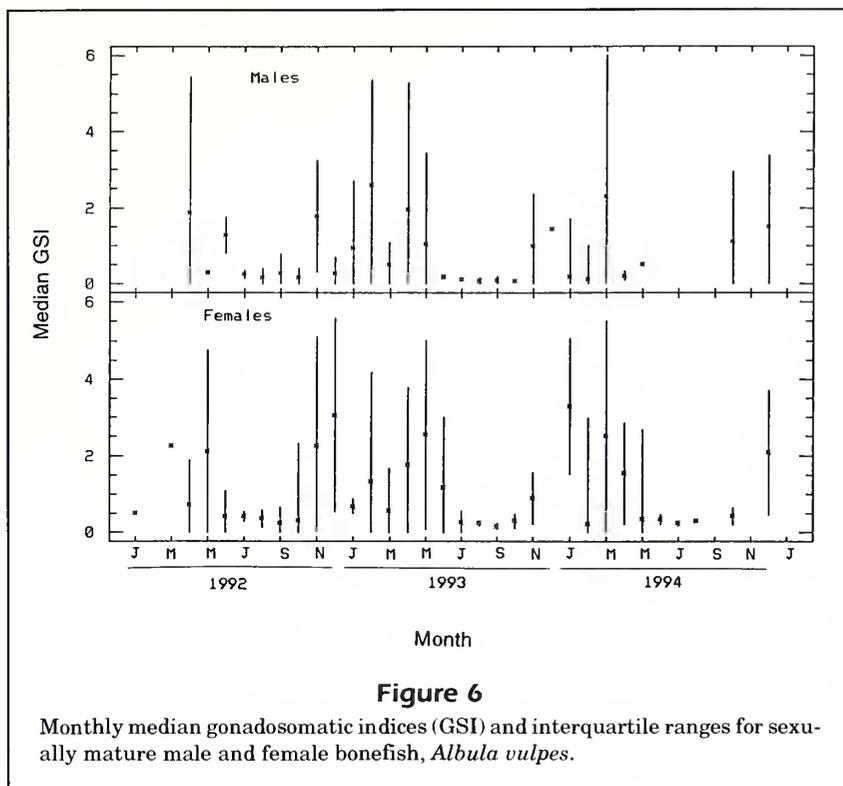


Figure 6
Monthly median gonadosomatic indices (GSI) and interquartile ranges for sexually mature male and female bonefish, *Albula vulpes*.

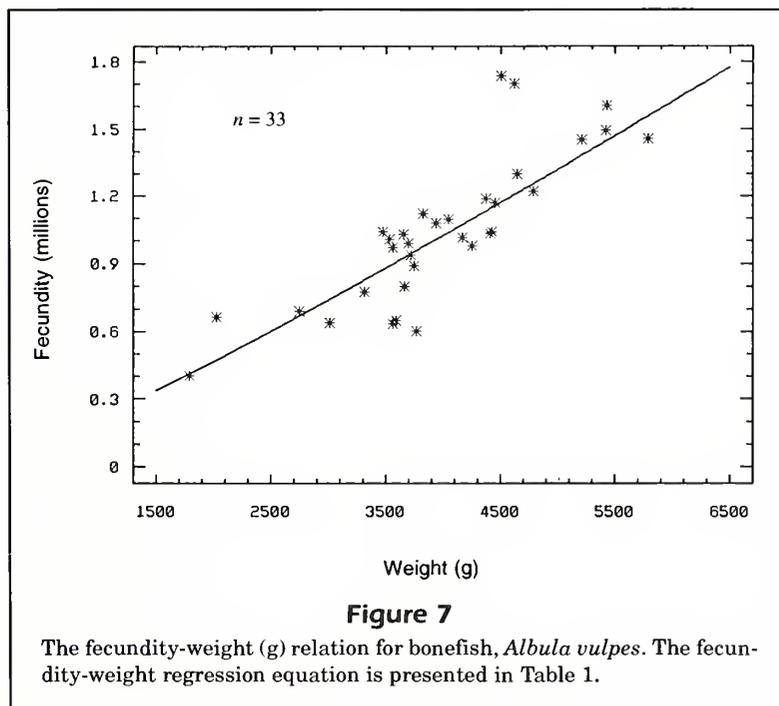


Figure 7
The fecundity-weight (g) relation for bonefish, *Albula vulpes*. The fecundity-weight regression equation is presented in Table 1.

shallow nearshore areas where the fishery exists. It is possible that bonefish had spawned in our sampling area but did not feed before or after spawning and so were not available for capture with hook-and-

line gear until after they had completed the resorption of recognizable postovulatory follicles. This possibility seems unlikely because most collections of premetamorphic bonefish larvae are from offshore waters (Alexander, 1961); thus spawning bonefish probably move out of the shallow waters (<2 m) where fishing usually occurs. Alexander (1961) suggested that bonefish either spawn offshore or in areas where currents are likely to carry the eggs offshore.

Fecundity

We did not examine any bonefish ovaries containing oocytes in the final stages of oocyte maturation or showing definitive evidence of recent spawning, such as postovulatory follicles. Consequently, we do not know if bonefish are isochronal or multiple-batch spawners, and we could not estimate batch fecundity. If annual fecundity in bonefish is indeterminate (Hunter et al., 1992), our estimate of total fecundity may not accurately represent total annual egg production. The bonefish spawning season is prolonged, and the potential exists for additional vitellogenic oocytes to mature from the standing stock of unyolked oocytes during the spawning season. Some ovaries contained vitellogenic oocytes, widespread atresia, and were loosely organized and highly vascularized. These females may have spawned earlier in the season and were developing an additional batch of oocytes that would have been spawned later in the season. It is unclear whether these oocytes were recruited from the standing stock of unyolked oocytes after previous spawning or if they were vitellogenic oocytes already present in the ovary that did not ovulate during previous spawning. Another bias of our fecundity estimates is that we could not correct them for atretic losses of vitellogenic oocytes during the spawning season; these losses could have caused us to overestimate egg production.

Acknowledgments

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Abstract.—A total of 1,237 tagged American lobsters, *Homarus americanus*, with a carapace length (CL) range of 48 to 198 mm (mean CL of 104 mm) were liberated at three release stations off the eastern shore of Cape Cod, MA, between 1969 and 1971. By 1973, 332 (26.8%) of the tags were returned. Mean time at large was 112.5 days (range 0–897 d).

One hundred and thirty (39.2%) of the recaptured lobsters moved less than 10 km from their points of release. One hundred and fifty-one (45.5%) were recaptured within 10 to 40 km from their points of release; 51 (15.4%) at 40 km or more.

Recapture depths and distances traveled were significantly greater in colder months. The distribution of these recaptures with time, depth, and location indicates seasonal movement to and from the edge of the continental shelf between fall and spring.

The apparent reshooling of these inshore-tagged lobsters to the eastern shore of Massachusetts in successive summers and the greater movement shown by females with ripe eggs at tagging, versus the movement of sublegal and nonovigerous female classes, suggest that the migration of this group of offshore lobsters is stimulated by seasonal changes in environmental cues in relation to hatching or reproductive needs (or both). Their relation to the Georges Bank–Southern Offshore stock unit, reproductive potential, and extensive seasonal movement into the southern and western Gulf of Maine, represent important considerations for resource managers and emphasize the need for further research on rate of stock interchange.

Seasonal movement of offshore American lobster, *Homarus americanus*, tagged along the eastern shore of Cape Cod, Massachusetts

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The traditional American lobster, *Homarus americanus*, fishery consists of a small-boat fleet that fishes with traps within a few miles of shore in depths up to 20 fathoms. This inshore fishery is centered in the northern Gulf of Maine and produces annually approximately 47% of the U.S. pounds landed. Massachusetts, the next largest producer, contributes about 28% of U.S. landings. Exploitation of inshore stocks is intensive. In the coastal waters of Maine, over 85% of the commercial inshore catch consists of new recruits (Krouse et al.¹). In Massachusetts coastal waters, approximately 90% of the inshore catch falls into this category (Estrella and Armstrong²).

Prior to 1948, small numbers of lobsters were caught incidentally by trawls in groundfish operations. These incidental catches accounted for less than 1% of U.S. landings. About 1945, trawlers began to fish specifically for lobsters, principally in deep water in the offshore region south of the Gulf between southeast Georges Bank and Hudson Canyon. This fishery was developed moderately and by 1968 offshore lobsters accounted for 16.9% of all U.S. lobster landings (Skud and Perkins,

1969). The introduction of deep-water trap fishing in the late 1960's rapidly accelerated development of the offshore fishery. Vessels that fish with traps have largely replaced the original trawl fleet, and the number of vessels in the offshore lobster fishery have increased greatly. Substantial numbers of vessels in the 40' to 60' class, as well as larger vessels, were built or converted specifically for offshore trap fishing. Offshore landings averaged 24% of U.S. landings (3,400 metric tons [t]) between 1970 and 1974 but declined to a 1978–83 average of 17% or 2,500 t per year (NEFC, 1983). Despite short-term increases (5,000 t in 1990), offshore landings have not accounted for more than 18% of total U.S. lobster landings since the mid 1970's (NEFSC, 1994).

¹ Krouse, J. S., K. H. Kelly, G. E. Nutting, D. B. Parkhurst Jr., G. A. Robinson, and B. C. Scully. 1994. Maine Dep. Marine Resources lobster stock assessment project 3-IJ-61-2. Maine Dep. Mar. Resources, Marine Resources Laboratory, P.O. Box 8, West Boothbay Harbor, ME 04575. Annual Rep., 53 p.

² Estrella, B. T., and M. P. Armstrong. 1995. Massachusetts coastal commercial lobster trap sampling program, May–November, 1994. Mass. Div. Mar. Fish., 20 p.

The continued development of the offshore fishery has subjected American lobster in all remaining segments of its range to intensive exploitation. Thus, stock identification and determination of any interrelations between stocks of lobsters is of increasing importance to management of the lobster fishery (Pezzack³). Earlier studies indicated that lobsters were relatively nonmigratory. Numerous tagging experiments conducted primarily in more northern inshore areas showed that most lobsters usually remain within a radius of 3–5 km (Templeman, 1935, 1940; Wilder and Murray, 1958; Wilder, 1963; Cooper, 1970; Cooper et al., 1975; Krouse, 1980; Stasko, 1980; Campbell, 1982; Lawton et al., 1984). Accordingly, management practices were based largely on the concept of discrete local stocks. Findings of extensive lobster movement in tagging experiments conducted in offshore areas (Saila and Flowers, 1968; Cooper and Uzmann, 1971, 1980; Uzmann et al., 1977; Fogarty et al., 1980; Campbell et al., 1984) and in more southern inshore areas (Morrissey, 1971; Briggs and Muschacke, 1984) show significant movement of large, sexually mature lobsters which become intermixed with the inshore resource. Thus, the concept of discrete inshore stocks, characterized by a particular size range or maturity status (Campbell and Stasko, 1986; Campbell, 1989) becomes speculative.

Intermingling of offshore lobsters with inshore stocks off southern New England is shown from recaptures of offshore-tagged lobsters in inshore areas. Cooper and Uzmann (1971, 1980) and Campbell (1986) hypothesized that seasonal depth-related movements are important to the biology of the species in providing optimal temperatures for mating, molting, egg extrusion, and egg development.

In an effort to obtain information that would augment offshore tagging studies off the Massachusetts coast, we undertook a three-year tagging experiment beginning in 1969 in the inshore waters of Cape Cod where previous work (Morrissey, 1971) showed the existence of a seasonal population of large, highly mobile lobsters. Additional lobster tagging in this area in 1984–85 also confirmed highly migratory behavior.⁴

Estrella and McKiernan (1989) described the extensive size range of this segment of the lobster resource, which is only seasonally available east of Cape Cod, as characteristic of an offshore migrant

group. This area exhibits the smallest percentage of sublegal-size lobsters in commercial trap catches of any other Massachusetts coastal region (10% compared with 89% in waters off Boston, MA, in 1995⁵). Catch per trap haul of sublegal-size lobster off outer Cape Cod was four to eight times lower than that for other Massachusetts coastal regions sampled in 1994 (Estrella and Armstrong²). Outer Cape Cod habitat is not “classic” lobster habitat conducive to supporting a resident (burrowed) resource; it is characterized by expansive sandy bottom and is dynamic owing to its exposure to strong easterly winds. Some local lobster production apparently occurs in the Nauset Marsh area of outer Cape Cod where limited numbers of early benthic-phase lobster have been found (Able et al., 1988). However, it is the larger, more common, offshore migrant lobster which supports the commercial fishermen in this area and which shapes the style of fishing deployed there. Long strings of traps are set parallel to the shoreline to intercept incoming migrations each season. In late spring, traps are initially set by day-boat lobstermen approximately thirteen miles from shore. This gear is gradually fished shoalward as migrations proceed closer to land in warmer months, until declining autumn temperatures reverse the trend.

It is informative that the intense outer Cape Cod lobster fishery has not been successful in reducing the size structure of this resource as definitively as in other inshore Massachusetts regions. A greater number of size-age groups are represented in outer Cape Cod catches. In most other inshore areas, lobsters exhibit minimal migration and are exposed to fishing pressure throughout the year. New recruits (lobsters which, upon molting, become legal size) may represent as much as 95% of the legal catch, compared with only 55% in the outer Cape Cod area. The seasonal occurrence of these offshore lobsters in the outer Cape Cod area thus limits their exposure to intense fishing pressure.

The size structure of this portion of the resource is similar to that from southern Georges Bank. Accordingly, the Sixteenth Northeast Regional Stock Assessment Workshop (16th SAW) of NMFS assigned this migratory group of lobsters to the Georges Bank-Southern Offshore stock unit (NEFSC, 1993).

Estrella and McKiernan (1989) discussed the geography as a potential factor in concentrating migrants. The outer Cape Cod area is adjacent to steeply sloping gradients which lead to a much greater depth range than that found in most other inshore regions.

³ Pezzack, D. S. 1987. Lobster (*Homarus americanus*) stock-structure in the Gulf of Maine. Int. Coun. Explor. Sea. Shellfish Comm. Council Meeting 1987/K:17, 18 p.

⁴ Estrella, B. T. 1997. American lobster tagging studies conducted in Massachusetts coastal waters. MA Div. Mar. Fish. In prep.

⁵ Estrella, B. T. 1997. Massachusetts Division of Marine Fisheries, 50 A Portside Drive, Pocasset, MA 02559. Unpubl. data.

Materials and methods

Tagged lobsters were released at three specific locations along the eastern shore of Cape Cod (Fig. 1). Lobsters used in tagging were collected in the immediate vicinity of each release station and released within a day of capture. At station 1 (Provincetown), tagged lobsters were liberated in the periods 21–25 July 1969; 6–9 July 1970; and 23–25 June 1971. Lobsters used in the tagging at station 1 were collected by SCUBA teams that attempted to capture all lobsters observed on each dive. At station 2 (Truro) and station 3 (Eastham), tagged lobsters were liberated over the period 20 July to 18 August 1970. Lobsters used at these two stations were collected in the traps of a local commercial fisherman.

Sphyron anchor tags were used. These consisted of a coded polyvinyl-chloride-tubing pennant connected by a monofilament thread to a stainless steel anchor. The anchor was inserted in the lobsters with a hypodermic needle through the membrane connect-

ing the carapace and first abdominal segment and implanted in dorsal extensor musculature below the carapace hypodermis as described in Cooper (1970). The implanted tag can endure successive molts.

A reward of \$1 was paid for each tag, as well as the market value of each tagged lobster returned with information on the date and location of recapture. During 1971, the reward was increased to \$5 for each tagged lobster submitted for examination, and the fisherman was permitted to retain possession of the lobster.

Distance traveled by recaptured lobsters was determined as the shortest distance, avoiding landmass, from point of release to point of recapture. Direction of travel was computed to the nearest 0.1 degree true north.

Results

A total of 1,237 tagged lobsters with carapace length (CL) range of 48 to 198 mm (mean CL of 104 mm),

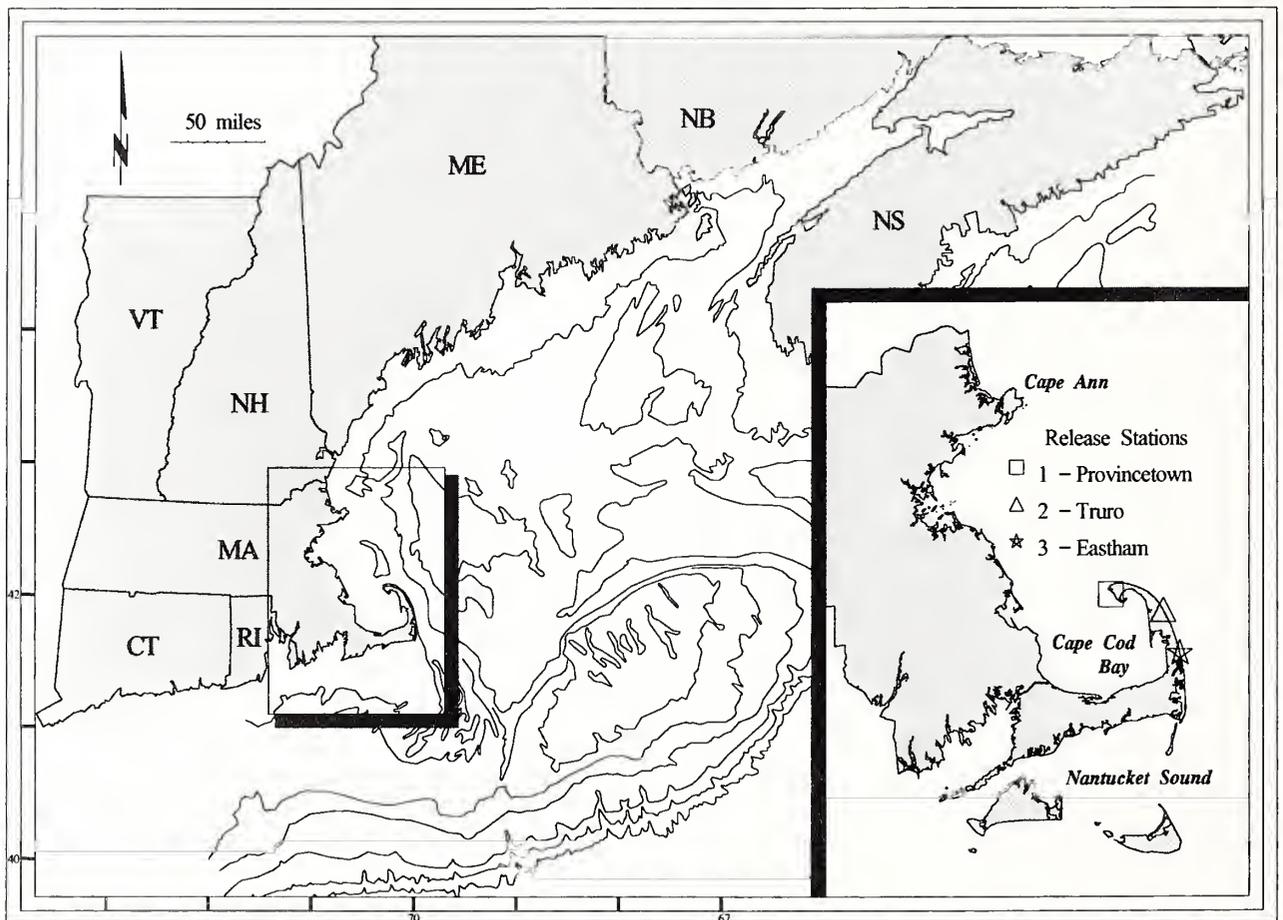


Figure 1

Map of northeast coast of the United States and Canada showing eastern Cape Cod, Massachusetts, release stations for tagged American lobster, *Homarus americanus*.

were liberated at three release stations (Table 1) between 21 July 1969 and 25 June 1971. By 22 December 1972, 332 or 26.8% of the tags were returned (Fig. 2). Mean distance from point of release to point of recapture was 22.6 km (median=140.4 km), mean time at large 112.5 days (median = 448.5 d).

One hundred thirty (39.2%) of the recaptured lobsters moved less than 10 km from their points of release (Table 2). One hundred fifty-one (45.5%) were recaptured within 10 to 40 km, and 51 (15.4%) were recaptured at 40 km or more from point of release. Four lobsters moved farther than 100 km, one of the four as far as 281 km.

The distances traveled by lobsters grouped in classes based on size, sex, and the presence or absence of ripe and immature external eggs at tagging are shown in Table 3A. Legal-size females without eggs moved the shortest distance of all groups. Ripe ovigerous lobster moved farthest (average 30.3 km), followed by females with immature eggs (average 23.8 km). Analysis of variance of log-transformed data indicated there were significant differences among groups ($P<0.01$). Several multiple-range test procedures, Tukey-HSD test, Student-Newman-Keuls (SNK), and Duncan, were run on log-transformed data. A common result among the tests was

Table 1
Tagged lobsters liberated and recaptured from three release stations at Cape Cod, Massachusetts.

Release station	Number tagged	Carapace length (mm)			Tags returned		Movement		
		Mean	Range	SD	Number	Percent recovery	Mean distance traveled (km)	Mean time at large (days)	Velocity (km/day)
1 Provincetown									
Male	190	84	48-198	25.2	54	28.4	22.4	220.4	0.49
Female	683	113	49-189	21.2	200	29.3	21.4	83.6	0.65
2 Truro									
Male	39	75	67-80	3.8	8	20.5	25.3	228.9	0.37
Female	105	106	67-149	21.0	21	20.0	21.7	104.7	1.50
3 Eastham									
Male	75	76	69-90	3.8	14	18.7	22.6	198.1	0.49
Female	145	96	66-146	21.6	35	24.1	29.6	55.1	1.18
Total or weighted mean	1237	102	48-198	24.9	332	26.8	22.6	112.5	0.72

Table 2
Distance traveled by lobsters liberated from three release stations at Cape Cod, Massachusetts.

Distance traveled (km)	Provincetown		Truro		Eastham		Total	
	Number of tags returned	Percent of total	Number of tags returned	Percent of total	Number of tags returned	Percent of total	Number of tags returned	Percent of total
Less than 10	100	39.4	2	6.9	28	57.1	130	39.2
10-19	49	19.3	15	51.7	1	2.0	65	19.6
20-29	26	10.2	2	6.9	2	4.1	30	9.0
30-39	46	18.1	8	27.7	2	4.1	56	16.9
40-49	20	7.8	1	3.4	5	10.3	26	7.8
50 or more	13	5.2	1	3.4	11	22.4	25	7.5
Total	254	100.0	29	100.0	49	100.0	332	100.0

that the distance traveled by legal-size nonovigerous females was significantly shorter than that of all other groups except sublegal females.

Only fourteen of the returned lobsters molted while at large. These were distributed among most of the lobster classes. Sample size was insufficient to assess effects of molting on movement.

The relatively long mean distances traveled by sublegal male and female lobster groups (22.5 km and 17.0 km, respectively) were likely due to their number of days at large being, on average, consider-

ably greater than the number of days at large for other lobster groups (Table 3A). The mean time at large was less for legal-size females with and without external eggs than for legal-size males and sublegal males and females.

Lobster "velocities" greater than 3 km/day were not exhibited by individual sublegal males or sublegal females. However, these rates were calculated for the larger lobsters, including 6.6% of legal-size males, 1.1% of legal-size nonovigerous females, 7.6% of females with immature eggs, and 4.2% of females with

ripe eggs. Females with immature and ripe eggs exhibited greatest mean velocities (1.55 and 0.95 km/day, respectively, Table 3A).

Because variability in days at large among classes of lobster could affect comparisons of distance traveled, standardization was warranted. An additional data analysis was conducted which was limited to lobsters at large < 200 days (Table 3B). This eliminated potential misleading recapture locations that could occur after circuitous (homing) movement patterns, i.e. those from lobsters which, after tagging, may move offshore and return inshore in the following year, and subsequent years. Because lobsters were tagged and released in the months of June through August, a 200-day limit was considered reasonable to avoid spring recaptures in our data treatments.

Analysis of these "standardized" data reaffirmed that legal-size females with ripe external eggs exhibited the greatest mean distance traveled, 25.6 km, followed by females with immature external eggs, 24.2 km. Legal-size males ranked third, with a mean of 16 km; nonovigerous females and sublegal females and males averaged 12.2 km, 13.1 km, and 14.2 km, respectively. Analysis of variance of log-transformed distance data indicated that there were signifi-

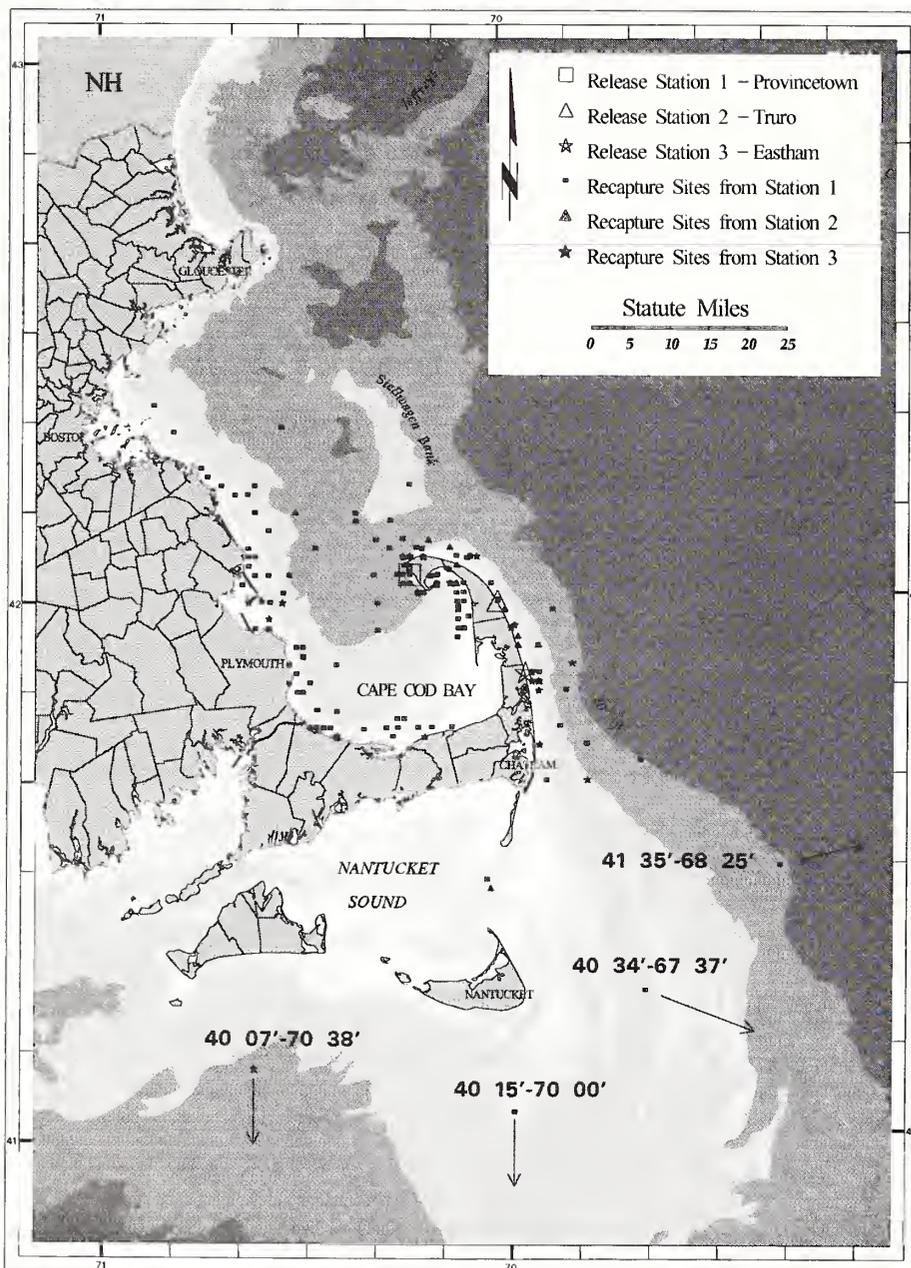


Figure 2

Tagged American lobster, *Homarus americanus*, release stations and return locations off the coast of Massachusetts. Some inshore recapture sites represent multiple recaptures.

Table 3A

Tag returns from various classes of lobsters liberated at Cape Cod, Massachusetts, for all days at large.

Lobster class	Number liberated	Number recovered	Percent tag recovery	Mean carapace length (mm)	Mean distance traveled (km)	Mean time at large (days)	Velocity (km/day)
Male sublegal-size ¹	213	46	21.6	72	22.5	308.0	0.31
Female sublegal-size without external eggs	128	20	15.6	75	17.0	153.0	0.37
Male legal-size	91	30	33.0	106	23.1	79.0	0.74
Female legal-size without external eggs	295	91	30.8	106	13.4	77.0	0.46
Female with immature external eggs	130	26	20.0	112	23.8	34.2	1.55
Female with ripe external eggs	380	119	31.3	118	30.3	83.0	0.95
Total or weighted mean	1,237	332	26.8	104	22.6	112.5	0.72

¹ Lobsters less than 81 mm carapace length. During this study, the minimum legal carapace length in Massachusetts was 3 and 3/16 inches (80.96 mm).**Table 3B**

Tag returns from various classes of lobsters liberated at Cape Cod, Massachusetts, which were at large <200 days.

Lobster class	Number liberated	Number recovered	Percent tag recovery	Mean carapace length (mm)	Mean distance traveled (km)	Mean time at large (days)	Velocity (km/day)
Male sublegal-size ¹	213	21	9.9	75	14.2	34.1	0.59
Female sublegal-size without external eggs	128	14	10.9	75	13.1	47.2	0.51
Male legal-size	91	26	28.6	104	16.0	38.1	0.82
Female legal-size without external eggs	295	81	27.5	106	12.2	35.0	0.51
Female with immature external eggs	130	25	19.2	112	24.2	22.8	1.61
Female with ripe external eggs	380	107	28.2	117	25.6	36.1	1.04
Total or weighted mean	1,237	274	22.2	107	19.1	35.2	0.85

¹ Lobsters less than 81 mm carapace length. During this study the minimum legal carapace length in Massachusetts was 3 and 3/16 inches (80.96 mm).

cant differences among groups ($P < 0.01$). Tukey-HSD, SNK, and Duncan test results were similar to results from tests on all data. They indicated that distances traveled by sublegal and legal nonovigerous lobster groups were significantly less than those of egg-bearing female groups ($P = 0.05$). The trend in mean velocity and proportion of lobsters traveling

greater than 3 km/day was similar to that calculated for each lobster class from all data. Maximum velocities, calculated by lobster class, were 2.98 km/day for a 79-mm-CL sublegal male, 2.36 km/day for sublegal females (80 mm CL), 5.19 km/day for legal size males (106 mm CL), 4.15 km/day for legal-size nonovigerous females (101 mm CL), 7 km/day for le-

gal-size females with immature eggs (103 mm CL), and 5.8 km/day for females with mature eggs (118 mm CL).

Time at large for recaptured lobsters ranged from 0 to 897 days (Table 4). Approximately 78% of recaptured lobsters were at large less than 60 days. The number of tags returned and the percentage recovery of tagged lobsters at large decreased sharply in the fourth month after release (October) coincident with the start of the fall season. Only three tags were returned from lobsters recaptured in the colder months from December through April (all years combined). All three tagged lobsters were recovered in deep water. Two were recaptured on 7 and 22 March 1972, at depths of 54 m and 59 m, respectively, off Provincetown, MA, and the third was recaptured offshore on 22 December 1972, at a depth of 95 m, NE of Veatch Canyon.

Depth of recapture data were log-transformed and analyzed with equality of means test and found to be related to season (Welch: $F=4.41$, $P=0.0411$;

Brown-Forsythe: $F=4.41$, $P=0.0411$). Depth of recapture for the combined months of June through September (63 m) was significantly different from October through May (93 m).

Distance traveled was also significantly different by season ($t=-3.50$, $P=0.001$). Distance from release site was greatest during the October–May period of recapture (41.3 km), in comparison with June–September period of recapture (22.5 km).

Distance of travel northeastward of the Cape Cod landmass was apparently limited compared with distance of travel in other directions; recapture points tend to be distributed in a northwest-southeast plane (Fig. 2).

To test inshore versus offshore migrational tendencies, tag-return locations were grouped with consideration for the curvature of the “arm” of the Cape. Exclusive of lobster recaptured within Cape Cod Bay, recapture points east to south of all landmass between 90° and 225° true north (for lobsters liberated at stations 2 and 3), and 1° and 225° (for lobsters

Table 4

Tags returned by month of recapture and days at large for tagged lobsters liberated at Cape Cod, Massachusetts (recapture years combined).

Recapture month	Mean days at large	Number of returns	Tags returned		Mean distance (km)	Mean depth (meters)
			Percent of total	Cumulative percent		
1st season						
June	4.0	2	0.6		3.2	70.0
July	10.1	70	21.1	21.7	10.1	62.5
August	33.2	112	33.7	55.4	20.0	53.0
September	50.6	76	22.9	78.3	26.2	78.5
October	89.9	9	2.7	81.0	21.1	81.2
November	111.0	5	1.5	82.5	19.5	128.2
2nd season						
March	258.0	1	0.3	82.8	4.6	176.0
May	302.1	10	3.0	85.8	69.7	91.3
June	338.8	9	2.7	88.5	22.5	54.3
July	359.8	5	1.5	90.0	37.0	33.8
August	381.6	8	2.4	92.4	33.1	51.9
September	434.5	2	0.6	93.0	7.6	92.5
October	449.8	4	1.2	94.2	39.8	48.3
November	486.0	1	0.3	94.5	33.8	50.0
3rd season						
March	582.0	1	0.3	94.8	38.5	192.0
May	670.0	2	0.6	95.4	19.9	30.5
June	703.5	2	0.6	96.0	35.7	60.5
July	726.3	6	1.8	97.8	23.2	81.5
August	742.5	2	0.6	98.4	33.9	93.0
October	807.5	2	0.6	99.0	30.2	70.0
November	843.5	2	0.6	99.6	11.5	61.0
December	897.0	1	0.3	99.9	223.5	312.0

liberated at station 1) were grouped as southeast (offshore) in direction. All other recapture points, including those within Cape Cod Bay, were grouped as northwest (inshore) in direction. Inshore versus offshore travel was tested with chi-square by month of recapture for lobsters at large up to one year and which traveled more than 3.7 km. Direction of travel was biased significantly toward inshore during warmer months (Table 5).

Discussion

Our findings of greater directed movement toward the north and west during summer months is in agreement with the summer movement along the eastern shore of Cape Cod and into Cape Cod Bay as reported by Morrissey (1971). The Cape Cod landmass is interjacent to inshore grounds to the north and west and offshore grounds along the edge of the continental shelf to the south and east. The overall northwest-southeast distribution of recapture points suggests an interchange of inshore and offshore stocks in the Cape Cod area. Cooper and Uzmann (1971) and Uzmann et al. (1977) found that lobsters tagged in offshore canyon areas moved into shoal water in late spring and early summer, returning to deep water in late fall and early winter. Lobsters migrating from that offshore area to the inshore area of eastern Massachusetts would pass along the eastern shore of Cape Cod. The northwest-southeast pattern of recapture locations is consistent with movement to and from the Georges Bank and southern offshore canyon area which exhibits a similar population structure to the lobster group which is only seasonally available east of Cape Cod.

Lawton et al. (1984) found minimal movement in an inshore tagging study of 4,761 sublegal lobster at nearby Rocky Point, Plymouth, Massachusetts during 1970–75. Only 19 lobsters (<1% of returns) were retrieved 16 or more km from their release points and all 19 were within state territorial waters. A study by Fair⁶ on legal-size lobster in the same area several years later yielded similar results. Additional studies affirmed the nonmigratory nature of inshore lobsters (Templeman, 1935; Wilder, 1963; Cooper et al., 1975; Krouse, 1980; Stasko, 1980; Campbell, 1982). Ennis (1984) noted small-scale seasonal depth movements in relation to temperature with lobsters moving to shallow water in warmer months and deeper water in colder months. More extensive seasonal migrations were demonstrated by Campbell (1986) and Pezzack and Duggan (1986).

We conclude that lobsters tagged in the present experiment are onshore migrants from an offshore stock that seasonably becomes "superimposed" on the endemic inshore stock. Recapture depths were significantly greater in colder months than during summer. The movement of lobsters off southeastern Massachusetts is cyclical, with lobsters moving to deep water in late fall. Uzmann et al. (1977) found that lobsters returned to the continental shelf margin and slope in fall and winter. In our study only three lobsters were recaptured during December through April, consequently, we did not clearly establish if lobsters winter specifically on the edge of the shelf or in deep-water areas in general. However, four of our lobsters were recaptured in clearly offshore areas: at 40°07', 70°38', 119 m depth, on 26 September 1970; at 40°34', 67°37', 110 m depth, on 9 May 1970; at 41°35', 68°25', 55 m depth, on 23 May 1971; and at 40°15', 70°00', 95 m depth, on 22 December 1972. The

occurrences of these recaptures in time, depth, and location suggest seasonal movement to and from the edge of the continental shelf between fall and spring. With an average recovery rate of only 7.0% of lobsters tagged offshore by Cooper and Uzmann (1971), it is probable that substantial numbers of our inshore tagged lobsters wintered on the edge of the continental shelf.

Cooper and Uzmann (1971) concluded that offshore lobsters actively orient to optimum temperature according to season. Uzmann et al. (1977) provided further sup-

Table 5

Seasonal distribution of recapture points of lobsters at large up to one year and that had traveled more than 3.7 km.

Recapture period	Direction of travel			χ^2
	Number inshore	Number offshore	Total	
1st season of release				
July–August	106	43	149	$P < 0.0001$
September–October	59	15	74	$P < 0.0001$
1st winter of release				
November–May	11	5	16	$P = 0.134$
2nd season of release				
June–August	8	4	12	$P = 0.248$
Total	184	67	251	

⁶ Fair, J. J., Jr. 1977. Lobster investigations in management area 1: southern Gulf of Maine. NOAA, NMFS State-Federal Relationships Div., Mass. Lobster Rep. No. 8, 21 April 1975–20 Apr. 1977, 8 p. Appendix, 5 p.

port with their finding that through random or directed movements (or both), the offshore lobster population maintains itself within temperatures of 8°–14°C. Cooper and Uzmann (1971) hypothesized that seasonal shoalward migration to warmer water compensates for a lack of sufficiently high temperature during summer in the continental slope habitat to permit extrusion and hatching of eggs and subsequent molting and mating. They found that offshore lobsters that demonstrated the most extensive onshore migrations were predominately females and that the migration of offshore lobsters to inshore grounds is generally confined to areas south and west of Cape Cod (no recoveries were made north of Cape Cod in the Gulf of Maine proper).

While diving to collect lobsters for tagging at station 1, we observed lobsters always to be concentrated in a narrow stratum where a thermocline intercepted the steeply sloping surfaces of a sandy escarpment paralleling the beach in that area, about 1.8 km from shore. Morrissey⁷ conducted semiweekly SCUBA surveys throughout the summer of 1966 at Provincetown, where station 1 is located, and found lobsters only in close proximity to the thermocline-sediment interface, which occurred at 24 m in late May and ranged between 9 and 19 m during June, July, and August. During a vertical transect along the bottom from the shoreline to a depth of 22 m, 14 July 1966, 15 of 16 lobsters observed were within a stratum (11 to 14 m) in which a bathythermograph cast showed a change of 12.8°C in water temperature. On the basis of observed activity of individual lobsters, he concluded that the lobsters were not concentrated by a thermal block but rather were attracted to the warmer epilimnion layer and used the reduced light intensity associated with the thermocline as cover. These observations support the conclusion of Cooper and Uzmann (1971) and Uzmann et al. (1977) that offshore lobsters orient to optimum temperature.

Our test results indicated that sublegal and legal-size females with no eggs moved significantly less than egg-bearing female groups. An explanation for why legal-size females without eggs move less than those with eggs may be that they tend to congregate in the warmer shoal water where egg extrusion occurs. During this study, three tagged females, which extruded eggs after tagging, moved only an average distance of 4.2 km before recovery. Although this sample size is small, the inference from it is supported by fishing activity in this area. Fishermen

report concentrations of females with immature eggs in the shoals east of Cape Cod during August and September.

The fact that tagged inshore female lobsters with ripe external eggs moved greater distances than other classes of tagged lobsters may be a verification of the findings of Cooper and Uzmann (1971), that offshore lobsters demonstrating the most extensive inshore migrations are predominantly female. However, unlike Cooper and Uzmann (1971), our recoveries indicate that lobster migration occurs north of Cape Cod into at least the southwestern portion of the Gulf of Maine with one recovery made as far north as latitude 42°39'. Our subsequent tagging work in this study area (1984–85) yielded the return of a female after 362 days at large from even farther north, 43°33' (off Cape Elizabeth, Maine).⁴

None of our lobsters were recovered in the inshore grounds south and southwest of Cape Cod where most of the inshore recoveries were made by Cooper and Uzmann. The distribution of recapture points of the 58 lobsters recovered after their first season of release (Table 4) suggests that our inshore tagged lobsters returned to the shoal waters along eastern Massachusetts in successive summers.

The movement described by the findings of Cooper and Uzmann (1971) suggests that offshore lobsters migrate to secure more suitable hydrographic conditions. The areas involved, i.e. the edge of the continental shelf and shoaler waters extending into inshore grounds south and west of Cape Cod, are quite generalized. The apparent return of our inshore tagged lobsters to the eastern shore of Massachusetts in successive summers, and the greater movement shown by females with ripe eggs at tagging, suggest that the migration of offshore lobsters may be anastrophic or gametic (Heape, 1931; Wilkinson, 1952) in character, i.e. nonrandom, stimulated by metabolic needs or reproductive cues. Campbell (1986) provided calculations that suggest ovigerous lobster need to make seasonal deep-shallow water migrations to obtain sufficient heat units for egg development within any 9–12 month period. Using a threshold temperature of 3.4°C, he determined that shallow water had more degree days than deeper water in summer months and that the reverse was true in winter months.

Although significant American lobster migrations have been reported, Saila and Flowers (1968) provided the first reference in the literature to long-distance homing by this species. They found a pronounced directional tendency toward the original area of capture in the movements of berried female lobsters transplanted from Veatch Canyon on the edge of the continental shelf to Narragansett Bay,

⁷ Morrissey, T. D. 1970. Observations on behavior of the American lobster, *Homarus americanus*, at Provincetown, Massachusetts during the summer of 1966. MA Div. Mar. Fish., 50 A Portside Drive, Pocasset, MA 02559.

Rhode Island. They concluded that the lobsters tended to remain in shoal waters in suitable spawning habitat until they had shed their eggs or had molted, or both. Cooper and Uzmann (1971) referred to seasonal movement to and from generalized areas: the edge of the continental shelf and the shoaler waters of southern New England. Campbell (1986) and Pezzack and Duggan (1986), however, provided evidence from Canadian waters that lobsters undertake regular migrations between widely spaced and well-defined areas.

In contrast, the European lobster, *Homarus gammarus*, although biologically similar to *H. americanus*, displays minimal migratory behavior (Bannister and Addison, 1995). Tagging studies have shown that both juveniles and adults exhibit "strong site loyalty." The distribution of the *H. gammarus* resource and fishery is primarily coastal; "offshore" distribution occurs only 20 km from shore. The lack of substantial long-distance movement may be due to the more moderate water temperature off the British Isles (compared with the NW Atlantic) caused by proximity to the Gulf Stream. This may mitigate the biological "need" for extensive seasonal inshore-offshore movement by *H. gammarus*.⁸

There is an apparent affinity between the migratory group of lobsters east of Cape Cod, which are examined in this study, and those from Georges Bank and southern offshore canyons. Our evidence for movement of these lobsters north of Cape Cod into the Gulf of Maine seasonally, implies that genetic interchange between stock units continues, despite high exploitation rates. In light of this, management of fishing mortality rates on the offshore resource becomes an issue of increasing importance.

There is also increasing information on movements of lobster larvae, the distribution and behavior of newly settled and juvenile lobsters, concentrations of egg-bearing females, and the occurrence of long-distance homing behavior in American lobster both in the northern Gulf of Maine and southern New England waters. Some progress has been made in roughly delineating stock structure with the help of larval dispersion, hydrodynamic, and migration studies (NEFSC, 1993). Interpretation of these data, however, is tentative because migratory habits of larger lobsters appear extensive and may transcend the boundaries that some researchers attempt to draw solely on the basis of larval distribution. Despite many years of larval and postlarval lobster monitor-

ing, a definitive stock-recruitment relation has yet to be determined, although ecological knowledge has been enhanced. The relative importance of the offshore lobster resource to recruitment in shoaler waters of the Gulf of Maine or other areas must be assessed. We need to know the degree of interchange between the two lobster groups in order to refine stock assessments.

Acknowledgments

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Abstract.—We measured the daily abundance of larvae of eight species of ocean-spawned, estuarine-dependent fishes to determine the effect of sampling frequency on the mean and variance estimates during larval immigration past a permanent sampling station inside Beaufort Inlet, North Carolina, mid-November 1991 to mid-April 1992. Species of interest were *Brevoortia tyrannus*, *Lagodon rhomboides*, *Leiostomus xanthurus*, *Micropogonias undulatus*, *Mugil cephalus*, *Paralichthys albigutta*, *P. dentatus*, and *P. lethostigma*. Our data suggest that sampling at intervals >7 days can lead to excessive variance in abundance estimates. For all species, abundance varied as much as an order of magnitude from night to night. Proportional residuals from polynomial models of the seasonal recruitment pattern for a given species were used to assess the potential influence of nine environmental variables on daily densities. Twenty-seven of 72 correlations of proportional residuals with environmental variables were significant ($P < 0.05$). Proportional residuals were positively correlated with time after dusk for six of eight species and were negatively correlated with turbidity for five of eight species. However, interpretation of correlations must be done cautiously because a species' recruitment pattern may coincide with normal seasonal change in one or more environmental variables. Variability in transport of larvae, from offshore to near the inlet and then through the inlet to the station, probably influences species abundance at the sampling station more than locally acting environmental variables. Daily collections of *B. tyrannus* larvae provided otoliths ($n=1,341$) showing that a large number of younger larvae, averaging 55 days posthatch, arrived at the station in mid-March on the date of maximum observed daily density (160 larvae per 100 m³).

Daily variability in abundance of larval fishes inside Beaufort Inlet

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From 1985 to the present, weekly sampling has been conducted near Beaufort Inlet to collect fish larvae entering the estuary during fall, winter, and spring (Warlen, 1994). Such inlets provide locations for sampling larvae in order to assess potential year-class strength of ocean-spawned but estuarine-dependent species. Abundance, size, and age data on early larvae in the sea, on advanced larvae in the inlets, and on juveniles in the estuaries can be used to understand when significant events such as mortality or rapid growth occur during a species' early life history. To obtain accurate abundance, size, and age estimates from the population of recruiting larvae, appropriate sampling protocol must be employed (Morse, 1989; Davis et al., 1990). Errors resulting from sampling bias can arise when larvae selectively avoid the sampling device or when there is nonrandom spatial (patchy) distribution of the larvae (Wiebe and Holland, 1968). Decreasing the time interval between sampling and decreasing the distance between stations in ichthyoplankton surveys increases the resolution of temporal or spatial patterns of species with patchy pelagic egg and larval distributions at both microscale

(Houde and Lovdal, 1985) and mesoscale levels (Rowe and Epifanio, 1994).

Studies within NOAA's Southeast Atlantic Bight Recruitment Experiment (SABRE) are attempting to measure fluxes of larval fishes across the continental shelf and through inlets into estuaries amid myriad cyclical phenomena that bear directly on the larvae's abundance (Govoni and Pietrafesa, 1994; Stegmann and Yoder, 1996). The purpose of our SABRE study was to estimate the daily variation in abundance data collected on eight species of larval fish that seasonally ingress past the permanent sampling station at Pivers Island inside of Beaufort Inlet in order to determine an optimum sampling frequency for future sampling protocols. For one of these species, *Brevoortia tyrannus* (Atlantic menhaden), which has been the focus species in SABRE studies, additional analysis was conducted on age and growth with specimens collected daily. For all species, we used daily abundance data to calculate the decrease in precision of our relative abundance estimates as the interval between sampling events increased. Daily collections of larvae also allowed us to measure changes in size (length) of all eight

species. Finally, environmental variables were tested for their correlation with abundance.

Materials and methods

Sampling location and period

The sampling station for larval fish abundance, located 2 km inside of Beaufort Inlet, North Carolina (34°43'N, 76°40'W), was a platform attached to a bridge over a 6-m-deep tidal channel adjacent to the Beaufort Laboratory at Pivers Island and has been the site of weekly larval fish sampling since the 1985–86 larvae ingress season (Warlen, 1994). We sampled every night, 20 November 1991 through 15 April 1992, a period that more or less encompasses the annual periods of recruitment of ocean-spawned estuarine-dependent larvae that pass through North Carolina inlets from autumn to spring.

Fish and environment sampling

Oblique tows (bottom to surface) of a 1-m diameter, 800- μ mesh net were used to sample the water column for larvae. Three consecutive 4-min tows were made at 15-min intervals during the time of predicted maximum flood-tide current. Sampling was conducted only between dusk and dawn and about 50 minutes later each successive night because of the advancing tide stage. Oblique tows through the entire water column were chosen over surface, bottom, or other single-depth tows to eliminate depth bias. Species of concern, including *B. tyrannus*, are reported to be distributed by depth even in shallow, well-mixed North Carolina inlets (Lewis and Wilkens, 1971; Hettler and Barker, 1993).

The net was deployed by paying out the winch cable as the net, pulled downstream by the tidal current, sank to the bottom. It was then retrieved obliquely through the water column. A depth sounder with a deck readout (Standard Communications DS20) was attached to the net frame to indicate that the net had reached the bottom of the channel. Tow volume was measured with a General Oceanics model 2030R flow meter. Average tow time was 4.0 minutes. The target tow volume was 100 m³, and target net retrieval speed was 1 m/sec.

Data on several environmental variables were collected concurrently with biological sampling. Salinity and temperature measurements were taken with a Hydrolab H20 water quality multiprobe. Water clarity was measured with a Sea Tech 25-cm transmissometer with a 660-nm filter. Tidal current speed was measured with a Marsh-McBirney model 201 flow

meter. Wind speed and direction data were obtained from the NOAA C-MAN station at Cape Lookout, 15 km SE of the larval sampling platform. Tidal amplitude data were obtained from a NOAA tide gauge located on Pivers Island.

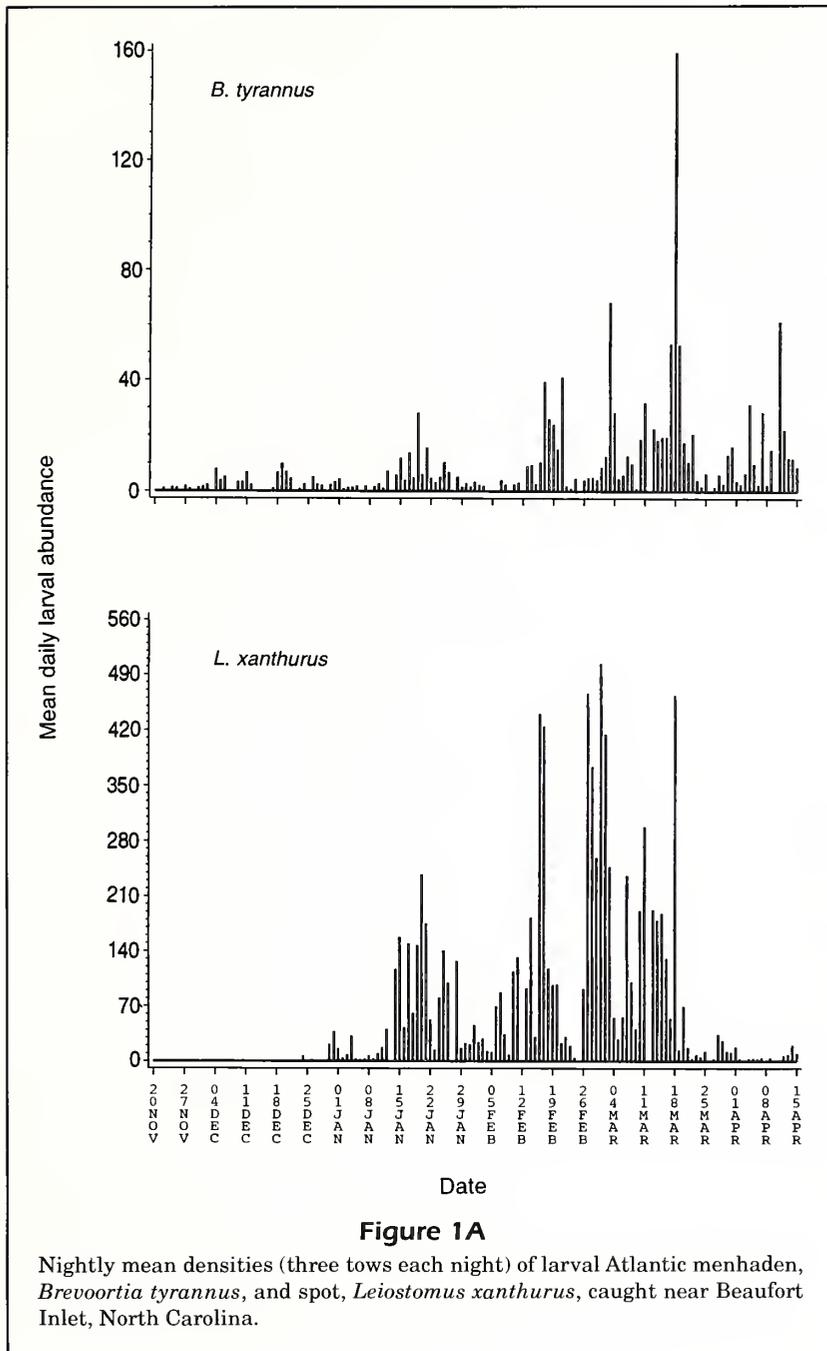
Processing of larvae

After preservation in 70% ethanol, fish larvae were identified, counted, and up to 20 individuals of each species were indiscriminately selected for measurement of standard length. Ages and birth dates of all menhaden larvae retained for length measurements (1,341 individual fish) were determined by otolith daily increment counts (estimated age in days = increment count + 5) following the methods of Warlen (1992).

Data analysis

Abundance was calculated from the number of larvae caught per tow and water volume sampled (density = number \times 100 m⁻³). Densities per unit volume were calculated rather than densities per unit area because all published relevant abundance data on these species is per unit volume. Mean densities by species for each date sampled were determined by averaging the densities from the three tows taken on that date. Although we sampled every night, no data were available for 10 dates during the sampling period (Fig. 1, A–D). This problem is explained by the following example. On 14 December, sampling started at 2359 h and ended around 0100 h, 15 December. The next night sampling began at 0033 h, 16 December. Thus, sampling never began on 15 December. Sampling on 15 December at the time of maximum flood tide current would have occurred before sampling on 14 December had ended. The same situation occurred on nine other dates.

Seasonal mean densities were determined by averaging the daily densities during the interval when each species was caught, including dates when no individuals of the species were caught. Variations in mean daily densities and associated variance estimates were derived by “sampling” individual density data sets for each species at intervals of 2, 3, 4, 5, 7, 14, and 30 days and by then comparing these with the actual data set (1-day intervals between sampling). From this exercise, a mean and standard deviation was generated for each sampling scheme. A 2-day cycle, for example, beginning on 20 November and continuing every other day at day 1, 3, 5 etc., produced one daily mean and standard deviation, whereas a 2-day cycle beginning a day later on 21 November and continuing every other day at day

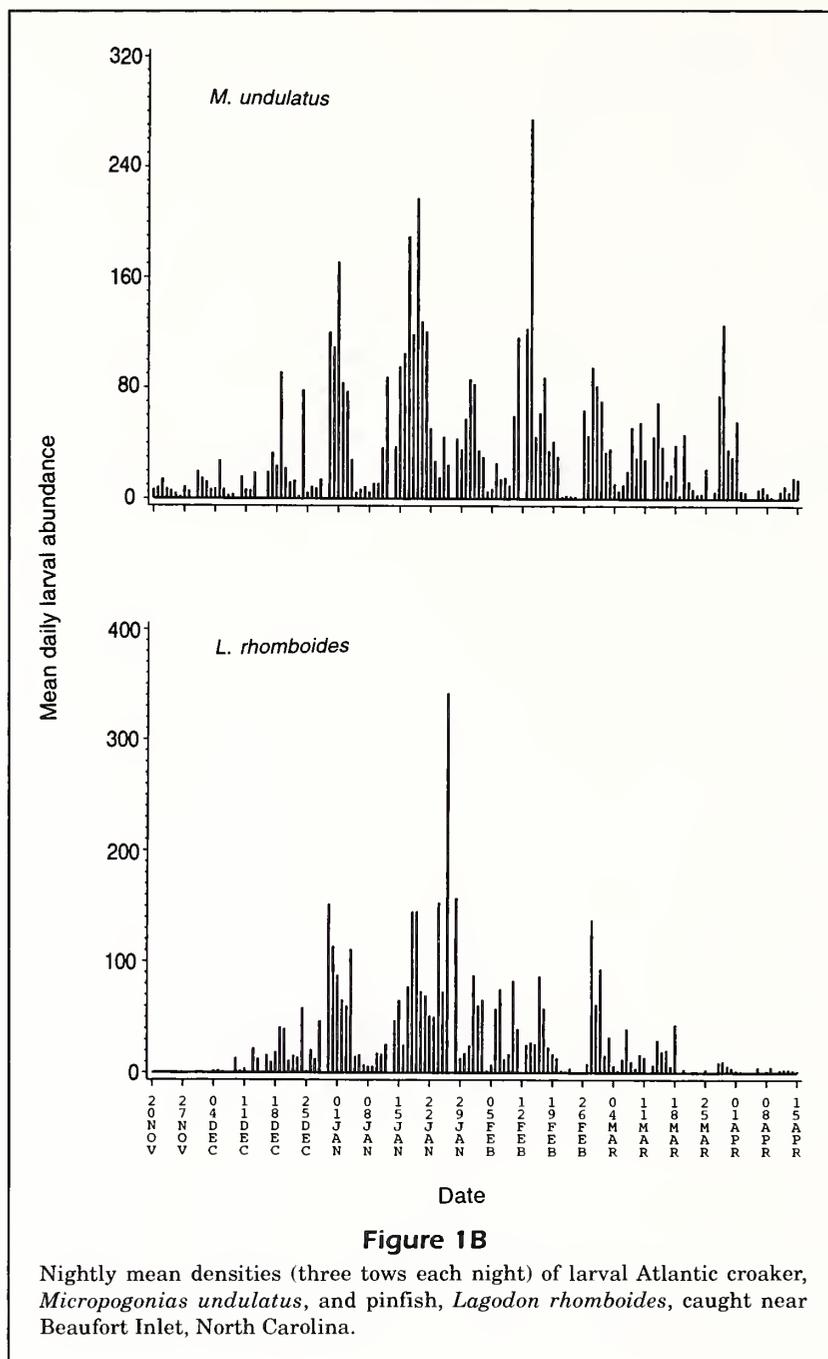


2, 4, 6 etc. produced a different daily mean and standard deviation.

Spectral analysis (ARIMA procedure) was used to examine the time series of densities for each species for evidence of periodicities. Weekly density data based on two methods were compared by using a paired-mean Wilcoxon Signed Rank test. The Laird version (Laird et al., 1965) of the log-transformed Gompertz growth equation (Zweifel and Lasker, 1976) was used to describe the average growth of *B.*

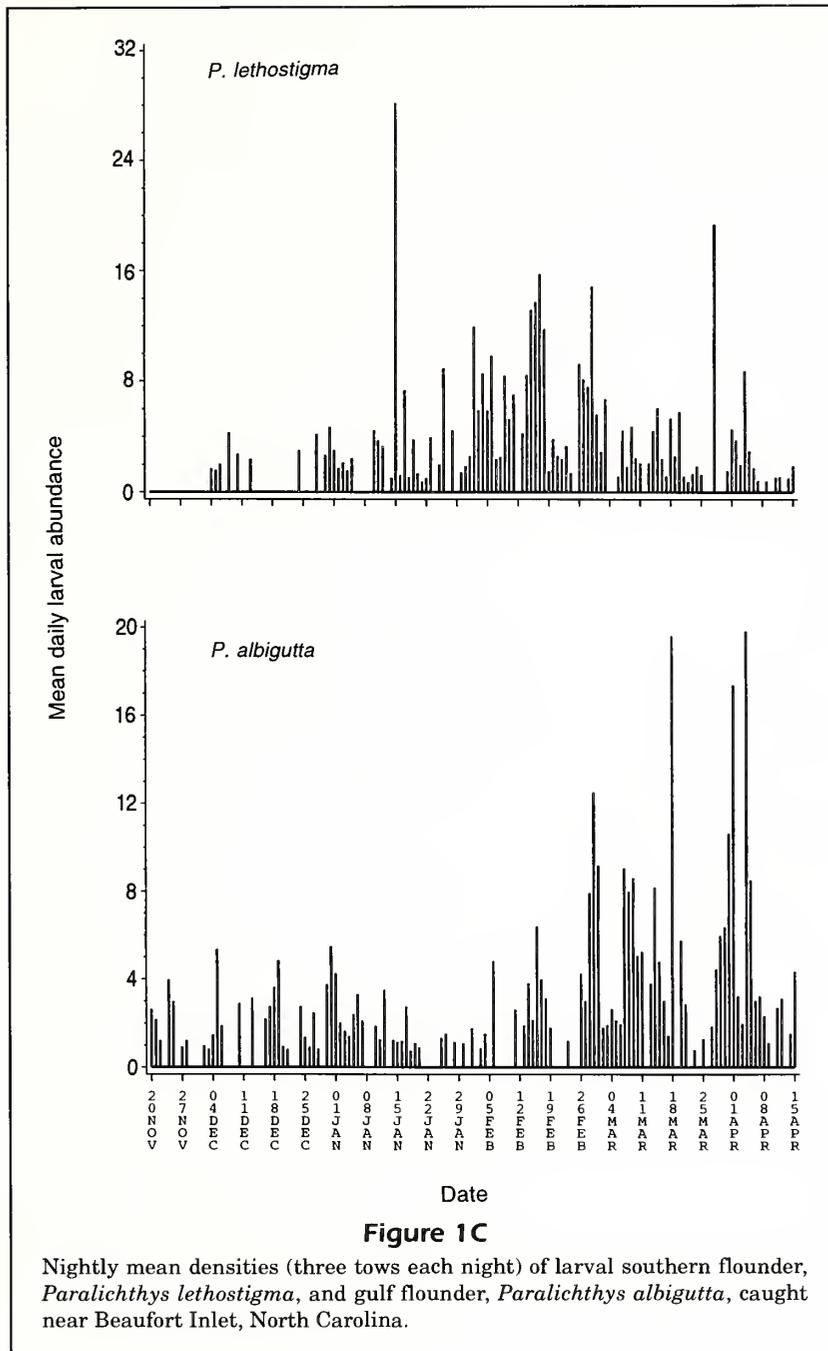
tyrannus larvae. The model was fitted to data for size and estimated age at time of capture. Log-transformed standard length (mm) and estimated age (in days) were used in the model (Warlen, 1992).

In order to examine the possible effects of environmental variables on observed larval densities, we first fitted polynomial regression models to the daily densities for each of the species' densities over time. Although a second-order polynomial was sufficient to describe the recruitment patterns of *Paralichthys*



dentatus and *Micropogonias undulatus*, most species required a fourth-order polynomial, and *Brevoortia tyrannus* required a fifth-order polynomial. The polynomial models provided a means of estimating each species' density for each day as well as the difference between the observed density and the estimated density (residual). One would expect that if an environmental factor influenced observed density, it would do so in a proportional sense, i.e. its effects would be exhibited in relation to the expected density of the

species at that date during the season of recruitment for that species. We therefore divided each residual by the expected density for that date to obtain a measure that took the species' recruitment pattern into account in looking at correlations with environmental variables. Durban-Watson statistics and first order autocorrelation coefficients were also computed to test the presence of autocorrelation and to measure its magnitude.

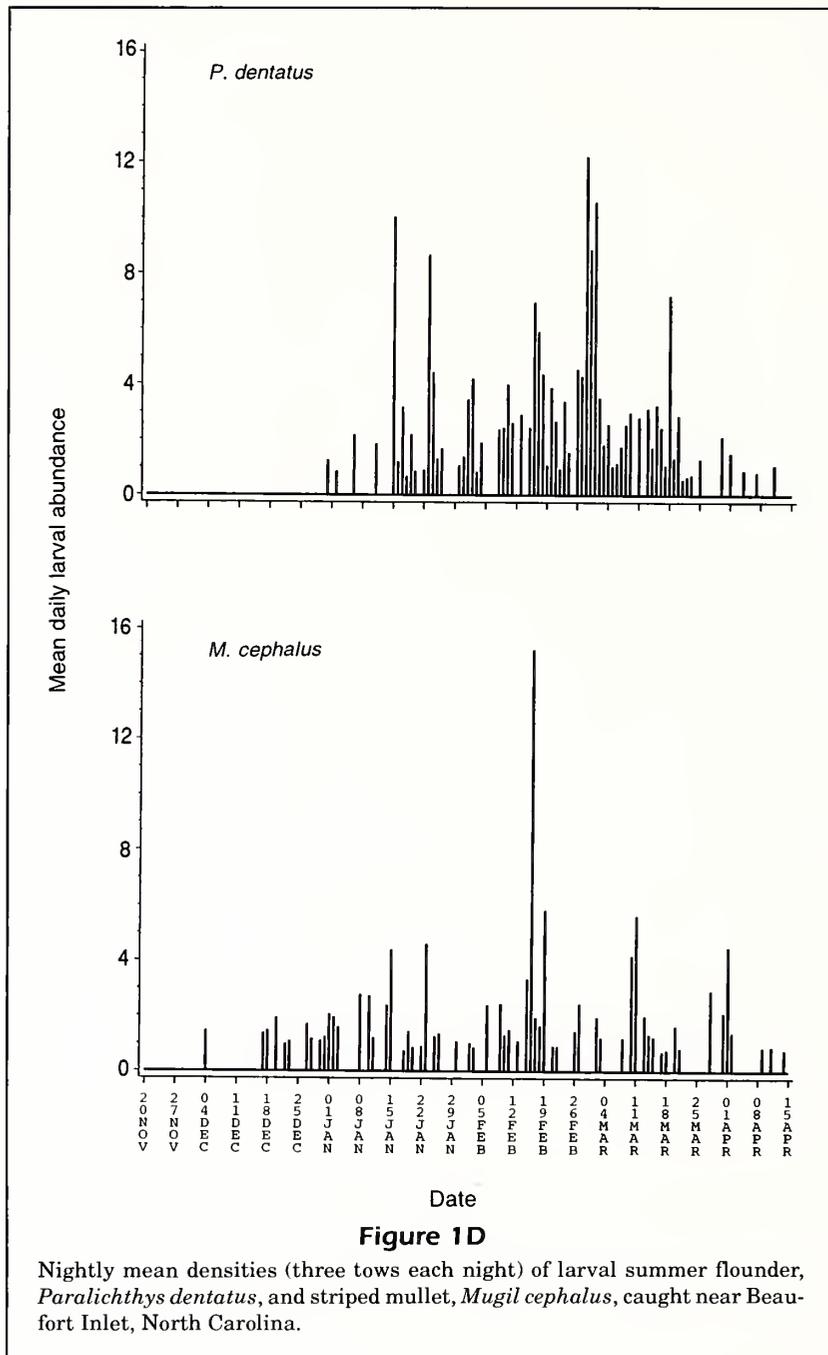


Results

Species abundance

The eight species selected for analysis accounted for 92% of the larvae caught during the period and are listed in Table 1 in order of decreasing abundance. Although abundance was not predictable from one night to the next for any species (Fig. 1, A–D), the Durban-Watson statistics for the polynomial regres-

sion models detected significant autocorrelation in the residuals for six of the eight species. However, one could not reject the null hypothesis that, for *Mugil cephalus* and for *Paralichthys albigutta*, the test was inconclusive. The first-order autocorrelations for the other six species ranged from 0.30 for *Paralichthys dentatus* to 0.52 for *M. undulatus*. These reflect the serial dependency between densities on successive nights. On many dates, densities were two or more times less or more than the night



before; in some cases the difference between two consecutive nights was an order of magnitude (e.g. *Leiostomus xanthurus* on 18–19 March).

Although periods of low and high abundance can be seen along the time axis for each species, oscillations in abundance by each species did not occur at the same time in all cases. However, most of the species share periods of high abundance (mid January, mid February, early March, and mid March). We presumed that our data set would be a good candidate for time-series analysis. Spectral analyses of the es-

timated densities for each species was employed to reveal evidence of periodicities of varying length. All eight species exhibited a strong 14-day signal, most likely dominated by the lunar cycle. However, this 14-day signal turned out to be an artifact in the sampling method which was unavoidable. This artifact was due to sampling 50 min later each night in the sampling scheme (sampling at the same stage in the flood tide) until dawn, at which time the next sampling opportunity would be either 12 h 25 min later or 37 h 15 min later. We chose the later option (to

Table 1

Average seasonal density (=AveDen) and maximum daily density (=MaxDen) of target species listed in order of decreasing average density (larvae per 100 m³). Sampling was conducted between 20 November 1991 and 15 April 1992.

Scientific name	Common name	AveDen	MaxDen	Capture date
<i>Leiostomus xanthurus</i>	spot	82.8	504.0	21 Dec–15 Apr
<i>Micropogonias undulatus</i>	Atlantic croaker	37.9	274.2	20 Nov–15 Apr
<i>Lagodon rhomboides</i>	pinfish	30.0	342.0	22 Nov–15 Apr
<i>Brevoortia tyrannus</i>	Atlantic menhaden	10.0	159.8	22 Nov–15 Apr
<i>Paralichthys lethostigma</i>	southern flounder	3.6	28.2	04 Dec–11 Apr
<i>P. albigutta</i>	gulf flounder	2.7	19.7	20 Nov–15 Apr
<i>P. dentatus</i>	summer flounder	2.0	12.2	31 Dec–15 Apr
<i>Mugil cephalus</i>	striped mullet	1.0	15.2	04 Dec–14 Apr

Table 2

Standard error of the mean abundance of larval species obtained at 2- to 30-day subsampling intervals of the actual daily sampling data set.

Scientific name	If the number of days between sampling had been						
	2	3	4	5	7	14	30
<i>B. tyrannus</i>	0.78	0.89	0.93	1.32	1.98	1.93	1.54
<i>L. rhomboides</i>	2.60	2.36	1.62	3.05	4.14	4.14	3.89
<i>L. xanthurus</i>	0.73	5.22	2.52	7.99	5.68	12.86	9.50
<i>M. undulatus</i>	1.96	2.28	1.17	1.37	1.90	5.90	3.65
<i>M. cephalus</i>	0.31	0.26	0.22	0.21	0.38	0.24	0.33
<i>P. albigutta</i>	0.37	0.14	0.44	0.19	0.27	0.26	0.31
<i>P. dentatus</i>	0.07	0.26	0.14	0.09	0.19	0.32	0.38
<i>P. lethostigma</i>	0.15	0.24	0.43	0.22	0.42	0.48	0.46

avoid sampling twice on the same date), but either option would have resulted in an irregular pulse interval in the time line every 14 days and would have precluded further time-series analysis.

Within-night variability

Variability between tows of the three tows each night was estimated by calculating the coefficient of variation (CV) for each night and for each species. The CV averaged about 50% for each species throughout the sampling period. Late in the immigration period, the CV in densities within a night increased for *Paralichthys lethostigma*; for all other species daily tow-to-tow variability was relatively constant throughout the time series.

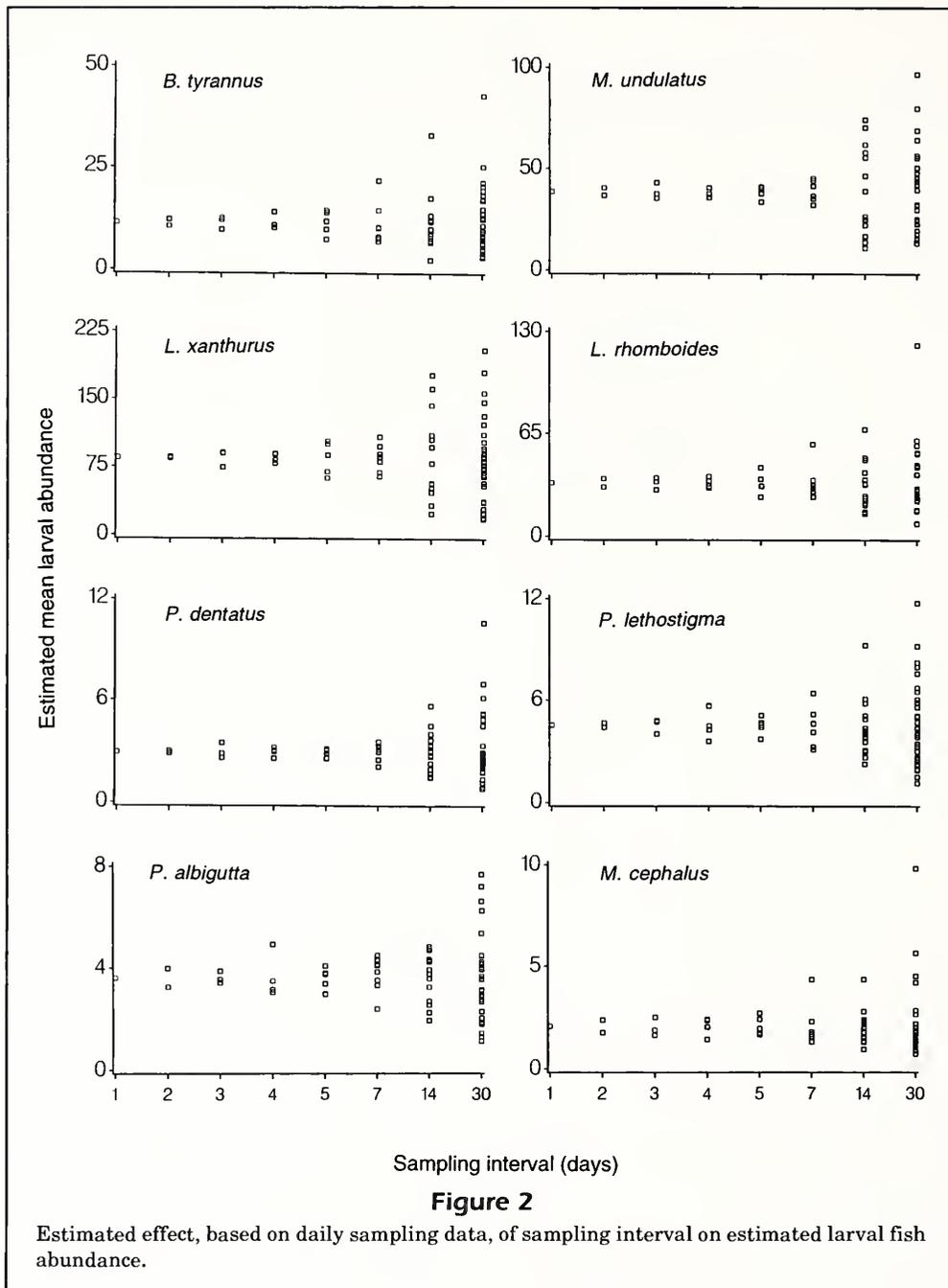
Sampling interval

The range in density estimates derived from subsampling the actual data set increased as the sub-

sampling interval increased (Fig. 2), as did the standard error of the mean for most species (except *Mugil cephalus* and *Paralichthys albigutta*) (Table 2). For example, sampling every night yielded a seasonal mean of 10 *B. tyrannus* larvae per 100 m³, but if we had sampled only every 30 days our estimate for the 1991–92 immigration season, seasonal mean abundance could have ranged from 3 to 43 larvae per 100 m³, depending on which date we began sampling. Similarly, had we sampled for *L. xanthurus* every 30 days, our estimated seasonal mean could have ranged from 11 to 249 larvae per 100 m³.

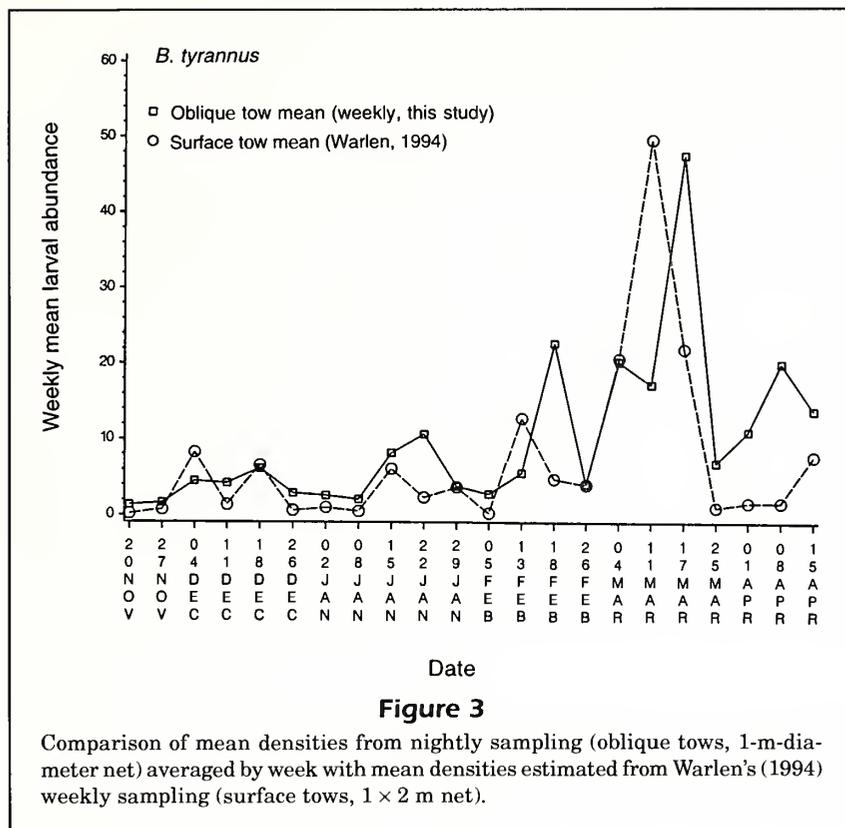
Daily versus weekly sampling

Sampling methods were compared to see if the increased effort required for daily sampling provided better abundance estimates than did weekly sampling. Weekly estimates were calculated by using *B. tyrannus* abundance data from our daily 1-m-net oblique-tows and are plotted (Fig. 3) along with



B. tyrannus data obtained with a 1×2 m net fished near the surface (Warlen, 1994). Sampling with a 1×2 m surface net occurred at night, at approximately the same hour, from the same sampling platform, and during the same immigration season (1991–92) as our basic study. The seasonal weekly mean of the weekly means calculated from daily means obtained with the 1-m net was significantly different ($P < 0.05$) from the seasonal weekly mean density obtained with the 1×2 m surface net. Sampling daily with the 1-m

oblique net resulted in an average of 10.0 *B. tyrannus* larvae per 100 m^3 compared with 7.2 larvae in weekly sampling during the same season with the 1×2 m surface net (Warlen, 1994). The abundance of *B. tyrannus* in catches of the 1-m oblique net tows made only on the nights that the 1×2 m surface net was fished appeared similar to the weekly average of the daily catches with the 1-m oblique net tows (10.2 vs. 10.0 larvae per 100 m^3), but this similarity could not be statistically tested because the samples were not independent.



Size of larvae

Plots of mean length for the larval species produced a variety of seasonal patterns (Fig. 4). Although *B. tyrannus* increased in average size until mid-March and then decreased, the mean length of *M. undulatus*, *L. xanthurus*, and *Lagodon rhomboides* peaked in mid-February, then decreased. *M. undulatus* seemed to share peaks in abundance with peaks in increasing mean lengths (e.g. 30 December, 17 and 26 January, and 28 February). Larvae of *Paralichthys* or *Mugil* did not change substantially in length over the season.

Age and growth of menhaden larvae

Because SABRE studies have centered around *B. tyrannus*, daily collections of this species provided a unique opportunity to test correlations of observed larval age structure with waves of immigrating larvae and environmental conditions. Otoliths of *B. tyrannus* (10–32 mm SL) showed a range in estimated age of 16 to 106 days (Fig. 5). The Gompertz growth equation predicted a size at hatching of 4.96 mm SL, which is above the reported size at hatching of 3.2–3.4 mm SL for laboratory-reared specimens (Powell, 1993). Average daily growth rate declined

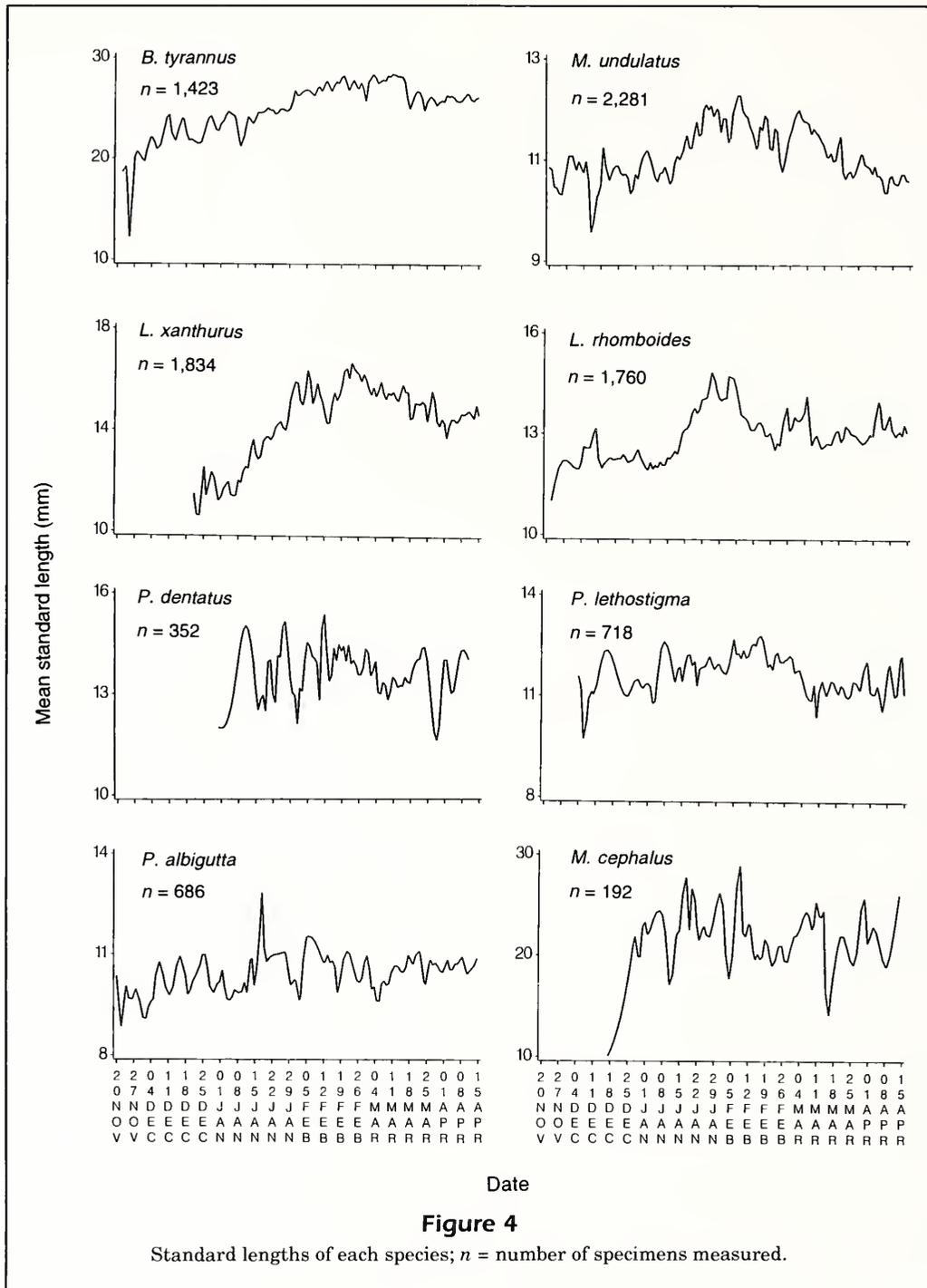
from 0.32 mm/day between days 30 and 40 to 0.03 mm/day between days 80 and 90.

According to back calculations from capture date, *B. tyrannus* ingressing Beaufort Inlet spawned from 12 October 1991 to 16 February 1992. Expressed as a percentage of the total Atlantic menhaden caught, two age cohorts, one in mid-December and another in late January, made up about 50% of the year's recruitment (Fig. 6). Almost 5% of the Atlantic menhaden larvae captured at the sampling station during the season were hatched on 13 December 1991.

The distribution of estimated ages of larvae by collection date is shown with an overlay plot of mean daily density (Fig. 7). The largest daily mean density of 159 larvae per 100 m³ (18 March 1992) occurred during a decrease in age distribution of about 25 days and would suggest a significant import of a younger cohort of *B. tyrannus*.

Environmental variables

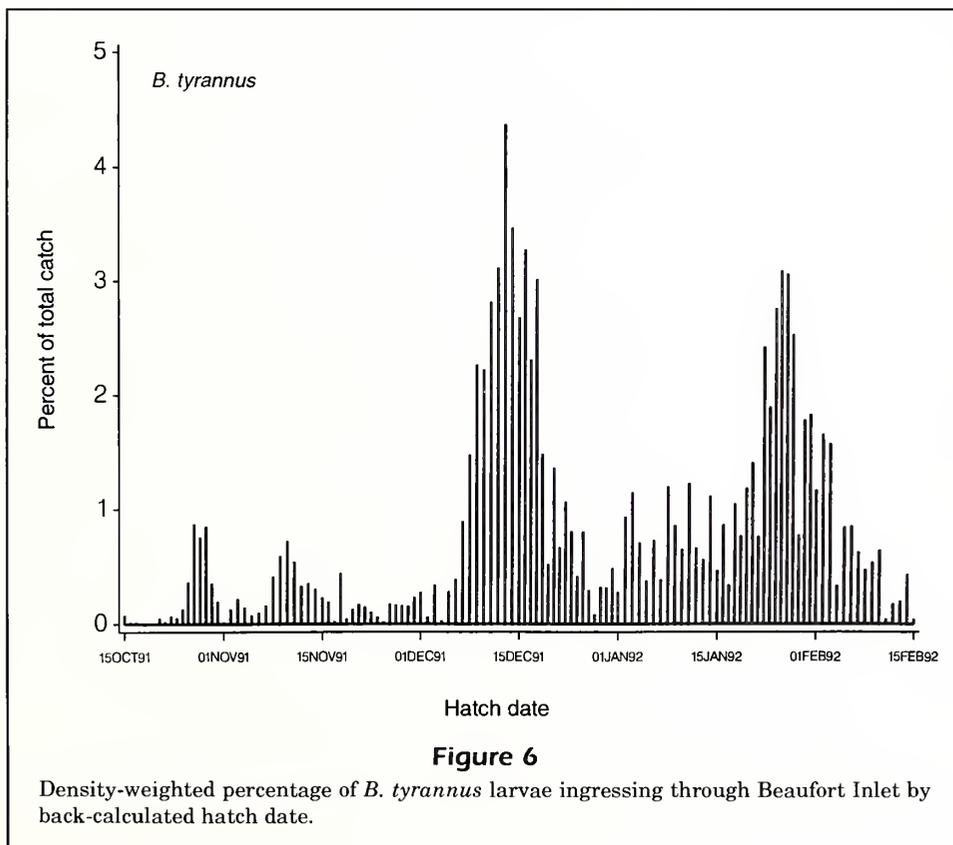
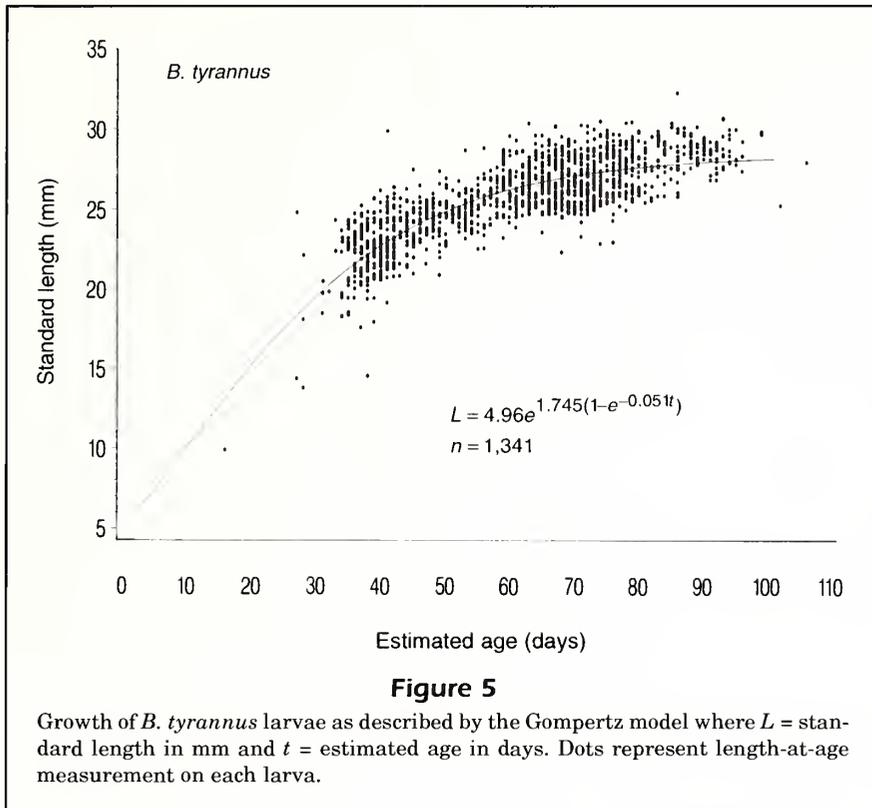
The environmental conditions (except barometric pressure) recorded at the time of sampling are shown in Figure 8. Spearman correlation coefficients were computed for each of the eight species with each of the nine environmental variables (Table 3). Twenty-seven of the 72 coefficients were significant ($P < 0.05$).



The proportional residuals were positively correlated with hour of capture after dusk for six species and negatively correlated with turbidity for five species. As an example, the regressions of abundance of *B. tyrannus* on each environmental condition are shown in Figure 9. Significant correlations for this species were found with tidal amplitude, current speed, moon phase (=spring vs. neap tide), water clarity, and hours

after dark when sampling occurred. *Paralichthys dentatus*, however, exhibited no correlations.

As would be expected, there were significant correlations between the nine environmental variables. The highest was between tidal amplitude and surface current (0.60), and the next highest was between atmospheric pressure and wind velocity (-0.44). However a principal components analysis yielded four



eigenvalues greater than 1.0, cumulatively accounting for only 66% of the variation, leading us to conclude that the structure of the environmental data was not simple.

Discussion

The periodic nature of seasonal changes in some environmental variables and in reproduction of the dif-

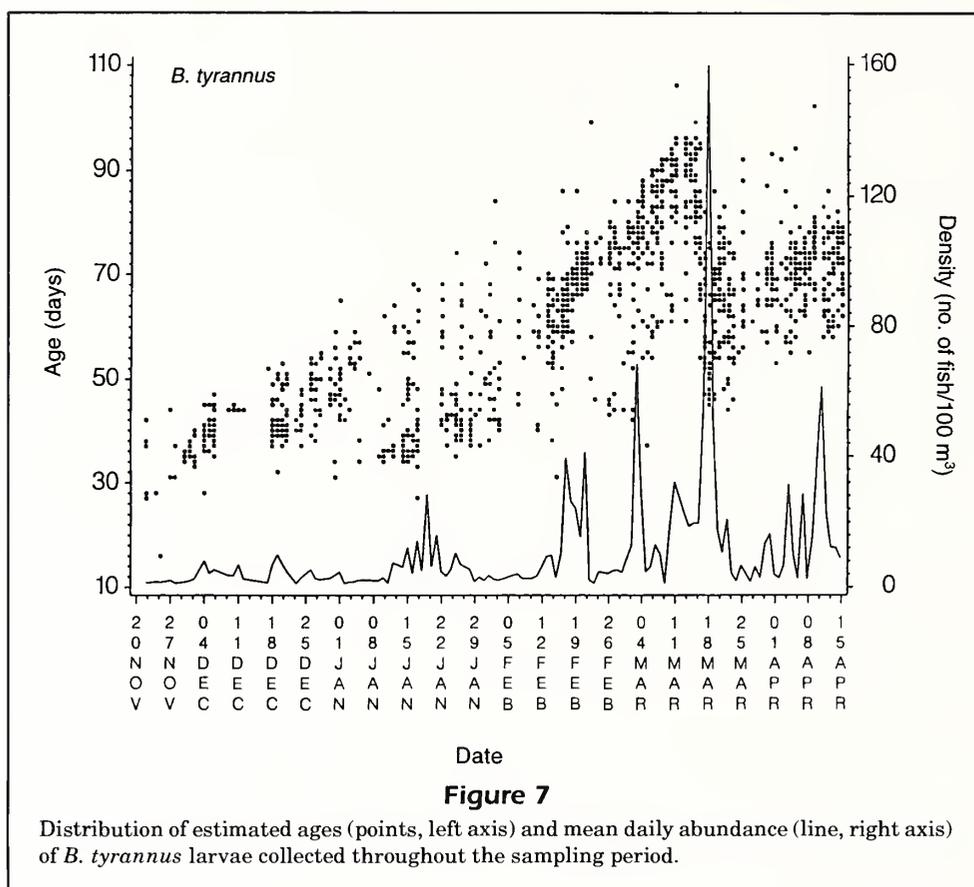


Table 3

Spearman correlation coefficients between proportional residuals for species' densities and various environmental variables: amplitude = tidal amplitude; pressure = barometric pressure; current = flood tide current; hours = hours after sunset; spring tide = spring tide (versus neap tide); temperature = water temperature; wind velocity = average daily wind speed. Bt=*B. tyrannus*, Lr=*L. rhomboides*, Lx=*L. xanthurus*, Mu=*M. undulatus*, Mc=*M. cephalus*, Pa=*P. albigutta*, Pd=*P. dentatus*, Pl=*P. lethostigma*. *= $P < 0.05$. **= $P < 0.01$. ***= $P < 0.001$.

Variable	Bt	Lr	Lx	Mu	Mc	Pa	Pd	Pl
Amplitude	0.40***	0.19*	0.12	0.08	-0.24	-0.02	0.20	0.08
Pressure	0.11	-0.09	0.04	0.03	-0.24	-0.08	-0.02	-0.20*
Current	0.29***	0.22*	0.06	0.14	-0.11	0.15	0.10	0.20*
Hours	0.19*	0.30***	0.30**	0.43***	0.01	0.24**	0.17	0.22*
Salinity	0.06	0.01	-0.20*	-0.11	-0.08	-0.18*	0.14	-0.19*
Spring tide	-0.26**	0.04	-0.22*	-0.24**	-0.00	0.00	-0.19	0.09
Temperature	-0.07	-0.24**	-0.05	-0.06	0.18	0.02	0.08	0.00
Turbidity	-0.28***	-0.42***	-0.32***	-0.29***	0.10	-0.19*	0.03	-0.17
Wind velocity	0.14	0.28*	0.22*	0.06	0.31*	0.11	0.16	0.15
(Sample size)	133	116	102	133	61	138	91	125

ferent species implies that care must be taken in the interpretation of correlations between these variables and fish densities. For example, temperature may be inappropriate to associate with observed densities owing to the spawning-season periodicities in-

involved with life history strategies of each species. Time of spawning (e.g. early winter) and the arrival at the inlet after a 2–3 month cross-shelf transport time, could result in higher abundance corresponding with rising temperatures. The multiple-regres-

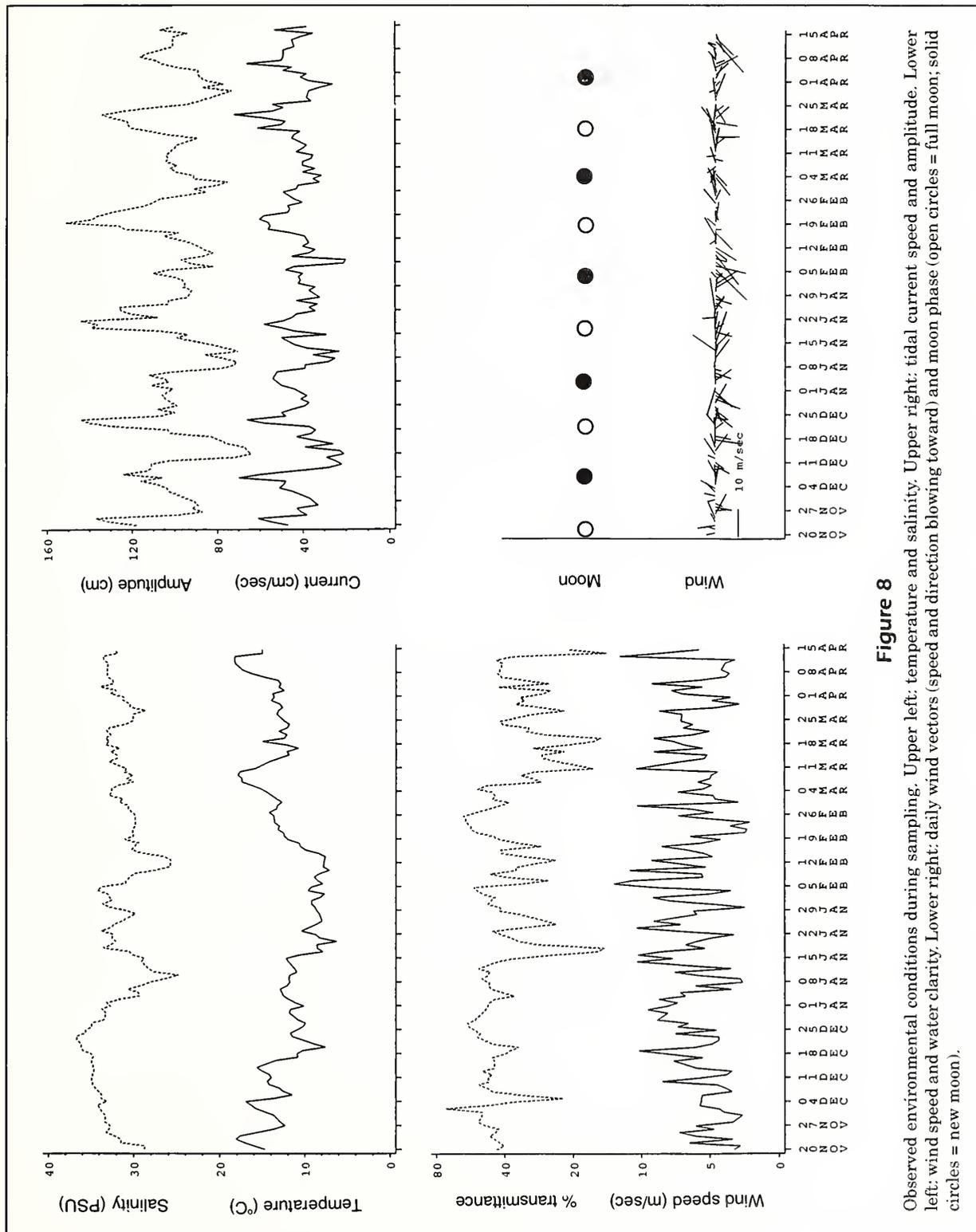
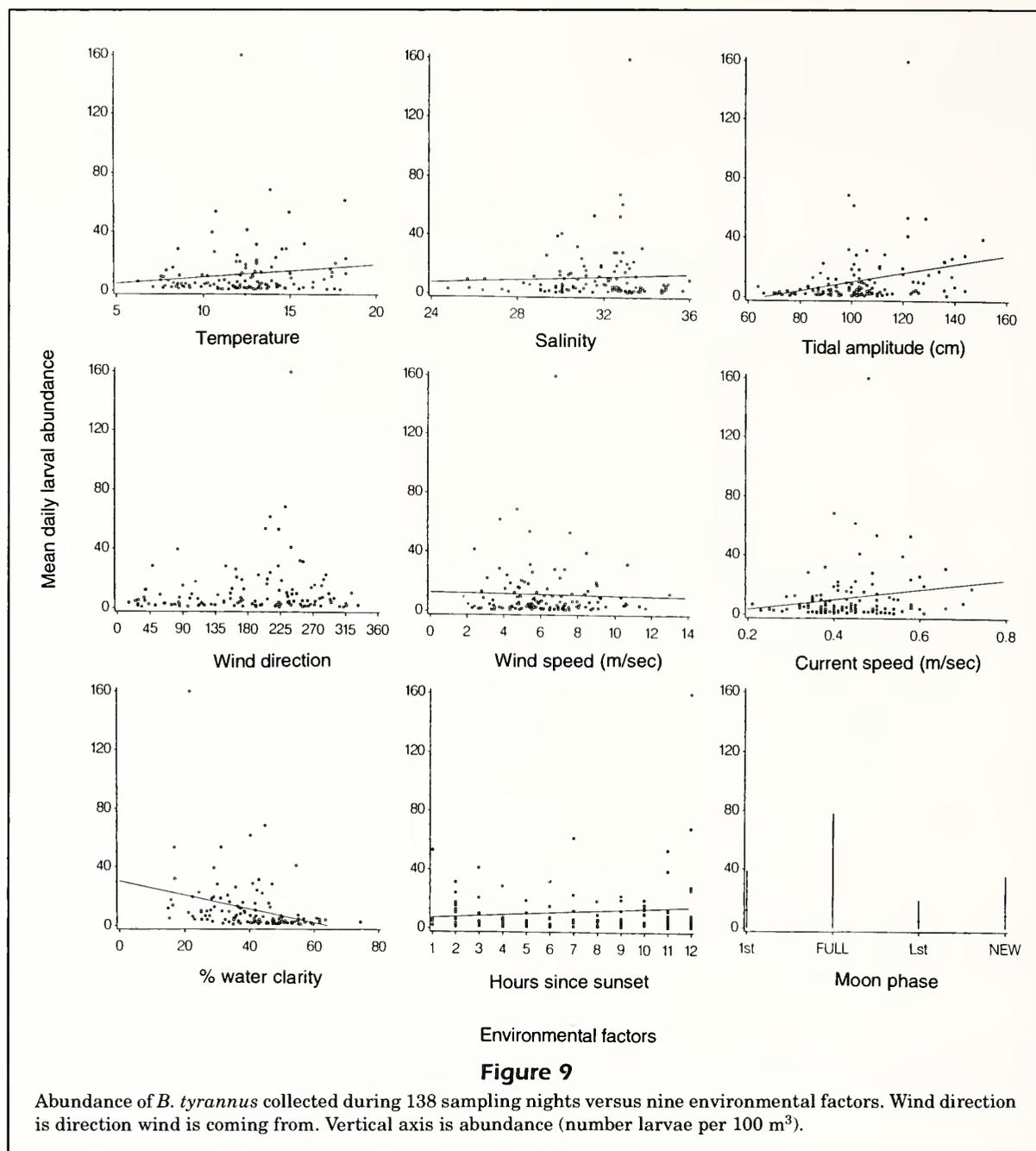


Figure 8

Observed environmental conditions during sampling. Upper left: temperature and salinity. Upper right: tidal current speed and amplitude. Lower left: wind speed and water clarity. Lower right: daily wind vectors (speed and direction blowing toward) and moon phase (open circles = full moon; solid circles = new moon).



sion analysis and the principal-component analysis suggested that unknown factors on a scale larger than the locally measured environmental conditions are probably more important in causing peaks in abundance of the immigrating larvae. Originating from wide-spread spawning sites during the fall-winter period, larvae of different spawning cohorts arrive near the inlet from many possible transport routes. The most likely factor is onshore displacement of warm Gulf Stream filaments containing patches of larvae (Stegmann and Yoder, 1996). Once under the influence of tidal exchange at the inlet,

patches of larvae merge as they ingress the estuary. Variables including temperature, salinity, turbulence, turbidity, odors, and currents differentially affect survival or active transport behavior into the estuary (Boehlert and Mundy, 1988). Larval behavior may have contributed to the fact that some species were more abundant in catches made later in the night (e.g. *L. rhomboides*, *L. xanthurus*, *M. cephalus*, and *P. dentatus*), acting to disperse larvae into the water column from the edges and bottom, thus making them more vulnerable to the sampling gear.

Daily ageing of *B. tyrannus* caught during the study revealed that a rapid and distinct shift in larval populations occurred in mid-March (Fig. 7). In early March, the recruiting larvae were primarily from a cohort that was spawned in mid-December, first reached the inlet in mid-January, and suddenly disappeared on 16 March. On 18 March a new cohort, spawned in mid-January, appeared. Its appearance was coincident with the year's highest daily mean density. This change in age structure coincided with a 3-day shift to southwesterly winds and full-moon spring tides. Advanced very high resolution radiometer sea surface temperature (AVHRR-SST) imagery revealed that sea surface temperatures 15 km off Beaufort Inlet warmed to 15°C on 9 March 1992, up from 11°C a week earlier (and down to 12.3°C a week later), possibly bringing in the younger *B. tyrannus* larvae from warmer offshore water to the vicinity of Beaufort Inlet (Stegmann¹). This warming was also detected by our temperature measurements at the sampling platform, rising to 17.9°C on 9 March followed by a decrease to 12°C on 18 March (Fig. 8), when the large number of younger larvae were caught. Until that date, the average estimated age of larvae caught in Beaufort Inlet increased from about 35 days in late November to about 80 days in mid-March. About 57% of the menhaden captured in the 1991–92 season were spawned in two 2-week periods (mid-December and late January). Although substantial spawning may have occurred at other times, the population from which these larvae were caught contained the survivors of the cross-shelf transport. It appears that size at estimated age was significantly larger, about 3 mm SL, for ages between 40 and 80 days for the 1991–92 collections than the larval size reported by Warlen (1992) for *B. tyrannus* collected mainly offshore of Beaufort Inlet in 1979–80. Because the daily ageing method was the same, this observed difference in growth rates of the 1991–92 ingressing larvae is attributed to a higher growth rate among the larvae that survive to reach the inlet.

Coastal marine environments experience periods of diurnal or semidiurnal tidal cycles imbedded within lunar and semilunar cycles, and these have been shown to influence a broad range of organisms and processes (Hutchinson and Sklar, 1993). Cyclical phenomena impose a particular set of requirements for their adequate measurement and for the avoidance of bias arising from aliasing (Kelly, 1976) because the temporal sequence of observations will be

autocorrelated. A circannual rhythm is a feature of the life history of most vertebrates, and one manifestation of this is the restriction of reproduction of a species to a season of several weeks or months. If the purpose of a sampling program is to compare recruitment of a species of larval fish from year to year, then it should be designed so that it describes each year's temporal pattern accurately. In this respect it differs from the normal random sampling situation designed to estimate the mean and variance of some statistical population. Because its purpose is to enable description of a temporal pattern, a systematic design is normally chosen to ensure equal (or near equal) spacing of samples. Equal spacing of samples is required for many approaches for the analysis of a time series. However, if there are other, shorter cycles within the seasonal pattern, then care must be taken to avoid spurious results (aliasing) that can arise when the sampling interval is greater than one half the wavelength of a significant component cycle. Sampling to determine a seasonal flux of larvae should be designed to detect temporal patterns, as well as estimate a mean abundance and variance.

The question of sampling frequency may have a lower priority than considerations of sampling costs and vessel availability, and thus it is important to quantify the effect that sampling frequency has on estimates of larval abundance, size, and age. For example, one may be interested in estimating the flux of larvae across a boundary over some unit of time. If one is interested in the strength of a year class, the sampling effort must include the entire season of larval recruitment of that species. If one is interested in evaluating the influence of a meteorological event on larval distribution, then the appropriate sampling interval would be measured in hours. As we shall see, both sampling designs also require due consideration of various physical and biological rhythms that have an important bearing on the number of larvae collected at a given point in space and time (e.g. tidal, circadian, circannual). Prior to establishing sampling protocol for future studies, we attempted to determine a sampling interval that would provide acceptable larval fish abundance estimates. Larval fish surveys have been made in Beaufort Inlet and other North Carolina inlets on different sampling intervals, i.e. weekly (Warlen, 1994), bi-weekly (Lewis and Mann, 1971), every new and full moon period (Hettler and Chester, 1990) and every new moon period (Hettler and Barker, 1993). When we compared the weekly sampling method that has been used for monitoring at Pivers Island for the past 10 years (Warlen, 1994) with our daily sampling experiment, a difference in estimated abundance of *B. tyrannus* was detected. Differences in the two types of nets may have

¹ Stegmann, P. 1996. Graduate School of Oceanography, Univ. Rhode Island, S. Ferry Road, Narragansett, RI 02882. Personal commun.

been responsible for the differences in catches. The 1-m net is an active gear, retrieved obliquely at a rate of about 1 m/sec through the water column, whereas the 1 × 2 m net is fished passively in the surface current (flowing 0.2–0.5 m/sec, Warlen²). Also, the mesh of the 1-m net is 200 m smaller and may have reduced extrusion of larvae. Density estimates derived from sampling one night per week with the 1-m net were similar to estimates derived from sampling every night per week with the 1-m net made on the same night as the 1 × 2 m surface net sets and further support our suspicions regarding the differences in sampling with the two gears. Finally, we have assumed for 10 years (Warlen²) that the Pivers Island station serves as a proxy for Beaufort Inlet. An intensive SABRE study conducted in March 1996, during which larval fish were sampled synchronously at seven locations in and near the inlet, including Pivers Island, is under analysis to determine how closely Pivers Island larval fish densities reflect Beaufort Inlet densities.

We conclude that at least one sampling event each week is required for estimating late autumn through early spring seasonal abundance of fish larvae in North Carolina inlets, although more frequent sampling is preferred if the standard error of estimates is to be reduced. Bias may be introduced by sampling only at a specific period of the lunar cycle, because larval abundance appeared to decrease following spring tides. Studies where sampling is done exclusively at the same lunar phase may consistently over or under estimate abundance. This attribute may be acceptable for interannual comparisons, if the same methods are followed from year to year, but would not be acceptable for calculating the flux of larvae through an inlet. Sampling at intervals of 7 days or less can reduce this bias.

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² Warlen, S. 1996. Southeast Fish. Sci. Center, Natl. Mar. Fish. Serv., 101 Pivers Island Rd., Beaufort, NC 28516. Personal commun.

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Abstract—Length at age, length at maturity, and age at maturity of yellowfin sole, *Pleuronectes asper*, in the eastern Bering Sea, are influenced by area of sampling and bottom depth. Yellowfin sole sampled during spring and summer bottom trawl surveys (1982–94) grew faster in the northwest area compared with the southeast area. Mean lengths at age were generally more than 2 cm greater than those for southeast fish at ages greater than 10 years. Length at 50% maturity in females during 1993 and 1994 was respectively 2.3 cm and 0.94 cm larger in the northwest area than in the southeast area. In contrast, there was no apparent difference in age at 50% maturity between areas.

Spring-summer patterns in bathymetric habitation of yellowfin sole differ for immature and mature individuals and cause a potential bias in estimates of growth and maturity. There is a clear relation between length and depth for immature fish, with older, immature fish inhabiting deeper water. In contrast, mature fish distribute similarly by size across a wide range of bottom depths. As a result, estimates of length and age at 50% maturity (L_{50} , A_{50}) tended to increase with increasing bottom depth. Because current resource assessment surveys do not sample the shallowest areas of the summer distribution of yellowfin sole, estimates of L_{50} and A_{50} are inherently biased high.

Effects of geography and bathymetry on growth and maturity of yellowfin sole, *Pleuronectes asper*, in the eastern Bering Sea

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Yellowfin sole, *Pleuronectes asper*, inhabit the nearshore shelf areas of the eastern Bering Sea, from Bristol Bay to north of Nunivak Island (60°N lat.) (Fig. 1), during spring and summer months. Adult individuals overwinter near the shelf-slope break at approximately 200 m. Two main eastern Bering Sea overwintering groups, composed mainly of sexually mature adults (Krivobok and Tarkovskaya, 1964) have been identified: a southern complex near Unimak Island and a central complex located west of the Pribilof Islands (Fadeev, 1970; Bakkala, 1981; Wakabayashi, 1989). During spring, as the edge of the shelf ice recedes toward the coast, yellowfin sole migrate across the shelf to nearshore spawning areas in Bristol Bay and off Nunivak Island (Bakkala, 1981). Yellowfin sole generally spawn at bottom depths less than 50 m (Wilderbuer et al., 1992); most spawning activity, however, occurs at depths less than 30 m, May through August (Nichol, 1995). Juvenile yellowfin sole probably do not undergo the long cross-shelf migration. At least some juveniles (<6 years) are known to overwinter nearshore (Fadeev, 1970; Wilderbuer et al., 1992), whereas relatively few juveniles overwinter offshore (Krivobok and Tarkovskaya, 1964; Fadeev, 1970).

Bottom trawl surveys for groundfish resource assessment are conducted annually in the eastern Bering Sea to obtain abundance estimates of commercially important fish and invertebrate species. Differences in fish distributions and oceanographic factors have prompted scientists who analyze survey results to stratify the eastern Bering Sea into discrete northwest and southeast areas, and three different depth regimes (Walters and McPhail, 1982; Walters, 1983; Wakabayashi, 1989; Bakkala, 1993). Thus, both geographic and bathymetric factors affect fish distribution and abundance in the eastern Bering Sea. In this paper I describe regional differences in growth of yellowfin sole (*P. asper*) from the eastern Bering Sea and effects of geographic area and bottom depth on estimates of length and age at maturity.

Commercial catch records (Norris et al.¹) indicate that yellowfin sole occur in substantial numbers in waters shallower than 30 m, where

¹ Norris, J. G., J. D. Berger, and K. T. Black. 1991. Fisherman's guide to catch per unit effort and bycatch data from the National Marine Fisheries Service Observer Program: Bering Sea/Aleutian Island yellowfin sole trawl fishery. AFSC Proc. Rep. NOAA-NMFS 91-07, 200 p. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

research surveys are not routinely carried out. Thus, current survey biomass estimates underestimate population abundance of the species; exclusion of juveniles in shallow water, as well as sexually mature yellowfin sole that inhabit these nearshore spawning areas during the survey period (June–August), may introduce a sampling bias into estimates of growth and estimates of size at maturation. To determine the extent of this potential problem, I considered the effects of bottom depth on fish size.

Materials and methods

Survey area

Resource assessment surveys were conducted in the eastern Bering Sea (Bakkala, 1993; Wakabayashi et al., 1985), from June to mid-August. Standard survey stations were based on a 20 by 20 nautical mile grid that covered the area from inner Bristol Bay west to the continental slope edge and from the Alaska Peninsula north to approximately latitude 61°N (Fig. 1). Bottom trawl tows of approximately 1.5 nautical miles and of 30-min duration were made at each station. Surveys began in inner Bristol Bay and generally followed north- and south-directed transects, proceeding westward with each finished transect.

Data

Yellowfin sole otoliths were collected from 3,891 males and 5,209 females during AFSC surveys, 1982–94 (Table 1). Fish were measured to the nearest centimeter total length (TL) and sagittal otoliths were removed and stored in 50% ethanol for subsequent age determination. Ages were determined by using the break-and-burn technique (Chilton and Beamish, 1982).

Female maturity data were collected during 1992–94 surveys (Table 2). Maturity codes were based on macroscopic gonadal appearance (Nichol, 1995). For the purpose of this study, codes were simplified to either mature or immature. Females were consid-

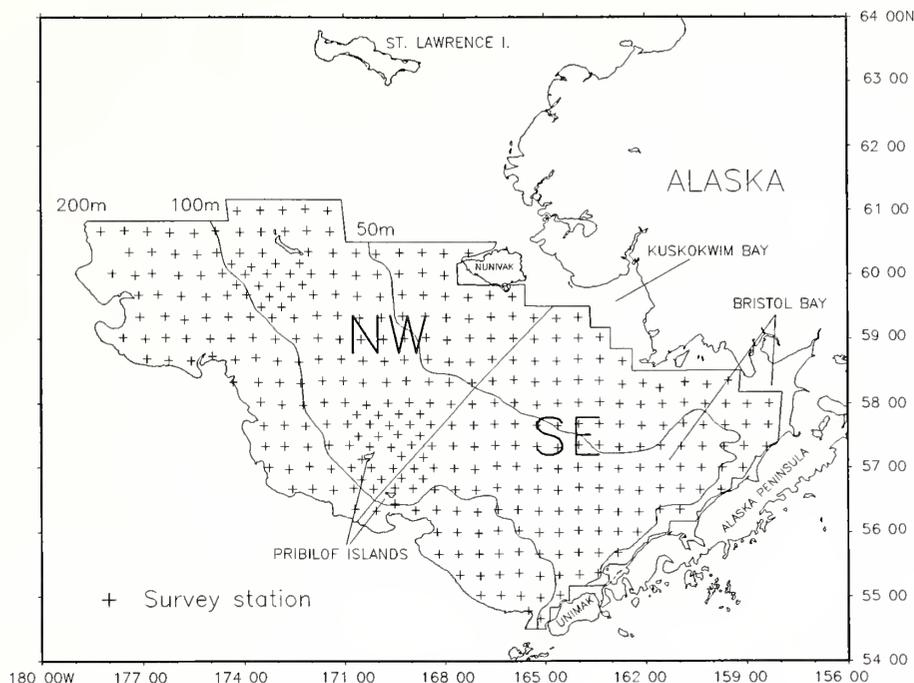


Figure 1

Map of the survey stations where yellowfin sole were sampled by the eastern Bering Sea crab-groundfish bottom trawl survey of the Alaska Fisheries Science Center from 1982 to 1994. Northwest (NW) and southeast (SE) areas are delineated by the strata boundary line extending from north of Kuskokwim Bay, southeast through the Pribilof Islands.

ered mature if ovaries contained yolked or hydrated oocytes, or were recently spent. Immature ovaries contained no visible oocytes. Data collected during 1993 (Table 2) were best for examining spatial differences in female length at maturity because samples were collected at nearly all survey stations within the 50-m contour line, and maturity code assignments were verified by histological examination (Nichol, 1995).

Analysis

The total survey area was subdivided into northwest and southeast areas (Wakabayashi, 1989; Bakkala, 1993) extending from north of Kuskokwim Bay southeast through the Pribilof Islands (Fig. 1).

Length at age Factorial analysis of variance (ANOVA) models (Reish et al., 1985) was constructed independently for males and females to examine the variance in length at each age due to geographic area (northwest or southeast) and to bottom depth. For ANOVA, bottom depths were grouped into three levels (<30 m, 30–49 m, and ≥50 m; Table 1). A model, which included interaction terms and which was pooled across years, was analyzed for both males and

females. Preferred models were estimated by a least-squares backward stepwise procedure that sequentially removed the highest-order nonsignificant factor until only significant terms remained. Nonsignificant ($P \geq 0.05$) main effects were retained if they were included in one or more significant interaction terms. Residual plots were examined to test assumptions of homoscedasticity and normality of error terms. Least squares estimates of model coefficients were obtained by means of the Statistical Analysis System procedure GLM (SAS Institute, 1989).

Length at maturity Logistic regression was used to assess the effects of area and bottom depth on the

probability that an individual of a given length (cm) was mature or immature. The following equation was fitted independently to 1992, 1993, and 1994 female yellowfin sole length-maturity data by using the Statistical Analysis System maximum likelihood procedure LOGISTIC (SAS Institute, 1989):

$$MAT = \frac{1}{1 + e^{-(\mu + \beta L + \alpha \text{area} + \delta D + \Delta L \cdot D)}}, \quad (1)$$

where MAT = mature proportion of female yellowfin sole given its length (L), area, and bottom depth (D) of capture.

Area was treated as a factor indicating either northwest or southeast areas. Depth was treated as a continuous variable. Length, area, and depth coefficients were represented by β , α , and δ , respectively, and μ denoted the intercept (on the logit scale). A length \times depth interaction term ($L \cdot D$; Eq. 1) with coefficient Δ was also tested for significance. Nonsignificant ($P \geq 0.05$) highest order terms were removed from the model.

Length at 50% maturity (L_{50}) was calculated by substituting 0.5 for MAT in Equation 1 and solving for L as follows:

$$L_{50} = - \left(\frac{\mu + \alpha \cdot \text{area} + \delta \cdot D + \Delta \cdot L \cdot D}{\beta} \right). \quad (2)$$

Due to sample-size inequalities (Table 2), length at maturity comparisons between northwest and southeast areas were limited to females sampled in 1993 and 1994.

Table 1

Number of male and female yellowfin sole sampled for age and length by the Alaska Fisheries Science Center during resource assessment surveys conducted in northwest and southeast areas of the eastern Bering Sea from 1982 to 1994.

Year	Bottom depth (m)					
	Northwest			Southeast		
	<30	30-49	≥ 50	<30	30-49	≥ 50
Males						
1982	26	58	26	65	97	45
1983	0	52	85	56	87	27
1984	14	102	31	31	109	42
1985	28	99	36	26	65	84
1986	0	100	42	39	74	66
1987	133	30	13	38	111	31
1988	44	33	13	27	28	98
1989	29	35	39	23	105	87
1990	49	58	48	36	74	92
1991	82	64	26	0	65	97
1992	32	0	25	73	79	39
1993	31	50	18	47	0	46
1994	24	64	21	72	13	37
Total	492	745	423	533	907	791
Females						
1982	15	110	49	65	97	83
1983	0	80	129	57	102	41
1984	0	143	71	33	137	83
1985	41	154	40	43	57	129
1986	0	113	97	48	57	103
1987	152	67	24	36	112	51
1988	58	38	46	47	31	100
1989	0	82	113	39	92	96
1990	47	81	86	54	38	129
1991	85	73	35	0	69	146
1992	35	0	91	86	79	67
1993	28	67	100	61	0	101
1994	29	55	49	61	20	76
Total	490	1,063	930	630	891	1,205

Table 2

Summary of female yellowfin sole length-maturity collections during the 1992-94 Alaska Fisheries Science Center eastern Bering Sea groundfish bottom trawl surveys. A = Age, length, and maturity data collected by sex-cm interval; L = Length and maturity (random measurements); O = Ovaries, lengths, and maturity data collected by size category, ≥ 25 cm TL. Ages were determined for 53 of these specimens.

Year	Sample type	Number of samples	
		Northwest	Southeast
1992	A	107	218
	L	0	1,260
1993	A	98	162
	O	256	512
1994	A	133	158

Age at maturity Analysis of female age at maturity was treated in the same manner as with length at maturity, substituting age (A) in years for length (L). Owing to smaller sample sizes (Table 2), data for years 1992–94 were pooled.

Results

Length at age

The general effects of area and bottom depth on length at age were highly significant for both males and females (Table 3). Mean length-at-age plots for both male and female yellowfin sole indicated greater

sizes at age in the northwest than in the southeast area of the eastern Bering Sea shelf (Fig. 2). Male and female yellowfin sole were on average 1.22 and 1.02 cm larger at age, respectively, in the northwest area than in the southeast area. Average length-at-age differences between areas (northwest-southeast) increased with increasing age to more than 2 cm for both males and females (Fig. 3). Total lengths were generally greater at age in deeper (≥ 50 m) waters than in shallow waters (< 50 m) for males and females less than 8 and 9 years of age, respectively (Fig. 3).

Length at maturity

Female yellowfin sole lengths corresponding to 50% maturity (L_{50}) were greater in the northwest than in the southeast area, and L_{50} increased with increasing bottom depth (Fig. 4). Area accounted for a 2.3 cm female length-at-maturity difference ($P=0.0001$) in 1993 and a 0.91 cm difference ($P=0.049$) in 1994 (Fig. 4; Table 4). Female L_{50} increased with increasing bottom depth ($P\leq 0.013$), varying by as much as 4 cm between shallow and deeper waters (Fig. 4; Table 4). Annual variation (1992–94) in L_{50} appeared to be approximately 1 cm (Fig. 4).

Age at maturity

In contrast to length-at-maturity results, no significant age-at-maturity difference ($P=0.080$) was found for females between the two areas (Fig. 5; Table 5). A similar increase in female age at maturity, however, did occur with increasing bottom depth ($P=0.0001$), with age at 50% maturity increasing by 3 years from shallow to deeper waters (Fig. 5).

Discussion

Larger northwest fish lengths corresponding to a particular age or percent maturity, combined with no apparent age-at-maturity difference between areas, indicate faster yellowfin sole growth in the northwest area than in the southeast area. Bottom depth effects on length-at-age, length-at-maturity, and age-at-maturity estimates, however, were more the result of sampling uneven fish distributions, as discussed below.

Area effects

The length-at-age and length-at-maturity differences found between areas support the hypothesis that northwest and southeast complexes are functionally allopatric during the summer spawning period. Tag-

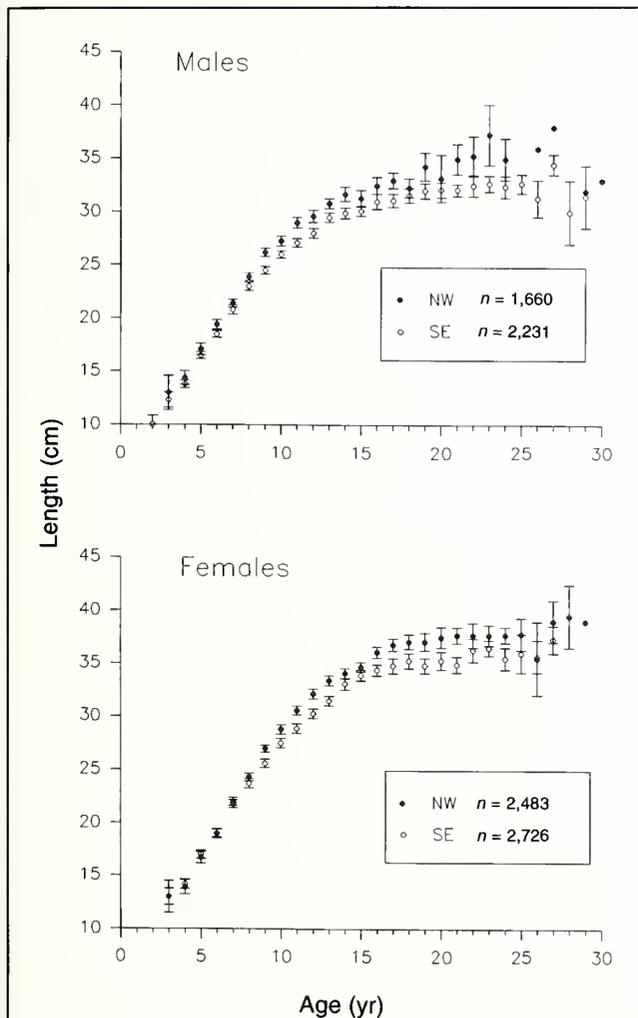


Figure 2

Comparison of male and female yellowfin sole mean length at age between northwest (NW) and southeast (SE) areas of the eastern Bering Sea (1982–94). Error bars indicate 95% confidence intervals.

ging studies (Wakabayashi, 1989) indicated only limited movements of yellowfin sole between northwest and southeast areas as they migrate inshore, and Kashkina (1965) supported a two-stock concept, cit-

ing differences in egg-stage advancement and abundance between northern and southern regions of the eastern Bering Sea. Despite the lack of genetic evidence supporting the coexistence of two independent

Table 3

Factorial analysis of variance of male and female yellowfin sole length (cm) at age (years), by area (northwest and southeast) and bottom depth (<30, 30–49, and ≥50 m), pooled across years 1982–94. Note that nonsignificant ($P \geq 0.05$) main effects were retained because they were included in one or more significant interaction terms. SS = sum of squares.

Source	df	SS	Mean square	F-value	$P > F$
Males					
Age	29	68,007.6	2,345.1	360.0	0.0001
Area	1	295.5	295.5	45.4	0.0001
Depth	2	5.7	2.8	0.4	0.6457
Age × depth	49	1,906.9	38.9	6.0	0.0001
Age × area	24	160.4	6.7	1.0	0.4268
Area × depth	2	51.8	25.9	4.0	0.0188
Age × area × depth	34	366.9	10.8	1.7	0.0098
Error	3,749	24,421.2	6.5		
Females					
Age	29	152,746.0	5,267.1	667.9	0.0001
Area	1	408.1	408.1	51.8	0.0001
Depth	2	2.1	1.1	0.1	0.8738
Age × depth	49	3,219.2	65.7	8.3	0.0001
Age × area	24	411.2	17.1	2.2	0.0008
Area × depth	2	44.7	22.3	2.8	0.0589
Age × area × depth	44	593.1	13.5	1.7	0.0025
Error	5,057	39,880.8	7.9		

Table 4

Logistic regression coefficients for the equation $MAT = 1 / (1 + e^{-(\mu + \beta L + \alpha \text{area} + \delta D + \Delta L D)})$ relating female yellowfin maturity status to fish length (L), binary variable area (northwest or southeast), and continuous variable depth (D). $L \times D$ denotes the interaction between length and depth. SE = standard error of the estimate. $L \times D$ coefficients were considered nonsignificant ($P \geq 0.05$) and were therefore removed from the model. Remaining coefficients and estimates result from model runs with $L \times D$ removed (underlined values).

Year	n	Variable	Symbol	Coefficient		
				Estimate	SE	$P > \text{chi-square}$
1992 ¹	1,478	Length	β	-0.82	0.047	0.0001
		Depth	δ	0.046	0.0048	0.0001
		$L \times D$	Δ	0.0046	0.0024	<u>0.057</u>
		Intercept	μ	22.22	1.36	0.0001
1993	1,028	Length	β	-0.83	0.063	0.0001
		Area	α	2.29	0.30	0.0001
		Depth	δ	0.042	0.0078	0.0001
		$L \times D$	Δ	-0.0065	0.0035	<u>0.063</u>
		Intercept	μ	21.70	1.81	0.0001
1994	291	Length	β	-0.69	0.085	0.0001
		Area	α	0.91	0.46	0.049
		Depth	δ	0.042	0.012	0.0004
		$L \times D$	Δ	0.0046	0.0048	<u>0.34</u>
		Intercept	μ	17.92	2.52	0.0001

¹ Southeast area only. Small sample size in the northwest area ($n=107$) limited a comparison by area.

stocks (Grant et al., 1983), the persistence of area-based differences suggests that mixing of adults between northwest and southeast complexes may be minimal.

Growth-rate differences may be associated with geographic differences in yellowfin sole density or bottom temperature (or both). Yellowfin sole mean density (1982–94; author, unpubl. data), measured in catch per unit of effort (kg/hectare) during spring-

summer, has been consistently higher in the southeast area (88.9 kg/ha) than in the northwest area (27.8 kg/ha). Spring-summer bottom temperatures have also been consistently higher in the southeast area than in the northwest area (Fig. 6). The higher yellowfin sole growth rate in the northwest areas is consistent with density-dependent hypotheses (Beverton and Holt, 1957; Cushing, 1975; Rijnsdorp, 1994) that suggest a negative correlation between fish growth and fish density. Reasons why fish growth appears faster in cooler northwest waters are less clear.

Age-composition data used in stock assessments for yellowfin sole in the eastern Bering Sea (Wakabayashi et al., 1985) have been based upon age-length keys generated from annual age-length collections (Armistead and Nichol, 1993). Although independent age (otolith) collections have been made for the southeast and northwest areas, age-length keys are currently pooled across areas. The resulting estimates of growth are considered accurate because Alaska Fisheries Science Center age-structure collections have been spread fairly evenly between areas. However, given the spatial patterns described here, separate northwest-southeast age-length keys might improve the precision of these estimates.

Implications of depth-related sampling biases

Immature yellowfin sole, like many other fish species (Hunter et al., 1990; Macpherson and Duarte, 1991; Jacobson and Hunter, 1993), undergo an ontogenetic migration, distributing themselves along a size-depth continuum where smaller individuals inhabit shallow waters and larger individuals inhabit deeper waters. A single cohort can also distribute itself along this size-depth continuum. In doing so, faster-growing individuals can be found at

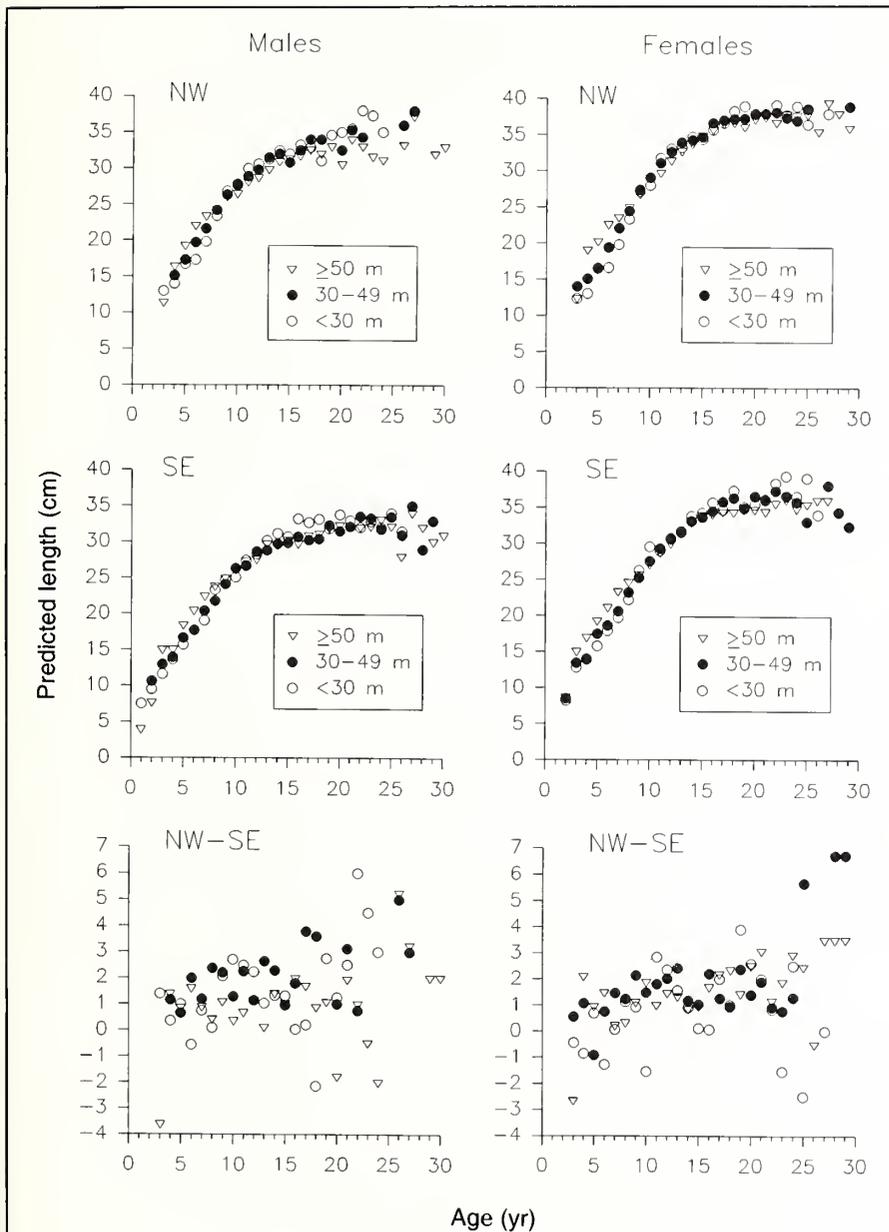
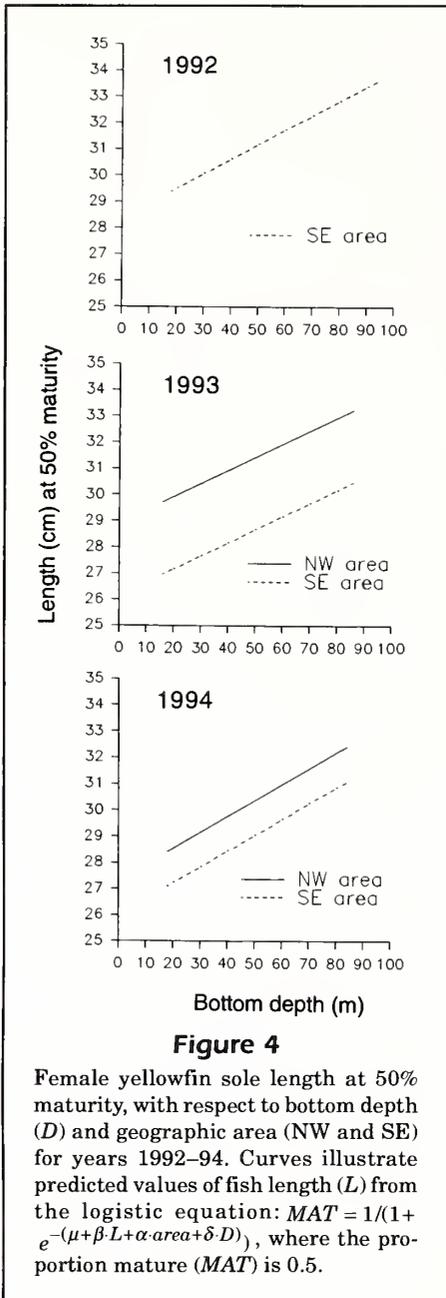
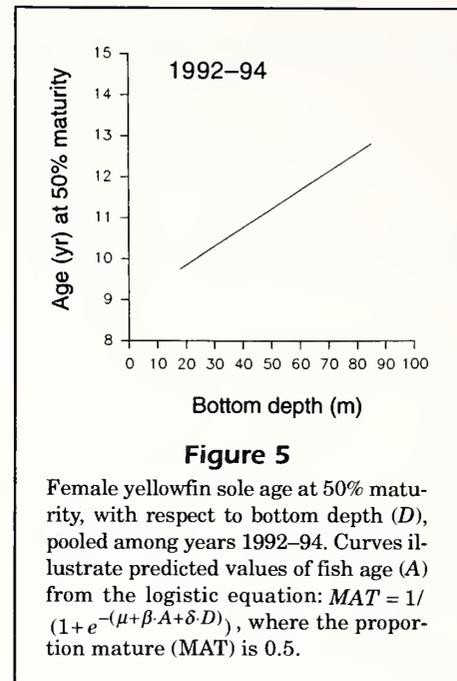


Figure 3

Factorial length at age model results comparing length at age of male and female yellowfin sole across bottom depths (m) in both northwest (NW) and southeast (SE) areas of the eastern Bering Sea. Age × Area × Depth interactions are included with data pooled across 1982–94 age-length collections.



deeper depths than can slower-growing individuals. Length-at-age estimates for immature yellowfin sole (<8 years of age) from shallower waters, therefore, are biased low in comparison with those from deeper waters (Fig. 3). The cessation of this depth effect with increasing bottom depth after 8 years of age (Fig. 3) may indicate the approximate age at which immature yellowfin sole leave the size-depth continuum and become migratory (i.e. to shelf-slope waters in winter and back to nearshore waters in spring-summer). The timing of first maturity may very well coincide with the initiation of a “spawning” migration.



The increase in female length and age at maturity with increasing bottom depth was largely due to the variation of immature female length distributions as depth increased. In spring-summer, when yellowfin sole have migrated nearshore for spawning, distributions of mature migratory individuals and immature “ontogenetically driven” individuals overlap. The differences between these two migration patterns act to separate immature and mature fish of similar lengths (and ages) along a bottom depth gradient. Immature females were distributed unevenly by size across depth; larger sizes (25–32 cm TL) were more common at deeper depths (Fig. 7). In contrast, mature females were distributed similarly by length between shallow (<30 m) and deeper (≥ 30 m) bottom depths (Fig. 7).

The absence of these larger immature females in shallow water resulted in lower values of length at maturity for shallow waters and higher values for deeper waters (Fig. 7). Trippel and Harvey (1991) demonstrated how age at maturity of white suckers (*Catostomus commersoni*) could be affected if year classes falling within the progression from immaturity to maturity are missing. Missing length classes, similarly, affect estimates of length at maturity. Sampling of female yellowfin sole in shallow waters (<30 m) misses critical length and age classes of immature individuals on the verge of maturity.

Length or age at maturity, as with growth relations, are often measured simultaneously across multiple cohorts and are therefore approximations

Table 5

Logistic regression coefficients for the equation $MAT=1/(1 + e^{-(\mu + \beta \cdot A + \alpha \cdot \text{area} + \delta \cdot D + \Delta \cdot A \cdot D)})$ relating female yellowfin maturity status to fish age (*A*), binary variable area (northwest or southeast), and continuous variable depth (*D*). *A* × *D* denotes the interaction between age and depth. SE= standard error of the estimate. *A* × *D* and age coefficients were considered nonsignificant ($P \geq 0.05$) and were therefore removed from the model. Remaining coefficients and estimates result from model runs with *A* × *D* and age removed (underlined values).

Year ¹	n	Variable	Symbol	Coefficient		
				Estimate	SE	P > chi-square
1992-94	929	Age	β	-0.70	0.048	0.0001
		Area	α	0.38	0.21	<u>0.080</u>
		Depth	δ	0.032	0.0056	0.0001
		A × D	Δ	-0.0040	0.0021	<u>0.054</u>
		Intercept	μ	6.25	0.50	0.0001

¹ Data were pooled among years 1992-94.

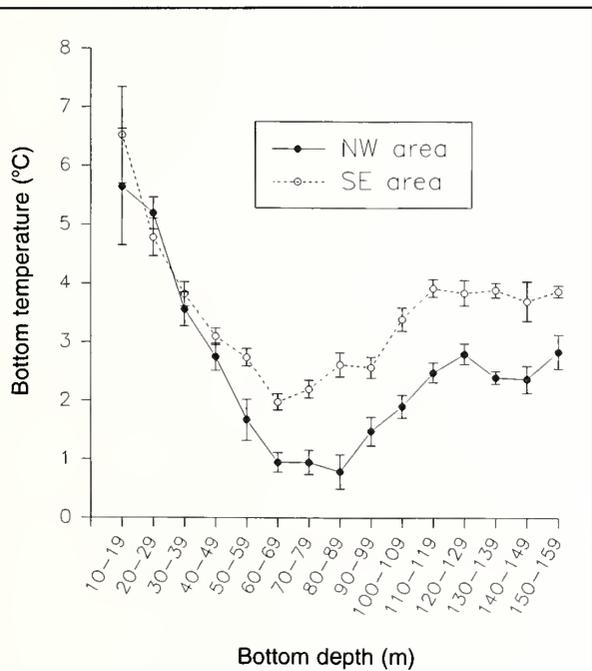


Figure 6

Mean bottom temperatures of the southeast and north-west areas of the eastern Bering Sea shelf, averaged across years 1982-94 at 10 m bottom depth intervals. Error bars indicate 95% confidence intervals.

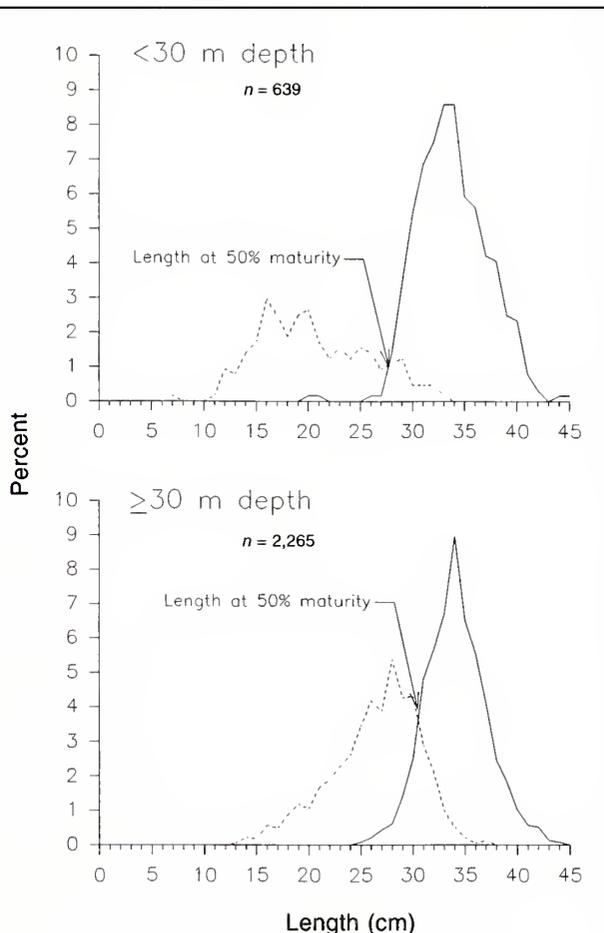


Figure 7

Length distribution of mature (solid line) and immature (dashed line) female yellowfin sole at bottom depths less than 30 m and greater than 30 m, 1992-94 data combined.

of individual growth and length or age at maturity. This estimation assumes that there is no between year-class growth or maturity differences with respect to a given age and that samples within each age class are random with respect to the population

(Ricker, 1975). Obtaining representative samples from each age class becomes difficult when fish size and age vary with bottom depth. Considering also that during spring-summer, yellowfin sole abundance increases with decreasing bottom depth (Nichol, 1995), population estimates of yellowfin sole growth and length or age at maturity should be weighted accordingly. Because groundfish assessment surveys in the eastern Bering Sea do not cover the shallowest areas of yellowfin sole distribution during spring-summer, current estimates of yellowfin sole growth, as well as size and age at maturity, are inherently biased high. Given that most demersal fish distribute themselves along a size-depth continuum (Macpherson and Duarte, 1991), the potential for similar depth-related sampling biases in other demersal fish species appears probable.

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Abstract.—Juveniles of four species of pleuronectid flatfishes were abundant in bays and nearshore areas around Kodiak Island, Alaska, during August 1991 and 1992. The four most abundant species of juvenile (age-0 or age-1) flatfishes were rock sole (*Pleuronectes bilineatus*), flathead sole (*Hippoglossoides elassodon*), Pacific halibut (*Hippoglossus stenolepis*), and yellowfin sole (*Pleuronectes asper*). These species appeared to share nursery areas; however, physical characteristics of the nursery areas occupied by each species limited the amount of true overlap among species. Tree-based regression of catch-per-unit-of-effort data on physical parameters was used to refine conceptual models of species distribution, which were originally based only on 1991 data.

Threshold values of the physical parameters were specified that best discriminated among stations with different abundances. Highest abundances of age-0 rock sole were found on sand or muddy sand at temperatures greater than 8.7°C, as well as on other mixed sand stations less than 28 m deep. Age-0 flathead sole were most abundant at temperatures less than 8.9°C and on mixed mud substrates. At warmer temperatures, abundances were high only if the depth was greater than 48 m, regardless of sediment type. Age-0 Pacific halibut were most abundant in depths less than 40 m at sites more than 2.9 km outside the mouths of bays. Inside bays, halibut were found in lower abundances in water over 9.0°C and on sediments containing both sand and mud. Age-1 yellowfin sole were always found in depths less than 28 m on mixed mud substrates. They were usually found within bays, with highest abundances at heads of large bays more than 32 km from the bay mouth. These four most abundant flatfishes therefore appeared to partition the available habitat in ways that minimized resource competition.

Habitat models for juvenile pleuronectids around Kodiak Island, Alaska*

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In the Gulf of Alaska, there are directed fisheries for deep-water and shallow-water complexes of fishes. The deep-water complex is made up of rex sole (*Errex zachirus*), Dover sole (*Microstomus pacificus*), Greenland halibut (*Reinhardtius hippoglossoides*), arrowtooth flounder (*Atherestes stomias*), and rockfishes (*Sebastes* spp.). The shallow water complex incorporates all other flatfishes found in the area, including rock sole (*Pleuronectes bilineatus*), flathead sole (*Hippoglossoides elassodon*), yellowfin sole (*Pleuronectes asper*), English sole (*Pleuronectes vetulus*), starry flounder (*Platichthys stellatus*), Alaska plaice (*Pleuronectes quadrituberculatus*), butter sole (*Pleuronectes isolepis*), and sand sole (*Psettichthys melanostictus*), in addition to Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Theragra chalcogramma*). The groundfish harvest from the Gulf of Alaska has been over 190,000 metric tons (t) annually from 1990 through 1995, for a total of 1,320,000 t, not including Pacific halibut (*Hippoglossus stenolepis*) or discards. Of that, in 1995, 716,000 t were landed in Kodiak, Alaska, for a value of \$34 million (NMFS, Fisheries Management Div., P.O. Box 21668, Juneau, AK 99802-1668). When Pacific halibut, a species regulated separately from

other groundfishes, is included, the total landed at Kodiak in 1995 was 75,000 t at \$49 million. Although rockfishes (Carlson and Straty, 1981; Krieger, 1992, 1993), cod (Wespestad et al., 1986; Dunn and Matarese, 1987), and pollock (Janusz, 1986; Dunn and Matarese, 1987; Kendall et al., 1994; Müter and Norcross, 1994; Swartzman et al., 1994) have been studied in the Gulf of Alaska, very little is known about flatfishes (Parker, 1989; Moles and Norcross, 1995). The large abundance and value of these commercially important flatfishes and lack of knowledge of their early life history led us to investigate distribution of juvenile flatfishes around Kodiak Island.

In general, recently metamorphosed flatfishes recruit to shallow, nearshore nursery areas with fine-grained sediments (Edwards and Steele, 1968; Gibson, 1973; Toole, 1980; Hogue and Carey, 1982; de Ben et al., 1990). Intertidal zones, estuaries, and shallow protected bays are nursery areas for flatfishes in the continental United States (Krygiel and Percy, 1986; Allen, 1988; Rogers et al., 1988; Wyanski, 1990), Canada (Tyler, 1971), Europe

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(McIntyre and Eleftheriou, 1968; Gibson, 1973; Lockwood, 1974; Poxton et al., 1982; Poxton and Nasir, 1985; van der Veer and Bergman, 1986), and Japan (Tanaka et al., 1989). Abundance and size distributions have been related to water depth (Edwards and Steele, 1968; McIntyre and Eleftheriou, 1968; Lockwood, 1974; Riley et al., 1981; Poxton et al., 1982; Wyanski, 1990), sediment size (Poxton et al., 1982; Poxton and Nasir, 1985; Wyanski, 1990; Jager et al., 1993; Keefe and Able, 1994; Moles and Norcross, 1995), and food availability (McIntyre and Eleftheriou, 1968; Allen, 1988; Jager et al., 1993). The generally accepted rationale for juvenile recruitment to shallow, fine-grained nursery areas includes escape from predation, increased cover and food availability, and decreased intraspecific food competition (Toole, 1980; de Ben et al., 1990; Minami and Tanaka, 1992). The examination of diet diversity among a subset of the fishes in the present study showed a reduction of both interspecific and intraspecific dietary overlap when flatfishes coexisted in large abundances (Holladay and Norcross, 1995).

The coastline of Kodiak Island, Alaska, encompasses a variety of habitats from shallow, fine-grained tidal flats to deep and rocky areas. Kodiak Island is mountainous and cut by many fjords and open bays with shallow waters (<10 m) usually within 0.5 km of the beach. The tidal range is 3 to 4 m. The region is characterized by deep bays, rough bottom topography, strong currents, and bottom characteristics that change rapidly over relatively short distances. Around Kodiak Island, juvenile flatfishes occupy fine-grained sediments in bays and nearshore waters, as do flatfishes in other locations, but waters less than 10 m in depth are only a minor component of the area that is used (Norcross et al., 1995).

A nursery may be partitioned into areas dominated by individual species or intraspecific age groups (Edwards and Steele, 1968; Zhang, 1988; Harris and Hartt¹; Smith et al.²). Habitats occupied by juvenile rock sole, flathead sole, Pacific halibut, and yellowfin sole collected on the east and south sides of Kodiak Island in August 1991 can be differentiated on the basis of depth, substrate, and within-bay distribution (Norcross et al., 1995).

We used linear discriminant functions to identify tentatively the habitat characteristics of juvenile flatfishes with data collected in August 1991 along east and south Kodiak Island (Norcross et al., 1995). In this study, we repeated the linear discriminant function analysis with combined 1991–92 data to include observations from a much wider geographic area around the entire island of Kodiak collected in August 1992. We refined our previous habitat models by using tree-based regression methods (Venables and Ripley, 1994) on catch-per-unit-of-effort data.

Materials and methods

Sample collections

Two cruises were conducted in the nearshore waters of Kodiak Island, Alaska, during August 1992 (Fig. 1). These cruises were similar to, but covered more area than, two cruises conducted in August 1991 (Norcross et al., 1995; Norcross et al.³). Cruise KI9201 consisted of collections taken with a 7.3-m skiff from Kalsin, Middle, and Womens Bays near the town of Kodiak during 9–14 August 1992. Because these bays were sampled with a skiff, extremely shallow collections could be made. Collections ranged in depth from 1 to 60 m. Ten stations were occupied in Kalsin Bay, six stations in Middle Bay, and five stations were occupied within Womens Bay. Kalsin and Middle Bays were also sampled during August 1991.

Immediately following the sampling from the skiff, a counterclockwise circuit of Kodiak Island was completed aboard a 24.7-m chartered trawling vessel (FV *Big Valley*, cruise KI9202). Collections during KI9202 were made from 16 to 29 August 1992 and ranged in depth from 5 to 180 m. Areas sampled in 1992, but not sampled in 1991, included 52 stations in bays on the north and west sides of the island. Collections were also made at 41 stations off south Kodiak, Sitkalidak Strait, and in Ugak Bay, which were sampled during August 1991.

Sampling gears, vessels, and vessel operators were the same in both 1991 and 1992 (Norcross et al., 1995; Norcross et al.³; Norcross et al.⁴). At each station one sediment sample was collected with a 0.06-m³ Ponar grab for analysis of grain size, and a portable conductivity, temperature, and depth (CTD) profiler was deployed to measure temperature and salinity. Fishes

¹ Harris, C. K., and A. C. Hartt. 1977. Assessment of pelagic and nearshore fish in three bays on the east and south coasts of Kodiak Island, Alaska: final report. In Volume 1: Environmental assessment of the Alaskan continental shelf, p. 483–688. U.S. Dep. Commer., and U.S. Dep. Interior Quarterly Reports of Principal Investigators, Anchorage, AK.

² Smith, R. L., A. C. Paulson, and J. R. Rose. 1976. Food and feeding relationships in the benthic and demersal fishes of the Gulf of Alaska and Bering Sea. In Volume 7: Environmental assessment of the Alaskan continental shelf, p. 471–508. Annual Report RU 0284.7. U.S. Dep. Commer. and U.S. Dep. Interior Environmental Research Laboratories, Boulder, CO.

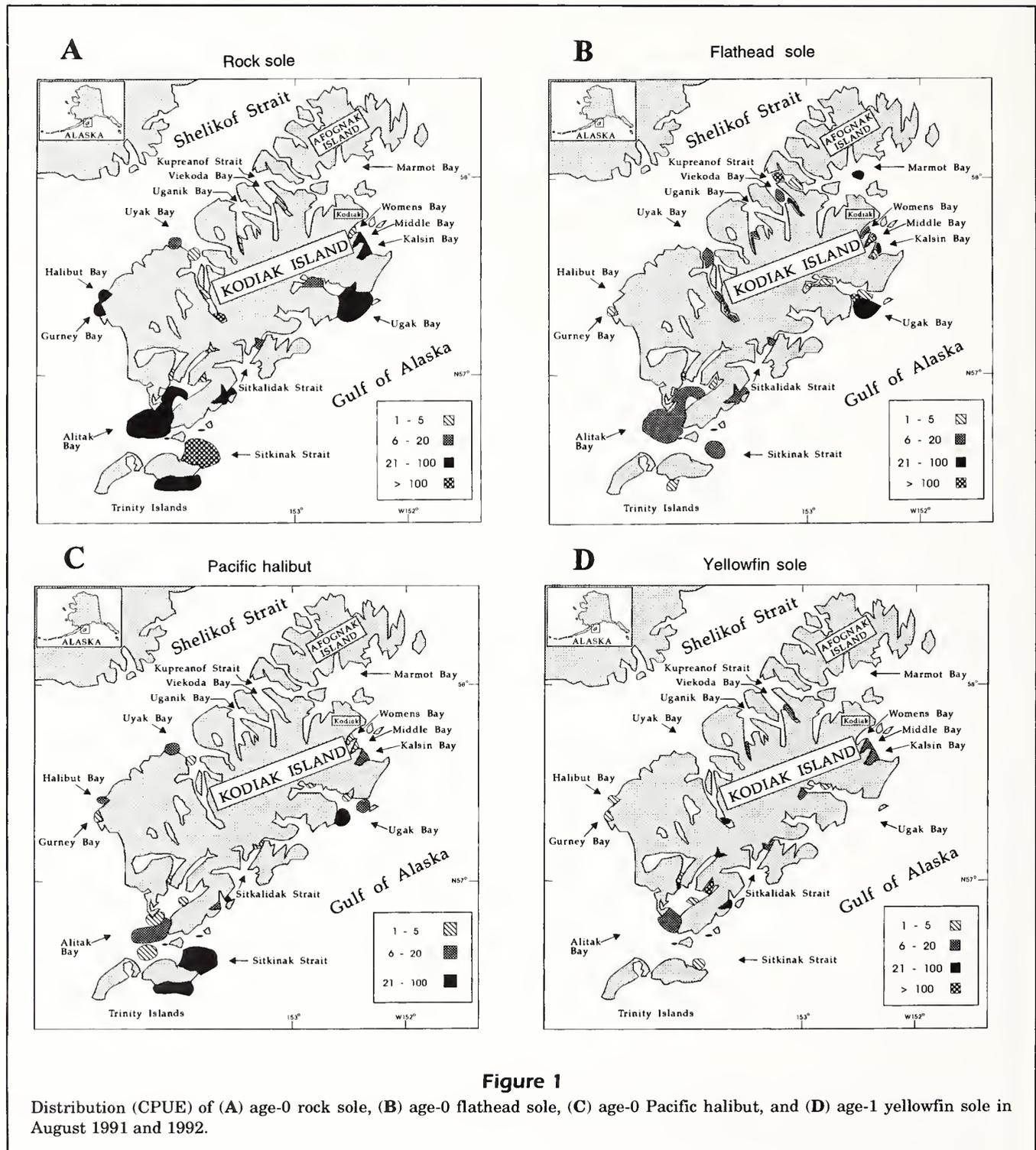
³ Norcross, B. L., B. A. Holladay, and M. Frandsen. 1993. Recruitment of juvenile flatfish in Alaska, phase 1. Final Contract Report, NOAA NA-16FD0216-01, 504 p.

⁴ Norcross, B. L., B. A. Holladay, F.-J. Muter, and M. Frandsen. 1994. Recruitment of juvenile flatfish in Alaska, phase 2. Final Contract Report, NOAA NA-26FD0156-01, 653 p.

were collected on rising tides during daylight hours by using a modified 3.7-m plumb staff beam trawl with a double tickler chain (Gunderson and Ellis, 1986). Tows of 10-min duration were made at the approximate speed of 0.5–1.0 kn from both the skiff and the trawler.

Sample processing

Substrate type, water depth, bottom temperature, bottom salinity, and distance from the mouth of the nearest bay were evaluated for each station. Sediment samples were analyzed, as in 1991, by means



of a simplified sieve and pipette procedure to obtain the percents of gravel, sand, and mud (Norcross et al., 1995).

Distance from the mouth of the bay was used as a relative index of fish distribution with respect to station position within or outside the bay. Distance from each station to the nearest position at the mouth of a bay was calculated by drawing a line on a chart across the bay mouth between the two outermost capes. The shortest distance from the station to any position on this line was measured. Stations inside the mouth were designated as positive distances, and stations outside of bays were assigned negative distances. The narrowest point of Sitkinak Strait was considered the "mouth" of the bay; stations to the west of that point were considered within the bay and the exposed stations in the open ocean on the east side of Sitkinak Strait were considered outside the mouth.

Flatfishes were identified, and total length (mm) was measured in the field with a Limnoterra electronic, digital fish-measuring board. Ages of flatfishes captured in August 1992 were estimated with 1) length-frequency plots of fishes collected August 1992 (Norcross et al.⁴), 2) length-frequency plots (Norcross et al.³) and analysis of regional differences in total lengths (Norcross et al., 1995) of fish caught during August 1991, and 3) available literature (Southward, 1967; Best, 1974, 1977; Walters et al., 1985; Harris and Hartt¹; Blackburn and Jackson⁵). Fish lengths were used to separate age classes of juvenile flatfishes. Catch per unit of effort (CPUE) based on a 10-min tow time was calculated for age-0 and age-1 individuals of each species. Habitat models were developed for the most abundant species and age-class combinations.

Statistical analyses

Linear discriminant function analysis of combined 1991–92 data included the broad range of conditions sampled around Kodiak Island. Canonical loadings of each variable and misclassification rates based on cross-validation were evaluated as outlined in Norcross et al. (1995) to test whether the same parameters had been selected as the best discriminators as those that had been selected solely on 1991 data. The magnitude of the canonical loading of each variable in the discriminant analysis is a measure of the importance of that variable in separating the sta-

tions with (presence) and without (absence) the fish species under consideration. The success of each combination of variables in assigning a new station to the presence or absence group can be evaluated by using misclassification rates from cross-validation.

The combined 1991 and 1992 data were further used to calculate Spearman's rank correlation (ρ) between the abundance of each fish species and each physical parameter. The significance of rank correlations was evaluated at the 95% level. The nonparametric test with Spearman's ρ was chosen because of non-normality of the CPUE data (even after transformation) and because of the high sensitivity of the parametric correlation coefficient (Pearson's r) to outliers. To maintain an overall confidence level of 95%, a Bonferroni-adjusted critical level of $\alpha = 0.025/28 = 0.001$ was used for the two-tailed test and for 28 comparisons (4 species \times 7 variables).

To refine our previous habitat models, which were based primarily on presence or absence data (Norcross et al., 1995), we used regression trees to model CPUE as a function of habitat parameters. We used the same parameters as in the discriminant analysis, except instead of percentages of gravel, sand, and mud in the substrate, we used a categorical description of sediment type based on Folk (1980), i.e. sand (S), mud (M), gravel (G), and the modifiers of these substrates, such as sandy mud (sM), sandy gravelly mud (sgM), etc., 12 categories in all. This categorical classification avoided problems with high correlations among the three sediment variables. Both continuous and categorical predictor variables can easily be accommodated in regression trees.

The regression tree used the logarithm of CPUE ($\log(\text{CPUE}+1)$) as the response variable and depth, distance from mouth of bay, bottom temperature, bottom salinity, and sediment type as predictor variables. A regression tree progressively splits stations on the basis of their values for one of the predictor variables until a leaf or terminal node is reached. Each leaf gives a predicted value of the response variable for the stations assigned to the leaf. The fit of the model is measured by the deviance, which is defined as

$$D = \sum_i (y_i - \mu_{[i]})^2,$$

or the sum of the squared differences between $y_i = \log(\text{CPUE}+1)$ at each station i and $\mu_{[i]} =$ the mean for all stations i at a leaf. The deviance is defined for the entire tree, as well as for each leaf, and is the analogue of the sum of squares in regression models. Each successive partitioning of the data reduces the deviance. For noisy data, the regression tree may overfit the data, resulting in an overly complex tree

⁵ Blackburn, J. E., and P. B. Jackson. 1982. Seasonal composition and abundance of juvenile and adult marine finfish and crab species in the nearshore zone of Kodiak Island's east side during April 1978 through March 1979. *In* Outer continental shelf environmental assessment program, p. 377–570. U.S. Dep. Commer., Final Reports of Principal Investigators 54.

(Venables and Ripley, 1994). Therefore the initial tree was pruned to an optimum number of terminal nodes as determined by cross-validation.

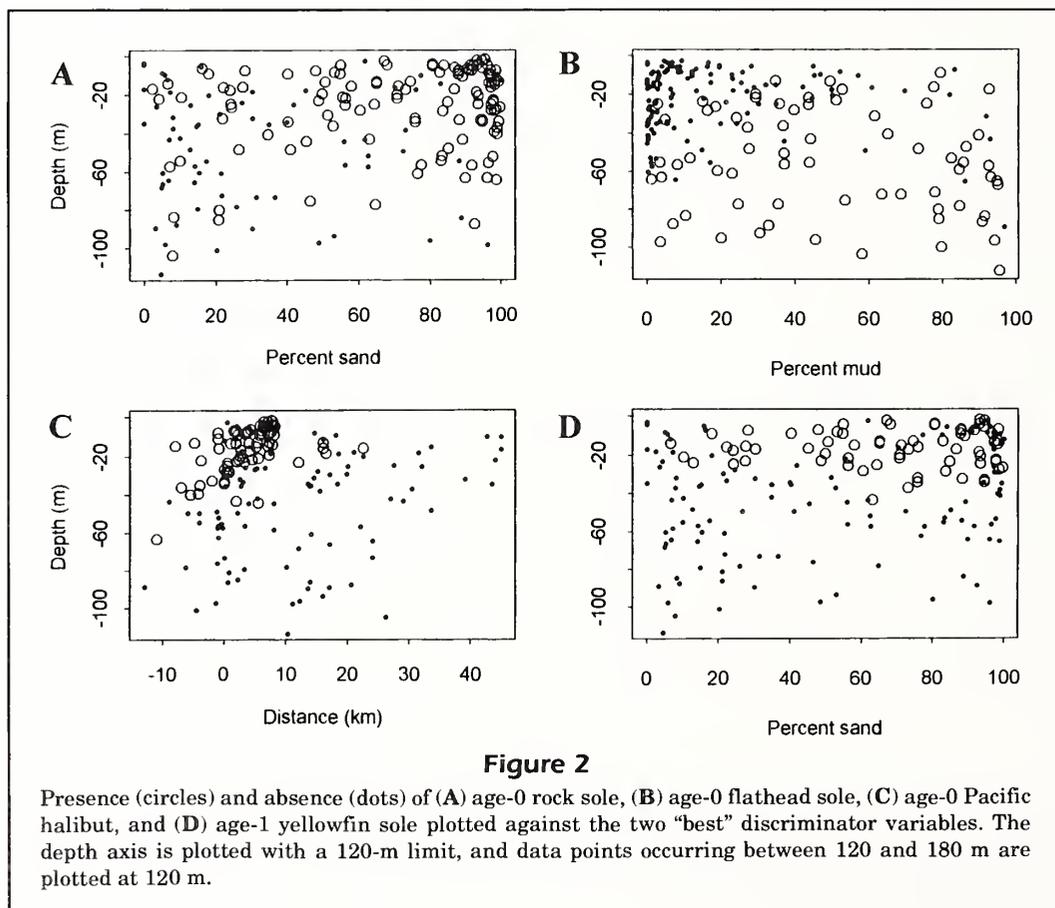
Cross-validation as implemented in S-Plus (Venables and Ripley, 1994) uses 90% of the data as a training set to grow the tree and test it on the remaining 10%. This procedure is repeated 10 times with nonoverlapping test sets. Predictions on the test set are done for the initial tree as well as for trees pruned to smaller sizes. The resulting deviances are computed and plotted against tree size. Deviances typically are minimized at an intermediate tree size. We chose as optimum tree size the largest size before a marked increase in deviance occurred.

Results

Rock sole was the most abundant flatfish captured in our 1992 sampling (67% of flatfish), as in 1991 (51% of flatfish). In 1992, a total of 4,625 age-0 rock sole (17–60 mm TL) were collected across almost all locations, with the highest CPUE in the Sitkinak Strait region (Fig. 1A). Age-0 rock sole were found mainly near the mouths of bays \pm 8–10 km, except for

a single large catch at the head of Uyak Bay. Age-0 rock sole were somewhat more abundant with increasing depth between 0 and 30 m, and were collected in high numbers to 70 m, although they were also found deeper than 70 m. Age-0 rock sole were collected in large numbers between 7.5°C and 9.5°C and were most often found at salinities of 32.5–33.0 psu (Norcross et al.⁴). Rock sole were predominantly distributed on sand and mixed sand substrates. Although found at almost all combinations of depth and sand, rock sole were somewhat more concentrated in shallow, sandy locations (Fig. 2A). Spearman's rank correlation coefficients (Table 1) indicated that rock sole abundance was positively correlated with percent sand in the substrate and negatively correlated with depth, distance from mouth of bay, gravel, and mud. Rank correlation was highest with percent sand in the substrate.

Flathead sole increased from 12% of the 1991 catch to 18% of the 1992 catch. We captured 1,079 age-0 flathead sole (23–52 mm TL) during 1992. The distribution of flathead sole was more restricted than that for rock sole. Age-0 flathead sole were found almost everywhere around the island but were found in reduced numbers in Southeast Kodiak (Fig. 1B).



They were concentrated mainly in central, deep areas of bays at depths of 80–120 m, 6.0–9.0°C, 31.5–33.5 psu, on mud or mixed mud substrates (Norcross et al.⁴). High abundances of flathead sole were associated with deep stations, low temperatures, high salinities, low sand content, and high mud content; the highest rank correlations for flathead sole were obtained for depth and mud (Table 1). Flathead sole were predominantly collected in depths > 40 m, except on substrates with a high mud content (Fig. 2B).

Pacific halibut composed 5% of the catch in 1991 and 7% in 1992. During 1992, 627 age-0 halibut (22–84 mm TL) were found in exposed sites at all locations on the east and south sides of Kodiak Island (Fig. 1C). In northwestern Kodiak, halibut were collected only at the mouth of Uyak Bay. Age-0 halibut were found mainly at 10–70 m depth, 7.0–10.5°C, 32.0–33.0 psu, on mixed sand substrates, outside of or within 7 km of bay mouths (Norcross et al., 1995). Pacific halibut abundances were positively correlated with temperature and sand content and negatively correlated with depth, distance from mouth of bay, and mud content in the substrate. The highest rank correlations were with sand and mud (Table 1). Unlike rock sole, halibut were seldom found in water deeper than 50 m. Halibut juveniles, like rock sole, were concentrated most often in shallow waters with sandy substrate, near or outside mouths of bays (Fig. 2C).

Yellowfin sole was very abundant in 1991, composing 28% of captured flatfishes, but this species represented only 4% of the 1992 total catch. Unlike the other three species examined, in which age-0 fish predominated, age-1 yellowfin sole (41–105 mm TL) were analyzed in both 1991 and 1992 because of the small number ($n=4$) and size (15–20 mm TL) of age-0

yellowfin sole collected during the second year. During 1992, 268 age-1 yellowfin sole were collected at depths less than 40 m, mainly between 5 and 30 m. Age-1 yellowfin sole were found near the heads of bays, in warm (9.0–11.5°C) saline (31.0–33.5 psu) water (Norcross et al., 1995). They were collected on sandy mud, gravelly muddy sand, and muddy sand. Unlike rock sole and halibut, yellowfin sole were collected in the inner reaches of bays around Kodiak Island (Fig. 1D). The only significant correlation between yellowfin sole abundance and an environmental variable was a negative rank correlation with depth (Table 1). Yellowfin sole were never found deeper than 50 m and were always on mixed substrate, i.e. not predominantly on one grain size (Fig. 2D).

Linear discriminant function analysis for the combined 1991–92 data resulted in depth having the highest correlation with discriminant scores (canonical loadings) for flathead sole and yellowfin sole (Table 2). Sand was most highly correlated with the discriminant scores for rock sole and Pacific halibut. For all species, except flathead sole, the three highest canonical loadings were obtained for depth, temperature, and sand. In the case of flathead sole, mud was more highly correlated with the discriminant score than was sand.

Sand was clearly a good predictor for rock sole presence and was included in the habitat model for rock sole. Depth and temperature performed equally well in the discrimination owing to their high (negative) correlation. However, although rock sole abundance was significantly correlated with depth, the correlation with temperature was not significant. Therefore, sand and depth seemed to be the most important variables determining rock sole distribution (Fig. 2A).

The three best predictor variables for flathead sole were depth, gravel, and mud. Of these, depth and mud resulted in the lowest total error rates. Because

Table 1

Spearman's rank correlation coefficients between CPUE of four flatfish species and environmental parameters with 1991 and 1992 data combined. * indicates significance at an overall 5% confidence level.

Parameter	Rock sole	Flathead sole	Pacific halibut	Yellowfin sole
Depth	-0.258*	0.644*	-0.284*	-0.369*
Distance	-0.308*	-0.074	-0.314*	0.204
Temperature	0.193	-0.467*	0.346*	0.212
Salinity	-0.083	0.246*	-0.163	-0.192
Gravel	-0.240*	-0.219	-0.078	-0.168
Sand	0.583*	-0.219	0.449*	0.113
Mud	-0.310*	0.540*	-0.417*	0.188

Table 2

Canonical loadings from linear discriminant function analysis for combined 1991 and 1992 flatfish data.

Parameter	Rock sole	Flathead sole	Pacific halibut	Yellowfin sole
Depth	-0.557	-0.776	-0.620	-0.696
Distance	-0.379	-0.011	-0.501	0.234
Temperature	0.474	-0.597	0.647	0.545
Salinity	0.180	-0.225	-0.026	-0.005
Gravel	-0.453	0.321	-0.249	-0.377
Sand	0.783	0.220	0.655	0.406
Mud	-0.391	-0.624	-0.473	-0.099

these variables also had the largest rank correlations with abundance (Table 1), they were likely to be the most important parameters for flathead sole distribution. The error rates for predicting absence of flathead sole were consistently much lower than those for predicting presence.

Pacific halibut presence or absence could be most accurately predicted by using either depth or temperature with either distance or sand. Halibut abundance had a higher rank correlation with temperature than with depth and a higher correlation with sand than with distance from the mouth of the bay (Table 1). It is difficult to evaluate the relative importance of depth and temperature and of sand and distance owing to high correlations among these variables (Fig. 3). The depth-temperature factor explained most of the observed distribution. The error rates for predicting presence or absence changed significantly only if both depth and temperature were excluded. Error rates for stations where Pacific halibut were present were consistently much lower than those for stations where no halibut were found, thus this species appears to be strongly associated with specific habitat characteristics.

The three best predictors for yellowfin sole were depth and gravel combined with either sand or temperature. Of these, depth and gravel resulted in the lowest total error rates. Only depth was significantly correlated with yellowfin sole abundance (Table 1). The sediment parameters added very little information because yellowfin sole occurred over a wide range of substrate types. Error rates for stations where yellowfin sole were present were much lower than those for stations where this species was absent, reflecting the restricted depth range within which yellowfin sole were encountered. Presence and absence patterns for all four species are plotted against the two best discriminator variables (Fig. 2).

Regression trees were constructed by using CPUE for each species to refine our habitat models. The initial trees were allowed to grow, provided the number of stations in a node was five or greater. The resultant regression trees had sizes of 22 terminal nodes for rock sole, 16 for flathead sole, 19 for Pacific halibut, and 18 for yellowfin sole. The total deviances for the initial trees were 1.24, 0.57, 0.38, and 0.44 respectively, indicating that the model fitted for rock sole was much poorer than that for the other species and that the tree for Pacific halibut had the best fit.

The trees for all species seemed to overfit the data, as indicated by cross-validation. Plots of deviance against tree size (number of terminal nodes) for the four flatfish species indicated that deviance was usually at a minimum at very small tree sizes, consist-

ing of only two or three nodes (Fig. 4). The deviance for each species tended to increase steeply at a tree size between 4 and 6 nodes, and we chose the largest size before a steep increase as optimum size for the tree. The initial tree was pruned to six terminal nodes for rock sole and halibut and to four terminal nodes for flathead sole and yellowfin sole.

The pruned regression tree for rock sole indicated that sediment, depth, and temperature were the best predictor variables for rock sole CPUE. The deviance of the pruned tree increased to 1.852 from 1.242 for the initial tree. This relatively poor fit may again be due to the widespread distribution of rock sole, a species that does not seem to be limited to any particular habitat type. Stations were first separated by sediment type into 89 stations on sand or muddy sand with a high mean CPUE (18 fish/10-min tow) and 80 stations on other sediment types that had a much lower mean CPUE (1.6 fish/10-min tow) (Fig. 5). The highest mean CPUE (25 fish/10-min tow) occurred at stations on sand or muddy sand which had a bottom temperature of more than 8.7°C. The colder stations on sand and muddy sand were separated into seven low salinity stations with low mean CPUE (0.58 fish/10-min tow) and 10 high salinity stations with medium to high CPUE (11 fish/10-min tow). Most stations on other sediment types, which included gravel, mud, gravelly mud, gravelly sand, gravelly muddy sand, gravelly sandy mud, muddy gravel, muddy sandy gravel, sandy gravel, and sandy mud, had low CPUE values except for a group in shallow water (<27.5 m) on gravelly muddy sand, sandy gravel, or sandy mud (13 fish/10-min tow). Thus, by combining results from the correlation analysis, presence and absence patterns, and regression trees, rock sole were found to be most common on sand or mixed sand substrates and most abundant in shallow and relatively warm water.

The regression tree for flathead sole indicated that temperature, sediment type, and depth were the best predictors of flathead sole abundance. The deviance of the pruned tree was 0.774 compared with 0.569 for the initial tree. Highest CPUE values tended to occur at stations where bottom temperature was less than 8.9°C (Fig. 6). At warmer stations, mean CPUE of flathead sole was very low (0.17 fish/10-min tow) if stations were less than 48 m deep, which was the case for the majority ($n=109$) of the stations. Mean CPUE at warm stations was higher, however, for the six stations located in water deeper than 48 m (4.6 fish/10-min tow). Stations with bottom temperatures below 8.9°C had a low flathead sole CPUE if the sediment was categorized as gravel, sand, muddy sandy gravel, or sandy gravel (1.6 fish/10-min tow). The CPUE was much higher on pure mud or mixed mud

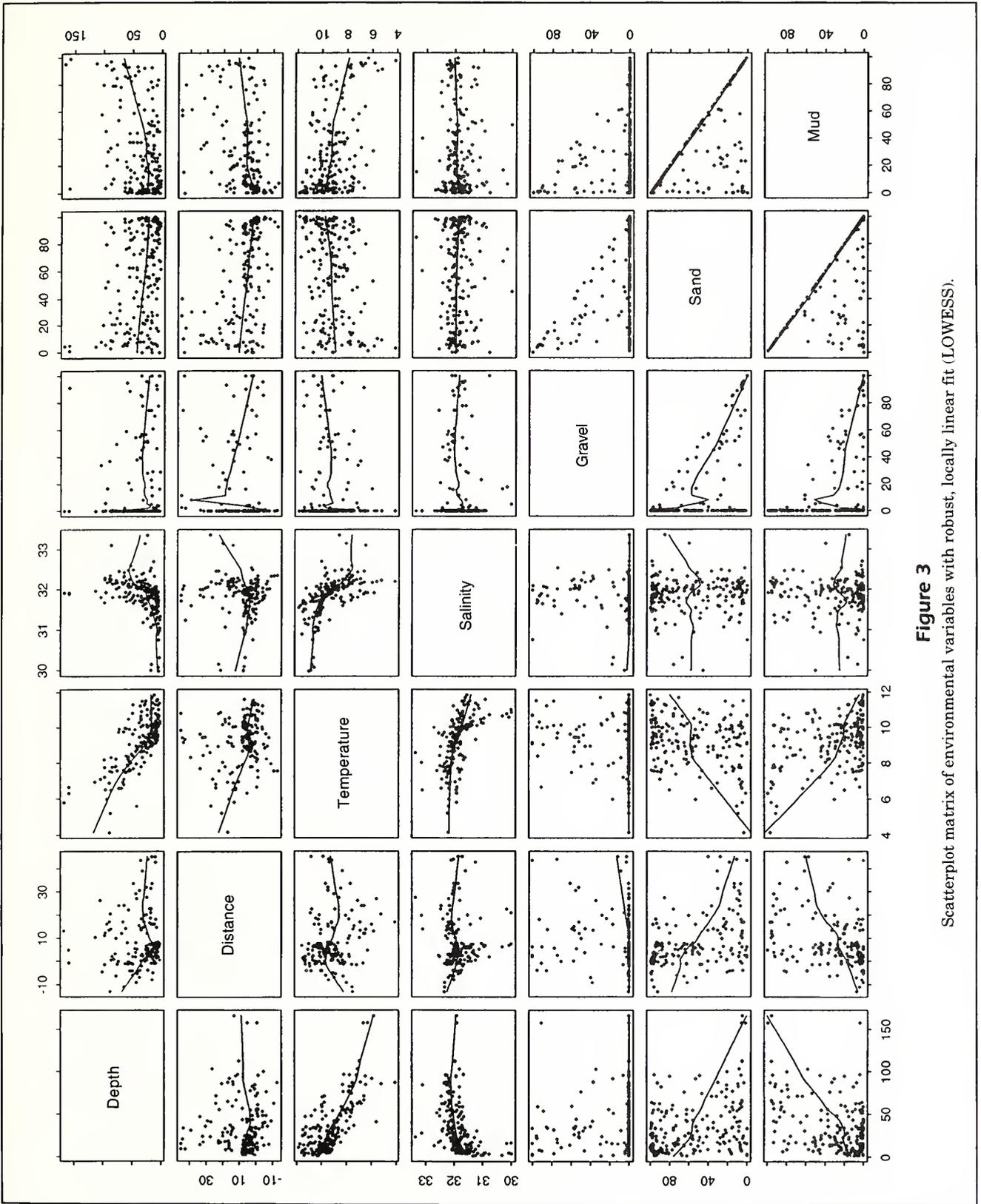
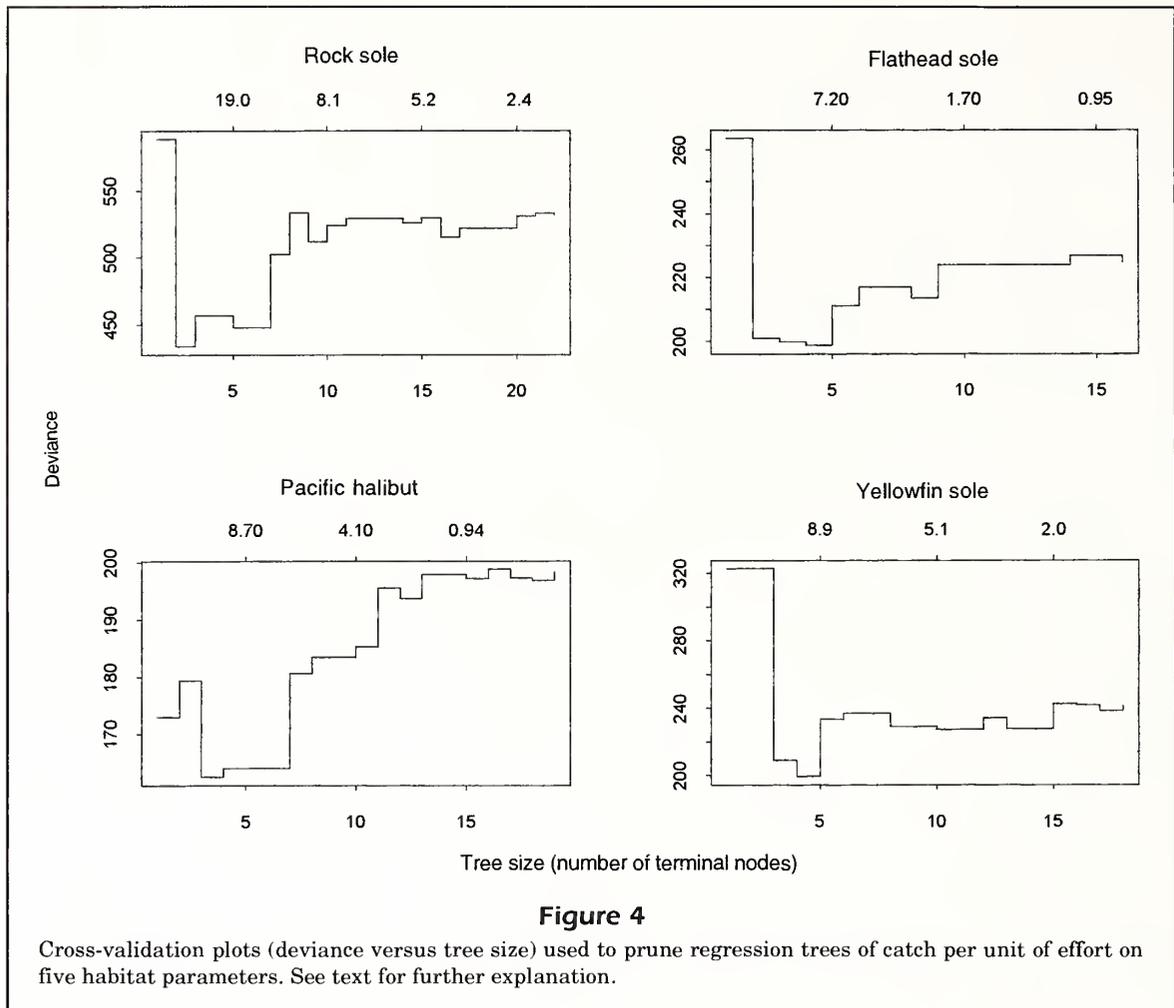


Figure 3 Scatterplot matrix of environmental variables with robust, locally linear fit (LOWESS).

sediments at low temperatures (8.0 fish/10-min tow). Thus, the highest CPUE values for flathead sole were on mixed mud sediments at stations with a bottom

temperature of less than 8.9°C, as well as at warmer stations if they were deeper than 48 m. This suggests that temperature should be used in addition to



sediment and depth selected by linear discriminant analysis as an important factor in determining the distribution of juvenile flathead sole.

Distance from the mouth of the bay and depth were the best predictors of halibut CPUE (Fig. 7). The deviance of the pruned tree was 0.587 compared with 0.384 for the initial tree. Highest CPUE values occurred at stations less than 40 m deep and more than 2.9 km outside the mouth of bays (10 fish/10-min tow). Very low abundances or no halibut were found at stations more than 7.9 km up the bay (0.13 fish/10-min tow). Intermediate CPUE values were found at 61 stations near the mouth of bays (-2.9 km to 7.9 km) which had high bottom temperature (>9.0°C) on sand or mixed sand substrates (2.9 fish/10-min tow). This confirmed our earlier finding that halibut tend to remain outside or near the mouth of bays in water less than 40 m deep on sandy substrates.

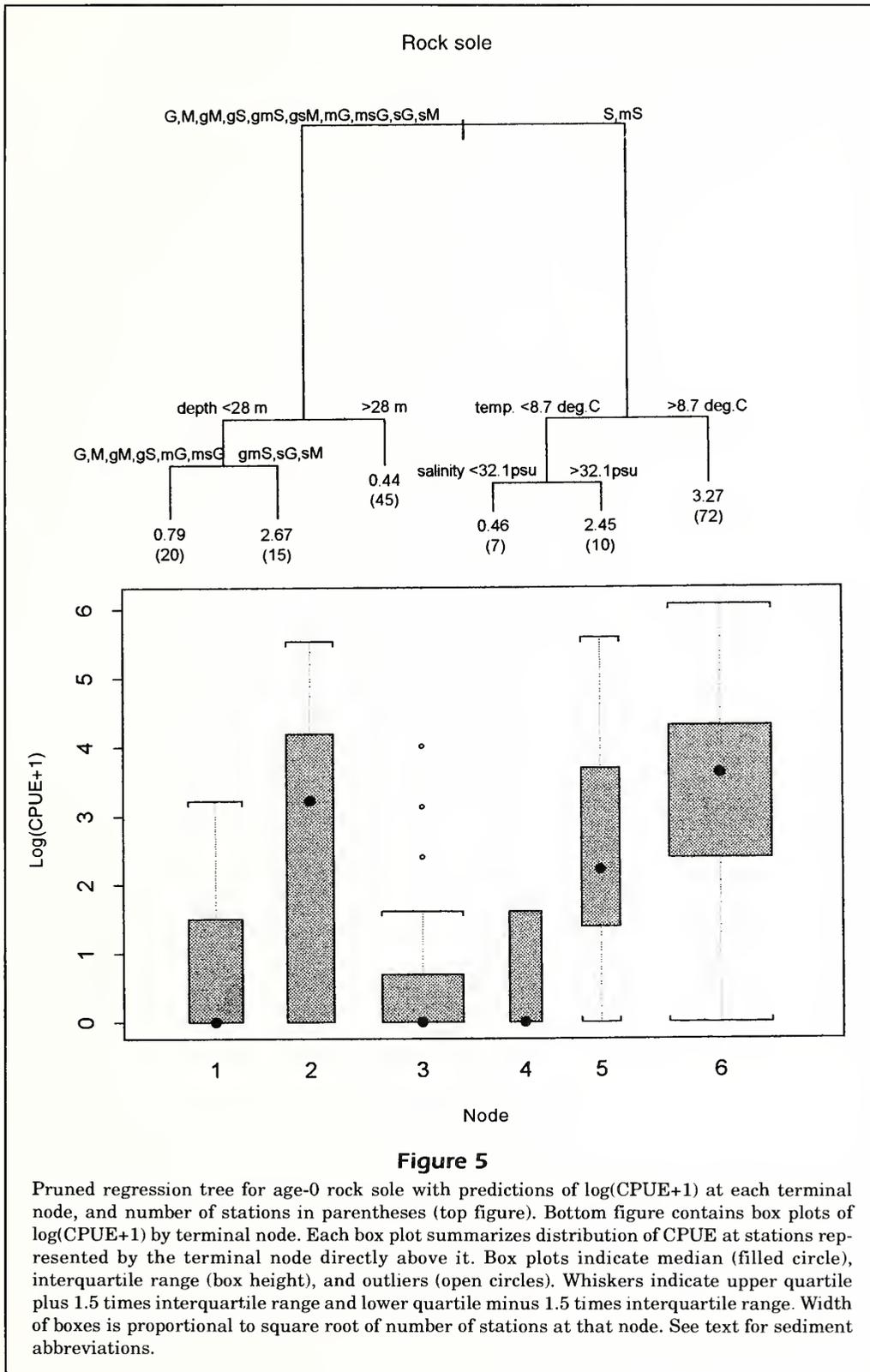
The most important variables used in predicting yellowfin sole abundance were depth, sediment, and distance. Deviance was increased from 0.442 for the

initial tree to 0.895 for the pruned tree. The first split separated 100 stations less than 28 m deep from 69 stations deeper than 28 m (Fig. 8). The deeper stations had a very low mean CPUE (0.17 fish/10-min tow), and yellowfin sole were absent at 64 of the 69 stations that were deeper than 28 m. The shallow stations had a low mean CPUE (0.82 fish/10-min tow) if the substrate type was pure gravel, sand, or mud, or had mixed gravel sediment, whereas stations on mixed mud sediments had medium to high abundances of yellowfin sole (9.0 fish/10-min tow). The 53 shallow stations on mixed mud substrates were further split by distance, indicating that the highest CPUE values occurred near the heads of long bays. Thus yellowfin sole tended to be concentrated in very shallow locations on mixed mud sediments near the head of bays. This finding agreed with results of the linear discriminant function in its identification of depth and sediment as important factors, but further added distance from the bay mouth as a third important factor.

Discussion

Our results show that relations among flatfish dis-

tributions and habitats found within the geographic restrictions of eastern Kodiak Island in 1991 can be applied more broadly to other areas around Kodiak



Island, i.e. to those areas sampled during 1992. Two groups of variables explain much of the observed distribution. These variables are substrate composition

and a depth-temperature factor. The relative importance of depth and temperature or of gravel, sand, and mud is difficult to assess because each group is

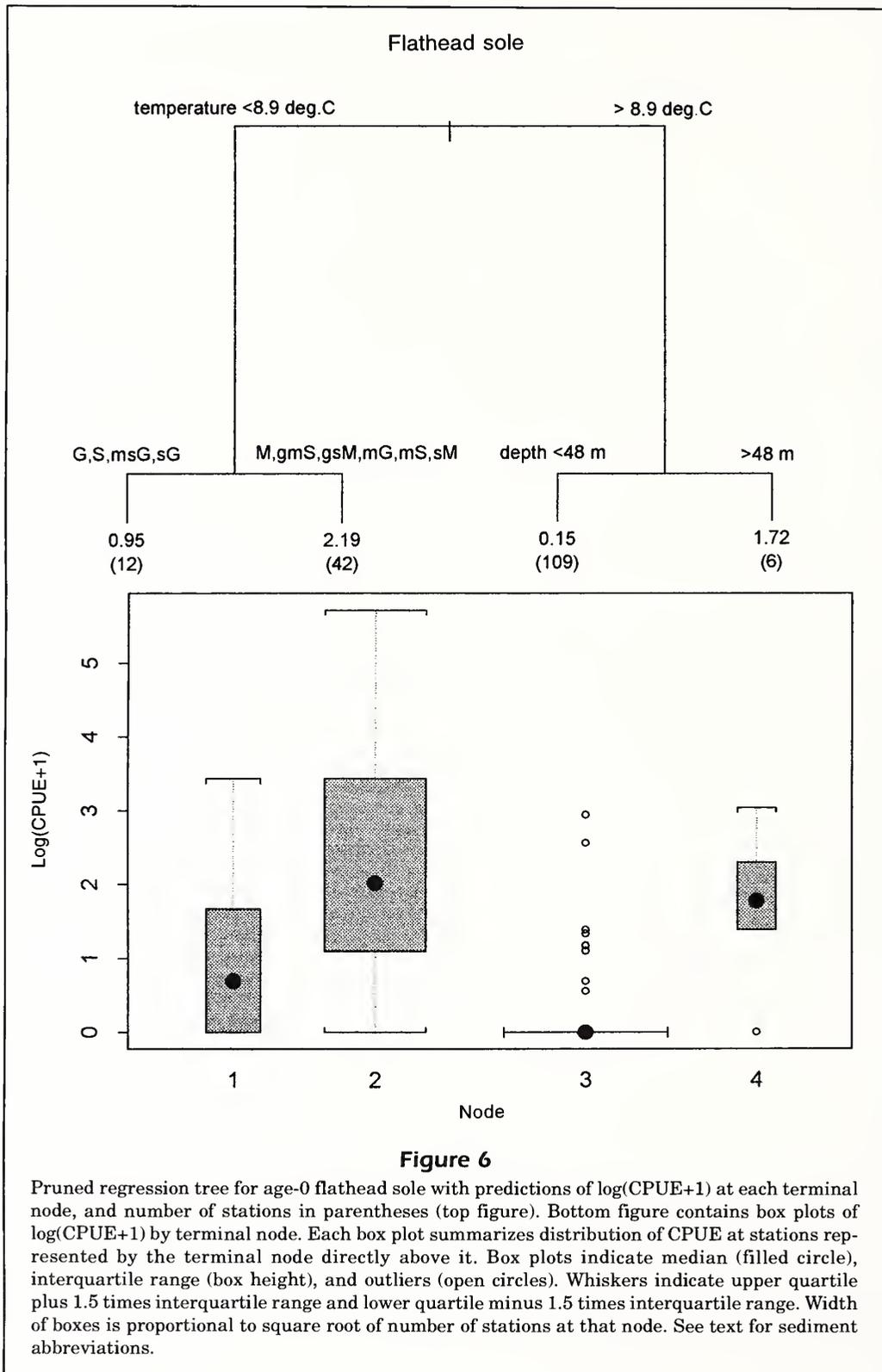


Figure 6

Pruned regression tree for age-0 flathead sole with predictions of $\log(\text{CPUE}+1)$ at each terminal node, and number of stations in parentheses (top figure). Bottom figure contains box plots of $\log(\text{CPUE}+1)$ by terminal node. Each box plot summarizes distribution of CPUE at stations represented by the terminal node directly above it. Box plots indicate median (filled circle), interquartile range (box height), and outliers (open circles). Whiskers indicate upper quartile plus 1.5 times interquartile range and lower quartile minus 1.5 times interquartile range. Width of boxes is proportional to square root of number of stations at that node. See text for sediment abbreviations.

highly intercorrelated (Norcross et al., 1995; Fig. 3). These parameters have been linked to the habitat quality of juvenile flatfishes in many other locations

(Gibson, 1994). Larvae of many flatfish species are known to settle either in shallow water (Edwards and Steele, 1968; Lockwood, 1974) or offshore water

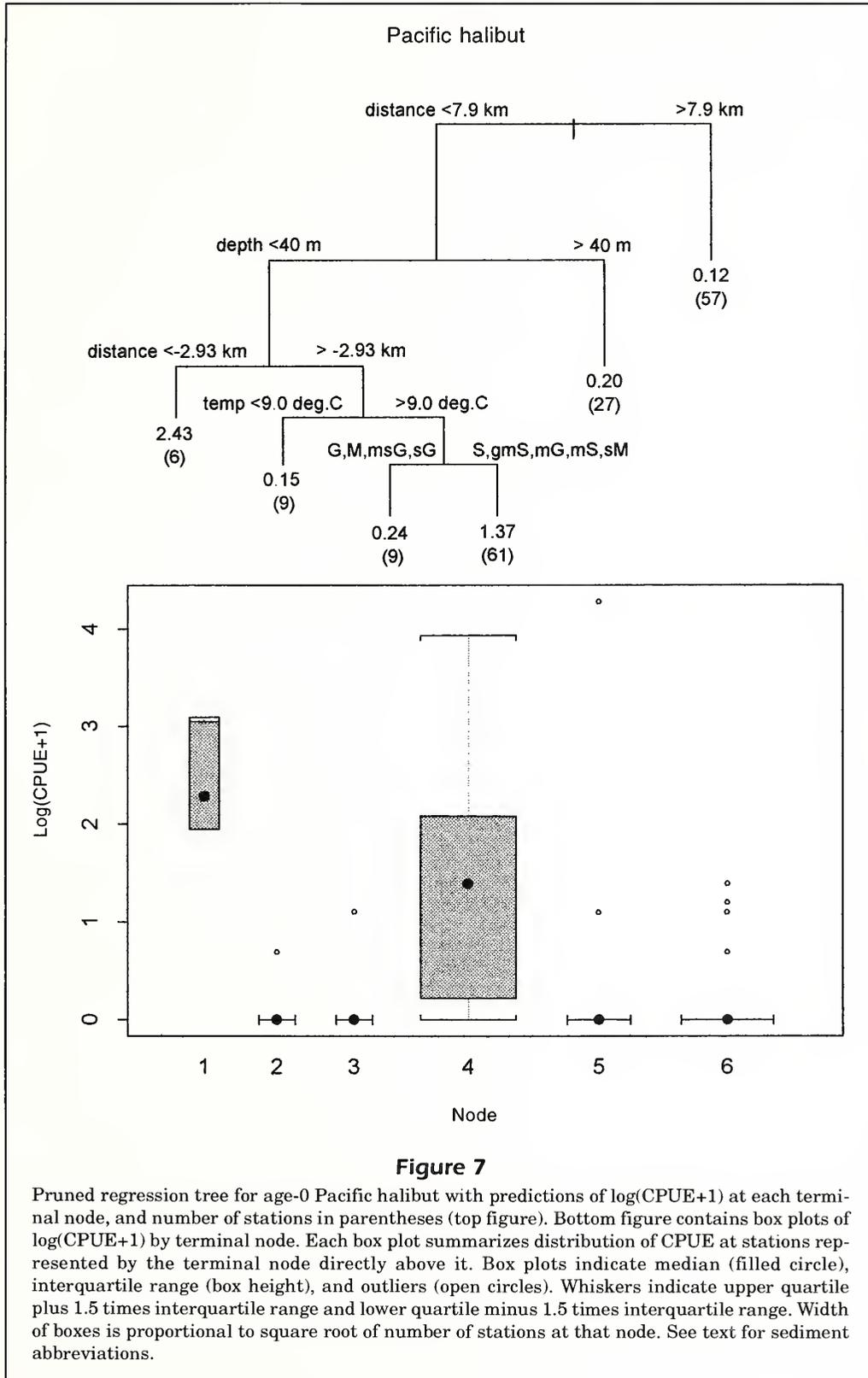
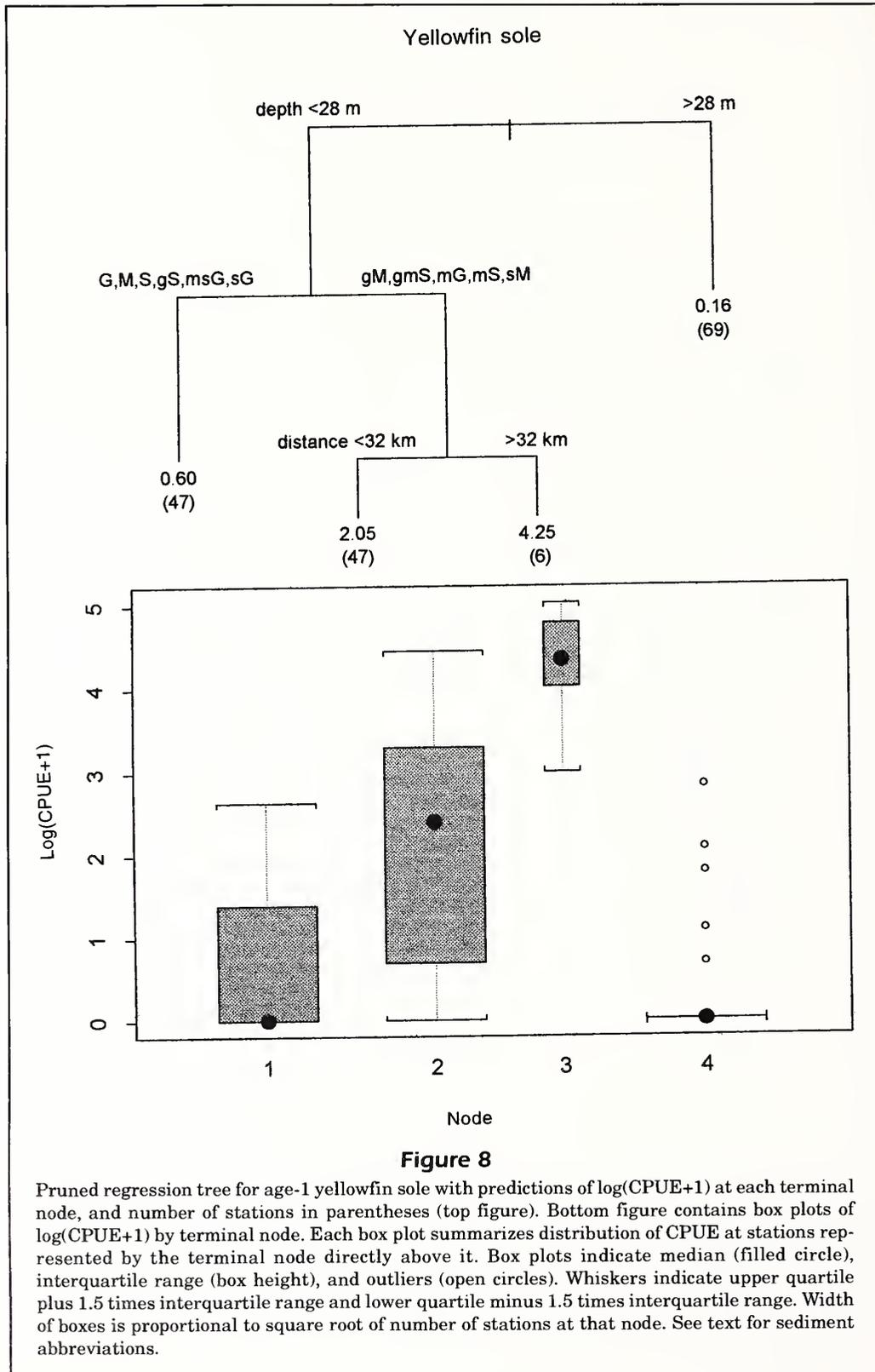


Figure 7

Pruned regression tree for age-0 Pacific halibut with predictions of $\log(\text{CPUE}+1)$ at each terminal node, and number of stations in parentheses (top figure). Bottom figure contains box plots of $\log(\text{CPUE}+1)$ by terminal node. Each box plot summarizes distribution of CPUE at stations represented by the terminal node directly above it. Box plots indicate median (filled circle), interquartile range (box height), and outliers (open circles). Whiskers indicate upper quartile plus 1.5 times interquartile range and lower quartile minus 1.5 times interquartile range. Width of boxes is proportional to square root of number of stations at that node. See text for sediment abbreviations.

and then to move into shallow water as age-0 juveniles (Gibson, 1973; Lockwood, 1974; Tanaka et al., 1989). In prior studies (Gibson, 1994) as well as this

one, depth and its effect on water temperature may play an important part in determining distribution of juveniles. Water temperature affects growth and



feeding rates, and shallow, warm waters promote faster growth (Malloy and Targett, 1991; van der Veer et al., 1994).

Distribution of juvenile flatfishes has been linked to substrate type (Tanda, 1990; Kramer, 1991; Gibson and Robb, 1992). Juvenile flatfishes appear to avoid coarse sediments (Moles and Norcross, 1995) and choose fine-grained sediments (Rogers, 1992; Keefe and Able, 1994) which vary in size from mud (Wyanski, 1990; van der Veer et al., 1991) to sand (Jager et al., 1993). In laboratory tests, rock sole prefer sand and mixed sand substrates, halibut prefer a combination of mud and fine sand, and yellowfin sole prefer mud and mixed mud sediments (Moles and Norcross, 1995); these findings are in agreement with the classification and regression trees of our study. Choice of settlement location is affected by the ability of a fish to bury itself in the sediment (Gibson and Robb, 1992) as well as by the availability of prey in the substrate (Burke et al., 1991). When diets of juveniles of the four species were examined from the same collections in 1991 that were used in these models, it was found that epibenthic crustacean taxa composed most of the diets (Holladay and Norcross, 1995). Stomach contents were related to physical parameters of capture, including location, depth, and substrate. When distribution of juveniles overlapped, dietary overlap was sometimes reduced, in that one or more groups of flatfishes appeared to alter their feeding (Holladay and Norcross, 1995), i.e. preference for specific prey types did not appear to be a primary factor governing distribution of these species.

A discriminant analysis was employed in this study to test whether stations could be accurately classified into groups defined by the presence or absence of a given flatfish species. The classification based on the observed parameters resulted in relatively high error rates for all species; between one-sixth and one-third of the stations were incorrectly classified.

Although no discrimination method is able to predict perfectly the presence or absence of populations that have a gradation in abundance in marginal habitats, there are several possible reasons for the observed high error rates found in this study. For rock sole, halibut, and yellowfin sole, error rates for predicting presence were generally much lower than error rates for predicting absence. This finding may indicate that these species were mostly confined to relatively well-defined depth-substrate characteristics. The high misclassification rate for predicting absence of rock sole, halibut, and yellowfin sole suggests that many stations may offer suitable depth, temperature, and substrate conditions for these species but that the species are not collected there be-

cause their physical habitat preferences may be different. The situation is different for flathead sole; their presence is not as predictable as their absence. Flathead sole are generally absent from shallow areas with little mud, whereas they are usually, but not always, present in deep, muddy places.

The classification results suggest that although the seven environmental variables (%sand, %mud, %gravel, depth, temperature, salinity, and distance from bay mouth) used in our discriminant analysis do not account fully for observed flatfish distributions, they do provide a useful first step at defining juvenile flatfish habitat near Kodiak. The initial linear discriminant function models developed with the 1991 data (Norcross et al., 1995) are still applicable after incorporating 1992 data. Similar linear discriminant methods have been used to examine nursery grounds of *Solea solea* (Rogers, 1992).

Regression trees of CPUE for each species generally agree with the results of the linear discriminant analyses. They determine specific values of the physical parameters as related to the abundance of juvenile flatfishes and, as easily comprehensible diagrams, can be used to predict species abundance based on habitat parameters.

This detailed analysis, based on CPUE and incorporating both 1991 and 1992 data, does not disagree with the original models that we were testing (Norcross et al., 1995) but rather refines those models and incorporates actual abundances (CPUE) in the multivariate analysis. The previous models characterized nursery areas of age-0 rock sole, flathead sole, Pacific halibut, and age-1 yellowfin sole on the basis of correlations and discriminant analyses by using presence or absence for 1991 data. Depth and substrate were statistically significant variables previously, and a measure of distance in relation to mouth of the bay was included qualitatively for each species. Depth, temperature, sediment composition, and distance from bay mouth were all found to be important predictors of the abundance of juvenile pleuronectids with regression trees for the combined 1991 and 1992 data.

Additional factors influence the presence or absence of these flatfish species at any given site. Possible factors that were not included in this study are additional measures of location (such as position around the island or distance from shore), abundances of prey or predators, and a substrate or habitat parameter that would account for microhabitat features not reflected in sediment composition.

A location parameter may be a categorical variable that assigns each station to a well-defined geographical area. For example, we observed large differences in the abundance of halibut and rock sole

between the east and west sides of Kodiak Island and among different bays. These differences possibly reflect oceanographic conditions that lead to variable levels of recruitment into different nearshore areas around Kodiak Island. Habitat models incorporating geographical and oceanographic information may help to reveal these mechanisms but would require larger sample sizes than are presently available.

The abundance of prey (McIntyre and Eleftheriou, 1968; Minami, 1986; Allen, 1988) and predators (van der Veer et al., 1991; Seikai et al., 1993) may influence the distribution and abundance of flatfish species but cannot be quantified without extensive surveys. Incorporating prey or predator abundance into a general habitat model is therefore probably of little practical use in applying the model to other areas. Postmetamorphic flatfishes in southeastern Alaska (Sturdevant, 1987) and juvenile flatfishes near Kodiak (Holladay and Norcross, 1995) feed primarily on small meiofaunal, benthic, and epibenthic crustaceans, including mysids, amphipods, cumaceans, and copepods. The diets of flathead sole, Pacific halibut, yellowfin sole, and rock sole were different in different capture sites, when region, depth, and substrate were the parameters used for the sites. This finding suggests that these species are opportunistic and feed on the prey available in their locale, rather than that they are discriminating, determining locale on the basis of prey availability.

Additional information is desirable to describe the microhabitat at each station more precisely. During our sampling, we obtained qualitative descriptions of the benthic flora and fauna that were collected at each station and a very broad quantification of the dominant invertebrates that were caught together with the fishes. In the future, we will attempt to consolidate this information into a categorical "community descriptor" for each station. This "community descriptor" can then be used as an additional explanatory variable in future models.

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Abstract.—Laboratory analyses were conducted on age-0 weakfish, *Cynoscion regalis*, to determine if deposition rate of otolith increments was daily and to examine the relation among otolith increment growth, daily feeding rate, specific growth rate, and condition factor. Tetracycline-marked juveniles ($n=58$) had a mean deposition rate of 0.98 (0.03 SE) increments/d. Feeding rate significantly affected increment width and was positively correlated with somatic growth rate and condition factor. Increment width response to changes in ration level was immediate, significant differences occurring between day 7 and 14. Mean increment width and specific growth rate were positively correlated ($r=0.86$). The continuation of otolith growth during periods of negative fish growth reflects the conservative nature of otolith growth and the lack of otolith resorption. An established relation between known growth rates of juvenile weakfish in the laboratory and otolith increment width will allow otolith increment widths to be applied to field samples. Such analyses could be used to examine closely factors affecting growth, survival, and recruitment.

Daily growth increments in otoliths of juvenile weakfish, *Cynoscion regalis*: experimental assessment of changes in increment width with changes in feeding rate, growth rate, and condition factor

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Growth rates in fishes can be determined by using scales, otoliths, modal analysis, RNA-DNA ratios, and assorted skeletal structures (Bagenal, 1978; Campana and Neilson, 1985; Summerfelt and Hall, 1987). Interpretations from these structures are based upon assumptions that increments within otoliths are added periodically and that the change in thickness of consecutive rings is proportional to fish length (Campana and Neilson, 1985). Otoliths have also proven to provide an accurate record of fish growth because there has been no evidence of resorption (Degens et al., 1969; Dunkelberger et al., 1980; Watabe et al., 1982; Mugiya, 1987), except under extreme physiological stress (Mugiya and Uchimura, 1989).

The periodicity of increment addition has been shown to be daily

in larval and juvenile fishes (Campana and Neilson, 1982; Hettler, 1984; Schmitt, 1984; Tsukamoto, 1985; Wilson et al., 1987; Tzeng and Yu, 1989; Monaghan, 1993). Otolith microstructure has more recently been used to compare growth of different cohorts within a year class (Townsend and Graham, 1981; Warlen, 1982; Methot, 1983; Jones, 1985), examine life history transitions (Brothers and McFarland, 1981; Laroche et al., 1982; Powell, 1982; Miller and Storeck, 1982; Victor, 1986; Thresher and Brothers, 1989), estimate mortality and survival (Crecco et al., 1983; Graham and Townsend, 1985; Neilson and Geen, 1986; Essig and Cole, 1986; Dalzell et al., 1987; Post and Prankevicius, 1987; Rice et al., 1987), and determine the effects of biotic and abiotic factors on microstructure

(Taubert and Coble, 1977; Tanaka et al., 1981; Campana and Neilson, 1982; Neilson and Geen, 1982, 1985; Neilson et al., 1985; Maillet and Checkley, 1991; Moksness, 1992).

Growth histories of fish are determined primarily through back calculation by using either a direct proportion or some nonlinear relation between otolith size and fish age (Maciena et al., 1987; Thorrold and Williams, 1989). Recent studies have used the relation between increment width (IW) and growth rate to show growth histories (Maillet and Checkley, 1990; Molony and Choat, 1990; Wright et al., 1990). Key assumptions for this use are that distance between increments is proportional to growth rate and that the increments are produced daily (Beamish and McFarland, 1983).

The objectives of this study were to validate the daily periodicity of otolith increments in juvenile weakfish, *Cynoscion regalis*, and to describe the relation between otolith IW and changes in feeding rate, specific growth rate, and condition factor.

Materials and methods

Experiment 1 (daily otolith increment validation)

Juvenile weakfish were captured in Delaware Bay in August, 1987, maintained in the laboratory in a recirculating seawater system under a photoperiod of 14 h light/10 h dark at 22°C (0.20 SE), 20‰, and fed ad libitum on squid. Fifty-eight fish were injected with a 200-mg oxytetracycline hydrochloride/0.1 mL saline solution and held in recirculating seawater for 26 days. Throughout the 26-d period, between 1 and 5 fish were removed and measured (SL), and their otoliths were removed for analysis. Fish sizes ranged from 68 to 150 mm SL.

Experiment 2 (effect of ration level on increment width and specific growth rate)

Weakfish were reared from eggs fertilized in the laboratory and raised to the juvenile stage in recirculating seawater (photoperiod=14L/10d at 22°C, 20‰). Individual fish were held in 20-L circular containers and fed ad libitum for two days to determine maximum ration (pretreatment period). Each day, fish were fed a known weight of live mysid shrimp (*Neomysis americana*) in excess of what they could consume. Fish were allowed to feed for 24 hours whereupon uneaten mysids were collected and weighed. Maximum ration was determined to be approximately 20% body weight/d.

Experimental treatment rations were randomly assigned on the third day of the experiment. Fish were weighed to the nearest 0.1 g and randomly assigned one of six daily rations: 100% maximum ration (MR, $n=5$), 90% MR ($n=4$), 80% MR ($n=4$), 60% MR ($n=4$), 40% MR ($n=4$), 20% MR ($n=4$, Table 1). Feeding levels were also calculated as percentages of body weight for individual fishes. For 14 days, fish were fed daily at these assigned levels; that is to say, they were allowed to feed for 24 h whereupon uneaten mysids were removed and collectively weighed. Fish were reweighed on day 7, and final weights and lengths were measured on day 14. The absolute weight of the daily feeding level offered (as a percentage body weight) was adjusted on day 7 to account for growth and maintain ration levels as a function of fish weight. Specific growth rate (SGR) was calculated for each fish as

$$SGR = [(\ln W_{14} - \ln W_0) / 14] \times 100,$$

where W_{14} = the wet weight (g) on day 14;
 W_0 = the initial wet weight (g); and
 14 = the duration of the treatment period in days.

Mean specific growth rates were calculated for each treatment. Fulton's condition factor (K) at the end of the experiment was calculated for each fish as

$$K = W / L^3 \times 10,000,$$

where W = the wet weight (g); and
 L = the standard length (mm).

Daily ration (percentage body weight/d) was calculated for each fish for each day on the basis of the

Table 1

Summary of ration levels. Actual treatment feeding levels and daily ration calculated based on calculated daily fish weights.

Estimated feeding level	Feeding levels (% of maximum ration)		Daily ration (% body weight/day)		
	Actual feeding level		Mean	Week 1	Week 2
100	100		23.8	26.4	21.3
90	66		15.6	16.1	15.0
80	58		13.9	14.6	13.3
60	46		11.0	11.1	10.9
40	32		7.6	7.7	7.5
20	17		4.1	4.1	4.1

weight of mysids consumed (weight of mysids offered minus weight of mysids not eaten) and estimated fish weights (assuming exponential growth between weighings). Mean daily ration was calculated for each feeding level treatment (Table 1). Henceforth, feeding will refer to daily ration, whereas treatment levels will continue to be referred to as percentage of maximum ration (MR).

Because measurements of feeding depended upon the reliability with which uneaten mysids were collected, retrieval efficiency was determined. Live mysids, in amounts comparable to the feeding levels described above, were weighed to the nearest mg and placed in all ten containers with recirculating seawater. After 24 hours, the mysids were retrieved and reweighed. Mean weight of retrieved mysids was 89% (0.017 SE) of initial weight. Therefore, differences between the weight of mysids provided and the weight retrieved was considered to be a useful estimate of feeding.

Otolith preparation and analysis

Otoliths were ground by hand following modified procedures of Neilson and Geen (1981) and Volk et al. (1984). Both sagittal otoliths were embedded in EPON resin. Otoliths were attached to a glass slide with thermoplastic and ground to half their thickness across a transverse plane by using a series of 400–600 grit carborundum paper. Otoliths were polished with 0.3 μm alumina oxide paste, reattached to a glass slide with the polished side down, then ground and polished to produce a thin section through the nucleus. All counts and measures were made from the origin along the dorsal edge of the neural groove to the otolith margin. All other transects lacked precision.

Tetracycline-marked otoliths were examined with UV light at 400 \times magnification. Increment counts were made from the fluorescent mark to the edge of the otolith. Each otolith was counted twice, without knowledge of the previous measurement, and confirmed by an independent counter. Otoliths from experiment 2 were examined under 400 \times magnification with transmitted light. Mean IW was calculated from three "blind" measurements. We made all counts and measurements with an Olympus Cue 2 Image Analysis System. One pair of otoliths from the 66% ration treatment was not readable and was subsequently discarded.

Statistical analyses

Experiment 1—daily otolith increment validation To validate the daily nature of otolith increment, the regression slope of increment count on day

was tested to determine if it differed from one (Students' *t*-test). Outliers were detected by calculating the leverage coefficients and by computing the standard residuals from the regression equation line. Only 2% of the otoliths were reexamined because the leverage coefficient was greater than $4/n$ and the standard residual was greater than the *t*-value for a sample size of *n* (Sokal and Rohlf, 1981).

Experiment 2—effect of ration level on increment width and specific growth rate Mean IW among ration treatments for increments formed during the pretreatment period was compared with ANOVA ($\alpha = 0.05$), followed by Tukey's multiple comparison tests (Zar, 1984). Mean IW among ration treatments for weeks 1 and 2 and between weeks within ration treatments was analyzed with two-way ANOVA ($\alpha = 0.05$). Mean specific growth rate for each treatment was regressed against mean increment width following confirmation of normality (Kolmogorov-Smirnov test) and homogeneity of variances (Cochran's *C* test) with $\alpha = 0.05$ for all treatment levels. Increment width was compared with SGR, daily ration, and Fulton's *K* at the end of the experiment for each fish (Pearson product-moment). Regression analysis was used to determine the relation between IW and SGR ($\log\{G+1\}$) for each fish. Regression lines were fitted by using a second-order regression against daily ration (Zar, 1984).

Results

Experiment 1—daily otolith increment validation

The slope of the regression increments on days after injection was not significantly different from one ($y = 0.975x + 0.825$, $P > 0.05$), thus supporting the daily periodicity of otolith increment formation in this species (Fig. 1).

Experiment 2—effect of ration level on increment width and specific growth rate

No differences were found in mean IW among treatments during the 2-d pretreatment period. Initially, IW narrowed in the lower feeding levels: 17%, 32%, and 46% maximum MR (Fig. 2). Mean daily IW ranged from a low of 2.3 μm (17% MR or 4.1% body weight/d) during week 2 to a high of 4.5 μm (66% MR or 15.6% body weight/d) during week 1 (Table 2).

Mean IW was significantly lower for the 17%, 32%, and 46% MR treatments during the entire 14-d period as compared with the higher ration treatment

(Table 2; Fig. 3). Increments in the higher ration treatments remained relatively wide throughout the experimental period. Narrowing of increment width in the 17% and 32% MR treatments ensued immediately and continued to decrease after the first week of the experiment (Fig. 2). For all treatments, mean IW was lower during week 2 than week 1; significant differences occurred between weeks in the 17%, 32%, and 66% MR treatments (Table 2). By week 2, there were significant among-treatment differences in mean IW among the 46% MR and the 32% and 17% MR treatments. Mean IW among the higher feeding levels did not differ throughout the entire experiment except for the 66% MR level. During several days of the first week, this group had a significantly higher mean IW compared with other treatments (Table 2). Daily variability in IW was high in all treatments (Fig. 2).

There was a positive correlation ($IW = 2.58 + 1.49(\log\{G+1\})$, $r=0.86$, $P<0.05$) between mean daily IW and mean specific growth rate for each treatment (Fig. 4). Although some fish lost weight at the lowest ration level, daily increments continued to be produced. There was a positive correlation between mean IW and mean daily

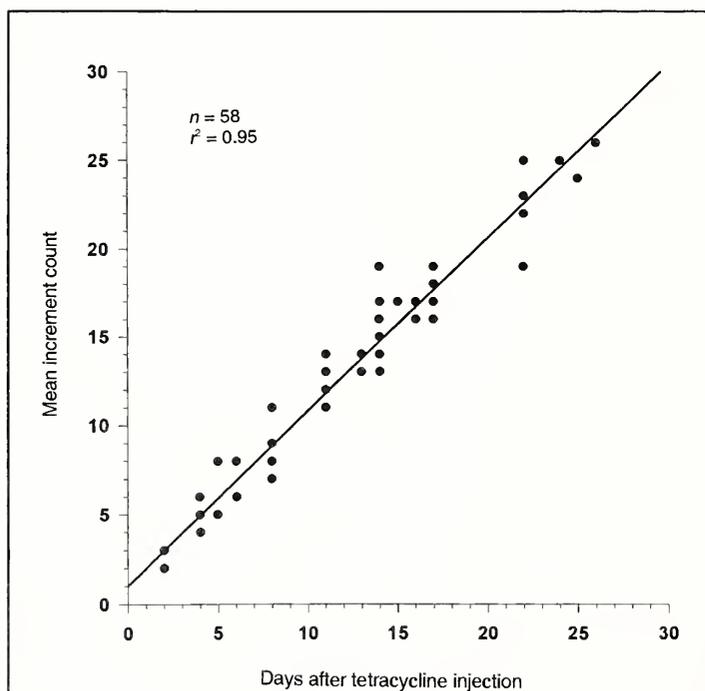


Figure 1

Relation between otolith increments distal to the fluorescent mark and days after tetracycline injection in juvenile weakfish, *Cynoscion regalis*. Symbols may represent more than one observation.

Table 2

Results of two-way analysis of variance and multiple-range tests from comparisons of mean weekly increment width from different ration treatments and one-way analysis of variance between weeks. MR is the maximum ration. * = $P<0.05$, ns = not significant; letters indicate the results of Tukey's HSD comparison among treatments. SE is the standard error associated with treatment means.

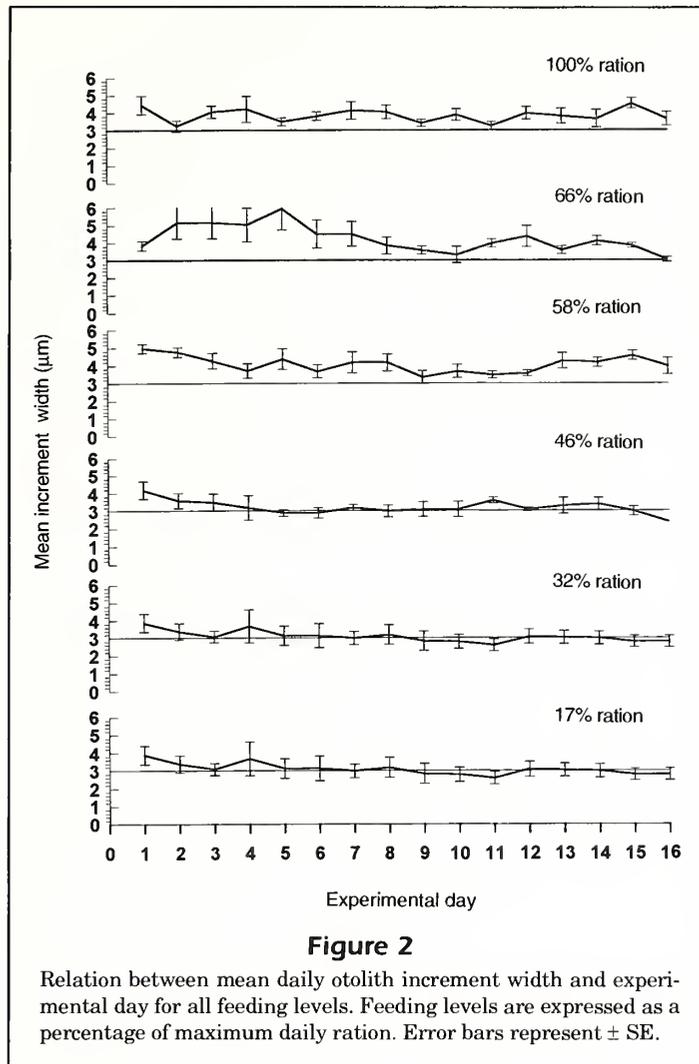
Treatment feeding levels (% MR)	Week 1	SE	Week 2	SE	Treatment means
17	3.042	0.0243	2.310	0.0378*	2.68 ^a
32	3.021	0.0465	2.616	0.1203*	2.82 ^{ab}
46	3.121	0.1402	3.027	0.1495ns	3.07 ^b
58	3.823	0.7427	3.817	0.5864ns	3.82 ^c
66	4.514	0.2835	3.766	0.8348*	4.14 ^c
100	3.864	1.2942	3.755	0.6493ns	3.81 ^c
Overall	3.538		3.215*		3.38

feeding rate and between mean specific growth rate and K at day 14 (Table 3; Figs. 3 and 4). This relation ($P<0.05$) developed during week 1 of the experiment and strengthened during week 2 (Table 3).

Discussion

Injection of oxytetracycline hydrochloride solution produced clear fluorescent bands in the otoliths of juvenile weakfish, and increment deposition occurred daily. Several other juvenile sciaenids have shown daily increments: spot (*Leiostomus xanthurus*), red drum (*Sciaenops ocellatus*), spotted seatrout (*Cynoscion nebulosus*), and silver perch (*Bairdiella chrysoura*) (Gjosaeter et al., 1984; Hettler, 1984; Peters and McMichael, 1987; McMichael and Peters, 1989; Hales and Hurley, 1991). The present study provides validation for ageing juvenile weakfish, thus enabling estimates of growth and providing, in combination with abundance data, a means of estimating accurate age specific mortality rates during this life history stage.

The rapid response of IW to changes in ration and the strong relation with SGR suggest that IW's may be used to infer growth history. Furthermore, significant differences in IW between high (58–100% MR) and low (17–46% MR) feeding levels suggests that IW may be used to approximate feeding history. Because of approximately a one-week lag time prior to stabilization of IW among treatments, the full magnitude of the change in IW cannot be assessed by examining just a few increments. At



least one week is required before IW responses to feeding and growth are statistically detectable although the physiological processes that result in IW differences begin acting sooner (Molony and Choat, 1990). Therefore, mean IW taken over several consecutive days would be most useful for making inferences regarding recent feeding and growth history for small sample sizes.

The magnitude of variability in IW observed in this study, particularly for the higher rations, has been documented for other species (Volk et al., 1984; Neilson and Geen, 1985; Maillet and Checkley, 1991). The reduced variability under the stress of lower ration may be related to reduced growth and utilization of food and stored reserves for maintenance (Molony and Choat, 1990). Continuation of otolith increment formation during periods of negative fish growth suggests that otolith growth is conservative and otolith resorption is not likely (Campana and Neilson, 1985; Secor et al., 1989).

Table 3

Results of Pearson product-moment correlation analysis (*r*) between daily increment width, daily feeding rate, and specific growth rate.

	Increment width		
	<i>r</i>	<i>n</i>	<i>P</i> <0.05
Daily feeding rate			
Week 1	0.5100	168	0.000
Week 2	0.6552	168	0.000
Specific growth rate			
Week 1	0.3961	168	0.000
Week 2	0.6232	168	0.000
Condition factor	0.3576	336	0.000

Otolith increments of spot, like those of weakfish, were found to have an immediate response to changes in ration (Govoni et al., 1985), although deposition

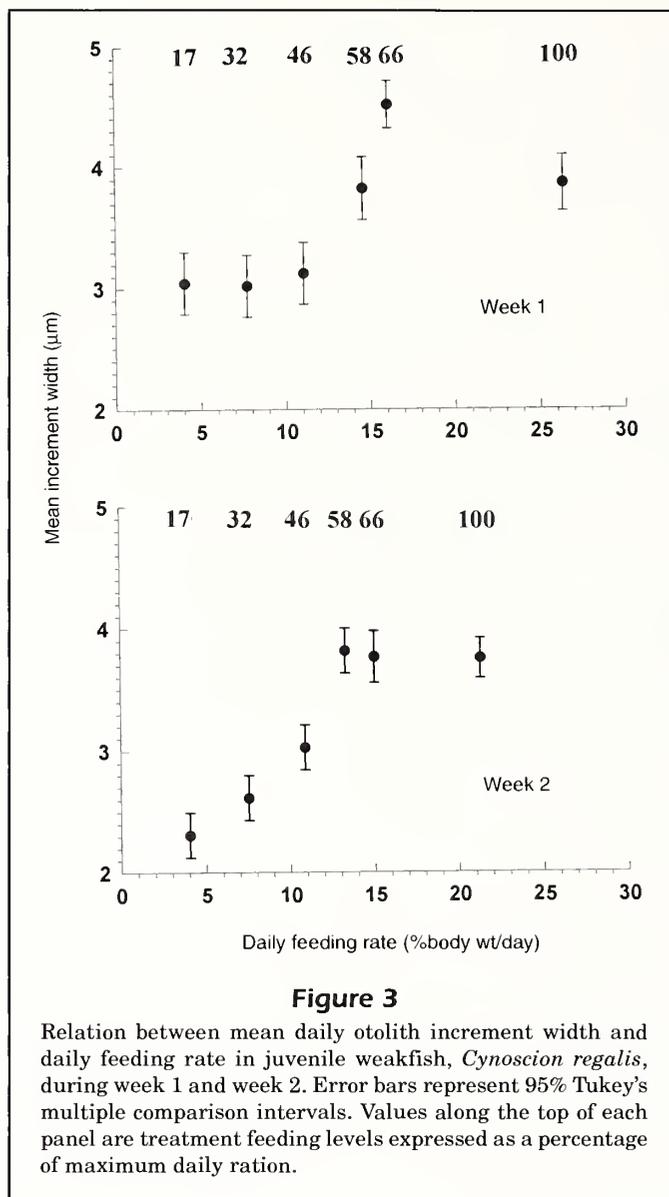


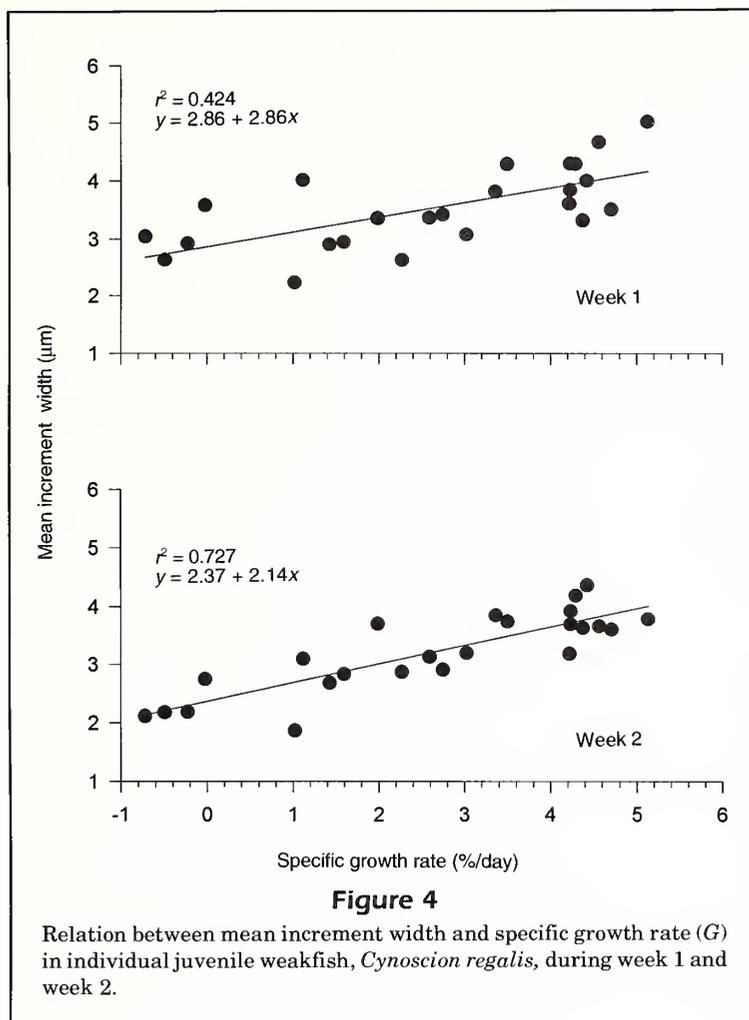
Figure 3

Relation between mean daily otolith increment width and daily feeding rate in juvenile weakfish, *Cynoscion regalis*, during week 1 and week 2. Error bars represent 95% Tukey's multiple comparison intervals. Values along the top of each panel are treatment feeding levels expressed as a percentage of maximum daily ration.

was found to be less than daily under low ration conditions (Siegfried and Weinstein, 1989). However, for the bloater (*Coregonus hoyi*) there was a loss of contrast between the hyaline and opaque bands and no effect on relative increment width (Rice et al., 1985). Maillet and Checkley (1990) found that starved Atlantic menhaden (*Brevoortia tyrannus*) larvae produced narrower increments with IW, increasing during a 3–6 day recovery period. In contrast to these examples of rapid otolith response to ration, changes in IW in juvenile chum salmon (*Oncorhynchus tshawytscha*) and the tropical glass fish (*Ambassis vachelli*) do not become discernible for three weeks and two weeks, respectively (Neilson and Geen, 1985; Molony and Choat, 1990). Recent experimental data

suggest that the IW-growth relation may be more complex than originally thought (Reznick et al., 1989; Secor et al., 1989; Francis et al., 1993; Jenkins et al., 1993). The result of these studies suggests that the IW response to feeding and growth is variable, may be of limited use in some species, and needs to be evaluated on a species by species basis.

For species in which the relation of IW to growth has been established, otolith increment analysis can provide a means by which an investigator may relate recent environmental conditions to recent growth history during the important early life stages. Thus, a more complete understanding of the role of the environmental conditions relating to feeding, growth, and ultimately survival may be obtained.



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Abstract.—Age and growth of larval and juvenile Spanish mackerel, *Scomberomorus maculatus*, were determined by examining increments of daily growth on the otoliths (lapilli) of specimens collected along the southeastern Atlantic coast, 1983–89. Marginal increment analysis was performed on 152 fish (7.4–97.0 mm SL) to validate the deposition of daily rings. A mean standardized marginal increment (SMI) was calculated by comparing the width of the marginal increment to the adjacent increment on the lapilli of fish captured over a diel cycle. The distribution of mean SMI was unimodal. A nonlinear equation was used to model growth ($\ln SL = 6.2 - 55.1/ \text{Age}$). Based on this growth equation, predicted absolute growth rates for the first 23 days of life were approximately 1.9 mm/day, followed by a surge of rapid growth approaching 5.0 mm/day over the next 17 days. Absolute growth rates subsequent to 40 days of age were 2.1 mm/day.

Daily age and growth of larval and early juvenile Spanish mackerel, *Scomberomorus maculatus*, from the South Atlantic Bight*

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The Spanish mackerel, *Scomberomorus maculatus* (Mitchill), is an inhabitant of the Gulf of Mexico and the Atlantic coast of the United States. During winter months, Spanish mackerel are concentrated in waters off southern Florida. In late spring and summer, however, they are widely distributed along the Atlantic coast to the Gulf of Maine (Klima, 1959; MacEachran et al., 1980; Finucane and Collins, 1986).

Most life history studies on Spanish mackerel have focused on adults from southern Florida and the Gulf of Mexico (Klima, 1959; Powell, 1975; Finucane and Collins, 1986; Fable et al., 1987; Schmidt et al., 1993). Except for work by DeVries et al. (1990) on growth rates of larval and early juvenile Spanish and king mackerel (2.8–22.0 mm SL), very little has been done on the early life history of *S. maculatus*, particularly in the South Atlantic Bight (SAB).

Daily growth increments on otoliths of juvenile scombrids (skipjack, *Euthynnus pelamis*, and yellowfin tuna, *Thunnus albacares*, bluefin tuna, *T. thynnus*, black skipjack, *Euthynnus lineatus*, Atlantic mackerel, *Scomber scombrus*, and southern bluefin tuna, *Thunnus maccoyii*) have been tentatively validated (Uchiyama and Struhsaker, 1981;

Radtke, 1983; Wild and Foreman, 1980; Brothers et al., 1983; D'Amours et al., 1990; Jenkins and Davis, 1990; Wexler, 1993). However, no published study has been directed at the validation of daily growth increments on the otoliths of Spanish mackerel.

The validation of the consistent periodic deposition of growth rings generally requires that fishes be held in captivity under conditions that approximate the natural environment. However, Spanish mackerel larvae and juveniles are difficult to rear in the laboratory. Another method that has moderate reliability involves demonstrating that initiation of increment formation is synchronous throughout the population (Tanaka et al., 1981; Geffen, 1987; Jenkins and Davis, 1990). If fishes deposit increments in response to external environmental cues of diel periodicity, or an endogenous daily rhythm, then individuals experiencing the same environmental conditions (light, temperature, feeding activity) would be expected to initiate increment deposi-

* Contribution 377 from the South Carolina Department of Natural Resources, Charleston, South Carolina 29422 and contribution 135 from the University of Charleston's Grice Marine Laboratory, Charleston, South Carolina 29412.

tion at approximately the same time of day. A review of this approach is presented in Tanaka et al., 1981; Brothers and MacFarland, 1981; and Geffen, 1987.

The age and growth data used in this paper came from two separate studies, one dealing primarily with larvae and small juveniles less than 100 mm SL, the other with larger young-of-the-year (YOY) juveniles. The primary objectives of this paper are to combine these studies to present a more comprehensive analysis of age and growth of larval and juvenile (7–353 mm SL) Spanish mackerel and to validate the daily deposition of increments on their otoliths.

Methods

Collection and treatment of specimens

Past studies attempting to describe the age, growth, and distribution of Spanish mackerel have resulted

in the collection of a relatively small number of specimens over a limited size range (MacEachran et al., 1980; Collins and Stender, 1987; DeVries et al., 1990). Because of the apparent difficulty in capturing Spanish mackerel larvae and juveniles, we attempted to increase our sample size by pooling ancillary collections of Spanish mackerel from unrelated studies when they became available. This allowed us to use a wide size range of specimens collected over an entire diel cycle.

Most of the Spanish mackerel larvae and juveniles (7.4–353.8 mm SL) were collected with a 1 m × 2 m neuston net (2.0 mm mesh) from Breach Inlet bridge, near Charleston, SC, during the entire nighttime flood tide (Fig. 1). The sampling effort was designed by the South Carolina Department of Natural Resources (SCDNR) to capture larval gag that enter the estuaries during the spring of each year. Spanish mackerel were obtained from samples that were taken during the month of June from 1986 through

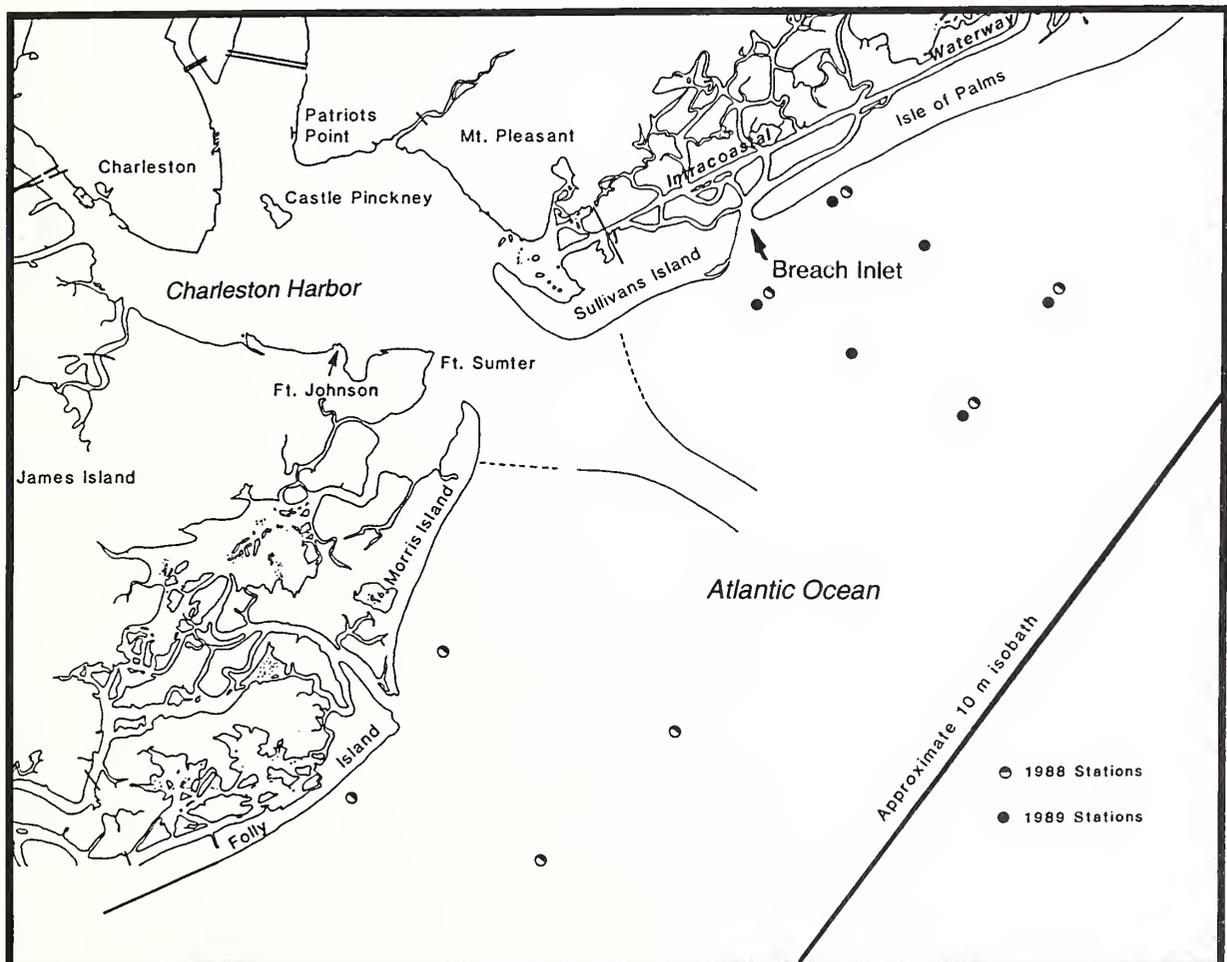


Figure 1

Locations of nearshore ichthyoplankton stations sampled during 1988 and 1989 and location of Breach Inlet, off Charleston, SC, where sampling was done for this study.

1988. In addition, 25 larval and juvenile Spanish mackerel were collected in ichthyoplankton samples from coastal waters off Charleston, SC, during May–October 1988 and 1989 (Fig. 1). During 1988, samples were obtained with a 0.5 m × 1 m (0.505-mm mesh) side-towing neuston net. The 1989 samples were taken with a 1 m × 2 m (0.947 mm mesh) neuston net. In addition, larger juvenile Spanish mackerel (> 60 mm SL) were obtained during 1983–89 along the coast of North Carolina, South Carolina, and Georgia from SCDNR research cruises aboard the RV *Oregon* and RV *Lady Lisa* with trawls, gill nets, seines, and from commercial shrimp trawling bycatch (Collins et al., 1988; Beatty et al.¹).

Larvae and juveniles (<100 mm SL) were preserved in 95% ethanol and measured (standard length [SL], fork length [FL], and total length [TL]) to the nearest 0.1 mm with dial calipers or ocular micrometer (Wild, M5 dissecting scope). Owing to the poor condition of the caudal fin on many of the smaller fish, standard length was used in the age and growth analysis. A factor of 3% was added to the length of each fish to account for shrinkage in ethanol (Schmidt, unpubl. data, 1988). All fish were identified following Wollam (1970) and Richardson and MacEachran (1981). Sagittae and lapilli were excised from larvae and small juveniles by immersing the head region in 5% sodium hypochlorite solution for no more than 30 minutes (Brothers, 1987). Otoliths were separated from undissolved tissue and bone under a dissecting microscope with transmitted crossed polarized light. Otoliths from larger juveniles were removed by dissecting out the entire otic capsule and by separating the otoliths from their respective ampullae. Excess tissue was dissolved in sodium hypochlorite solution. Otoliths were then rinsed in water, mounted whole (concave side down, unpolished) in immersion oil on a microscope slide and examined on a video-enhanced (Hitachi, MOS) compound microscope (Nikon, Labophot). Lapilli were used to estimate age in Spanish mackerel larvae and juveniles because increments were more discernible in the lapilli than in the sagittae. Young-of-year juveniles (>100 mm SL) were treated according to the same procedures used for YOY king mackerel by Collins et al., 1988.

Marginal increment analysis

To confirm the hypothesis of daily increment deposition, a marginal increment analysis was performed.

In this analysis, the stage of completion of the marginal increment was compared with the adjacent fully formed increment on the lapilli from fish captured over a daily cycle (Fig. 2). Because Breach Inlet specimens were captured over an entire flood tide, it was impossible to know their precise time of capture. Therefore, the mean stage of completion of the marginal increment of several specimens, captured over 5–6 hour periods that progressed throughout the day and night, was compared. Large collections were subsampled by selecting as many as 35 individuals representing the size range of fish captured in the sample. Additional mackerel taken in SCDNR trawls and nearshore ichthyoplankton samples were also used. The time of capture of these specimens was known to within 30 minutes. A total of 165 larval and juvenile Spanish mackerel (7–97 mm SL) were examined. Attempts to find evidence for the daily nature of otolith rings in larger juveniles by measuring diel variation in marginal increments with SEM were not successful.

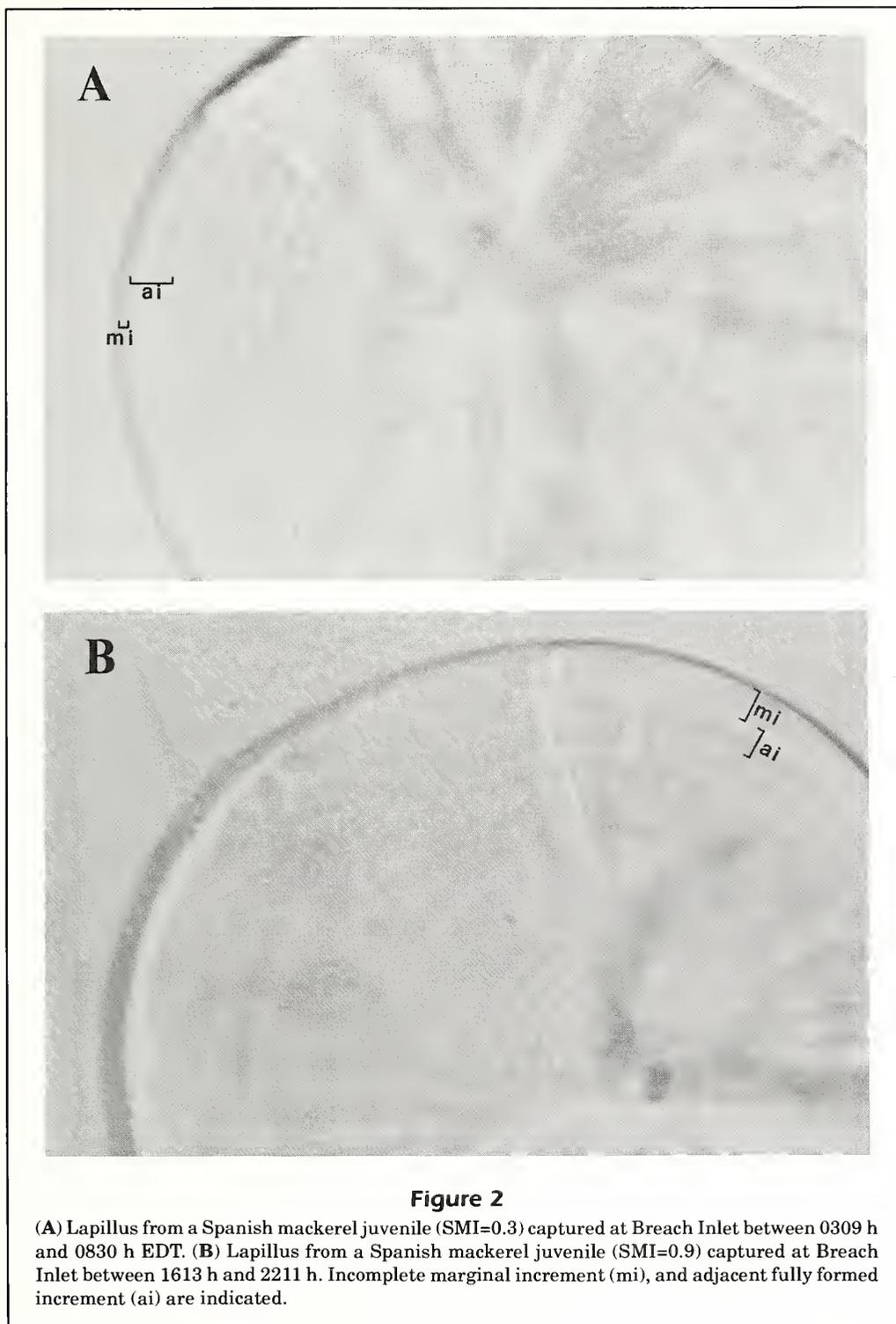
Measurements of the marginal increment and the adjacent increment were made along each of three separate axes on each otolith. These axes were chosen because their optical properties allowed acceptable ring resolution. Occasionally, it was not possible to measure all three axes owing to opacity or damage to the otolith. Increments were displayed on a video monitor at 1,000× and measured to the nearest 0.1 mm with dial calipers. Care was taken in observing the opaque and transparent zones because different focal planes may invert their appearance. Consistent counts and marginal increment measurements were obtained at a “high” focal point (the distance [with the highest lens power] to object that will produce a well-defined image). We were unaware of time of capture while performing the measurements. A standardized marginal increment (SMI) for each axis of measurement was calculated as

$$SMI = \frac{W_n}{W_{(n-1)}}$$

where W_n = width of marginal increment; and $W_{(n-1)}$ = width of complete adjacent increment.

The SMI's for each of the axes were averaged to obtain a mean SMI for each otolith. Two independent mean SMI's were calculated for each otolith from separate measurements. Although there was no significant difference between the two measurements (paired *t*-test, $P=0.153$), the second measurement was used in the analysis because we were more experienced at locating and measuring the marginal increment.

¹ Beatty, H. R., J. W. Hall, and E. L. Wenner. 1988. Results of trawling efforts in the coastal habitat of the South Atlantic Bight 1987–1988. South Carolina Division of Natural Resources, P.O. Box 12559, Charleston, SC 29422. SEAMAP Report, 94 p.



Age and growth analysis

Whole lapilli from 415 larval and juvenile Spanish mackerel were examined. For larvae and juveniles <100 mm SL, otolith radius was measured from the center of the primordium to the margin of the otolith

along a consistent axis. Measurements were made with an ocular micrometer at magnifications of 100× or 400× depending upon the size of the otolith. Presumed daily increments on the lapilli were counted on a video monitor under 1,000× magnification. Two independent counts of presumed daily increments

were made; we were unaware of fish length and any prior age determination during counting. Incomplete marginal increments were not counted. Furthermore, counts of right and left otoliths were conducted separately. In situations where the first two counts differed, a third independent count was performed. The assigned age corresponded to the two counts that were in agreement. If agreement could not be reached on two of the three counts, the otolith was considered unreadable and was not used. Otoliths in YOY juveniles (>100 mm SL) were counted according to the procedures used for YOY king mackerel in Collins et al. (1988).

Nonlinear regression analysis was used to describe the relation between age and length. Statistical analyses were performed with SYSTAT software (Wilkinson, 1988) and Table Curve (Jandel Scientific) and were based on a significance level of 0.05.

Results

Several features of increment deposition were observed to be consistent among the otoliths examined. Two diffuse and poorly defined increments (core increments) surrounded the primordium (Fig. 3). Mean core width was 11.4 mm and there was little variation with fish length (SD=0.54 mm, $n=40$, length range=9.0–300.1 mm). Although these increments

were counted as daily, the nature of their deposition was clearly different from that of subsequent rings. This finding indicated that they were formed during a separate developmental stage. The absence of fish younger than 9 days precluded precise determination of the time period represented by these two increments. Subsequent increments were clearly defined on most lapilli and were easily discernible in whole otoliths examined under a light microscope without any special preparation (grinding or polishing). Subdaily increments occurred, particularly in older juveniles, and were discernible from the daily increments (Fig. 4).

Marginal increment analysis

Of 165 fish examined for marginal increments, 13 were not used in the final analysis owing to damage to the otoliths or to uncertainties in distinguishing the marginal or adjacent increments (or both). No significant difference in SMI was found between left and right lapilli (paired t -test, $P=0.191$). Examination of fish captured during the 1613–2330 h time period revealed an obvious split in the stage of marginal increment completion (Table 1). A unimodal distribution of mean SMI, for fish captured over a 24-h period, was obtained if the mean SMI of those otoliths whose margin was bordered by a translucent zone

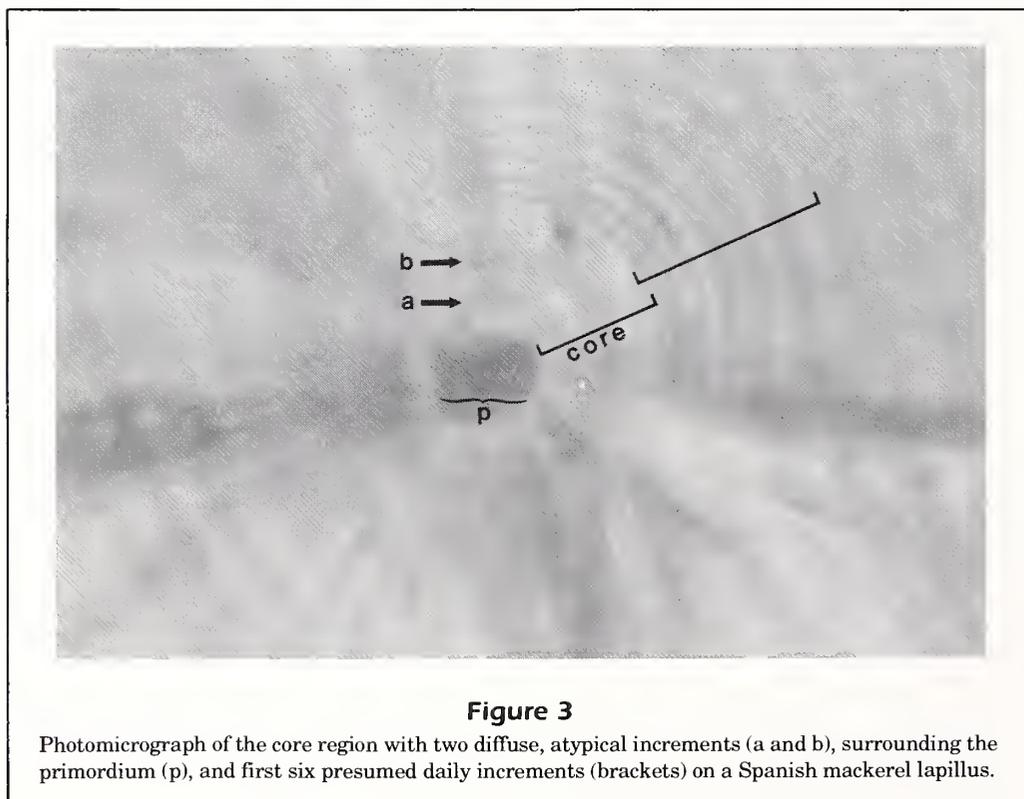


Figure 3

Photomicrograph of the core region with two diffuse, atypical increments (a and b), surrounding the primordium (p), and first six presumed daily increments (brackets) on a Spanish mackerel lapillus.

(late stage of increment formation) was plotted separately from the mean SMI of otoliths whose margin was bordered by an opaque zone (early stage of increment formation) (Fig. 5). The observed separation in the stage of increment formation would be expected if initiation of increment formation occurred between 1613 h and 2330 h.

Age and growth

Otolith radii measurements revealed no significant difference between right and left lapilli (paired sample *t*-test, $P=0.127$). The relation between SL versus lapillus radius was described by the following regression equation:

$$SL = -4.78 + 0.68(Radius) \quad [r^2=0.99, n=364].$$

No significant difference was found between increment counts for left and right lapilli (paired *t*-test, $P=0.190$). Therefore, if left and right counts differed, the otolith whose increments were more clearly defined, or which was in better condition, was used to assign an age to the fish. Growth in young Spanish mackerel was quite variable within age classes, particularly in juveniles older

Table 1

Mean standardized marginal increment (MSMI), range, standard deviation for left (L) and right (R) lapilli, and size range for *S. maculatus* captured from 1613 to 2211 h and 1755 to 2330 h. Lapilli with opaque margins are considered separately from lapilli with translucent margins. (*n* refers to the number of specimens, no. refers to the number of right or left lapilli.) Hours are those of eastern daylight time.

	Lapilli from fish collected 1613-2211 h				Lapilli from fish collected 1755-2300 h			
	Opaque		Translucent		Opaque		Translucent	
	R	L	R	L	R	L	R	L
<i>n</i>	34				10			
No.	18	18	16	16	6	6	2	4
MSMI	0.19	0.22	0.88	0.86	0.25	0.23	0.75	0.75
SD	0.05	0.07	0.08	0.15	0.06	0.05	0.07	0.13
Range	0.3	0.2	0.3	0.5	0.1	0.1	0.1	0.3
Size range (SL)(mm)	17.1-97.0				22.6-79.0			

than 23 days (Fig. 6). Nonlinear regression analysis provided the following growth equation:

$$\ln SL = 6.2 - 55.1/Age.$$

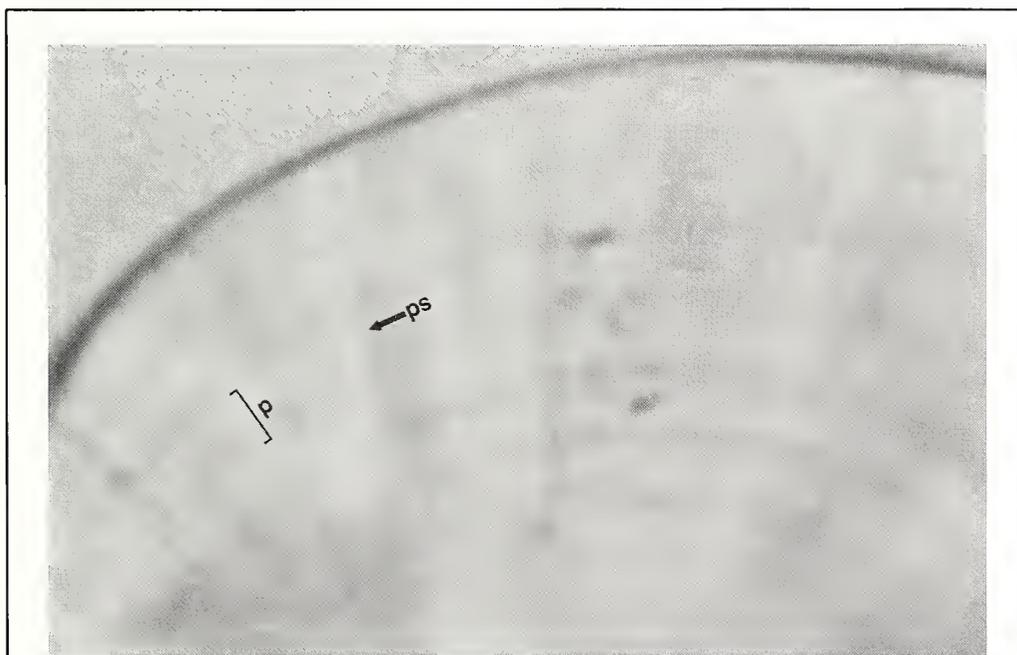


Figure 4

Lapillus of an 18-day-old juvenile Spanish mackerel (18.7 mm SL). Note occurrence of subdaily rings as the fish ages. A daily growth increment (d) and a presumed subdaily increment (sd) are indicated.

Based on this growth equation, predicted absolute growth rate (predicted SL/age in days) was 2.4 mm/

day for the first 150 days of life. Early growth was characterized by relatively slow growth for the first 23 days of life (1.9 mm/day) followed by a surge of rapid growth from 23 to 40 days, during which growth rates approached 5.0 mm/day. Predicted absolute growth of older juveniles (40–150 days) was 2.0 mm/day.

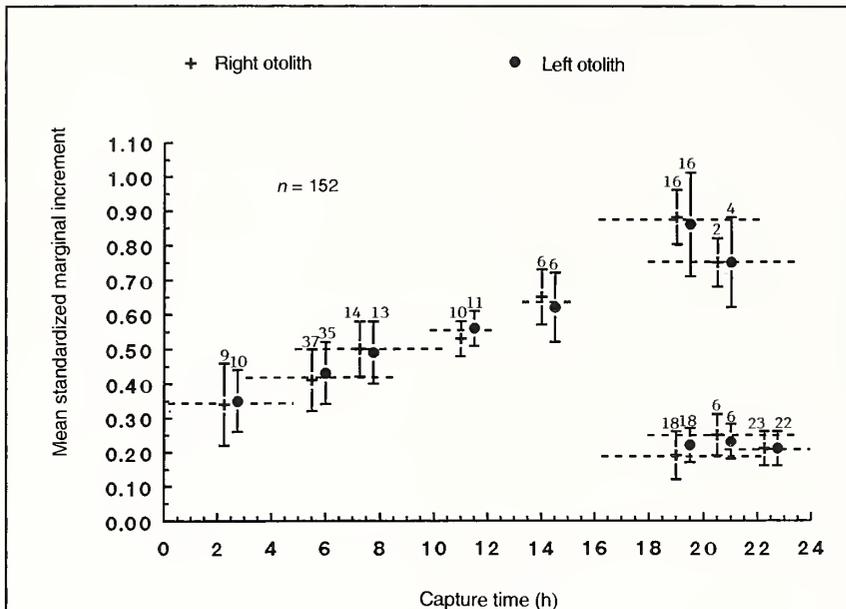


Figure 5

Mean standardized marginal increment and standard deviation for left and right lapilli of Spanish mackerel larvae and juveniles collected throughout the day and night. Mean SMI for opaque bordered marginal increments are plotted separately from translucent bordered marginal increments in samples taken from 1613–2330 h. Capture time ranges (dashed lines) and sample sizes are indicated.

Discussion

Validation of daily formation of the microstructural increment is a necessary prerequisite to using otoliths for ageing larval and juvenile fishes. Determination of the stage of completion of the most recently formed increment over a daily light cycle does not directly validate daily increment formation but lends strong support to the hypothesis that increments are deposited daily.

Several studies have shown that increment deposition is most likely controlled by an endogenous rhythm that can be modified by physical or behavioral parameters (or both), such as light and dark periodicity,

temperature regimes, feeding frequency, food availability, activity patterns (such as daily vertical migrations), or a combination of these and other factors (Jones, 1986; Campana and Neilson, 1985, for review). There is presently no information available on the effects of changes in environmental factors on the periodicity or pattern of increment formation in larval or juvenile scombrids. However, work done with other teleosts (Taubert and Coble, 1977; Tanaka et al., 1981; Campana, 1984; Neilson and Geen, 1985; Jenkins and Davis, 1990) suggests that an internal diel clock alone is not responsible for daily increment formation but that it is entrained by some external environmental cue that can vary between species of fishes.

Observations on the seasonal occurrence and distribution of larval Spanish mackerel in the northern Gulf of Mexico and the South Atlantic Bight suggest that they are restricted to middle and inner continental shelf waters (Dwinell and Futch, 1973; MacEachran et al., 1980; Collins and Stender, 1987). Since daily fluctuations in salinity and turbidity are minimal in shelf waters outside estuarine influence, they are not likely to modify cyclic daily deposition of increments in larval Spanish mackerel. It seems more likely that feeding periodicity or diel vertical

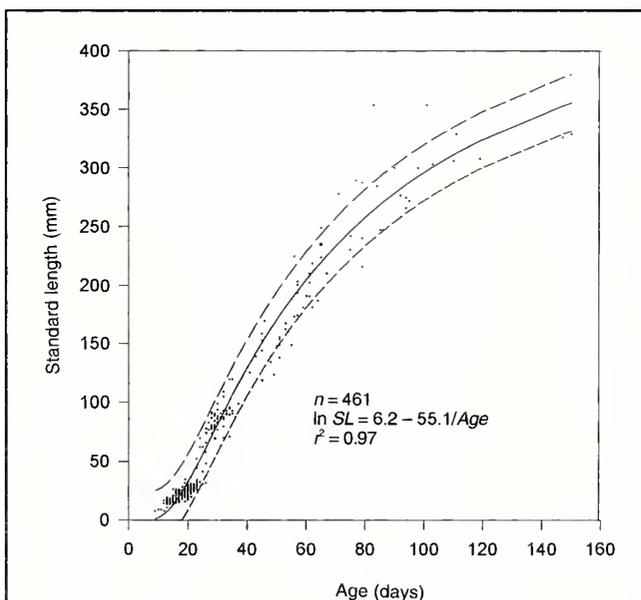


Figure 6

Relation between standard length (SL) and age in days and 95% confidence limits (dashed lines) determined from otolith increment counts for Spanish mackerel.

migrations, which are often strongly associated with light cycles, serve to increase daily increment definition (Campana and Neilson, 1985).

Other species of scombrid larvae and early juveniles (*E. pelamis*, *T. albacares*, *E. alletteratus*, *Auxis thazard*, and *Scomber scombrus*) are known to undergo vertical diel migration feeding primarily at the surface at night (Matsumoto, 1958; Grave, 1981). Collins and Stender (1987) found statistical evidence for vertical migration to the surface at night in both *S. maculatus* and *S. cavalla*. Spanish mackerel and other species of *Scomberomorus* are known to feed on ichthyoplankton during the larval stage and are almost completely piscivorous as juveniles (Naughton and Saloman, 1981; Jenkins et al., 1984). The large eyes of scombrids, even during the larval stage, suggest that they are visual predators. Therefore, light cycles probably have a strong influence on prey detection. Moreover, feeding opportunities related to diurnal vertical migrations of prey organisms, along with fluctuations in temperature associated with diel vertical migrations, may further serve to entrain this endogenous rhythm of calcium carbonate deposition.

Age and growth

Marginal increment analysis indicated that otolith increments are deposited daily in larvae and juveniles from 7 to 95 mm SL. However, because we were unsuccessful at capturing preflexion larvae, it was impossible to determine if increment counts truly reflected age from fertilization. Very little information is available on otolith formation in scombrids, although otoliths are among the first calcified structures and are present in scombrid embryonic stages (Matsumoto, 1958; Radtke, 1983; Brothers et al., 1983). In *E. pelamis* larvae reared from hatching (Radtke, 1983), the core region of the otolith (the primordium and two diffuse increments), along with the pattern of subsequent increment formation, is very similar in appearance to otoliths of *S. maculatus* (Fig. 3). Radtke (1983) observed that the two core increments were present at hatching.

The two core increments in *S. maculatus*, because of their atypical pattern of deposition, are likely to have been formed during the egg stage or prior to yolk-sac absorption. However, it is not known whether these increments are deposited daily. Because hatching and yolk-sac absorption of Spanish mackerel larvae usually occurs five days after fertilization at temperatures experienced during the spawning season in South Carolina waters (Berrien and Finan, 1977; Fritzsche, 1978), errors in age estimation are likely to be consistent among most fish, and growth rate calculations would remain unaffected.

Considerable variation was observed in the growth rates of individual fish, particularly among juveniles older than 23 days. The use of specimens collected over a wide spatial and temporal range was probably responsible for much of this variation. However, the overall predicted mean absolute growth rate of 2.4 mm/day is within the range of growth rates observed in other scombrids during the first few months of life (1 mm/day–6 mm/day) (see Brothers et al., 1983, for review). The regression lines estimating the relationship between age and length appeared to be a good approximation ($r^2=0.97$, $P<0.0001$) of growth in young Spanish mackerel.

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Spanish mackerel, *Scomberomorus maculatus* (Mitchill); (Pisces: Scombridae); in the western North Atlantic. Fla. Dep. Nat. Resour. Mar. Res. Lab. Tech. Ser. 61, 31 p.

Abstract.—Stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope measurements were used to differentiate groups of king mackerel, *Scomberomorus cavalla*, in the northwestern Gulf of Mexico and off the southeastern coast of Florida, as well as off the coast of Mexico. Northwestern (+13.1‰) and southeastern (Mexico=+10.8‰ and Florida=+10.8‰) groups, as well as the Atlantic group, had significantly different stable nitrogen isotope ratios. These were attributed to isotopic variations at the base of the food chain. Variability in $\delta^{13}\text{C}$ measurements was too large and did not corroborate the $\delta^{15}\text{N}$ results. The grouping suggested by the $\delta^{15}\text{N}$ data can be explained by the influence of the Mississippi River and the Gulf of Mexico Loop Current.

Use of stable isotopes to assess groups of king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico and southeastern Florida

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King mackerel, *Scomberomorus cavalla*, is one of the most sought after migratory pelagic resources in waters of the contiguous United States (Dwinell and Futch, 1973; Manooch et al., 1978; Manooch, 1979; Finucane et al., 1986). This species is strongly exploited by both sport and commercial fisheries, and fishing pressure may exceed maximum sustainable yields of the Gulf resource (Gulf of Mexico and South Atlantic Fishery Management Councils¹). In the United States, commercial catches of king mackerel were 2,013 metric tons (t) in 1994 (U.S. Dep. Commer., 1995). Recreational catches in the United States are thought to be larger than commercial landings (Deuel and Clark, 1968; Deuel, 1973; Manooch, 1979; U.S. Dep. Commer., 1985–1987). Recreational catches are reported as individuals rather than as weight; however, an estimated total weight of recreational catches for 1991 was 2,713 t (U.S. Dep. Commer., 1992).

Current management plans are based on a two-stock model, an Atlantic stock and a Gulf of Mexico stock (Gulf of Mexico and South Atlantic Fishery Management Councils¹). However, general consensus among scientists is that two stocks of king mackerel exist within the Gulf of Mexico. Evidence for two

stocks within the Gulf of Mexico includes fisherman observations of migration (Baughman, 1941), electrophoretic studies (Grimes et al., 1987; Johnson et al., 1994; May²), catch-per-unit-of-effort data from charter boats (Trent et al., 1987), and differences in spawning times (Grimes et al., 1990).

Stable isotopes (C, N) have been used to study trophic levels and feeding strategies of organisms (see Macko et al., 1984; Peterson and Fry, 1987; Koch et al., 1995). According to DeNiro and Epstein (1978), the carbon isotopic composition of a food source is not substantially altered during assimilation. DeNiro and Epstein (1981) found that animals also reflect the nitrogen isotopic composition of their diet; however, there is a trophic-level enrichment. Regardless of habitat, form of nitrogen excreted, and growth rate, an isotopic enrichment of +3.4

¹ Gulf of Mexico and South Atlantic Fishery Management Councils. 1992. Amendment 6 to the fishery management plan for coastal migratory pelagics in the Gulf of Mexico and South Atlantic includes environmental assessment regulatory impact review and initial regulatory flexibility analysis. Gulf Mex. S. Atl. Fish. Manage. Council, Tampa, FL, var. pagin.

² May, B. 1983. Genetic variation in king mackerel (*Scomberomorus cavalla*). Final Rep. FL Dep. Nat. Resour. Contract C-1434, 20 p.

$\pm 1.1\%$ occurs for nitrogen isotopes (Minagawa and Wada, 1984). Macko et al. (1984) also demonstrated that stepwise enrichment, which occurs from trophic level to trophic level, does not vary among locations. Finally, Minagawa and Wada (1984) suggested that individuals do not fractionate nitrogen isotopes differently at various ages.

Estep and Vigg (1985) observed that the carbon isotope discrimination between scale and muscle was consistent for a particular fish species, and stated that isotopic measurements in muscle and scales could be used to determine diet of fish. Studies that encompass time scales of months to years, however, may be compromised by fast turnover of muscle. Collagen, in contrast to muscle, has a slow turnover rate of carbon (Libby et al., 1964). Collagen amino acid composition varies only slightly among species (see Schoeninger and DeNiro, 1984); therefore, differences in collagen isotope ratios reflect isotopic changes in diet and not variations in chemical composition (Schoeninger and DeNiro, 1984). Additionally, we speculate that turnover of collagen may be slower in poikilotherms, such as fish, compared with homeotherms, such as mammals, owing to the lower metabolic rate of poikilotherms. The chemical uniformity and slow turnover time of collagen make it a suitable matrix for recording the dietary history of organisms that grow fin spines (fin spines consist of collagen fibers in a bony matrix) and live over periods of years.

In the Gulf of Mexico, Fry (1983) compared stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of several decapod crustaceans and two species of in-

shore fishes. The study revealed that groups feeding primarily in the eastern Gulf of Mexico have different $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from those feeding in the western Gulf of Mexico (Table 1). Macko et al. (1984) also reported geographical variations in isotopic ratios of sedimentary organic matter. From these studies, we hypothesized that stable carbon and nitrogen isotopes would aid in establishing group structure if 1) king mackerel feed in different regions of the Gulf of Mexico for extended periods of time, and 2) the carbon and nitrogen isotope composition of a food source is incorporated in a consistent manner into tissues of king mackerel. Dorsal fin spines were chosen for isotopic analyses because collagen has a slow turnover rate, and the isotopic ratio of the spine should reflect assimilated food at the time of formation. Therefore, the diet recorded within the spine is chiefly a record of early developmental years, when the majority of growth occurs. A previous study, however, showed a loss of the first annulus in fin spines of older swordfish (Tsimenides and Tserpes, 1989). We could find no such study of fin spine annulus of king mackerel to substantiate this loss in king mackerel. Loss of mass has not been investigated in swordfish research; therefore, we assumed that if any material is lost, it is minimal in comparison with the remaining material, because this phenomenon has been observed only in large individuals. Below, we report on the identification of two isotopically distinct groups of king mackerel in the Gulf of Mexico and compare our findings with previous studies conducted in order to determine location and number of king mackerel groups.

Table 1

Mean stable isotope (C and N) values of sediment, particulate organic matter, zooplankton, shrimp, and mackerel for Florida, Northwestern Gulf of Mexico, and Mexico. Standard error is presented when available. GOM = Gulf of Mexico. nd = no data. Florida king mackerel data comprise collection sites Panama City, FL, and Fort Pierce-Palm Beach, FL. Northwestern king mackerel data comprise collection sites Port Aransas, TX; Galveston, TX; Grand Isle, LA; and Gulf Port, MS. Mexico king mackerel data comprise collection sites Dzilam DeBravo, Celestun, and Veracruz.

Sample type	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
	Florida	Northwestern GOM	Mexico	Florida	Northwestern GOM	Mexico
Sediment ¹	-18.5 \pm 0.7	-20.6 \pm 0.6	nd	3.6 \pm 0.1	6.5 \pm 0.2	nd
Particulate organic matter ¹	-19.4 \pm 1.2	-21.0 \pm 1.4	nd	-0.9 \pm 1.4	7.5 \pm 0.8	nd
Zooplankton ¹	-18.4 \pm 1.1	-19.2 \pm 0.7	nd	5.9 \pm 0.7	8.9 \pm 0.9	nd
<i>Penaeus</i> shrimp ¹	-14.8 \pm 0.5	-15.6 \pm 1.1	nd	8.4 \pm 0.9	12.9 \pm 1.1	nd
<i>Penaeus</i> shrimp ²	-14.6	-15.9	nd	8.3	12.6	nd
King mackerel (this study)	-18.9 \pm 1.1	-18.1 \pm 0.9	-17.7 \pm 1.5	10.8 \pm 1.1	13.1 \pm 1.3	10.8 \pm 1.0

¹ Data, excluding the king mackerel data, were compiled from Fry (1983) and Macko et al. (1984).

² Data are based on estimated values from Figure 7 in Fry (1983).

Methods and materials

King mackerel were obtained from the Southeast Fisheries Center, National Marine Fisheries Service, Panama City, FL, and laboratory of John R. Gold, Department of Wildlife and Fisheries Sciences, Texas A&M University. These samples were collected within the Gulf of Mexico and Atlantic Ocean (Fig. 1) during November and December 1991; February, May, and July 1992; and March, May, and June 1993 (Table 2). Two to twenty fish were analyzed per site (average of seven per locality). Locality, date collected, fork length (standard measure of size), weight and sex of the fish specimens were recorded for most samples. According to the length-at-age study of DeVries and Grimes,³ all fish were between 1 and 19 years of age.

Stable carbon and nitrogen isotope measurements were performed on dorsal fin spines. Dorsal fin spines were extracted and frozen prior to laboratory processing. After thawing, fin spines were cleaned of epidermal and dermal tissue, soaked in a dilute solution of HClO_3^- (bleach) to remove excess tissue, and then washed thoroughly with double-distilled

water (no significant difference was observed with the dilute bleach method of cleaning and simply scraping the spine clean). Collagen was extracted according to the method of Tuross et al. (1988), who found that collagen extractions obtained with ethylenediaminetetraacetic acid (EDTA) yielded higher demineralization than those obtained with hydrochloric acid. Contamination of EDTA had been detected at less than 1 ng EDTA per mg of dry protein (Tuross et al., 1988). Spines of each individual were soaked separately in 50 mL of 0.5M EDTA, pH 7.2, at 4°C and shaken on a laboratory shaker for five days to remove mineralized bone. Mineralized bone was considered removed by evidence of a translucent, pale yellow appearance (Tuross et al., 1988). The remaining collagen was washed with dilute NaOH, rinsed thoroughly with double distilled water, and freeze-dried.

An investigation of sample preparation techniques was conducted to ensure accurate data collection. Incomplete removal of the mineral phase of the dorsal fin spine would cause erroneous ^{13}C -enriched values. In turn, poor conversion of collagen carbon to CO_2 would result in CO production and inaccurate ^{15}N -enriched values owing to $^{13}\text{C}^{16}\text{O}$, which interferes with the $^{15}\text{N}^{14}\text{N}$ signal on the mass spectrometer. These sources of contamination were most likely to occur in large samples, reflecting a relation between sample size and isotope value.

Owing to the large size of these dorsal fin spines, multiple sections were taken from all samples to ensure that the whole spine was measured isotopically. Spines were divided into approximately 3-mg sections; therefore, spines from larger mackerel had more sections than did spines from smaller mackerel. Each section of the dorsal fin spines was placed in a separate quartz tube with elemental copper and cupric oxide and sealed under vacuum. These sections were converted to CO_2 and N_2 gas with modified Dumas combustion (850°C for two hours) (Macko, 1981). The CO_2 and N_2 were then isolated cryogenically and analyzed on Finnigan MAT 251 and Nuclide 3-60-RMS isotope ratio mass spectrometers. The reproducibility of the measurements for $\delta^{13}\text{C}$ was $\pm 0.2\text{‰}$ and $\pm 0.3\text{‰}$ for N_2 . Minimum sample size was 50 μg for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

³ DeVries, D. A., and C. B. Grimes. 1991. Spatial and temporal variation in age composition and growth of king mackerel *Scomberomorus cavalla* from the southeastern U.S., 1986-1989; implications for stock structure and recruitment variability. U.S. Dep. Commer., NOAA, NMFS, 3500 Delwood Beach Rd., Panama City, FL 32408-7403. Unpubl. manuscript, 41 p.

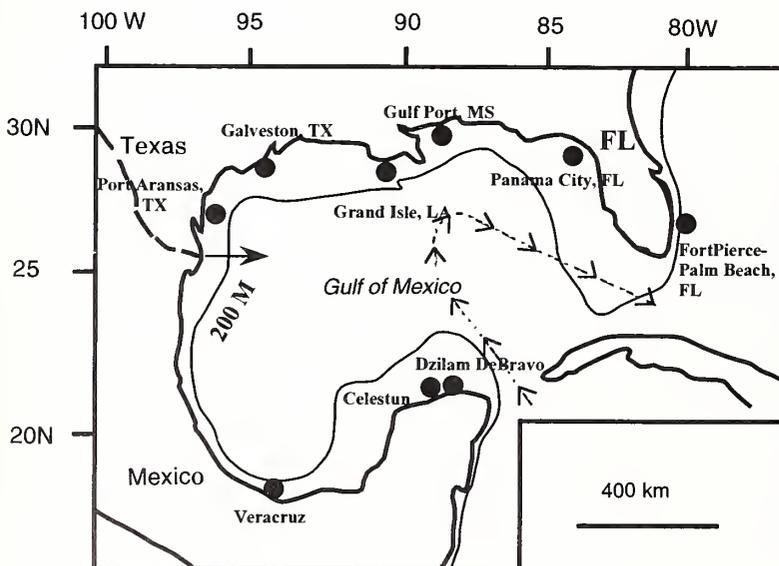


Figure 1

King mackerel study sites. Dotted line is mean position of the Loop Current. Arrow heads on the dotted line denote direction of flow. Solid arrow indicates convergence zone at Brownsville, TX.

Stable carbon and nitrogen isotope measurements were performed on 65 and 64 dorsal fin spines, respectively. Stable isotope ratios, denoted in parts per mil, were calculated in terms of δ as follows:

Table 2

Mackerel collection data and range of stable isotope (C and N) values for each dorsal spine analyzed. nd = no data.

Collection site	Sex	Fork length (cm)	Month of collection	Range of $\delta^{13}\text{C}$ (‰) for each spine	Range of $\delta^{15}\text{N}$ (‰) for each spine
Celestun, Mexico	male	91	12	4.1	0.9
Celestun, Mexico	female	81	12	1.5	0.8
Celestun, Mexico	male	78	12	2.5	0.7
Celestun, Mexico	female	76	12	3.3	4.3
Gulf Port, Mississippi	male	126	7	3.0	0.2
Gulf Port, Mississippi	female	120	7	2.1	0.9
Gulf Port, Mississippi	male	100	7	2.6	0.5
Gulf Port, Mississippi	male	117	7	2.3	0.2
Gulf Port, Mississippi	male	85	7	2.9	0.5
Gulf Port, Mississippi	female	113	7	2.5	1.1
Veracruz, Mexico	male	71	5	1.7	0.7
Veracruz, Mexico	male	68	2	3.1	0.3
Dzilam DeBravo, Mexico	unknown	73	11	3.3	0.9
Dzilam DeBravo, Mexico	unknown	51	11	0.7	1.0
Dzilam DeBravo, Mexico	unknown	54	11	1.8	0.5
Dzilam DeBravo, Mexico	unknown	71	11	2.3	0.2
Dzilam DeBravo, Mexico	unknown	78	11	1.8	1.4
Dzilam DeBravo, Mexico	unknown	70	11	1.4	3.5
Dzilam DeBravo, Mexico	unknown	64	11	0.7	nd
Dzilam DeBravo, Mexico	unknown	79	11	3.5	0.2
Dzilam DeBravo, Mexico	unknown	65	11	1.4	0.2
Dzilam DeBravo, Mexico	unknown	93	11	1.3	0.3
Dzilam DeBravo, Mexico	unknown	80	11	1.2	0.4
Dzilam DeBravo, Mexico	unknown	73	11	2.4	1.1
Dzilam DeBravo, Mexico	unknown	69	11	1.3	0.2
Dzilam DeBravo, Mexico	unknown	65	11	0.9	4.1
Dzilam DeBravo, Mexico	unknown	73	11	3.8	0.5
Dzilam DeBravo, Mexico	unknown	80	11	3.1	3.0
Dzilam DeBravo, Mexico	unknown	65	11	3.6	2.8
Dzilam DeBravo, Mexico	unknown	89	11	2.4	3.2
Dzilam DeBravo, Mexico	unknown	69	11	1.2	1.8
Dzilam DeBravo, Mexico	unknown	79	11	nd	0.9
Galveston, Texas	unknown	86	7	2.7	0.6
Galveston, Texas	unknown	70	7	2.3	0.7
Galveston, Texas	unknown	67	7	2.9	0.3
Port Aransas, Texas	unknown	81	7	3.9	0.2
Port Aransas, Texas	unknown	81	7	0.4	0.8
Port Aransas, Texas	unknown	113	7	4.3	0.5
Port Aransas, Texas	unknown	94	7	3.0	2.9
Port Aransas, Texas	unknown	75	7	3.0	1.1
Port Aransas, Texas	unknown	97	7	3.4	0.7
Port Aransas, Texas	unknown	88	7	2.2	0.6
Port Aransas, Texas	unknown	91	7	1.6	0.1
Port Aransas, Texas	unknown	121	7	5.4	1.0
Grand Isle, Louisiana	unknown	88	7	2.6	0.1
Grand Isle, Louisiana	unknown	99	7	2.5	0.9
Grand Isle, Louisiana	unknown	49	7	2.4	1.1
Grand Isle, Louisiana	unknown	74	7	1.1	0.3
Grand Isle, Louisiana	unknown	58	7	0.4	0.1
Grand Isle, Louisiana	unknown	73	7	2.7	0.2
Grand Isle, Louisiana	unknown	75	7	2.4	0.2
Grand Isle, Louisiana	unknown	96	7	4.2	0.2
Grand Isle, Louisiana	unknown	61	7	1.9	0.9
Grand Isle, Louisiana	unknown	80	7	3.1	0.4
Panama City, Florida	female	85	6	2.6	0.3
Panama City, Florida	female	80	6	2.9	0.2

Table 2 (continued)

Collection site	Sex	Fork length (cm)	Month of collection	Range of $\delta^{13}\text{C}$ (‰) for each spine	Range of $\delta^{15}\text{N}$ (‰) for each spine
Panama City, Florida	female	84	6	1.5	0.6
Panama City, Florida	female	81	6	3.0	0.6
Panama City, Florida	female	80	6	2.2	0.3
Panama City, Florida	female	90	6	2.0	0.4
Fort Pierce-Palm Beach, FL	female	102	5	2.2	0.5
Fort Pierce-Palm Beach, FL	male	100	5	3.5	0.3
Fort Pierce-Palm Beach, FL	male	87	5	3.5	0.7
Fort Pierce-Palm Beach, FL	male	71	3	1.3	nd
Fort Pierce-Palm Beach, FL	male	75	3	2.1	0.4
Fort Pierce-Palm Beach, FL	male	70	3	1.7	0.2

$$\delta X [\text{‰}] = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 10^3, \quad (1)$$

where X = the heavier isotope (either ^{13}C or ^{15}N); and R = the ratio (either $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$).

The working standard for carbon was tank CO_2 which was identified as $\delta^{13}\text{C}_{\text{PDB}} = -1.85\text{‰}$, and the standard for nitrogen was N_2 from air, which is 0‰ by definition (see Eq. 1).

Because spines were too large to measure whole, they were divided into segments that were analyzed separately, and the weighted average was calculated as

$$\frac{\sum_{n=1}^x (W_n)(\delta_n)}{\sum_{n=1}^x W_n} \quad (2)$$

where W_n = weight of the segment in milligrams;
and

δ_n = isotopic value for the segment.

Multivariate analysis of covariance (MANCOVA) was used to determine which independent variables had significant effects in the general linear models (GLM) (Eqs. 3 and 4) (SAS, 1990).

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = \text{collection site} + \text{season} + \text{sex};$$

[length was used as a covariate.] (3)

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = \text{region} + \text{season} + \text{sex};$$

[length was used as a covariate.] (4)

If an independent variable did not have a significant effect on the model, the variable was eliminated and the GLM was conducted again. Least squared means (LSmeans) and a pairwise comparison, with a 95%

confidence interval ($P=0.05$), were performed to determine significant differences in nitrogen and carbon isotope data between sample collection sites and regions. As king mackerel increased in fork length, an increase in ^{15}N was observed (Fig. 2B); therefore, analysis of covariance was used to control for differences in fish size. Fork length was used as the covariate.

Results

No significant correlation between weight of the fin spine sample segment and $\delta^{15}\text{N}$ ($r^2=0.03$) or $\delta^{13}\text{C}$ ($r^2=0.06$) was detected for any of the samples, suggesting that the mineral phase had been completely removed, and 100% collagen carbon and nitrogen as CO_2 and N_2 had been recovered, respectively.

Isotopic variations within individual spines were examined to try to determine the life history of individuals. Spines were delineated into three portions (tip, mid, and base) (Fig. 3). The base of the spine is believed to contain more recently acquired material. Isotopic trends in carbon, along the length of the spine, were observed for many sites. Isotopic values for carbon became lighter as the fish aged (from tip to base); however, few trends existed for nitrogen. In general, the isotopic difference within the spine was generally less for nitrogen compared with carbon.

Nitrogen and carbon isotopic differences were observed between various sites and regions (Table 1; Fig. 4). In the pairwise comparison, more significant differences were found between individual sites for nitrogen isotope ratios than for carbon isotopic ratios (Fig. 4). Nitrogen isotopic data displayed a geographical pattern (Fig. 5). In general, king mackerel from Mississippi, Louisiana, and Texas were ^{15}N -enriched in contrast with those from the Mexican

and Florida sites. Spines of individuals from Florida were typically ^{13}C -depleted in contrast with those from the Mexico, Mississippi, Louisiana, and Texas sites.

After the nonsignificant variable (sex) was eliminated from the GLM (Eq. 3), the season of sample collection ($P=0.0001$), fork length ($P=0.031$), and collection site ($P=0.0001$) influenced the variation in nitrogen isotope data ($F=9.27$; $P=0.0001$ for the overall model). Only collection site ($P=0.028$) significantly influenced the revised GLM (Eq. 3) for $\delta^{13}\text{C}$ ($F=2.38$; $P=0.0281$ for the overall model). A GLM was also constructed for the three regions in this study: Florida, Mexico, and northwestern Gulf of Mexico (Eq. 4). These regions were determined on the basis of previous king mackerel stock structure studies (Baughman, 1941; Trent et al., 1987; Johnson et al., 1994; May²) and isotopic patterns observed in previous studies (Fry, 1983; Macko et al., 1984) as well as in this study. The GLM (Eq. 4) for $\delta^{15}\text{N}$ ($F=26.42$; $P=0.0001$) showed that collection site ($P=0.0001$) and fork length ($P=0.0023$) were statistically significant regionally. Collection site ($P=0.023$) and fork length ($P=0.047$) also had a significant regional influence on $\delta^{13}\text{C}$ ($F=4.04$; $P=0.011$) (Eq. 4).

Discussion

Although the dorsal fin spines were divided into multiple sections, and isotopic trends were observed along a spine (Fig. 3, A and B), life history could not be determined from isotopic data because it was not possible to assign accurately an age to a particular portion of the spine. The length-at-age relation varies regionally and shows large individual variation (DeVries and Grimes³). For example, male king mackerel from the eastern Gulf of Mexico, with a fork length of 105–110 cm, ranged from 4 to 22 years of age (DeVries and Grimes³). Additionally, female king mackerel are larger than males at a given age (Beaumariage, 1973; Johnson et al., 1983; DeVries and Grimes³) and sex was not known for the majority of the fish analyzed (Table 2).

Isotopic differences within individual dorsal spines were studied. One would generally expect the king mackerel with the greater fork length to have a larger range of isotopic values within its dorsal spine owing to variation in trophic-level feeding with size; however, no clear trends were found (Table 2). For example one 113-cm-FL female king mackerel from Gulf Port, MS, exhibited little variation among the segments analyzed. The $\delta^{15}\text{N}$ varied by only 1.1 and

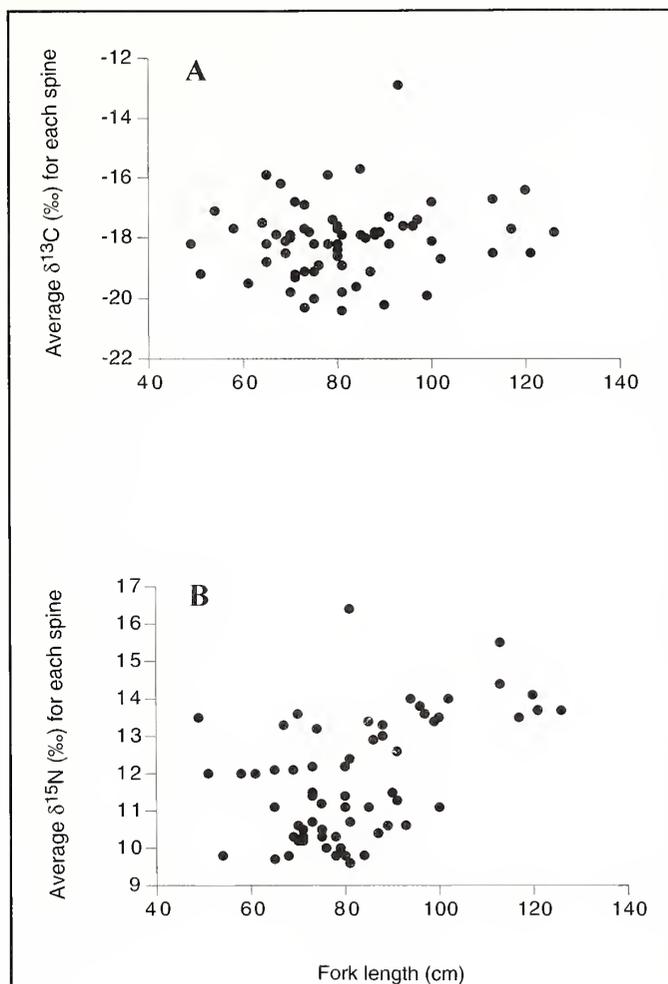


Figure 2

King mackerel fork length versus (A) stable carbon and (B) nitrogen isotopes. King mackerel fork length showed a positive relation to nitrogen isotopic values, but not to carbon isotopic values.

the isotopic ratio of carbon varied by only 2.5‰. Conversely, a 76-cm-FL female from Celestun, Mexico differed by 4.3‰ in nitrogen and 3.3‰ in carbon among the spine segments analyzed.

Additionally, an isotopic trend of an individual spine becoming heavier over time (from tip to base) would be expected because of an increase in trophic level feeding; however, this trend was not generally observed in the sites or regions for either carbon or nitrogen (Fig. 3). A greater enrichment in nitrogen, compared with carbon, would be expected for an increase in trophic level feeding (DeNiro and Epstein, 1978; DeNiro and Epstein, 1981); however this tendency was not observed. In fact, carbon isotopic trends were contradictory to this assumption, and no clear nitrogen isotopic trends could be detected

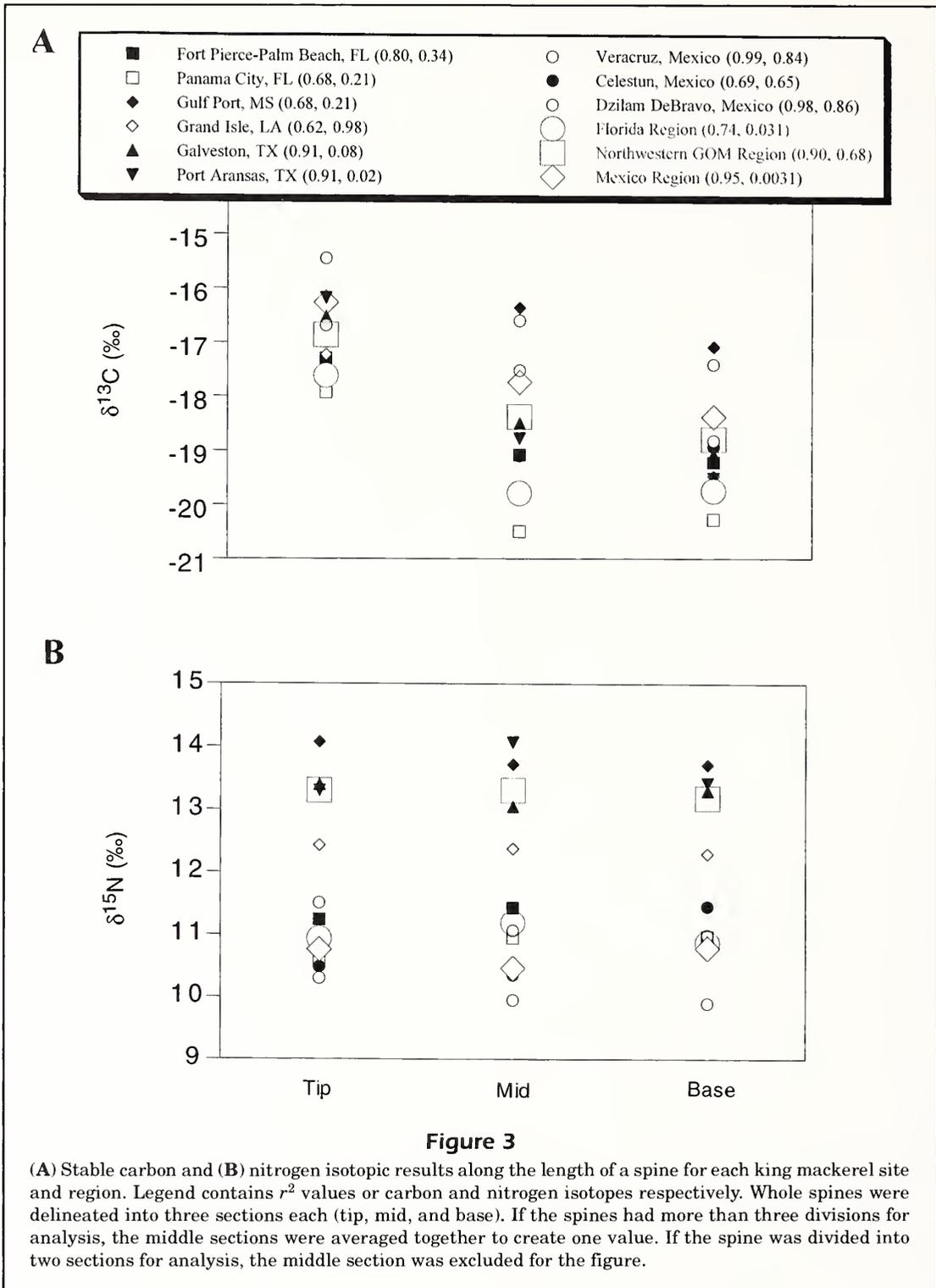


Figure 3
 (A) Stable carbon and (B) nitrogen isotopic results along the length of a spine for each king mackerel site and region. Legend contains r^2 values for carbon and nitrogen isotopes respectively. Whole spines were delineated into three sections each (tip, mid, and base). If the spines had more than three divisions for analysis, the middle sections were averaged together to create one value. If the spine was divided into two sections for analysis, the middle section was excluded for the figure.

along the individual spines for the sites or regions. The data suggest a factor other than change in trophic level determines isotopic values found within the spines. Numerous factors could influence the range and trend of isotopic values found within a dorsal spine, such as feeding region, trophic-

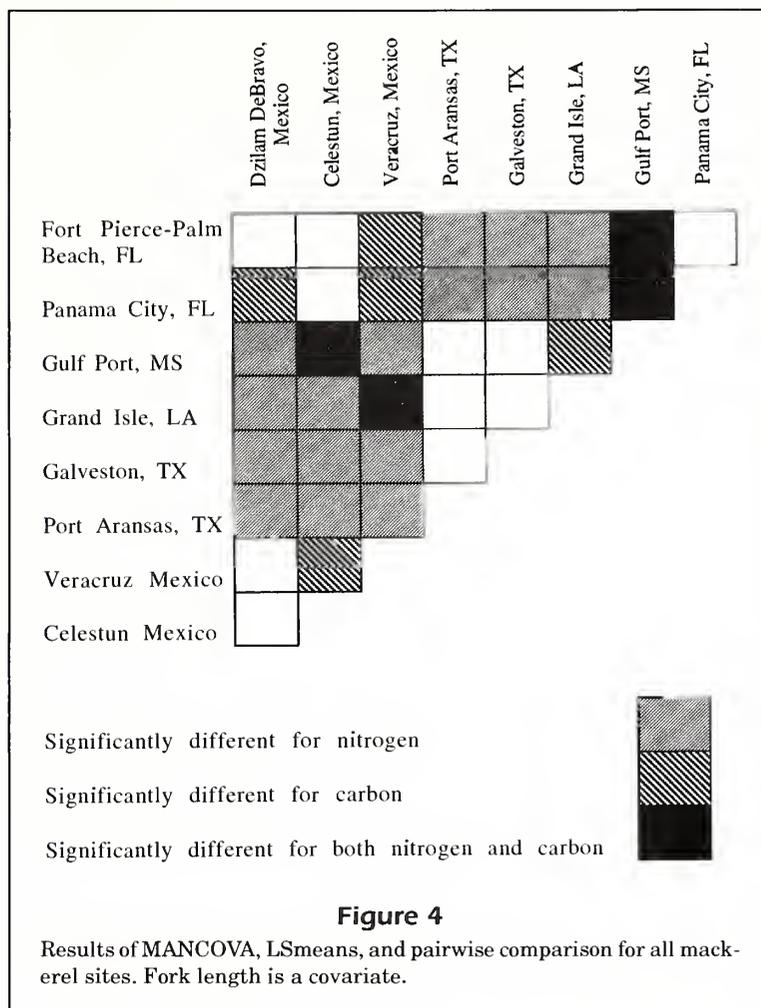
level status of the individual, and the manner in which the spine was segmented.

Stable carbon and nitrogen isotopic values at the base of the food chain vary within the Gulf of Mexico (Table 1), particularly among waters off southern Florida and the northwestern Gulf of Mexico. We

observed similar differences for mean $\delta^{15}\text{N}$ values of king mackerel spines collected in these regions. The $\delta^{15}\text{N}$ data of Macko et al. (1984), Fry (1983), and this study all showed an ^{15}N -enriched in the northwestern Gulf of Mexico relative to samples collected in Florida and Mexico. Enriched nitrogen values are often observed off the mouths of estuaries (e.g. Cifuentes et al., 1989). This enrichment often reflects the assimilation of isotopically altered inorganic nitrogen from riverine sources by algae. The influence of the Mississippi River could account for the more positive $\delta^{15}\text{N}$ values (Lopez-Veneroni⁴) detected in the northwestern Gulf of Mexico.

In contrast to the $\delta^{15}\text{N}$ data for the king mackerel, $\delta^{13}\text{C}$ measurements were not as discriminating between sites (Fig. 4) or regions (Table 1). Although not significant, the king mackerel $\delta^{13}\text{C}$ values for the northwestern Gulf of Mexico region were more negative than those for the Mexico region. More negative $\delta^{13}\text{C}$ values were also detected at the base of the food chain in the northwestern Gulf of Mexico region in comparison with those for Florida (Table 1). The influence of the Mississippi River on the northwestern Gulf of Mexico area is most likely the primary reason for $\delta^{13}\text{C}$ values being more negative. Although CO_2 depletion resulting from enhanced primary production can increase $\delta^{13}\text{C}$ values (Raven et al., 1993), the primary impact of the Mississippi River is the large terrestrial input of particulate organic matter (Trefry et al., 1994) leading to more negative $\delta^{13}\text{C}$ values.

Commonly, less variability is observed in carbon isotopes than with nitrogen. This trend was not observed in this study. Our results, however, are consistent with some previous studies that reported that $\delta^{15}\text{N}$ data could be more discriminating than $\delta^{13}\text{C}$ data. For example, Sholto-Douglas et al. (1991) used carbon and nitrogen isotopes to study food web relations among plankton and pelagic fish and found greater variability in $\delta^{13}\text{C}$ data than in $\delta^{15}\text{N}$ measurements. Perhaps these systems have numerous carbon sources that create greater than expected variation in stable carbon isotope values, thereby rendering them ineffective.



Numerous studies have observed seasonal migrations of king mackerel. King mackerel migrate along the eastern coast of the Gulf of Mexico and into the northern Gulf of Mexico from southeastern Florida (wintering grounds) in the summer (Trent et al., 1987; Sutter et al., 1991; see also Johnson et al., 1994). Migrations may extend as far as Galveston and Port Aransas, TX (Williams and Sutherland, 1978). A return migration from the northern Gulf of Mexico into southeast Florida occurs in late summer and early fall (Williams and Sutherland, 1978). While the king mackerel that winter in southeast Florida are migrating into the northern Gulf of Mexico, a simultaneous migration from the Yucatan area (wintering grounds) occurs along the western coast of the Gulf of Mexico into the northern Gulf of Mexico (Trent et al., 1987; see also Johnson et al., 1994).

Wind circulation along the Mexican and south Texas coast during the late spring and early summer may cause upwelling off the Texas-Mexico border (Dagg et al., 1991). Consequently, coastal bound-

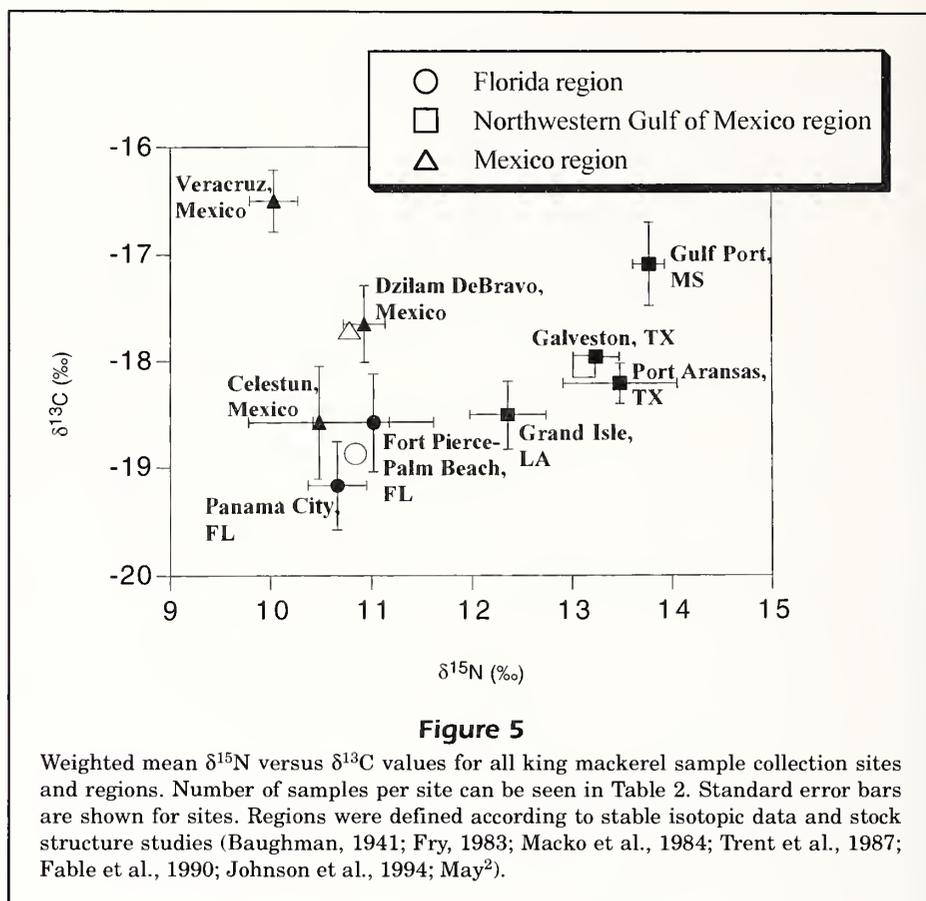
⁴ Lopez-Veneroni, D. 1997. Oceanography Department, Texas A&M University, College Station, TX 77843. Manuscript in prep.

ary water masses off Mexico and south Texas may collide and form a convergence zone that directs low-salinity waters offshore, near Brownsville, TX (Vastano⁵) (Fig. 1). This convergence zone may act as a temporary boundary between northwestern Gulf of Mexico fish and Mexico fish.

The innate migratory patterns of the king mackerel can influence the isotopic values observed in their dorsal spines. The location in which food is assimilated should directly influence the isotopic value recorded in the spine. Consequently, the area in which the individual fed, rather than collection site of the individual, would be detected in the spine. Therefore, determination of groups of king mackerel from collection site alone, may be inappropriate. In addition, regional groupings of the mackerel that were based upon isotopic data and on previous king mackerel studies may be more suitable for drawing conclusions.

Likewise, the migratory nature of king mackerel complicates the use of season of collection as a variable (Table 2). For example, the GLM (Eq. 3) indicated that the season in which the specimens were collected, fork length, and collection site influenced the nitrogen isotope results. However, when the data were divided into regions, fork length and region were the only variables that had a significant effect on the GLM (Eq. 4). Again, consideration of the data by region, as opposed to individual site, may be more appropriate, particularly because, in the former case, time of collection did not bias the isotopic findings.

Our method of using stable isotopes is a new approach in trying to determine the number and location of king mackerel groups. An advantage of isotopic analysis over that of genetics is that stable isotopes enable researchers to view significant changes in an individual, whereas genetic methods require generations to see significant variations. The disadvantage to stable isotopes is that the signal is ac-



quired only from areas in which food is assimilated, which may or may not represent the location and number of king mackerel groups. Although the number and location of king mackerel stocks have been researched previously by using genetic techniques (see below), several scenarios exist. Research by DeVries and Grimes (1991) has suggested the possibility of three stocks: a western Gulf of Mexico, an eastern Gulf of Mexico, and an Atlantic stock. From mitochondrial DNA data, Gold et al. (in press) found weak genetic differences between Atlantic and Gulf of Mexico king mackerel that implied more than one stock. Additionally, Johnson et al. (1994), using electrophoretic data, suggested the existence of two stocks, eastern and western, within the Gulf of Mexico. The idea of separate eastern and western stocks of king mackerel within the Gulf of Mexico has also been supported by Baughman (1941), May,² and Trent et al. (1987) with observational, electrophoretic, and catch results, respectively.

Our $\delta^{15}\text{N}$ data showed significant differences between king mackerel caught in Mexican and Florida waters in contrast to those collected in the northwestern Gulf of Mexico. Thus, our isotopic results suggest that at least two distinct groups exist within

⁵ Vastano, D. 1995. Oceanography Department, Texas A&M Univ., College Station, TX 77843.

the Gulf of Mexico (Fig. 5). Statistically, the Mexico and Florida regions are significantly different in carbon isotopes; however, neither region differs significantly from the northwestern Gulf of Mexico. It is conceivable that a separate Mexico and Florida group of king mackerel exists. Possibly neither site differed significantly from the northwestern Gulf of Mexico owing to individuals from both the Mexico and Florida regions being contained in the catch from the northwestern Gulf of Mexico. Recall, the northwestern Gulf of Mexico individuals were collected in the summer when migrations to the northwestern Gulf of Mexico from Florida and Mexico have been documented (Trent et al. 1987; Sutter et al. 1991). However, the similarity in nitrogen isotopic composition indicates that the Florida and Mexico regions are related.

A year-round sustained population in the northwest Gulf of Mexico would contribute to their isotopically different nitrogen values compared with Mexican and Florida fish. Other studies have surmised that Louisiana may have a resident population (Fisher, 1980; Fable et al., 1987) along a broad area from the Mississippi delta westward to regions off Texas, which are adjacent to oil rigs (Trent et al., 1983). These artificial structures may attract bait fish (Wickham et al., 1973). Northwestern Gulf of Mexico fish, being significantly ^{15}N -enriched, might be a nonmigrating or a separate group of king mackerel that feed on an isotopically enriched food source compared with king mackerel from Mexico and Florida. Alternatively, it is conceivable that the individuals are migratory and that the isotopic signal is due to assimilation of material from the northwestern Gulf of Mexico region although they are not permanent inhabitants of the region.

Physical dynamics within the Gulf of Mexico may influence mixing between sites and therefore the isotopic values in mackerel found at different sites. The primary current in the Gulf of Mexico is the Loop Current, which enters the Gulf of Mexico through the Yucatan Channel and exits through the Florida Straits (Leipper, 1970; Cooper et al., 1990) (Fig. 1). This current is formed by waters from the western, north, and south Atlantic and the Mediterranean Sea that flow into the Caribbean Sea (Koch et al., 1991). It has a mean position of 88° and 89°W and 27°N (Auer, 1987). Although the Loop Current reaches into the northern Gulf of Mexico, its influence is to the east of the Mississippi Delta. Thus, Mexican and Florida fish could be linked by the Loop Current to the extent that they consume isotopically similar food sources. In contrast, fish in the northwestern Gulf of Mexico are most likely minimally affected by the Loop Current.

Northwestern Gulf of Mexico fish may also be strongly influenced by runoff from the Mississippi River system (Dagg et al., 1991). The majority of this runoff (two thirds) is westward and contains high concentrations of dissolved nutrients in relation to the open Gulf of Mexico (Dagg et al., 1991). Dagg et al. (1991) also suggested that the Mississippi River system is the ultimate source of much of the biological productivity on the Louisiana and Texas shelf. The flow of the Mississippi River into the northwestern area influences the isotopic differences within these Gulf of Mexico sites (Lopez-Veneroni⁴). Although Gulf Port, MS, is east of the Mississippi river, specimens collected from this area could conceivably be feeding in or near the Mississippi River Plume region. Discharge from the Mississippi River is transported west along the shore (Dagg et al., 1991), and consumption of prey from this region would be heavily influenced by the Mississippi River leading to ^{15}N -enriched values found in this study. Furthermore, Dagg et al. (1991) stated that king mackerel from the northern Gulf of Mexico generally consumed prey that were estuarine dependent and are, therefore, most likely influenced by runoff.

Conclusions

Stable nitrogen isotope values of spines of king mackerel varied geographically. The northwestern Gulf of Mexico ($+13.1\text{‰}$) was isotopically distinct from the Mexican and Florida ($+10.8\text{‰}$ and $+10.8\text{‰}$) regions. We interpret these results to mean that there are, at least, two distinct groups of king mackerel within the Gulf of Mexico. Our results contrast with certain previous stock-structure assessments that distinguish only between Gulf of Mexico and Atlantic stocks. Stable carbon isotopes were able to distinguish between Mexico and Florida regions, although, not the northwestern Gulf of Mexico region. Although carbon isotopes were expected to be less variable than nitrogen, owing to the enrichment from trophic level to trophic level, they were found to be more variable within individual spines. The variability and perplexing isotopic trends within individual spines create difficulties in drawing conclusions from the data for stable carbon isotopes. In addition, fewer significant differences were detected between sites for stable carbon isotopes than for nitrogen isotopes. Stable carbon isotopes may be more useful when the isotopic discrimination among food resources is greater, which may be found when individuals also feed in coastal habitats. King mackerel, being of great commercial and recreational value, need to be managed with a clearer understanding of the number of groups

that exist. The isotopic data we have generated in conjunction with genetic research and tagging studies may be able to answer questions pertaining to location and number of king mackerel groups.

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Abstract.—Trawling was conducted in three areas of coastal Louisiana during the two inshore shrimp seasons of 1992 to evaluate the effectiveness of four industry-developed bycatch reduction devices (BRD's). Each BRD (Authement-Ledet excluder, Cameron shooter, Lake Arthur excluder, and Eymard accelerator) was towed alongside a control net 72 times; tows were equally divided between areas and seasons. The Authement-Ledet excluder, Cameron shooter, and Lake Arthur excluder BRD's caught fewer fish (-36%, -51%, and -21%, respectively), but also fewer shrimp (-18%, -16%, and -24%) than corresponding control nets. Biomass catch differences were -42%, -33%, and -21% for fish and -14%, -14%, and -17% for shrimp. The Eymard accelerator caught 26% more fish numerically, 19% less fish biomass, and more shrimp (38% in numbers, 26% in biomass) than control nets. Differences between catches obtained with BRD nets and those with control nets depended upon the organisms present in an area. Abundances and size distributions of many species differed between areas; thus BRD's may have to be selected for the area where they are intended to be used.

Effectiveness of four industry-developed bycatch reduction devices in Louisiana's inshore waters

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The inshore shrimping area of Louisiana is typically the waters landward of the barrier islands and the general Gulf of Mexico shoreline. The Louisiana inshore shrimp fishery is managed as three geographic zones (Fig. 1) and has two inshore shrimping seasons. Brown shrimp, *Penaeus aztecus*, dominate spring catches, whereas white shrimp, *P. setiferus*, dominate fall catches, although both species are caught during each season. In 1992, nearly 101 million kg of shrimp, valued at about \$389 million, were landed commercially in the Gulf of Mexico (National Marine Fisheries Service, 1993). From 1986 to 1989, 40% of the total commercial catch in Louisiana was caught inshore (Baron-Mounce et al.¹).

Although fishing gears and areas fished have varied, a survey in 1987 (Keithly and Baron-Mounce²) characterized Louisiana's commercial inshore shrimpers as follows. The average vessel size was 10.2 m for full-time shrimpers, 6.1 m for part-time shrimpers. Smaller boats tended to be constructed of fiberglass and powered by outboard motors. About 75% to 80% of the commercial inshore shrimpers partici-

pated in the fishery on a part-time basis. State law limited the size of each trawl to a headrope of 7.6 m length when two trawls were towed in inshore waters, except for Breton and Chandeleur Sounds. The inshore shrimp fleet was not highly mobile between management zones; only about 10% of the full-time shrimpers with boats in the 20–30 ft range and 2% of the part-time shrimpers fished in more than one zone during either season. The estimated inshore shrimping effort in 1987 by management zone was 18% (zone 1), 73% (zone 2), and 9% (zone 3) (Keithly and Baron-Mounce²).

The otter trawl has been the primary gear used by the inshore shrimp fishery in Louisiana (Keithly and Baron-Mounce²), although butterfly (wing) nets, cast nets, and skimmer (bay sweepers) nets have

¹ Baron-Mounce, E., W. Keithly, and K. J. Roberts. 1991. Shrimp facts. La. Sea Grant Coll. Prog., Communications Office, Louisiana State Univ., Baton Rouge, LA, 22 p.

² Keithly, W. R., Jr., and E. Baron-Mounce. 1990. An economic assessment of the Louisiana shrimp fishery. Final report to NMFS NA88WC-H-MF179. Coastal Fisheries Institute, Louisiana State Univ., Baton Rouge, LA, 129 p.



Figure 1

Map of the Louisiana coastline with locations of the three study areas and the three shrimp management zones (east-west zone boundaries are denoted by dark lines).

also been used. The minimum legal stretch mesh size at the time of the present study was 3.2 cm; however, shrimpers often use larger mesh to reduce the catch of small shrimp and nontargeted (bycatch) organisms.

Some methods that shrimpers have used to reduce bycatch have included relocating to areas of lower fish concentrations, cutting openings in nets, reducing tow speeds before haulback, and modifying nets in various ways. Heightened pressure by environmental organizations and pending legislation to reduce bycatch has furthered the development of shrimp trawls equipped with bycatch reduction devices (BRD's) to reduce the catch of nontargeted organisms. Previous research on BRD designs tested in the United States has been summarized by Watson and Taylor.³

Some of the BRD designs used successfully in other shrimp fisheries have proven ineffective in Gulf of Mexico waters. For example, a horizontal separator panel yielded a 75% reduction in bycatch but lost 30% of the shrimp (Seidel, 1975). Seidel (1975) tested six modifications of the Pacific Northwest shrimp

separator trawl, which has a vertical separator panel and several chutes for fish escapement. Shrimp losses ranged from 9.1% to 63.5%, and fish reduction ranged from 37% to 83.5%; however, the modification with the best fish reduction had a shrimp loss of 63.5%. The lowest attainable shrimp loss (6%) from a trawl with vertical separator panels of varying mesh had a 45% bycatch reduction (Watson and McVea, 1977).

The Gulf has a high diversity of bycatch species, many of which are similar in size to shrimp; shrimp, however, may represent as little as 10% of the total catch (Seidel, 1975). Prior to this study, most evaluations of BRD's in the Gulf had been conducted in offshore waters. Inshore organisms are often smaller than those caught offshore, inshore trawls and vessels are typically smaller, and trawling conditions, such as water depth and turbidity, may differ. Because of these differences, the present study was designed to determine the performance of four BRD's in inshore waters of Louisiana.

Materials and methods

Bycatch reduction devices

To gather regional expertise on trawling and BRD design, an advisory committee of shrimpers, net makers, and fishery-related agency personnel was

³ Watson, J. W., and C. W. Taylor. 1990. Research on selective shrimp trawl designs for penaeid shrimp in the United States: a review of selective shrimp trawl research in the United States since 1973. Proceedings ASMFC Fisheries Conservation Engineering Workshop, Narragansett, RI, April 1990, 21 p.

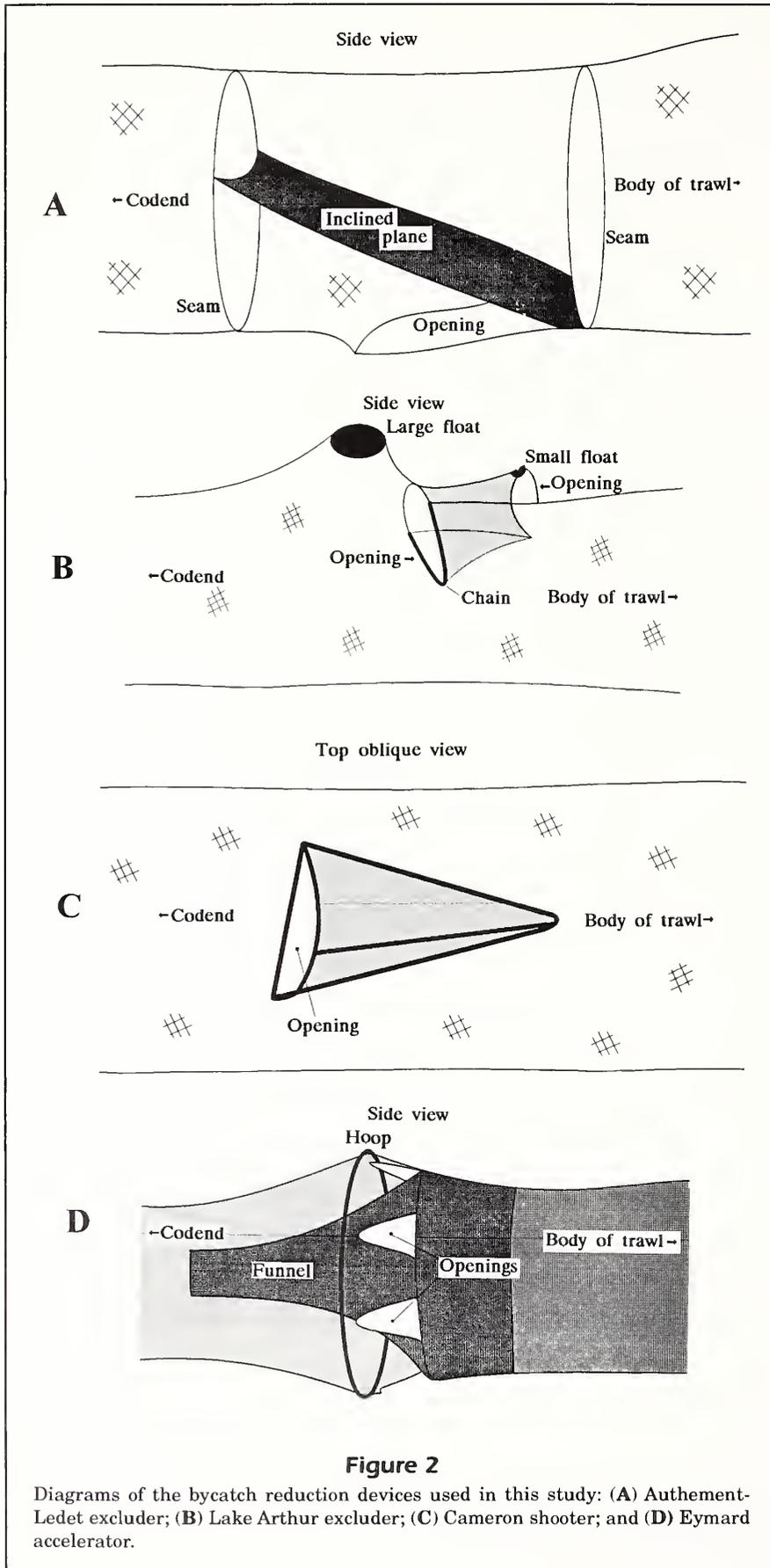


Figure 2

Diagrams of the bycatch reduction devices used in this study: (A) Authement-Ledet excluder; (B) Lake Arthur excluder; (C) Cameron shooter; and (D) Eymard accelerator.

organized. The industry committee members recommended basic trawl specifications and sampling areas. BRD's were selected from a pool of 14 industry- and NMFS-developed BRD and turtle excluder device (TED) designs suggested by members of the committee. Four industry-developed BRD designs were selected: Authement-Ledet excluder, Lake Arthur excluder, Cameron shooter, and Eymard accelerator (Fig. 2). The Cameron shooter, and very similar designs, such as the fisheye and Florida fish excluders, have had the widest use among commercial shrimpers along the U.S. Gulf of Mexico and Atlantic coasts. The other devices have been used on a limited basis in inshore and offshore waters of Louisiana, primarily in certain management zones: Eymard (zone 1), Authement-Ledet (zone 2), and Lake Arthur (zone 3).

Seven identical four-seam, nylon semiballoon trawls with 6.1-m headrope length were constructed; three were used as control nets and four were randomly selected for BRD installation. Each net had 3.5-cm stretch mesh in the body (no. 7 twine) and in the codend (no. 15 twine).

The Authement-Ledet excluder (Fig. 2A), constructed of 3.5-cm stretch mesh polyethylene webbing, was 35 meshes long and contained an inclined plane that was angled 20° from the net bottom to guide the catch upwards. The inclined plane was 18 meshes wide at the front and 30 meshes wide at the back; the back of the inclined plane was attached 18 meshes from the top seam of the trawl net. Fishes swimming forward from the codend were guided by the inclined plane to exit through the 18-mesh-wide, 40-mesh-long bottom opening.

The Lake Arthur excluder (Fig. 2B) was constructed by cutting 22 meshes across the top of the trawl

net beginning 30 meshes from the tail. A 3-mm chain was attached to the forward edge of this opening and a 10-mesh \times 12-mesh long cover was attached to the rear edge of this opening. Half of a 3.8 \times 7.6 cm float ("small float" in Fig. 2B) was attached under, and a 4.5-mm rope was threaded along, the forward edge of this cover. A 13 \times 28 cm conical float ("large float" in Fig. 2B) was attached 10 meshes behind the opening. The chain and floats created the escape opening.

The Cameron shooter (Fig. 2C) was a 30-cm wide, 45-cm long, 15-cm deep half cone of 12.7-mm aluminum round stock. A 30-mesh opening was cut in the top of the trawl net, and the forward edge of the cone was inserted into the codend, 20 meshes back from the body of the trawl. The semicircular frame opening faced the codend and protruded inside the trawl net.

The Eymard accelerator (Fig. 2D) had a polyethylene-webbing accelerator funnel, 45 meshes in diameter and 24 meshes long surrounded by six 10 \times 10 \times 10 mesh triangular openings. A 60-cm hoop of rubber coated cable was attached to pull the trawl net away from the funnel after initial dive tests indicated that the funnel blocked the escape openings.

Personnel from the National Marine Fisheries Service (NMFS) Harvesting Systems Branch examined the trawls several times by using scuba equipment, and adjustments were made to the trawl rigging and the BRD's. Dye was injected into various parts of the nets around the devices to observe water flow, and the behavior of escaping fish was documented.

Sampling

A 6.7-m Boston whaler, powered by twin 115-hp outboard motors and equipped with a single-drum winch and double boom, was used to tow twin trawls off the stern (Harrington et al., 1988); one trawl contained a BRD, the other a bare control net. The nets were equipped with tickler chains, connected to an aluminum dummy door, and spread by two 0.6 \times 1.07 m pinewood trawl doors. Although twin trawls are not typically towed behind commercial vessels in Louisiana, the use of twin trawls to replace single large trawls off outriggers is increasing, particularly in the Gulf of Mexico (Watson et al., 1984). Smaller inshore vessels in Louisiana, without outriggers, typically tow a single larger net behind the boat. Our twin-trawl rigging configuration was approved by the committee to ensure that the nets sampled an area as closely as possible, given the patchy nature of many species. Nets were towed for 20 minutes (time at towing speed); the speed over ground was maintained between 2.0 and 2.5 knots (2.2 kn, average)

by using a Global Positioning System, as recommended by the committee. Tows were made during daylight hours, near commercial shrimp boats whenever possible. Average water depth and the salinity were recorded for each trawl tow.

The four BRD's were evaluated in each inshore shrimp zone (Fig. 1). Eighteen two-day sampling trips were made, three trips to each area during each season. Each BRD net was towed 72 times over the year. Tows were divided among the areas and seasons. The towing order and trawl side for each BRD were initially selected randomly, although the same nets were not used on consecutive tows owing to the time taken to empty the nets. The three control nets were numbered and alternated to ensure equal pairing with a particular BRD net throughout the study. Sampling was conducted during the 1992 inshore shrimp seasons, although the short spring season necessitated sampling the week before the season opened in zone 1 and a few days after the season in zone 3. This schedule was approved by the advisory committee.

Samples were tagged and placed in mesh bags in ice and water. In the laboratory, organisms in each sample were identified, counted, and the biomass of each species in a sample was weighed to the nearest 0.1 g. When numerous, individuals of a species within a sample were subsampled and the total number estimated by weight. Standard lengths of most fishes, carapace widths of crabs, and total lengths of penaeid shrimp were measured. Organisms were measured in 5-mm length increments, designated by the lower end of the length range (e.g. 10-mm class=10.0 to 14.9 mm).

Statistical analysis

Residuals were examined for univariate normality and homogeneity of variances prior to accepting the analysis of variance model. Normality was tested with the Wilk-Shapiro test, and a modified Levene test was used to test for homogeneity of variances. These tests indicated that the raw data were not distributed normally and variances were not homogeneous. The transformation $\ln(\text{catch}+1)$ was used to create a new variable that met the criteria of being approximately normally distributed with homogeneous variances. This transformed variable was used in the analysis of variance (ANOVA). Statistical analysis was performed by using the Statistical Analysis System (SAS).

Control nets The transformed catch (both numbers and biomass of abundant species) of the three control nets was used as the dependent variable in an ANOVA with season, area, and season-by-area terms

and with the interaction of these terms with the control net number, with tow as the experimental unit. Length-frequency distributions of abundant organisms collected by the control nets in each area were visually examined.

BRD's versus control nets Catches of shrimp, fish, and the nine most abundant species were analyzed. An ANOVA model was used to compare the difference between control and BRD net catches between areas and seasons. ANOVA was also used to detect differences caused by towing a BRD on the port or starboard side of the twin trawl.

The number of individuals and biomass of each species (or group) caught in a BRD net was compared with the number caught by the control net by using a univariate paired *t*-test. The univariate procedure is appropriate if one can assume that the probability of one species being retained within the net is independent of another species being retained. The short tow duration contributes to the chance that this assumption is valid. Paired *t*-tests were conducted on untransformed and log-transformed differences between BRD- and control-net catches. Percent catch differences of untransformed data were calculated to compare device nets:

$$\text{Percentage catch difference} = \frac{\text{Device net} - \text{Control net}}{\text{Control net}} \times 100.$$

Percent catch difference values could range from -100 to infinity.

Differences between areas and seasons

A univariate paired *t*-test was also used to compare differences between a BRD net and the control net within each area. This test had less power because the sample size was reduced by two-thirds and because the test was not able to detect as small a difference as the test with the areas combined. A similar analysis was conducted to examine device performance in each season.

For all analyses, differences between means with an alpha of 0.05 or less were considered significant. However, the exact probabilities are presented in the tables.

Results

Control nets

The control nets collected 88 species of fishes and invertebrates; fewer species were collected in the spring than in the fall in all areas (Table 1). More than 64% of the 84,919 organisms collected in the control nets were caught during the spring. Nine species represented nearly 89% of the total control-net catch. Bay anchovy, white shrimp, and hardhead catfish catches were higher in the fall, but the other

Table 1

Numbers of most abundant organisms collected in the control nets in inshore waters of Louisiana during the spring and fall of 1992.

Species	Spring				Fall				Combined total
	Area				Area				
	Borgne	Barre	Calcasieu	Total	Borgne	Barre	Calcasieu	Total	
Brown shrimp <i>Penaeus aztecus</i>	2,842	5,375	10,593	18,810	400	481	245	1,126	19,936
Atlantic croaker <i>Micropogonias undulatus</i>	597	8,346	5,162	14,105	240	207	2,015	2,462	16,567
Bay anchovy <i>Anchoa mitchilli</i>	712	976	1,106	2,794	1,011	2,387	2,166	5,564	8,358
White shrimp <i>Penaeus setiferus</i>	47	51	732	830	1,954	3,425	1,752	7,131	7,961
Hardhead catfish <i>Arius felis</i>	423	363	2,638	3,424	1,087	1,432	1,864	4,383	7,807
Spot <i>Leiostomus xanthurus</i>	846	2,059	1,603	4,508	180	161	339	680	5,188
Sand seatrout <i>Cynoscion arenarius</i>	353	196	2,097	2,646	153	689	408	1,250	3,896
Blue crab <i>Callinectes sapidus</i>	149	1,610	154	1,913	111	907	13	1,031	2,944
Gulf menhaden <i>Brevoortia patronus</i>	86	278	1,533	1,897	54	68	623	745	2,642
Other species	273	2,108	1,152	3,533	1,263	2,273	2,551	6,087	9,620
Total	6,328	21,362	26,770	54,460	6,453	12,030	11,976	30,459	84,919
Number of species	38	51	53	66	47	65	57	82	88

six species were much more abundant in the spring. The catches from Lake Borgne were typically much smaller than catches from the other areas. Brown shrimp, hardhead catfish, sand seatrout, and gulf menhaden were most abundant in Calcasieu Lake, whereas Atlantic croaker and blue crab were most abundant in Lake Barre. Penaeid shrimp constituted 36% of the catch in the spring and 27% of the catch in the fall.

The numbers of organisms collected by the three control nets did not differ significantly. Control-net catches did not differ significantly with respect to the excluder with which they were paired. Length-frequency distributions of the abundant species differed between areas (Fig. 3).

The side of the trawl on which the control or BRD net was towed did not significantly affect catches of the abundant species. Each BRD was towed equally on each side of the twin trawl.

BRD's versus control nets

Fish All BRD nets had significantly different catches of fish from those of the control nets. Numerically, the Cameron BRD had the highest overall reduction of fish (-51%) compared with the catch of the control nets (Table 2). The Eymard BRD caught 26% more fish than the control nets. In terms of biomass, the Authement-Ledet BRD had the highest reduction (-42%), and the Eymard BRD had a 19% lower catch than the control nets.

The Authement-Ledet, Lake Arthur, and Cameron BRD nets caught fewer fish than the control nets in

all size categories (Fig. 4). The Cameron BRD, in particular, had the highest reduction of small fish (≤ 75 mm). The Eymard BRD caught more small fish (≤ 85 mm) and fewer large fish than the control net.

The Cameron BRD had the best reduction in numbers of Atlantic croaker (49%), and the Authement-Ledet the best reduction in biomass (39%) (Table 3). The Authement-Ledet and Eymard BRD's caught 50% or fewer spot in terms of numbers and biomass; in contrast, the Cameron had very poor reductions for spot. Both the Cameron and Authement-Ledet BRD's caught 50% or fewer hardhead catfish than the control nets. The Cameron BRD caught 75% fewer bay anchovy than the control net, and the Authement-Ledet and Lake Arthur reduced bay anchovy by 37%. For most bycatch species, the Eymard BRD caught more than the control nets, although catches of the bay anchovy were markedly higher (83% numbers, 86% biomass).

Shrimp The catch of shrimp with all BRD nets differed significantly from the control net catch. The Cameron, Authement-Ledet, and Lake Arthur BRD's caught fewer shrimp than the control nets; shrimp catch with the Eymard was higher (38% numbers, 25% biomass) (Table 2). Numerically, the Cameron BRD had 16% fewer shrimp, and both the Cameron and Authement-Ledet had 14% lower shrimp biomass than the control nets.

Most of the catch difference between the BRD nets and corresponding control nets appeared to be smaller (≤ 85 -90 mm) shrimp (Fig. 5). Catch differ-

Table 2

Comparison of numbers and biomass of fish and shrimp collected in bycatch reduction nets and corresponding control nets in selected inshore waters of Louisiana in 1992. SD is the standard deviation of the difference. Significance levels are 0.01 (***) and 0.05 (*). $n=72$. Superscripted letters denote significance levels of paired t -tests on log-transformed data: 0.01 (^a). BRD = bycatch reduction device.

Type of catch and BRD	Numbers					Biomass (g)				
	Mean catch/tow		Percent catch difference	SD	$P>t$ -value	Mean catch/tow		Percent catch difference	SD	$P>t$ -value
	Control	Device				Control	Device			
Fish										
Authement-Ledet	170.5	109.0	-36	102.6	0.01*** ^a	2,541.8	1,464.1	-42	1,363.1	0.01*** ^a
Lake Arthur	171.4	134.7	-21	124.9	0.01*** ^a	2,904.4	2,282.6	-21	1,616.5	0.01*** ^a
Cameron	181.7	88.3	-51	109.8	0.01*** ^a	3,068.5	2,068.1	-33	1,233.3	0.01*** ^a
Eymard	190.4	239.7	26	167.6	0.01*** ^a	2,980.3	2,406.3	-19	2,059.8	0.02** ^a
Shrimp										
Authement-Ledet	84.8	69.3	-18	58.1	0.03** ^a	483.1	417.5	-14	240.7	0.02*
Lake Arthur	93.2	70.9	-24	57.5	0.01*** ^a	514.0	425.0	-17	218.1	0.01*** ^a
Cameron	110.9	93.0	-16	77.7	0.05** ^a	579.3	500.3	-14	220.5	0.01*** ^a
Eymard	98.9	136.4	38	97.4	0.01*** ^a	517.2	645.3	25	340.1	0.01*** ^a

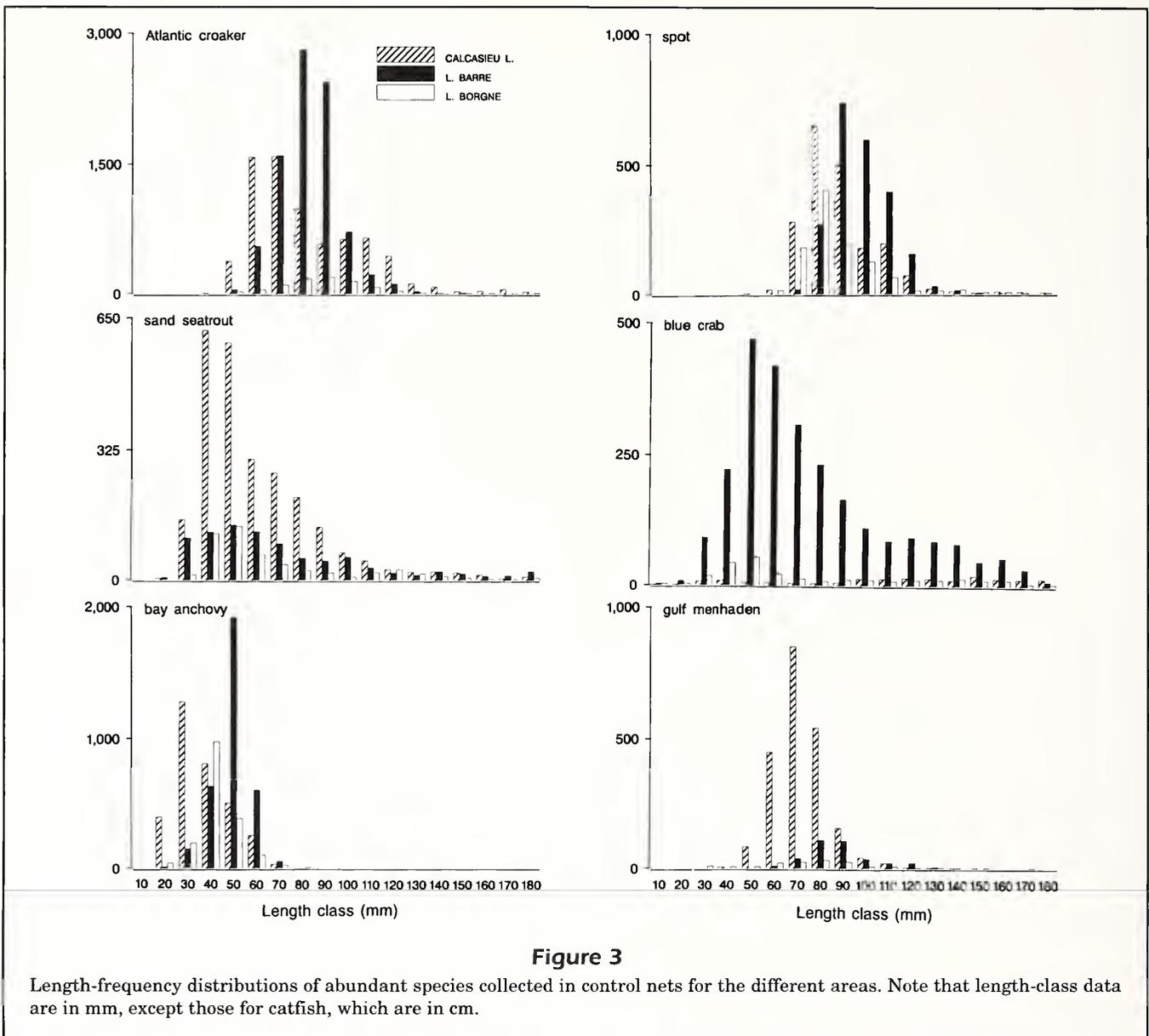


Figure 3

Length-frequency distributions of abundant species collected in control nets for the different areas. Note that length-class data are in mm, except those for catfish, which are in cm.

ences of brown shrimp and white shrimp differed for the BRD's (Table 3); fewer brown shrimp tended to be caught with the BRD nets.

Differences between areas and seasons

Although the Authement-Ledet BRD caught 18% fewer shrimp than the control nets overall, losses in Lake Barre were low and statistically nonsignificant (Table 4). Fish reduction was consistent across the areas for this BRD. The Lake Arthur BRD had a fairly consistent reduction of shrimp and fish across all areas but had the lowest shrimp catch difference in Lake Borgne and had poorer fish reductions in Calcasieu Lake. The Cameron BRD had the highest

fish reduction in Lake Borgne; however, this was accompanied by the highest shrimp loss. This BRD lost the fewest shrimp in Lake Barre. The Eymard BRD caught more shrimp than the control net in all areas and reduced fish biomass in all areas, by as much as 35% in Lake Borgne.

Mean water depths and salinities differed between Lake Borgne and the other two areas. Lake Borgne (2.7 ± 0.64 m) was slightly deeper than Lake Barre (1.9 ± 0.34 m) and Calcasieu Lake (1.5 ± 0.27 m). Mean salinities during sampling were $9.6 \pm 2.9\text{‰}$ (Lake Borgne), $22.5 \pm 2.8\text{‰}$ (Lake Barre), and $20.6 \pm 5.2\text{‰}$ (Calcasieu Lake).

There were some slight differences in BRD performance between seasons (Table 5), reflecting differ-

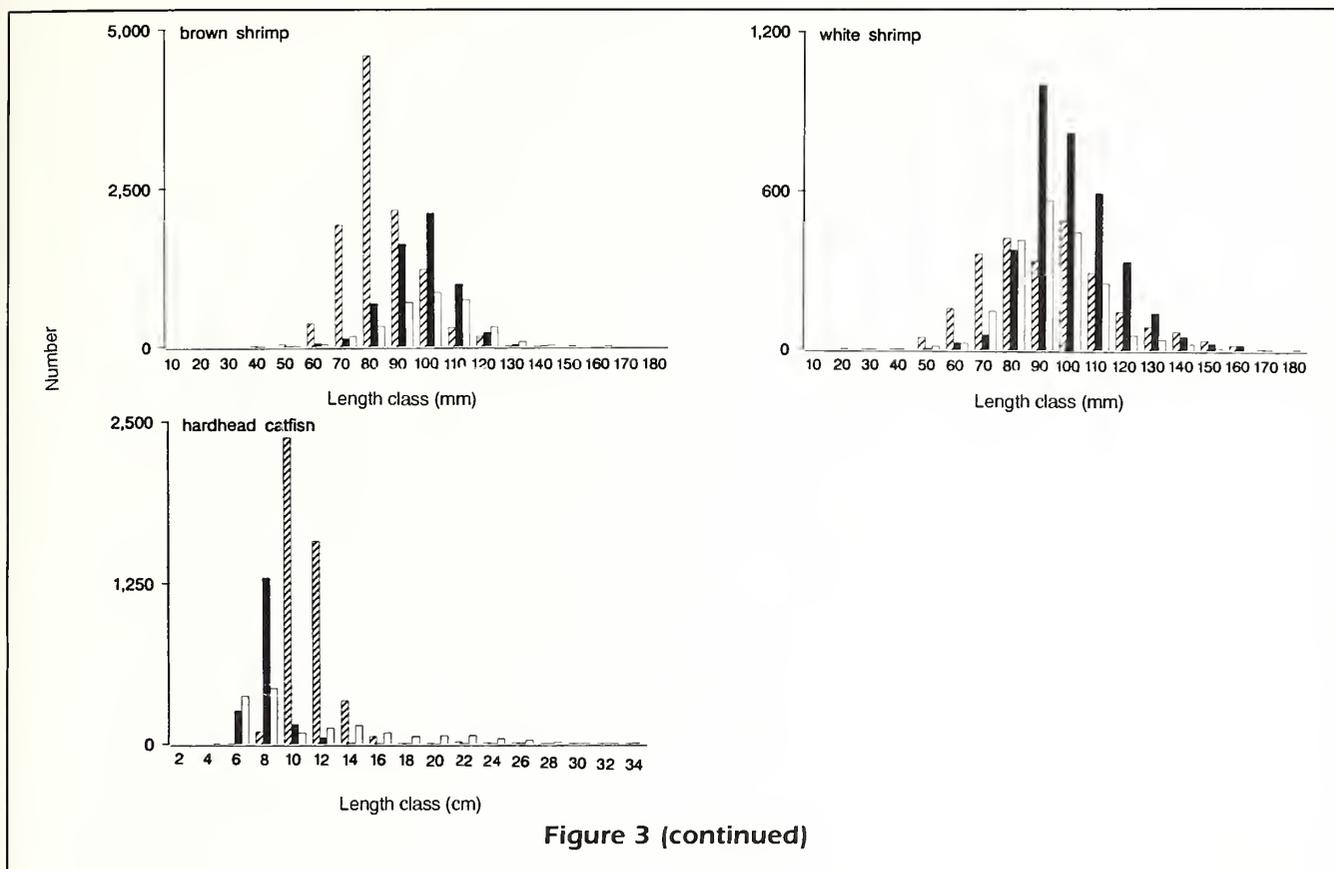


Figure 3 (continued)

ences in species composition and length-frequency distributions.

Discussion

The Authement-Ledet, Lake Arthur, and Cameron BRD's significantly reduced bycatch, but also the catch of shrimp. Excluded shrimp were primarily in the smaller size classes. The Eymard BRD caught significantly more fish and shrimp than the corresponding control nets.

The Lake Arthur and Cameron BRD's were designed with a similar opening, but the Lake Arthur BRD did not release as many fish. Because the weight of the aluminum frame of the Cameron BRD caused the device to sink slightly, the bottom of the Cameron opening was only about 15 cm from the bottom of the trawl net. In contrast, the floats of the Lake Arthur BRD raised the opening to about 30 cm above the trawl bottom. A design somewhat similar to the Lake Arthur BRD and placed 1.7 m from the end of the net did not significantly reduce bycatch in inshore waters of Alabama (Wallace and Robinson, 1994).

Reductions with the Cameron BRD (16% shrimp, 51% fish) were similar to those found by Watson et

al. (1993) for the fisheye top position excluder in offshore waters (17% shrimp, 70% fish). Inshore fish are typically smaller and less able to escape by swimming; this may account for the lower reductions with the Cameron BRD. This BRD also released shrimp of most size classes; Watson and McVea (1977) found that the fish escape device, a somewhat similar device, also lost shrimp over the entire size range. Changing the location of the Cameron shooter may affect performance, although Watson et al. (1993) noted that the top position appeared to have the best effectiveness for fish reduction and shrimp retention. A bottom-mounted Florida fish shooter, placed 1.7 m from the end of a 4.9-m trawl, reduced bycatch 26% by weight and 46% by number and caught 14% fewer shrimp than an unmodified net (Wallace and Robinson, 1994). McKenna and Monaghan⁴ reported that the efficiency of the Florida fish excluder depended on the size of the escape opening, placement of the excluder in the net, and the number of devices installed.

⁴ McKenna, A., and J. P. Monaghan Jr. 1993. Gear development to reduce bycatch in the North Carolina trawl fisheries. Completion report to Gulf and South Atlantic Fisheries Development Foundation Cooperative Agreement No. NA90AA-H-SK052. North Carolina Div. Mar. Fish., Morehead City, NC, 79 p.

The Eymard BRD was developed to reduce the catch of larger hardhead catfish, particularly in Louisiana waters east of the Mississippi River. Hardhead catfish reductions were 6% in terms of numbers, but 51% in biomass, resulting from the loss of larger catfish. Overall, the Eymard BRD caught 26% more fish, but fish biomass was 19% less than that caught by the control net. This finding was the result of the BRD catching more fish smaller than 80 mm and fewer large fish than the control nets. The Eymard BRD caught significantly more numbers and bio-

mass of shrimp, particularly smaller shrimp. The Eymard BRD design contained a webbing funnel, designed to carry shrimp and fish into the codend with accelerating water flow (Watson⁵). Because swimming speed of a fish is a function of size (Blaxter and Dickson, 1958), smaller fishes may not be able to swim in increased water flow, with the result that fewer shrimp and small fish can escape from the Eymard BRD than from a control net. However, dye released into the Eymard indicated that the water flow was not perceptibly increased by the funnel,

probably because the funnel diameter was only slightly smaller than the net diameter. However, the Eymard BRD had a 21.6-cm greater net spread than that of the control net; this greater net opening may have resulted in the higher catches of many species. Because the nets were otherwise constructed identically, we suspect this difference was most likely due to the presence of the hoop. The polyethylene webbing may have increased the incidence of anchovy being gilled, particularly during haul-back. Numerous small bay anchovies were found, upon retrieval, to be gilled in the polyethylene webbing of the Eymard BRD, and the device caught 83% more bay anchovy than the control net. In a subsequent study, a polyethylene net caught 245% more anchovies than a nylon net (Rogers et al.⁶).

Fish were observed escaping from several of the BRD's during diver evaluations in Florida. Divers observed several large juvenile pinfish (*Lagodon rhomboides*) escaping from the bottom openings of the Eymard BRD and numerous juvenile pinfish escaping the Authement-Ledet BRD

⁵ Watson, J. W. 1988. Fish behaviour and trawl design: potential for selective trawl development. In S. G. Fox and J. Huntington (eds.), Proceedings of the world symposium on fishing gear and fishing vessel design, p. 25-29. Newfoundland and Labrador Institute of Fisheries and Marine Technology, St. John's, Newfoundland.

⁶ Rogers, D. R., B. D. Rogers, J. A. de Silva, and V. L. Wright. 1994. Evaluation of shrimp trawls designed to reduce bycatch in inshore waters of Louisiana. School of Forestry, Wildlife, and Fisheries, Louisiana State Univ. Agricultural Center. Final report submitted to NMFS, St. Petersburg, FL. NOAA Award No. NA17FF0375-01, 230 p. Available from LSU library.

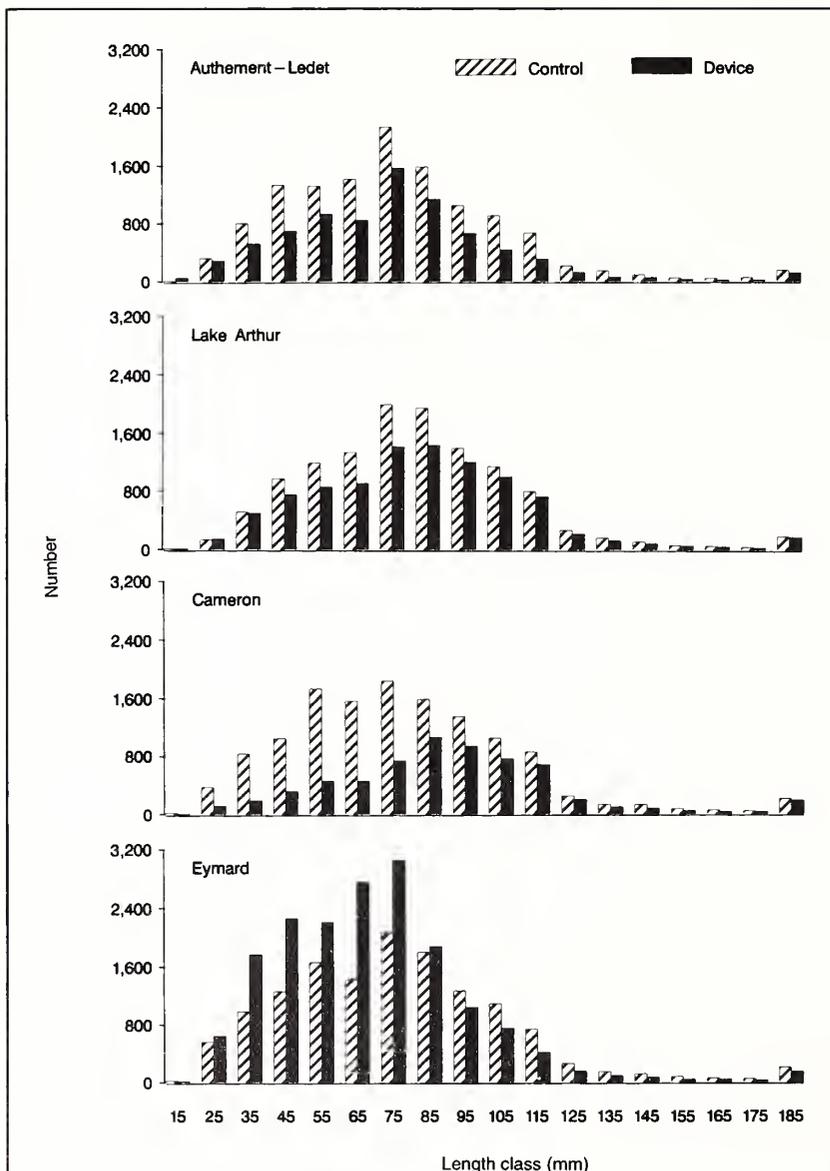


Figure 4

Length-frequency distribution of fish collected by the four devices and corresponding control nets. The 185-mm category includes all individuals greater than or equal to 180 mm.

Table 3

Comparison of numbers and biomass of the most abundant species collected in bycatch reduction device (BRD) nets and corresponding control nets. SD is the standard deviation of the difference. Significance levels are 0.01 (***) and 0.05 (*). $n=72$. Superscripted letters denote significance levels of paired t -tests on log-transformed data: 0.01 (^a), 0.05 (^b).

Species and BRD	Numbers					Biomass (g)				
	Mean catch/tow		Percent catch difference	SD	$P>t$ -value	Mean catch/tow		Percent catch difference	SD	$P>t$ -value
	Control	BRD				Control	BRD			
Atlantic croaker										
Authement-Ledet	58.0	38.0	-34	67.9	0.01*** ^a	832.9	509.8	-39	711.1	0.01**
Lake Arthur	56.8	41.6	-27	63.4	0.05** ^b	783.6	627.8	-20	450.9	0.01*** ^a
Cameron	58.5	29.6	-49	64.8	0.01***	859.8	570.2	-34	524.7	0.01***
Eymard	56.9	83.6	47	117.6	0.06 ^b	789.7	871.3	10	907.3	0.45
Spot										
Authement-Ledet	12.2	5.6	-54	12.4	0.01*** ^a	294.4	110.7	-62	318.0	0.01*** ^a
Lake Arthur	25.3	15.2	-40	52.3	0.10	575.5	372.7	-35	1,121.1	0.13
Cameron	12.0	9.8	-18	6.7	0.01***	322.5	269.4	-16	221.4	0.05*
Eymard	22.6	11.2	-50	49.4	0.05** ^a	562.0	234.0	-58	1,137.9	0.02** ^a
Sand seatrout										
Authement-Ledet	14.1	8.8	-38	26.3	0.09 ^b	101.0	63.5	-37	114.9	0.01**
Lake Arthur	9.8	8.5	-13	9.6	0.27	132.1	110.5	-16	138.8	0.19
Cameron	13.3	4.8	-64	14.5	0.01*** ^a	119.8	69.5	-42	105.5	0.01*** ^a
Eymard	17.0	20.1	19	21.7	0.22 ^b	165.5	160.1	-3	209.1	0.83
Hardhead catfish										
Authement-Ledet	22.3	11.0	-51	24.0	0.01*** ^a	625.5	244.9	-61	596.6	0.01*** ^a
Lake Arthur	26.2	20.8	-21	31.2	0.14 ^a	729.6	548.4	-25	380.4	0.01*** ^a
Cameron	35.3	14.4	-59	61.7	0.01*** ^a	960.0	549.1	-43	784.2	0.01*** ^a
Eymard	24.6	23.2	-6	51.3	0.82	802.0	393.7	-51	1,045.0	0.01**
Bay anchovy										
Authement-Ledet	29.3	18.3	-37	34.6	0.01**	40.1	22.1	-45	45.1	0.01*** ^b
Lake Arthur	23.3	14.7	-37	30.2	0.02** ^b	35.3	25.0	-29	49.3	0.08 ^b
Cameron	27.8	7.0	-75	31.2	0.01*** ^a	36.7	9.5	-74	41.8	0.01*** ^a
Eymard	35.8	65.4	83	67.4	0.01*** ^a	43.4	80.8	86	79.8	0.01*** ^a
Gulf menhaden										
Authement-Ledet	12.8	10.0	-22	18.5	0.20	135.2	110.8	-18	170.0	0.23
Lake Arthur	7.8	8.5	9	14.2	0.67	96.0	106.7	11	161.7	0.57
Cameron	7.6	7.1	-7	12.5	0.71	82.1	82.0	0	126.3	0.99
Eymard	8.5	12.1	42	22.8	0.19	96.0	109.7	14	173.0	0.50
Blue crab										
Authement-Ledet	9.9	9.0	-9	6.9	0.25	430.3	352.1	-18	353.3	0.06
Lake Arthur	9.0	6.4	-28	7.6	0.01**	378.6	295.9	-22	326.0	0.03*
Cameron	11.4	9.3	-19	15.8	0.24	571.0	457.2	-20	888.7	0.28
Eymard	10.5	9.3	-12	6.3	0.09	574.4	410.0	-29	647.9	0.03*
Brown shrimp										
Authement-Ledet	60.0	46.7	-22	52.0	0.03** ^b	332.4	270.7	-19	197.7	0.01**
Lake Arthur	64.3	48.2	-25	54.6	0.01*** ^a	333.8	268.8	-19	181.7	0.01*** ^b
Cameron	78.5	64.0	-19	72.4	0.09	375.6	315.6	-16	170.2	0.01**
Eymard	73.4	99.1	35	85.8	0.01**	356.3	438.6	23	273.4	0.01**
White shrimp										
Authement-Ledet	24.6	22.3	-9	22.9	0.40	150.3	146.3	-3	116.5	0.77
Lake Arthur	28.7	22.7	-21	20.9	0.02** ^a	179.6	156.2	-13	137.4	0.15 ^a
Cameron	32.0	28.8	-10	24.6	0.28	202.9	184.5	-9	124.1	0.21
Eymard	25.4	37.0	46	47.5	0.04** ^b	160.8	206.2	28	209.1	0.07

opening while the nets were being towed. Few fish were observed escaping from the Cameron and Lake Arthur BRD openings during these tests.

Although each BRD net contained escape openings, smaller species, such as the bay anchovy, could have escaped through the codend meshes. The devices may

have affected escape rates through the meshes by altering the shape of the codend. The percentage of fish and shrimp that escaped during trawling, as opposed to escaping during haulback, is also unknown. Watson et al. (1993) reported that most species escaped through escape openings during trawl haulback or when fish were crowded near the openings. Further diver evaluations are necessary to identify methods by which fish and shrimp escape.

Differences in catch rates of brown and white shrimp observed for many of the BRD's may have been due to species-specific behavior or size differ-

ences (or both). White shrimp swim more actively than brown shrimp during the day (Wickham and Minkler, 1975). The white shrimp caught by the control nets were larger, on average, than the brown shrimp, a finding that is typical for Louisiana catches (Keithly and Baron-Mounce²). In addition, the white shrimp caught in the spring were substantially larger than those in the fall.

These data are derived from a fishery-independent study; results from commercial shrimping could differ. Had the Eymard BRD been used in a larger trawl and without a hoop, the results might have been quite

different. Many fish and shrimp may have been lost during haulback and although we had mechanical retrieval, a larger commercial vessel may have had faster retrieval. Although we trawled near shrimp boats whenever possible, at times no shrimp boats were present in a sampling area. When this was the case, we began trawling in an area where shrimp had been caught previously; if few or no shrimp were caught, we moved to another area. Moving short distances (one or two km) could result in very different catches. Because of time and fuel limitations, however, movements of very long distances were not feasible. Provided that shrimp were being caught, we did not relocate if large quantities of fishes or crabs were also present. In this situation, a shrimper would most likely relocate in an attempt to find more shrimp or cease shrimping until conditions in the area become more favorable. We found higher ratios of fish to shrimp when shrimp catches were low. Other studies have reported that bycatch ratios depend on shrimp abundance; when few shrimp are present, fishing times are longer and result in high catches of bycatch species (Adkins⁷). The 20-minute tows used in our study were three to six times shorter than those typically used in commercial operations. Longer tows would have necessitated decreasing the number of

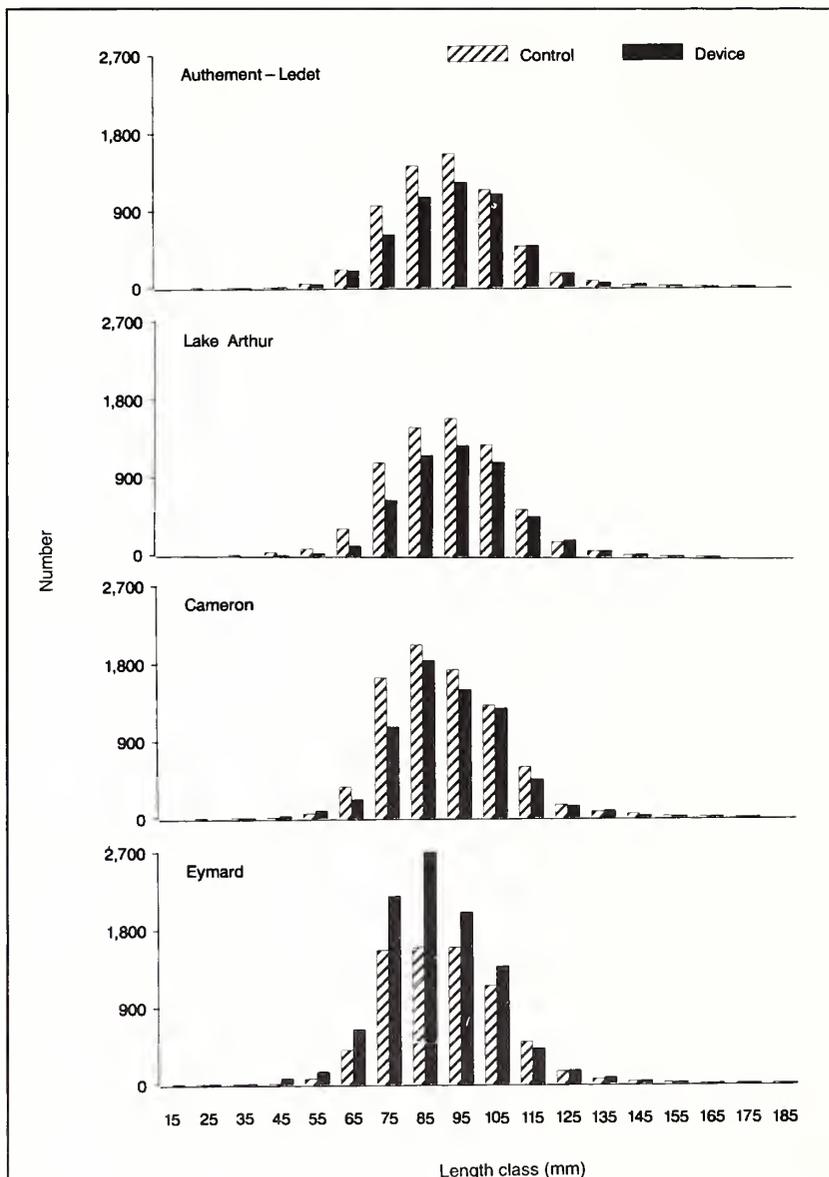


Figure 5

Length-frequency distribution of shrimp collected by the four devices and corresponding control nets.

⁷ Adkins, G. 1989. A comprehensive assessment of bycatch in the Louisiana shrimp fishery. Final report to NMFS NA89WC-H-MF006. La. Dep. Wildlife Fish., Bourg, LA, 75 p.

Table 4

Comparisons of numbers and biomass of fish and shrimp collected by the four bycatch reduction device (BRD) nets and corresponding control nets in the three areas. SD is the standard deviation of the difference. Significance levels are 0.01 (***) and 0.05 (*). $n=24$. Superscripted letters denote significance levels of paired t -tests on log-transformed data: 0.01 (^a), 0.05 (^b).

BRD and type of catch	Area	Numbers					Biomass (g)				
		Mean catch/tow		Percent catch difference	SD	$P>t$ -value	Mean catch/tow		Percent catch difference	SD	$P>t$ -value
		Control	Device				Control	Device			
Authement-Ledet											
Fish	L. Borgne	64.6	38.4	-41	45.7	0.01***	1,119.9	732.7	-35	588.1	0.01***
	L. Barre	202.7	134.8	-34	122.6	0.01***	2,425.2	1,458.9	-40	1,302.6	0.01***
	Calcasieu L.	244.0	153.8	-37	114.7	0.01***	4,080.2	2,200.8	-46	1,584.7	0.01***
Shrimp	L. Borgne	49.0	35.8	-27	21.3	0.01**	381.7	285.4	-25	178.1	0.01**
	L. Barre	90.5	86.7	-4	40.1	0.64	613.6	579.7	-6	233.9	0.49
	Calcasieu L.	115.1	85.5	-26	89.4	0.12 ^b	454.1	387.5	-15	300.6	0.29
Lake Arthur											
Fish	L. Borgne	65.4	47.0	-28	36.4	0.02* ^b	1,365.2	1,072.9	-21	638.6	0.03*
	L. Barre	215.3	151.3	-30	149.3	0.05*	3,046.8	2,263.0	-26	2,441.9	0.13
	Calcasieu L.	233.4	205.6	-12	152.9	0.38	4,301.0	3,511.9	-18	1,235.3	0.01***
Shrimp	L. Borgne	57.0	47.0	-18	20.1	0.02* ^a	389.1	350.6	-10	142.5	0.20 ^a
	L. Barre	95.3	70.3	-26	39.5	0.01***	649.4	509.4	-22	239.9	0.01***
	Calcasieu L.	127.4	95.4	-25	89.4	0.09	503.5	415.1	-18	252.1	0.10
Cameron											
Fish	L. Borgne	89.8	32.5	-64	113.0	0.02* ^a	1,987.7	1,170.2	-41	1,361.9	0.01***
	L. Barre	188.9	98.6	-48	75.1	0.01***	2,693.3	1,776.4	-34	869.6	0.01***
	Calcasieu L.	266.5	133.9	-50	125.9	0.01***	4,524.6	3,257.7	-28	1,402.8	0.01***
Shrimp	L. Borgne	59.8	45.0	-25	23.6	0.01***	419.8	338.2	-19	145.7	0.01*** ^b
	L. Barre	108.2	97.5	-10	42.8	0.23	719.6	655.1	-9	225.8	0.18
	Calcasieu L.	164.8	136.6	-17	126.7	0.29 ^b	598.4	507.7	-15	278.4	0.12
Eymard											
Fish	L. Borgne	81.6	114.4	40	83.9	0.07 ^a	1,970.0	1,288.0	-35	1,394.5	0.03*
	L. Barre	201.8	301.0	49	193.1	0.02* ^a	2,724.3	2,554.9	-6	2,158.8	0.70
	Calcasieu L.	287.8	303.7	6	195.7	0.69	4,246.5	3,376.1	-20	2,493.5	0.10 ^b
Shrimp	L. Borgne	52.7	84.1	60	79.2	0.06 ^a	365.2	510.4	40	343.3	0.05*
	L. Barre	97.5	120.6	24	34.1	0.01***	672.8	730.8	9	166.2	0.10 ^b
	Calcasieu L.	146.5	204.5	40	145.4	0.06 ^a	513.5	694.8	35	450.7	0.06 ^a

trips or evaluating fewer BRD's. Increasing the trawl-tow duration decreases the ability of a fish to maintain swimming speed (Bainbridge, 1960). Reductions over longer tow periods may differ; if most reduction occurs during haulback, fish may be too exhausted to escape. Longer tows also increase the chances of catching large quantities of fish and shrimp that may clog the net and cause organisms to be released from the BRD.

In terms of abundances and size distributions, bycatch varied between the areas and seasons; some species were very abundant in one or two areas. The capability of a BRD to reduce fish or shrimp depends on the species assemblage present in an area. A BRD may work well in one area under certain conditions but perform poorly in another area owing to assem-

blage differences. Species-specific size selectivity has been reported in other studies (e.g. Rulifson et al., 1992). Of the four BRD's, the Cameron had the best overall fish reduction. However, if spot and gulf menhaden were the most abundant species in an area, the Authement-Ledet may be a better choice. Bycatch reduction devices may have to be selected for particular areas or seasons, depending on the type and size distributions of predominant bycatch species, because a particular device may not be as effective in all areas or at all times of the year.

The high shrimp losses from the BRD's evaluated in this study would most likely be unacceptable for commercial operations. However, further modifications to these devices, such as altering the size or location of escape openings, could reduce these losses.

Table 5

Comparison of numbers and biomass of fish and shrimp collected by the four bycatch reduction device (BRD) nets and corresponding control nets for the different seasons. S_D is the standard deviation of the difference. Significance levels are 0.01 (***) and 0.05 (*). $n=36$. Superscripted letters denote significance levels of paired t -tests on log-transformed data: 0.01 (^a), 0.05 (^b).

BRD and type of catch	Season	Numbers					Biomass (g)				
		Mean catch/tow		Percent catch difference	SD	$P>t$ -value	Mean catch/tow		Percent catch difference	SD	$P>t$ -value
		Control	Device				Control	Device			
Authement-Ledet											
Fish	spring	218.3	137.8	-37	127.7	0.01*** ^a	2,895.3	1,667.1	-42	1,374.2	0.01*** ^a
	fall	122.6	80.2	-35	65.5	0.01*** ^a	2,188.3	1,261.2	-42	1,354.2	0.01*** ^a
Shrimp	spring	116.6	92.1	-21	73.2	0.05* ^b	650.3	556.6	-14	288.7	0.06 ^b
	fall	53.1	46.5	-12	36.4	0.29 ^b	316.0	278.5	-12	180.4	0.22
Lake Arthur											
Fish	spring	216.1	165.2	-24	157.1	0.06	3,459.1	2,761.7	-20	2,119.1	0.06 ^b
	fall	126.7	104.2	-18	80.9	0.10 ^b	2,349.6	1,803.6	-23	893.6	0.01*** ^b
Shrimp	spring	124.8	96.5	-23	75.4	0.03* ^b	642.3	541.1	-16	244.8	0.02* ^b
	fall	61.7	45.3	-27	31.0	0.01*** ^a	385.7	308.9	-20	190.3	0.02* ^a
Cameron											
Fish	spring	203.1	106.5	-48	101.5	0.01*** ^a	3,296.6	2,229.1	-32	1,187.8	0.01*** ^a
	fall	160.3	70.2	-56	118.9	0.01*** ^a	2,840.4	1,907.1	-33	1,290.5	0.01*** ^a
Shrimp	spring	157.9	134.9	-15	104.4	0.19 ^a	773.1	677.9	-12	252.8	0.03* ^a
	fall	64.0	51.2	-20	35.8	0.04* ^a	385.4	322.8	-16	184.8	0.05* ^a
Eymard											
Fish	spring	233.8	301.1	29	197.3	0.05* ^a	3,386.9	2,773.0	-18	2,029.4	0.08 ^b
	fall	147.1	178.3	21	131.7	0.16 ^b	2,573.8	2,039.7	-21	2,117.8	0.14
Shrimp	spring	145.1	199.8	38	119.5	0.01*** ^a	716.1	883.0	23	380.7	0.01*** ^a
	fall	52.6	73.0	39	65.9	0.07 ^a	318.2	407.7	28	294.3	0.08

The BRD nets tested here did not appear to slow water flow in the trawl net. Other studies, however, have indicated that flow rate around and through the BRD may be a key factor in fish and shrimp escapement. Watson et al. (1993) found that juvenile fish could exit a BRD at flow rates between 0.2 and 0.5 m/sec. However, shrimp accumulated in areas of reduced flow and crawled along the webbing against the flow to escape some devices (Watson et al., 1993). Devices can be designed to create a 0.2 to 0.5 m/sec flow rate, but debris can alter the flow rate and affect BRD performance. The ability to sustain swimming appears to be related to length, but this relationship often differs for each species (Bainbridge 1960). Further testing is necessary to acquire escape flow rates for the major species of concern.

Reduction rates for numbers and biomass of many species differed for the four BRD's, reflecting size-dependent selectivity. Escape rates of different species also varied considerably owing to differences in size and behavior. These differences, coupled with the high variability in organisms between areas, in-

dicating that the performance of BRD's should be evaluated at the species and size level.

Future studies should continue to involve members of the industry. The advisory committee provided suggestions and valuable insight that greatly enhanced the success of this project and the acceptability of the results. Other studies have reported successful industry involvement (Rulifson et al., 1992; McKenna and Monaghan⁴). The design and construction of BRD's should be a dynamic process which will benefit from the cooperation of industry, research, and management personnel.

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Abstract.—Yellowfin tuna, *Thunnus albacares*, were sampled from one region of the Atlantic Ocean, two regions of the Indian Ocean, and six regions of the Pacific Ocean. One of the Indian Ocean collections could not be allozymically analyzed; the remaining eight collections were examined for four polymorphic allozyme loci (*ADA**, *FH**, *GPI-A**, and *GPI-B**, $n=540$ to 677). All nine collections were examined for mitochondrial DNA variation ($n=767$), with two restriction enzymes (*Bcl* I and *Eco* RI) that detect polymorphic restriction sites in yellowfin tuna. Allele frequencies at three of the allozyme loci were homogeneous across collections, whereas *GPI-A** showed highly significant differentiation ($P<0.001$). The *GPI-A** data, taken together with the geographic location of the collections, suggested the existence of at least four yellowfin tuna stocks: Atlantic Ocean, Indian Ocean, west-central Pacific Ocean, and east Pacific Ocean. Mitochondrial DNA differentiation was more limited, but spatial heterogeneity of the 24 observed haplotypes over the nine regions ($P=0.048$) and three oceans ($P=0.009$) was significant. The mtDNA data did not differentiate west-central Pacific Ocean collections from east Pacific Ocean collections but did support the separation of Atlantic Ocean, Indian Ocean, and Pacific Ocean stocks.

Global population structure of yellowfin tuna, *Thunnus albacares*, inferred from allozyme and mitochondrial DNA variation

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The yellowfin tuna, *Thunnus albacares* (Bonnaterre), supports important fisheries in tropical and subtropical oceans. Catches have increased from about 600,000 metric tons (t) in 1982 and 1983 to about 1,100,000 t in 1993 and 1994; in 1994, about 63% of the catch came from the Pacific Ocean, about 24% from the Indian Ocean, and 14% from the Atlantic Ocean (FAO, 1996). Given the size and circumglobal nature of the resource, there is considerable management interest in determining stock structures.

It is only comparatively recently that yellowfin tuna has been recognized as a single species (Gibbs and Collette, 1967); its high degree of morphological variation led Jordan and Evermann (1926) to recognize seven yellowfin tuna species. However, a major morphometric study by Royce (1964) revealed that intra-oceanic differences could be greater than interoceanic differences and that several characters showed clinal variation. He concluded that the morphometric data are best explained by a single worldwide pan-tropical species, a conclusion confirmed by Gibbs and Collette (1967).

Most stock structure studies of yellowfin tuna have focused on the large Pacific Ocean component of

the catch. Here, tagging experiments indicated that yellowfin tuna usually migrate hundreds rather than thousands of kilometers and that their movements do not range far both east-west or north-south (Joseph et al., 1964; Bayliff, 1979; Hunter et al., 1986; Lewis, 1992). Morphometric studies have provided commensurate results, with Mexico and Ecuador fish being much more similar to one another than to fish from the central (Hawaii) and western (Australia, Japan) Pacific (Schaefer, 1991). Studies of the microchemical composition of larval portions of otoliths in West Pacific fish (Indonesia, Philippines, Coral Sea, Hawaii) have shown some differences, indicating that such analyses may be useful in determination of spawning origins (Gunn and Ward¹; Gunn²). Genetic studies of four to five polymorphic

¹ Gunn, J. S., and R. D. Ward. 1994. The discrimination of yellowfin tuna sub-populations within the AFZ. Phase 1: a pilot study to determine the extent of genetic and otolith microchemical variability in populations from different parts of the Pacific and Indian Oceans. Final Report (91/27) to Fisheries Research and Development Corporation, Deakin, ACT, Australia.

² Gunn, J. S. 1996. CSIRO Division of Marine Research, Hobart, Tasmania, Australia. Unpubl. data.

allozyme loci in Pacific Ocean collections have shown significant spatial heterogeneity at one locus (*GPI-A**); the common allele in western and central regions differed from that in the east (Sharp, 1978; Ward et al., 1994). This finding either indicates the existence of two reproductively isolated groups of yellowfin tuna in the Pacific Ocean or suggests that selection pressures are different in the two regions. There is no evidence of mitochondrial DNA (mtDNA) differentiation between eastern Pacific and western Pacific yellowfin tuna (Scoles and Graves, 1993; Ward et al., 1994).

In the Atlantic Ocean, where it was once assumed that there were separate eastern and western stocks, recent taggings of large yellowfin tuna have resulted in 15 trans-Atlantic recoveries (ICCAT, 1992b); a single stock is now assumed (ICCAT, 1995). There have been no genetic comparisons of eastern and western Atlantic yellowfin tuna.

The extent of genetic differentiation of yellowfin tuna from different oceans has been little studied. Suzuki (1962) found no differences in the incidence of the Tg2 blood group antigen in fish from the equatorial Pacific and Indian Oceans. Scoles and Graves (1993) found no significant differentiation in mtDNA from one west Atlantic collection and five Pacific collections (each of 20 fish). Here we compare genetic variation in collections from the Pacific, Indian, and Atlantic oceans. We used larger sample sizes than those used in the study by Scoles and Graves (1993) and examined both allozyme and mtDNA variation to see if the increased statistical power would enable us to reject the null hypothesis of no interoceanic genetic differentiation.

Materials and methods

Samples were collected from one region of the Atlantic Ocean, two regions of the Indian Ocean, and six regions of the Pacific Ocean. Details of most of the Pacific collections (Philippines, Coral Sea, Kiribati, Hawaii, California, and Mexico) are given in Ward et al. (1994). For the present paper, the 1991 and 1992 Hawaii collections were pooled. A second Philippines collection was collected in October–December 1994. This showed no significant genetic differentiation from the earlier collection; therefore the two collections were pooled for our study. The Atlantic collection was taken from the Caribbean Sea (Gulf of Mexico, approx. 28°N, 88°W) in September 1993. The Indian Ocean collections were taken from off Sri Lanka (approx. 6°N, 80°E) and off the Seychelles (approx. 7°S, 52°E) in December 1994. White muscle samples were flown (airfreight) frozen to Hobart and stored at –80°C.

Specimens were studied by allozyme and mtDNA analysis. The experimental methods are given in Ward et al. (1994). Four allozyme loci known to be polymorphic in white muscle were examined: *ADA** (adenosine deaminase, EC 3.5.4.4), *FH** (fumarate hydratase, EC 4.2.1.2), *GPI-A**, and *GPI-B** (glucose-6-phosphate isomerase, EC 5.3.1.9). MtDNA variation was examined by using two restriction enzymes (*Bcl* I and *Eco* RI) known to discriminate most of the mtDNA haplotypes revealed by eight restriction enzymes in an earlier survey (*Bam* HI, *Ban* I, *Bcl* I, *Eco* RI, *Hind* III, *Pvu* II, *Sal* I, and *Xho* I—see Ward et al., 1994).

The homogeneity of allele and haplotype frequencies of the collections was tested by the randomized Monte Carlo chi-square procedure of Roff and Bentzen (1989). For each test, 2,000 randomizations of the data were carried out, each giving a randomized chi-square value (χ^2_{null}). The probability that the null hypothesis of genetic homogeneity was correct was given by $P = n/2,000$, where n is the number of randomizations that generate $\chi^2_{null} \geq \chi^2$ and where χ^2 is the chi-square value given by the actual observations.

The extent of genetic differentiation among collections was quantified by Nei's gene diversity statistic G_{ST} (Nei, 1987), which estimates the proportion of total genetic variation attributable to differentiation between populations. For each allozyme locus, G_{ST} was estimated as $(H_T - H_S) / H_T$, where H_T represents total heterozygosity and H_S is average (Hardy-Weinberg expected) population heterozygosity. The mtDNA data were analyzed in a similar way, treating haplotypes as alleles and H_T and H_S as diversity estimates. The proportion or magnitude of G_{ST} generated by sampling error, which we have termed $G_{ST,null}$, was estimated with a bootstrapping program, with the observed allele or haplotype frequencies and collection sizes. Simulations were run 1,000 times to provide a mean value of $G_{ST,null}$ and a standard deviation. The probability of obtaining a value of $G_{ST,null}$ as large or larger than that obtained from the actual observations of G_{ST} was given by $P = n/1,000$, where n is the number of randomizations that generate $G_{ST,null} \geq G_{ST}$. Values of P less than 0.05 indicated significant differentiation between areas that could not be explained by sampling error alone.

Bonferroni adjustments of significance levels, to correct for multiple tests, were carried out with the sequential procedure advocated by Hochberg (1988). Tests are ordered according to their probability value. The highest probability value, P_m , is compared with the significance value α . Here we initially set $\alpha = 0.05$. If $P_m \geq \alpha$, that test is judged to be nonsignificant, and comparisons continue with subsequent probabilities, each compared with a modified signifi-

cance level = $\alpha/(1+i)$, where i is the number of tests already performed. When a test is significant, it and all subsequent tests are deemed significant.

Cluster analysis of the allozyme allele frequency data and the mtDNA haplotype frequency data used the UPGMA (unweighted pair-group method using averages) algorithm with Nei's (1978) unbiased genetic distance measure, as implemented in BIOSYS-1 (Swofford and Selander, 1981).

Estimates of mtDNA nucleotide sequence diversity and divergence (Nei and Tajima, 1981; Nei, 1987) were made with REAP vers.4.0 (see McElroy et al., 1992), and population divergences were clustered by using UPGMA.

Results

The Seychelles muscle samples were partially degraded on arrival, and could not be confidently screened for allozyme determinations, although mtDNA analysis presented no problems. Because it is sometimes difficult to distinguish tuna species, we usually find a small percentage (3–5%) of non-yellowfin tunas among nominal yellowfin tuna collec-

tions. These misidentified fish can be recognized by aberrant allozyme (Graves et al., 1988; Elliott and Ward, 1995) and mtDNA patterns (Grewe³). For example, five (3.7%) of the 135 Philippines samples collected in 1994 proved to be bigeye tuna, *Thunnus obesus*. However, at times, the proportion of misidentified fish can be much higher: 18 (46.2%) of the 39 "yellowfin tuna" from Sri Lanka proved to be bigeye tuna. The misidentified fish were excluded from the following analyses.

Allozyme allele frequencies at four polymorphic loci (*ADA**, *FH**, *GPI-A**, *GPI-B**) for eight collections (Table 1) and mtDNA haplotype frequencies for nine collections (Table 2) were determined.

No significant deviations from Hardy-Weinberg expectations were recorded for any allozyme locus. Heterogeneity chi-square analyses (Table 3) of allele frequencies revealed no significant differentiation for three loci (*ADA**, *FH**, and *GPI-B**), but highly significant heterogeneity at the fourth locus, *GPI-A** ($P < 0.001$, $\alpha = 0.0125$). Genetic diversity (G_{ST}) analyses (Table 3) indicated that for *ADA**, *FH**, and *GPI-B**,

³ Grewe, P. M. 1993. CSIRO Division of Marine Research, Hobart, Tasmania, Australia. Unpubl. data.

Table 1

Allozyme allele frequencies and sample sizes (n). GOM = Gulf of Mexico, S.Lan. = Sri Lanka, Philipp. = Philippines, Cl. Sea = Coral Sea, Calif. = California.

Locus	Allele	Atlantic		Indian		Pacific			
		GOM	S. Lan.	Philipp.	Cl. Sea	Kiribati	Hawaii	Calif.	Mexico
<i>ADA*</i>	125	0.005	—	0.003	—	—	—	—	—
	115	0.414	0.310	0.330	0.306	0.399	0.361	0.317	0.359
	100	0.548	0.643	0.622	0.638	0.567	0.609	0.671	0.628
	85	0.033	0.048	0.045	0.056	0.034	0.030	0.012	0.013
	n	105	21	176	98	89	115	41	39
<i>FH*</i>	130	0.118	0.091	0.081	0.117	0.086	0.076	0.051	0.075
	100	0.875	0.909	0.910	0.878	0.900	0.920	0.949	0.925
	75	0.007	—	0.009	0.005	0.014	0.004	—	—
	n	68	11	111	98	70	112	39	29
<i>GPI-B*</i>	-20	0.015	—	—	—	—	0.004	—	—
	-60	0.180	0.167	0.176	0.163	0.233	0.113	0.187	0.231
	-100	0.806	0.833	0.824	0.837	0.767	0.878	0.813	0.769
	-125	—	—	—	—	—	0.004	—	—
	n	103	21	176	98	88	115	40	39
<i>GPI-A*</i>	145	—	—	0.003	—	—	—	—	—
	135	0.045	—	0.015	0.036	0.011	0.035	0.122	0.077
	100	0.624	0.286	0.651	0.683	0.673	0.609	0.305	0.231
	75	0.332	0.714	0.328	0.281	0.316	0.357	0.573	0.692
	40	—	—	0.003	—	—	—	—	—
	n	101	21	175	98	87	115	41	39

slightly less than 1% of the observed diversity arose from differences between collections and could be attributed to sampling error alone ($G_{ST.null}$). For $GPI-A^*$, the observed value of G_{ST} , at 12%, was much larger than the value attributable to sampling error (about 1%). The "true" G_{ST} estimate of $GPI-A^*$ —the difference between G_{ST} and $G_{ST.null}$ —is thus around 11%, indicating that about 11% of the observed diversity at the $GPI-A^*$ locus comes from differences between collections.

The $GPI-A^*$ heterogeneity (Fig. 1) was further explored by comparing all collections pairwise (Fig. 2; Table 4). This comparison essentially revealed two groups of collections: 1) the west-central Pacific Ocean and the Atlantic Ocean (Gulf of Mexico) collections; and 2) the Indian Ocean (Sri Lankan) and eastern Pacific Ocean (Californian and Mexican) collections. Within each of these two groups there was

no significant differentiation, but between them differentiation was marked. This conclusion holds after Bonferroni corrections of α levels for multiple tests. The $GPI-A^*100$ allele was the most frequent allele in the west-central Pacific Ocean and the Atlantic Ocean group, whereas the $GPI-A^*75$ allele was the more frequent allele in the Indian Ocean and the eastern Pacific Ocean group. The genetic differentiation of the Atlantic Ocean collection from the Indian Ocean collection suggests that fish from these areas constitute separate stocks; the separation of the Indian Ocean collection from the west-central Pacific Ocean collections suggests that fish from these areas constitute separate stocks; the separation of the west-central Pacific Ocean collections from the eastern Pacific Ocean collections suggests that fish from these areas constitute separate stocks; and the separation of the eastern Pacific Ocean collections

Table 2

Mitochondrial DNA haplotype frequencies (*Bcl* I and *Eco* RI haplotypes respectively), sample sizes (n), haplotype diversities (h) and percent nucleotide diversities (% n.d.). Abbreviations are defined in Table 1. Seych. = Seychelles.

Locus	Haplotype	Atlantic		Indian		Pacific				
		GOM	Seych.	S. Lan.	Philipp.	Cl. Sea	Kiribati	Hawaii	Calif.	Mexico
mtDNA	AA	0.266	0.319	0.381	0.286	0.340	0.443	0.276	0.294	0.325
	AB	0.543	0.407	0.333	0.509	0.402	0.364	0.537	0.463	0.425
	AC	—	—	—	—	—	0.011	0.015	—	—
	AF	—	0.011	—	—	—	—	0.007	0.049	0.025
	AG	—	—	—	0.006	—	—	0.007	—	—
	BA	0.011	0.011	—	0.025	0.010	—	0.007	0.049	—
	BB	0.064	0.066	—	0.031	0.052	0.068	0.060	0.073	0.025
	CA	0.032	0.011	—	0.031	0.062	0.011	0.015	0.024	0.050
	CB	0.021	0.088	0.286	0.068	0.103	0.057	0.045	0.024	0.125
	CO	0.021	—	—	—	—	—	—	—	—
	DB	—	—	—	—	—	0.010	—	—	—
	EB	—	—	—	—	—	0.021	—	—	—
	LB	—	—	—	—	—	—	0.011	—	—
	MB	—	—	—	—	—	—	0.011	—	—
	NB	—	—	—	—	0.019	—	—	0.007	—
	PB	—	—	—	—	—	—	—	0.015	0.024
	OA	—	—	—	—	0.006	—	—	—	0.025
	OB	—	—	—	—	0.006	—	0.023	—	—
	QA	—	0.011	—	—	—	—	—	—	—
	QB	0.011	0.011	—	—	—	—	—	0.007	—
	WA	0.032	0.033	—	—	—	—	—	—	—
	ZB	—	0.022	—	—	0.006	—	—	—	—
A2B	—	—	—	—	0.006	—	—	—	—	
Q2B	—	0.011	—	—	—	—	—	—	—	
n		94	91	21	161	97	88	134	41	40
h		0.634	0.727	0.695	0.655	0.712	0.670	0.633	0.705	0.712
% n.d.		0.998	1.263	1.017	1.017	1.174	1.027	0.901	1.099	1.047



Figure 1

Map of sample sites showing *GPI-A** gene frequencies in yellowfin tuna, *Thunnus albacares*. Larger circles represent our data (Table 1), the three smaller circles (Bismark Sea, Roca Partido, and Ecuador) data are from Sharp (1978). The location of the Seychelles sample, examined for mtDNA variation but not for *GPI-A** variation, is identified. The shaded area represents the approximate global distribution of yellowfin tuna.

from the Atlantic Ocean collection suggests that these fish constitute separate stocks. Thus the *GPI-A** data, taken together with the spatial orientation of these collections, indicate the existence of at least four yellowfin tuna stocks: Atlantic Ocean, Indian Ocean, west-central Pacific Ocean, and east Pacific Ocean.

Six of the 24 mtDNA haplotypes (CO, QA, WA, ZB, A2B, Q2B, see Table 2) were not recorded in the ear-

lier survey of Ward et al. (1994) but were rare (frequencies less than 3.5%). Fragment sizes for most haplotypes are given in Ward et al. (1994), but a full list is available on request. Haplotype (nucleon) diversities per collection ranged from 0.633 to 0.727 (mean estimate of 0.683) (Table 2). Percent nucleotide diversities per collection ranged from 0.998 to 1.263 (mean estimate of 1.061) (Table 2).

Table 3

Analyses of genetic differentiation among the samples.

Locus	Number of fish	Number of alleles/haplotypes	Heterogeneity χ^2 analysis		Genetic diversity analysis		
			χ^2	<i>P</i>	G_{ST}	$G_{ST.null} \pm SD$	<i>P</i>
<i>ADA*</i>	684	4	17.326	0.666	0.006	0.008 \pm 0.004	0.569
<i>FH*</i>	538	3	9.241	0.821	0.006	0.011 \pm 0.008	0.736
<i>GPI-B*</i>	680	4	29.256	0.128	0.008	0.008 \pm 0.005	0.370
<i>GPI-A*</i>	677	5	131.416	<0.001	0.118	0.008 \pm 0.004	<0.001
mtDNA	767	24	227.743	0.048	0.023	0.015 \pm 0.005	0.071

Table 4Pairwise comparisons of *GPI-A** allele frequencies (*P* above, chi square below). GOM = Gulf of Mexico.

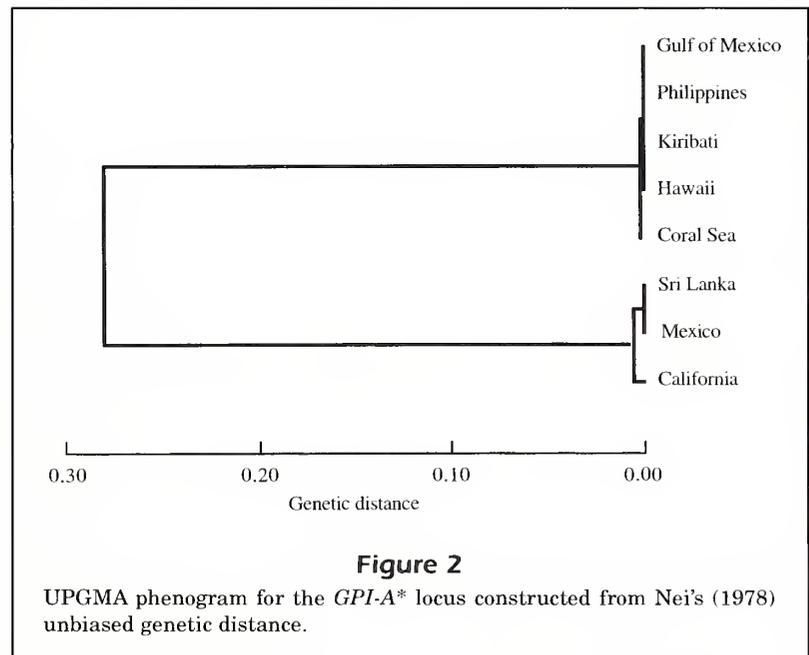
	GOM	Sri Lanka	Philippines	Coral Sea	Kiribati	Hawaii	California	Mexico
GOM	—	<0.001	0.156	0.468	0.129	0.769	<0.001	<0.001
Sri Lanka	21.700	—	0.001	<0.001	<0.001	0.001	0.031	0.214
Philippines	5.938	24.115	—	0.264	0.965	0.291	<0.001	<0.001
Coral Sea	1.586	28.644	4.870	—	0.270	0.237	<0.001	<0.001
Kiribati	3.905	22.586	1.196	2.630	—	0.203	<0.001	<0.001
Hawaii	0.493	19.130	4.635	2.824	3.280	—	<0.001	<0.001
California	24.850	6.047	46.871	35.021	37.324	25.374	—	0.289
Mexico	34.934	3.579	51.193	46.401	44.495	33.366	2.526	—

Table 5Pairwise comparisons of mtDNA haplotype frequencies (*P* above, chi square below). GOM = Gulf of Mexico.

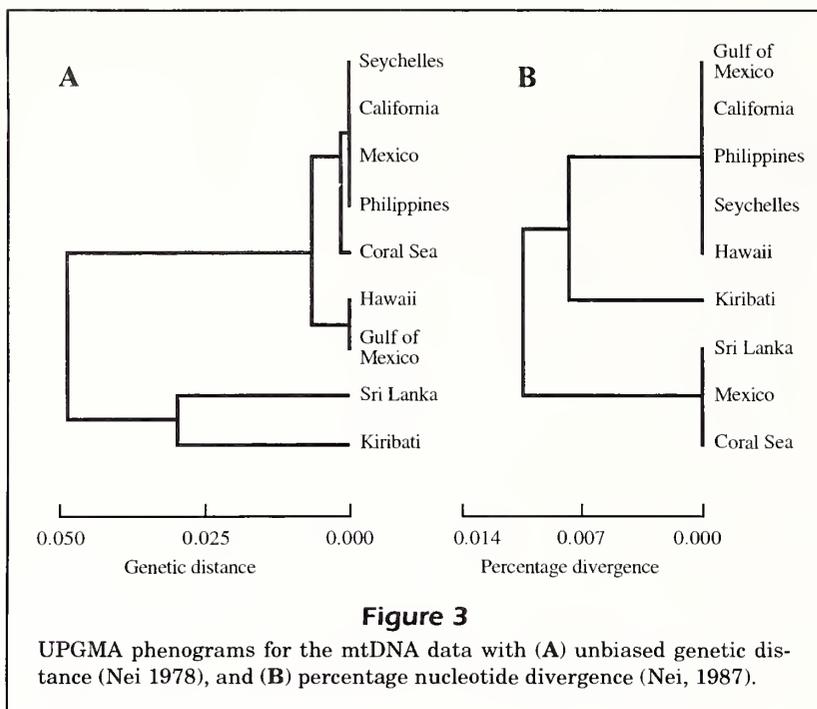
	GOM	Seychelles	Sri Lanka	Philippines	Coral Sea	Kiribati	Hawaii	California	Mexico
GOM	—	0.277	0.009	0.089	0.025	0.009	0.384	0.285	0.076
Seychelles	14.079	—	0.549	0.062	0.188	0.212	0.200	0.478	0.707
Sri Lanka	23.110	9.697	—	0.269	0.369	0.171	0.111	0.025	0.612
Philippines	19.823	22.529	14.013	—	0.223	0.025	0.428	0.207	0.597
Coral Sea	18.085	16.020	7.785	15.432	—	0.087	0.053	0.092	0.683
Kiribati	21.523	17.480	11.862	22.368	15.117	—	0.086	0.093	0.253
Hawaii	13.801	18.574	18.760	15.533	19.300	18.754	—	0.667	0.378
California	11.888	11.682	13.905	17.165	14.055	16.316	8.888	—	0.383
Mexico	15.622	9.718	5.017	10.188	7.203	12.214	13.080	8.473	—

A chi-square test (Table 3) showed that the mtDNA haplotype variation across all nine regions was just significant ($\alpha=0.05$, $P=0.048$, with the standard 2,000 replicates, and $P=0.045$, with 10,000 replicates). Genetic diversity analysis (Table 3) gave a result bordering on significance ($P=0.071$, with a "true" G_{ST} of about 1%). All collections were compared pairwise with chi-square tests (Table 5) to determine which collections contributed most to the marginal chi-square differentiation. Although some pairs appeared significantly different (e.g. Gulf of Mexico versus Sri Lanka, $P=0.009$; Gulf of Mexico versus Kiribati, $P=0.009$), none was significant after Bonferroni adjustments for table-wide comparisons.

Two UPGMA dendrograms were estimated. One, based on mtDNA haplotype frequencies alone (Fig. 3A), showed the maximal genetic-distance estimates among collections to be about 0.05 — much less than the major *GPI-A** split of nearly 0.30 (Fig. 2). The second,



based on percent sequence divergence (Fig. 3B), confirmed the high degree of similarity among the collections. After correcting for within-collection nucle-



otide divergence, pairwise nucleotide divergence ranged from 0.040% to -0.025% (mean 0.004%). There was little correspondence between these two mtDNA dendrograms, and this lack of correspondence, together with the low distances observed, suggests that the tree topologies are unreliable.

Because there is no significant mtDNA differentiation between the six Pacific Ocean collections (Table 5; and Ward et al., 1994) nor between the two Indian Ocean collections (Table 5), the collections within each ocean were pooled to test for interoceanic differences. A comparison of the three oceans yielded a chi-square analysis that was significant ($P=0.009$, $\alpha=0.05$) and a genetic diversity analysis bordering on significance (observed $G_{ST}=0.010$, $G_{STnull}=0.005 \pm 0.003$, $P=0.059$). A pairwise comparison of the oceans showed that all pairs were significant (Indian versus Atlantic, $P=0.047$, $\alpha=0.05$; Pacific versus Atlantic, $P=0.017$; Pacific versus Indian, $P=0.009$).

Finally, the mtDNA data were analyzed to see whether they offered any support to the conclusion from the *GPI-A** data that there are (at least) four yellowfin tuna stocks. The four putative stocks consisted of the following units: Atlantic (Gulf of Mexico), Indian (Seychelles and Sri Lanka), west-central Pacific (Coral Sea, Kiribati, Philippines, Hawaii), and east Pacific (California and Mexico). Chi-square analysis of mtDNA data from these four regions indicated limited but significant ($P=0.024$) heterogeneity. Although none of the six pairwise comparisons

was significant following Bonferroni correction to α levels (west-central Pacific versus east Pacific, $P=0.456$, $\alpha=0.05$; Indian versus east Pacific, $P=0.316$, $\alpha=0.025$; Atlantic versus east Pacific, $P=0.119$, $\alpha=0.017$; Atlantic versus Indian, $P=0.047$, $\alpha=0.0125$; Atlantic versus west-central Pacific, $P=0.032$, $\alpha=0.010$; Indian versus west-central Pacific, $P=0.0135$, $\alpha=0.008$), the three pairwise comparisons of the Atlantic Ocean, Indian Ocean, and west-central Pacific all showed P -values less than 0.05.

Clearly, the mtDNA data do not differentiate west-central Pacific Ocean collections from east Pacific Ocean collections but, considering the interoceanic analyses alone, do provide some support for the delineation of Atlantic Ocean, Indian Ocean, and Pacific Ocean stocks.

Discussion

Samples of yellowfin tuna from the Pacific, Indian, and Atlantic oceans were compared with respect to four polymorphic allozyme loci and with respect to mtDNA variants.

No significant allele frequency differences were observed for three of the allozyme loci, but the fourth locus, *GPI-A**, showed considerable differentiation. Across all collections, the "true" G_{ST} indicated that about 11% of the variation at this locus was attributable to differences between collections. Two genetically distinguishable groups were apparent. One consists of eastern Pacific Ocean and Indian Ocean fish, with a high frequency of the *GPI-A**75 allele, the other of Atlantic Ocean and west-central Pacific Ocean fish, with a high frequency of the *GPI-A**100 allele. Because there are no migration routes between the eastern Pacific Ocean (California and Mexico) and the Indian Ocean that avoid the west-central Pacific Ocean, and between the Atlantic Ocean and west-central Pacific Ocean that avoid the Indian Ocean, there is reason to believe that there are at least four stocks of yellowfin tuna: Atlantic Ocean, Indian Ocean, west-central Pacific Ocean, and eastern Pacific Ocean.

Sharp (1978) also examined *GPI-A** allele frequencies in western and eastern Pacific populations. His *GPI-A** allele frequencies for collections from Ecuador and Mexico were very similar to our California and Mexico frequencies, and his *GPI-A** frequencies

from the Bismarck Sea in the western Pacific were very similar to our western Pacific Ocean frequencies (Ward et al., 1994), supporting the separation of western and eastern Pacific stocks. Another allozyme study (Fujino, 1970) failed to find differences between Hawaiian and eastern Pacific fish for an esterase and for transferrin, although the esterase was nearly monomorphic.

We interpret the *GPI-A** differentiation as being indicative of stock differences, resulting from restricted gene exchange between the four identified regions. However, the alternative explanation, that of differential selection in the presence of gene flow, cannot be ruled out. Indeed, the very limited mtDNA differentiation observed could be held to support this interpretation. Microsatellite analysis, currently underway, may help to resolve this question. Selection acting on these noncoding genetic markers is presumed to be minimal or nonexistent; therefore microsatellite differentiation paralleling the *GPI-A** differentiation would suggest drift of neutral *GPI-A** alleles, whereas lack of microsatellite differentiation would indicate significant gene flow and thereby implicate selection as the cause of the *GPI-A** differentiation. Pogson et al. (1995) have recently suggested that the highly heterogeneous distribution of anonymous nuclear RFLP markers among populations of cod, *Gadus morhua*, reflects limited gene flow and that the much more homogeneous distribution of allozyme alleles reflects stabilizing selection rather than extensive gene flow. Such an argument applied to yellowfin tuna data would interpret the *GPI-A** heterogeneity as indicative of limited gene flow, and the *ADA**, *FH**, and *GPI-B** homogeneity as indicative of stabilizing selection at these three loci.

Differences between collections in mtDNA was only just significant ($P=0.048$), with a "true" G_{ST} value across all nine collections of around 1%. When collections were pooled within oceans, i.e. the three groups (Atlantic, Indian, and Pacific), significant differentiation was detected ($P=0.009$), although the "true" G_{ST} was only of the order of 0.5%. All three pairwise ocean comparisons were statistically significant. However, because collections within oceans did not always pool together in the distance dendrograms (Fig. 3), possibly because of limited sample sizes, it would clearly be useful to have more data to confirm (or refute) this evidence of interoceanic differentiation. When collections were pooled into the four putative stocks indicated by the *GPI-A** data, limited but significant heterogeneity in mtDNA haplotype frequencies was apparent ($P=0.024$), but there were no significant pairwise comparisons.

Scoles and Graves (1993) were unable to detect significant mtDNA differentiation between Pacific

and Atlantic yellowfin tuna, whereas the probability of homogeneity in our tests of these two oceans was only 0.017. However, they adopted a different test strategy. Instead of examining relatively large numbers of fish (our study: Pacific fish, $n=561$; Atlantic fish, $n=94$) with relatively few restriction enzymes ($n=2$, but known to detect polymorphic sites), they chose to examine relatively few fish (Pacific fish, $n=100$; Atlantic fish, $n=20$) with a relatively large number of restriction enzymes ($n=12$, which included the two enzymes we used). Given that the common 12-enzyme haplotype in Scoles and Graves' study comprised 52 fragments or 304 bp and that the common 2-enzyme haplotype in our study comprised 7 fragments or 42 bp (see Ward et al., 1994) and that the mean size of the yellowfin tuna mtDNA genome is about 16,702 bp (Scoles and Graves [1993] estimate=16,549; Ward et al. [1994]=16,856), Scoles and Graves surveyed about 1.8% of the mtDNA genome, whereas we surveyed only about 0.3%. However, although it is of course true that had we surveyed more restriction enzymes, we would have uncovered many additional haplotypes, the two enzymes that we did select revealed most of the mtDNA diversity shown by Scoles and Graves (1993). For example, the (pooled) 12-enzyme haplotype diversity of 0.840 of Scoles and Graves was not much larger than our (pooled) 2-enzyme diversity of 0.677. Four of the enzymes used by Scoles and Graves showed no variation at all in the 120 fish and therefore were of no use for population discrimination. Twenty of the 34 12-enzyme haplotypes detected by Scoles and Graves (1993) among their 120 fish were seen only once, whereas only four of the 22 2-enzyme haplotypes in our 655 Atlantic and Pacific fish were seen only once: such rare haplotypes are of extremely limited use in population studies. Given that mtDNA heterogeneity among regions is very limited, it is not surprising that the approach of screening large numbers of fish for a small number of sequences known to be variable should be more powerful than screening small numbers of fish for a larger number of sequences, many of which are relatively invariant.

MtDNA data from another tuna, the albacore, *Thunnus alalunga*, showed a somewhat more pronounced separation of Atlantic Ocean and Pacific Ocean collections than did data for yellowfin tuna, but again no intraoceanic heterogeneity was detected (Chow and Ushiamo, 1995).

The limited mtDNA differentiation among yellowfin tuna sampled throughout their range contrasts with the marked population subdivision revealed by the *GPI-A** locus. Mitochondrial DNA has an effective population size only one quarter that of nuclear DNA (Birky et al., 1989) and evolves more rapidly

(Brown et al., 1979); in principle it should be a more effective indicator of population substructure than nuclear loci. Given that more mtDNA than nuclear DNA divergence is expected, how can an allozyme locus show differentiation when mtDNA haplotypes do not? The lack of mtDNA differentiation in yellowfin tuna does not appear to be the result of a lack of variation nor of a small sample size: although increasing haplotype diversities and sample sizes will increase statistical power, the mtDNA haplotype diversities of our populations, assayed for just two restriction enzymes, were quite high at around 0.65–0.70, and sample sizes were similar to those used in the allozyme analyses. Nuclear DNA differentiation can exceed mtDNA differentiation when either the migration rate or the breeding sex ratio is strongly biased towards females (because mtDNA is maternally inherited), but there is no evidence that either of these conditions holds for yellowfin tuna (e.g. IATTC, 1992). The explanation for the seeming discrepancy may be that several independent polymorphic allozyme loci were screened, whereas haplotypes of mtDNA are best treated as alleles at a single, nonrecombining locus. In a situation of low overall genetic divergence (resulting from gene flow or recent separation), the stochastic nature of genetic drift means that if several allozyme loci are screened, and notwithstanding the expected higher rate of mtDNA evolution, divergence might be first detected at an allozyme locus before it is detected for mtDNA. An alternative explanation, as intimated earlier, is that the *GPI-A** differentiation results from selection.

The delineation of the four stocks of yellowfin tuna does not seem unreasonable given what we know of their distribution and movements. Yellowfin are found circumglobally, but only in tropical and subtropical oceanic waters, approximately between the latitudes 40°N and 40°S (Collette and Nauen, 1983). Spawning occurs throughout the year in all core areas of distribution, peaking in the warmer months (Collette and Nauen, 1983). Waters off the southern regions of South America (approximately 55°S) are too cold for Atlantic Ocean and Pacific Ocean fish to migrate around Cape Horn. Furthermore, direct connections between the tropical Atlantic Ocean and the eastern Pacific Ocean were severed after the Isthmus of Panama closed about 3.5 million years ago (e.g. Keigwin, 1982; Coates et al., 1992), a closure likely to have predated the origin of yellowfin tuna (estimated by Elliott and Ward (1995) to have occurred within the last two million years). Thus Pacific Ocean and Atlantic Ocean fish could not mix. In contrast, Atlantic Ocean and Indian Ocean fish could mix (through southern Africa waters), as could In-

dian Ocean and Pacific Ocean fish (through Indonesian waters), but tagging experiments indicate that most yellowfin tuna move on a scale of hundreds rather than thousands of kilometers (Joseph et al., 1964; Bayliff, 1979; Hunter et al., 1986; Lewis, 1992). The extent of migration between ocean basins is therefore likely to be low, with intraoceanic recruitment predominating. Nonetheless, interoceanic movements are possible and could account for the low degree of genetic differentiation among areas. Further discussion of the genetic and other biological data with respect to Pacific Ocean fish is given in Ward et al. (1994).

At present, these suggestions on the global stock structure of yellowfin tuna are essentially based on gene frequencies at a single polymorphic allozyme locus, *GPI-A**, because no significant genetic heterogeneity was detected for three other polymorphic allozymes and the mitochondrial DNA variants showed little interpopulation differentiation. It may well be that the stock structure of yellowfin tuna, in management terms, is more complex than these present findings suggest: very limited migration between areas can effectively homogenise gene frequencies, and thus dispersal between areas can still be low even between populations that cannot be genetically discriminated.

Future genetic work should include the examination of more fish from the Indian Ocean because the identification of these fish as a separate stock is based primarily on the analysis of just 21 fish for a single allozyme locus. Further clarification of genetic stock structure issues in yellowfin tuna will require larger sample sizes, examination of more areas (especially from the Indian and Atlantic Oceans), and the deployment of genetic techniques, such as microsatellite analysis, with enhanced resolving power and less concern over neutrality and selection issues.

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Abstract.—The recruited biomass of orange roughy, *Hoplostethus atlanticus*, was estimated for the New Zealand mid-east coast orange roughy stock with the daily fecundity reduction method (DFRM). These fish migrate to Ritchie Bank and spawn between 850 and 900 m for about one month in winter. The biomass of spawning females was estimated by dividing mean daily planktonic egg production, N_0 (eggs/day), by mean daily fecundity, D (eggs/kg per day). The stock biomass was then estimated by multiplying the spawning female biomass by the ratio of all recruited fish to females that would spawn that year, estimated with a wide-area trawl survey made over the stock area two months before the spawning season.

The mean daily planktonic egg production was sampled near the peak of the spawning season, by using a stratified-random plankton survey. Eggs were staged and aged after accounting for their thermal history as they ascended the water column. Because young eggs were damaged by the net and older eggs were affected by advection out of the plankton survey area, relatively few egg stages were available for estimating N_0 (10.9×10^9 eggs/day), and the estimate was somewhat imprecise ($CV=0.46$). Mean daily fecundity (787 eggs/(kg \times day), $CV=0.11$) was estimated from the daily rate of decline in population fecundity per mature female weight (R_f). Fecundity per female weight was estimated from a trawl survey made in the spawning area during the spawning season and was calculated as the mature eggs/kg of active spawners multiplied by the proportion of active spawners in each trawl. Spawning female biomass was 14,000 t ($CV=0.50$), and stock biomass was 26,000 t ($CV=0.50$). Mean daily fecundity was probably under-estimated because spent fish appeared to migrate from the spawning area during the fecundity reduction measurement period and reduce stock biomass to about 18,200 t. The DFRM biomass estimate was of central importance in the introduction of greatly reduced total allowable catch levels in this fishery.

An estimate of orange roughy, *Hoplostethus atlanticus*, biomass using the daily fecundity reduction method

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The orange roughy (*Hoplostethus atlanticus*, Trachichthyidae) fishery on Ritchie Bank on the eastern New Zealand continental slope (Fig. 1) was the second largest orange roughy fishery in New Zealand during the late 1980's and early 1990's, with a total allowable commercial catch (TACC) of about 10,000 metric tons (t) per year. Trends in catch per unit of effort (CPUE) indicated that the stock size was diminishing rapidly under this management regime, although the stock reduction analysis for the fishery did not estimate stock size precisely (Field et al.¹). Experience with other major orange roughy fisheries in New Zealand (the "Box" fishery on northern Chatham Rise and the Challenger Plateau fishery [Fig. 1; Clark, 1995]) indicated that overfishing of the Ritchie Bank stock was likely because of low productivity. However, without adequate knowledge of stock size, it was difficult to set a TACC that would allow a sustainable fishery.

Zeldis (1993) concluded that both the annual egg-production method (AEPM; Saville, 1964; Picquelle and Megrey, 1993; Koslow et al., 1995) and the daily fecundity reduction method (DFRM; Lo et al., 1992; Lo

et al., 1993) would be feasible for the estimation of absolute spawning biomass of orange roughy. A voyage was made to Ritchie Bank from early June to early July, 1993 (*Tangaroa* voyage TAN9306), with the intention of using both types of egg-production survey method. With the AEPM, annual egg production is the sum of daily planktonic egg production estimates made over the entire spawning season from separate subsurveys. Unfortunately, the voyage failed to sample annual egg production for two reasons. First, although the voyage was executed as a series of five subsurveys, two of the subsurveys were not completed because of ship and equipment breakdowns and because of a lack of time at the end of the voyage. Second, the voyage period ended before spawning had finished for the season, so that the annual egg production was not completely sampled.

¹ Field, K. D., R. I. C. C. Francis, and J. H. Annala. 1993. Assessment of the Cape Runaway to Banks Peninsula (ORH 2A, 2B, and 3A) orange roughy fishery for the 1993–94 fishing year. MAF Fisheries, Fisheries Assessment Research Document 93/8. NIWA, Greta Point, Wellington, New Zealand, 17 p.

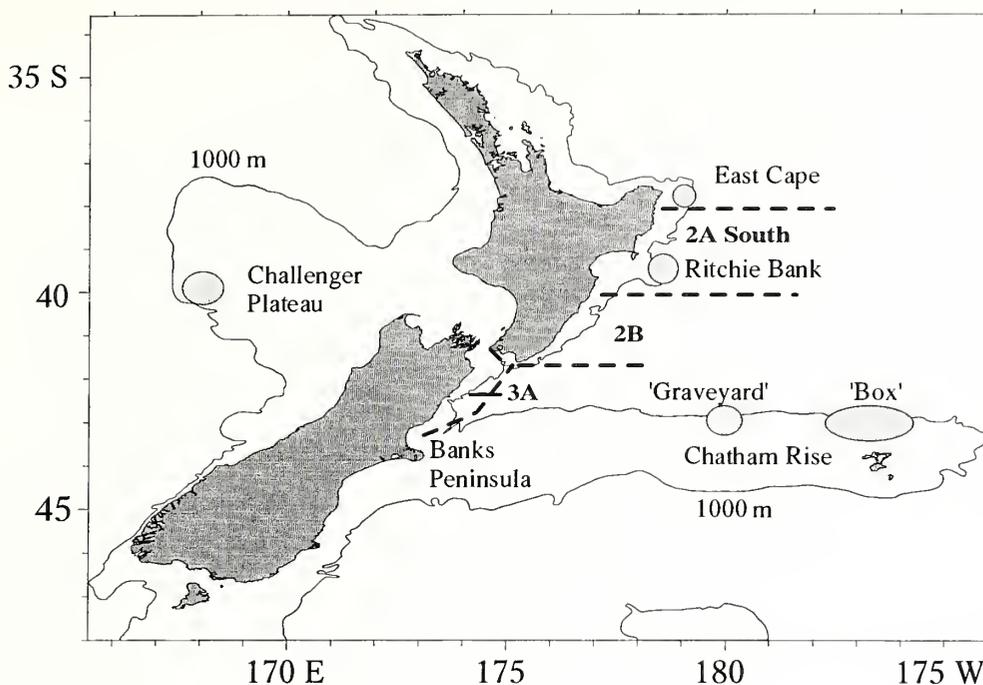


Figure 1

Map of New Zealand and location of spawning grounds (ovals) of orange roughy, *Hoplostethus atlanticus*. Also shown are the areas (2A, 3B, and 3A) of the east coast stock.

Unlike sampling for the AEPM, sampling for the DFRM did not need to cover the entire spawning season, allowing an estimate of spawning female biomass on Ritchie Bank to be produced from the portion of the voyage that did not suffer from ship and equipment breakdowns and that provided adequate data on planktonic egg production and fecundity. The DFRM was used to estimate the biomass of spawning females by dividing the daily planktonic egg production in the survey area (eggs/day) by the daily fecundity of females (eggs/(kg × day)). The biomass of spawning females was scaled by the maturity ogive, sex ratio, and spawning proportion to estimate the recruited biomass (≥ 32 cm standard length) of orange roughy in the stock (where the stock is defined as those fish assumed to spawn on Ritchie Bank). The latter data were taken from a wide-area trawl survey in March–April 1993 (*Tangaroa* voyage TAN9303; Field et al.²), that covered the area inhabited by the stock (Banks Peninsula to East Cape, Fig. 1).

A necessary biological prerequisite for using the DFRM is that the target species has determinate annual fecundity (Hunter and Lo, 1993). This enables total seasonal fecundity to be determined before final maturation so that the fecundity reduction rate can be monitored through the spawning season (Lo et al., 1993). Orange roughy have determinate annual fecundity (Pankhurst et al., 1987; Bell et al., 1992; Zeldis, 1993). Application of egg production methods to orange roughy also is possible, but only if the age of planktonic eggs at morphological stage can be estimated. Ageing of eggs was achieved by developing a model for ageing the eggs as they traversed the thermal gradient in the water column (Zeldis et al., 1995) and by describing the morphological stages of the eggs (Grimes et al.³).

DFRM model

To calculate the biomass of Ritchie Bank spawning females, the daily planktonic egg production in the

² Field, K. D., R. I. C. C. Francis, J. R. Zeldis, and J. H. Annala. 1994. Assessment of the Cape Runaway to Banks Peninsula (ORH 2A, 2B, and 3A) orange roughy fishery for the 1994–95 fishing year. MAF Fisheries, Fisheries Assessment Research Document 94/20. NIWA, Greta Point, Wellington, New Zealand, 24 p.

³ Grimes, P. J., A. C. Hart, and J. R. Zeldis. 1997. Embryology and early larval development of orange roughy (*Hoplostethus atlanticus* Collett). Unpubl. data.

survey area was divided by the daily fecundity/kg of the females:

$$B_{spf} = N_0 / (1,000D),$$

where B_{spf} = biomass of spawning females (tons);
 N_0 = daily egg production, (eggs/day);
 D = mean daily fecundity (eggs/(kg × day))
 for mature fish; and the factor 1,000
 converts kg to tons.

The recruited biomass, B_{rec} (defined as the biomass of fish of length ≥ 32 cm) was calculated from the biomass of Ritchie Bank spawning females, B_{spf} , as

$$B_{rec} = B_{spf}S,$$

where the scalar (S) was an estimate of the ratio B_{rec}/B_{spf} . This ratio allows for recruited females that did not spawn, females that did spawn but were < 32 cm, as well as the sex ratio.

To estimate the parameters of the above biomass model, the data analysis deals with three distinct data sets:

- daily planktonic egg production;
- daily fecundity per female weight; and
- proportions spawning, recruited, and female.

Daily planktonic egg production

Survey design The timing of plankton sampling coincided with the period when orange roughy females on the Ritchie Bank were in late maturation or spawning stages (mid-June to the end of the first week of July; Pankhurst, 1988). The location of plankton sampling was determined from research trawl catch rates (Fincham et al.⁴), which showed adult biomass to be highly aggregated on Ritchie Hill⁵ (Fig. 2, A and B) at the northern end of Ritchie Bank. Ritchie Hill catch rates accounted for 84% of the relative orange roughy biomass over the Ritchie Bank survey area in July 1986 (Fincham et al.⁴). In plankton sampling during the spawning season on Ritchie Bank in early July 1986,⁶ orange roughy eggs were

caught only at stations near Ritchie Hill, and samples taken ≥ 20 km away contained no eggs, indicating that eggs were aggregated near the spawners (Zeldis, 1993) and that plankton sampling would need to be highly concentrated near Ritchie Hill.

During their first 36 hours of development, orange roughy eggs ascend the water column at 300–350 m/day from a spawning depth of about 850 m (Zeldis et al., 1995). Geostrophic currents over Ritchie Bank during July 1986⁶ were to the south and averaged about 12 cm/sec between 700 m and 250 m; these currents would displace these eggs at least 15.5 km to the south of Ritchie Hill by the time the eggs had reached 36 h of development (this is a minimum estimate because there was probably some residual flow at the postulated level of no motion at 700 m). Considering that drift would probably vary in direction and speed but would lie predominantly along isobaths, we designed the survey area with eight strata, elongated alongshore and arranged symmetrically around a central stratum centred over the top of Ritchie Hill (Fig. 2B). This central stratum (10.0 × 7.6 km) was about the size of the area of high fish density observed during a trawl survey done in the area in June–July 1987 (Grimes⁷). The middle layer of four strata surrounding the central stratum had outer boundaries of 18.5 × 13.7 km. These dimensions were chosen to approximate the distance at which catch rates of 1-day-old orange roughy eggs on the St. Helen's seamount in eastern Tasmania were reduced to half (9.3 km from the spawners [Koslow⁸]). The outer layer of four strata had an outer boundary 40.0 × 30.0 km long, to allow for maximal drift of 36-h-old eggs.

The St. Helen's data were used to estimate optimal allocation of stations to Ritchie Hill strata. The St. Helen's data were collected over an entire spawning season, in six separate subsurveys, each of which had two spatial strata. The counts in each St. Helen's subsurvey and stratum were standardized such that their means equalled the mean across all of the subsurveys for each stratum. This procedure removed the within-season variation in mean egg density in each stratum. These standardized data were then laid over the Ritchie Bank stratum layers (central, middle, and outer), and mean egg densities (M_j) were estimated for each stratum layer, j . To allocate sta-

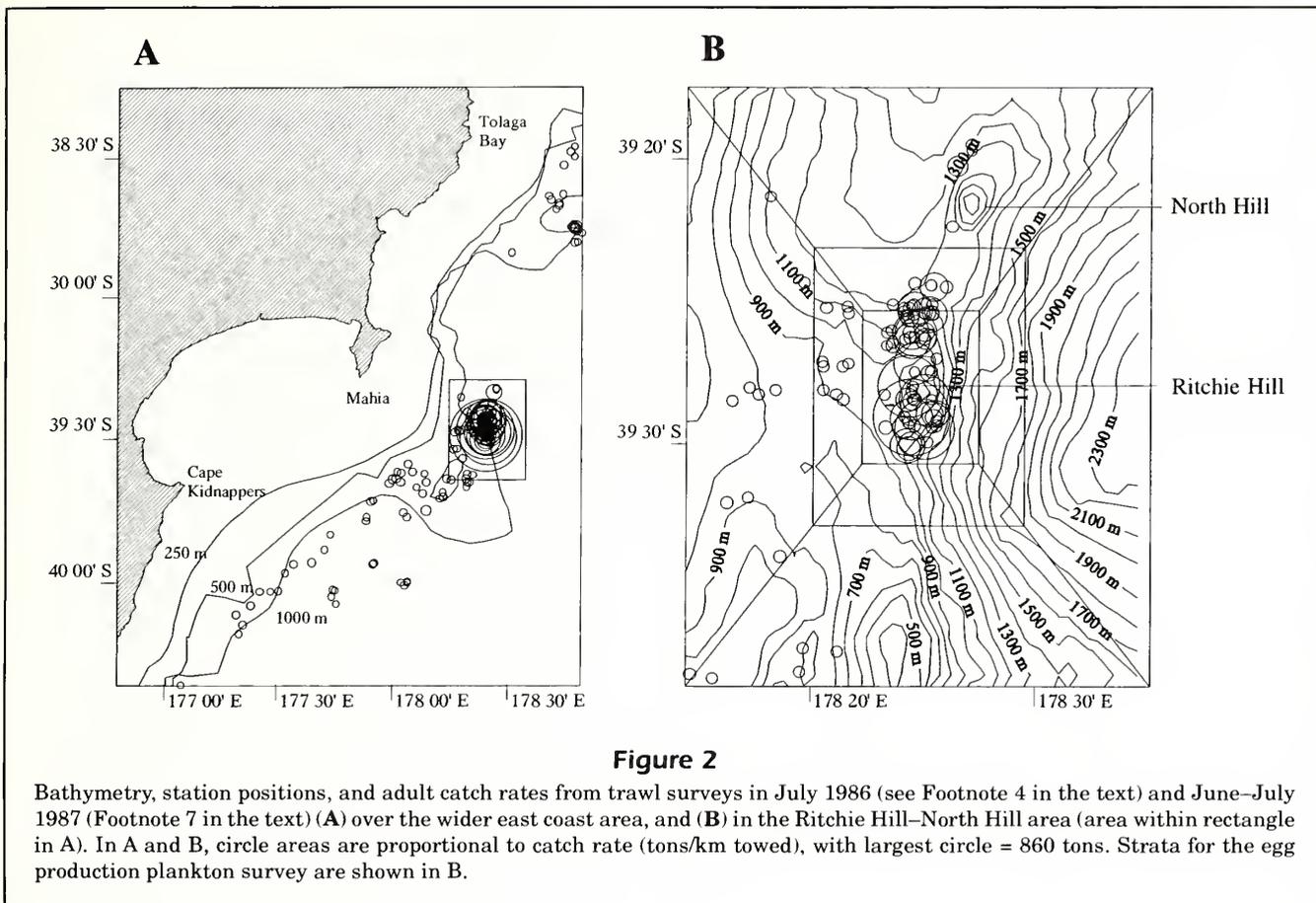
⁴ Fincham, D. J., D. A. Banks, and P. J. McMillan. 1987. Orange roughy trawl survey, Tolaga Bay to Cape Turnagain, 14 June to 11 July 1976: cruise report. Fisheries Research Division Internal Report 60. NIWA, Greta Point, Wellington, New Zealand, 38 p.

⁵ The names "Ritchie Bank," "Ritchie Hill," and "North Hill" used in this paper refer to the features called "Ritchie Ridge," "Calyptogena Bank," and "Pantin Bank," respectively, in the following: Arron, E. S., and K. B. Lewis. 1992. Mahia, 2nd ed. N.Z. Oceanogr. Inst. Chart, Coastal Series, 1:200,000. NIWA Greta Point, Wellington, New Zealand.

⁶ Zeldis, J. R. 1986. Cruise report J08/86 (second half). MAF Fisheries unpublished cruise report held in NIWA Library, Greta Point, Wellington, New Zealand, 7 p.

⁷ Grimes, P. 1987. NIWA, P.O. Box, 14-901, Kilbirnie, Wellington, New Zealand. Unpubl. data.

⁸ Koslow, T. 1992. CSIRO Division of Fisheries, GPO Box 1538, Hobart, Tasmania 7001, Australia. Personal commun.



tions optimally in a survey of size N stations, n_j stations were allocated to each stratum layer such that

$$n_j \propto A_j M_j$$

and

$$\sum_j n_j = N,$$

where A_j = the area of each stratum layer.

Allocation was done in proportion to the strata means (M_j) because they were highly correlated with the strata standard deviations and were probably estimated more reliably than the standard deviations (Francis, 1984). To estimate values of N that would yield a desired coefficient of variation for egg abundance estimates, the standardized counts in each stratum layer were randomly sampled with replacement (bootstrapped) to estimate M_j , where the number of samples taken from each stratum was n_j . The survey mean egg abundance combined across all strata, E , was estimated as

$$E = \sum_j M_j A_j.$$

This procedure was repeated 500 times and the mean of the 500 survey estimates was taken as the egg abundance estimate. The standard deviation of the 500 estimates divided by the mean was taken as the coefficient of variation of the egg abundance estimate.

This analysis suggested that the optimal allocation would have stations allocated to the central, middle, and outer strata in ratios of 1.5:0.38:0.25, respectively. It also suggested that 400 stations would provide adequate precision ($CV=0.15$) in the egg abundance estimate. Therefore, for the AEPM design, five 80-station subsurveys were planned with stations allocated to strata in the above ratios.

Using simulations, we found that by occupying stations within each stratum in an order which minimized steaming distance between stations, before moving to a new, randomly chosen stratum, about 50% less steaming time would be involved than by occupying stations in completely random sequence in each subsurvey. This procedure would be done, however, at the cost of variable (and possibly long) periods of no coverage of each stratum between subsurveys and could be a serious drawback if spawning intensity varies significantly and rapidly (over a few days) during

the spawning season, especially for coverage of the central stratum. To counteract this, the stations in the central stratum were divided randomly between two time strata to reduce the time between occupation of this high-density stratum between subsurveys.

In the DFRM analysis, the plankton samples used for the estimation of egg production were from two consecutive AEPM subsurveys that were occupied near the peak of the spawning season and that were not subject to "downtime" from ship and equipment failures. These two subsurveys had no time break between them and were treated as a single survey, in which the central stratum was occupied four times and each of the surrounding strata was occupied twice. The plankton sampling in the entire survey was done from 14 June to 7 July, and the two subsurveys used in the DFRM analysis were done from 28 June to 6 July (subsurveys 3 and 4).

Egg sampling and staging, count standardization, and production estimation The plankton net used in sampling had a cylinder-cone design with 900- μ m mesh, a mouth area of 2 m², and was fitted to a 125-kg flat-steel ring. It was designed to be efficient, with the ratio of the open area in the mesh to mouth area being >5:1 (Tranter and Smith, 1968). The net was deployed from a starboard crane while the ship was stationary (i.e. not under power) and its starboard side faced the wind. The winch had dynamic tensioning, to minimize surging of the net as a result of the rolling motion of the ship. Tow depths were within 30 m of the bottom to the surface if the bottom was less than 950 m and from 850 m if the bottom was deeper than 950 m. A conductivity-temperature-depth (CTD) probe or a net sonde within the mouth of the net was used to measure net depth. Warp payout was measured with winch instrumentation. Warp payout and recovery rates were 1 m/sec, also measured with winch instrumentation.

Eggs were staged (Grimes et al.³) on board, prior to preservation, and generally within 0.5 h of landing the net, except for two samples with many eggs. For these, staging was done partly on board and partly in the laboratory on 4% formaldehyde-preserved eggs. All eggs \leq stage 7 (32-cell) were grouped, because it was not possible to identify with confidence the stages from germinal disk through 32 cells within the plankton samples because most of these younger eggs were damaged (76% of the 8,293 eggs \leq stage 7), which caused the cell walls of the embryos to rupture, the cells to fuse, and the perivitelline space to collapse. Justification for assuming that the damaged eggs were all \leq stage 7 are given in Zeldis et al. (1995) and Grimes et al.³

The standardization from egg count to egg density (eggs/m²) was based on the formula $density = count$

\times correction factor, where the correction factor takes into account the mouth area of the net and the volume of water filtered by it. With a vertical haul, the correction factor is 0.5 (because the net mouth area=2 m²). However, because the vessel almost always drifted (owing to wind and current) during shooting and hauling, hauls were not vertical and therefore the correction factors were almost always <0.5. Distance towed was not estimated by using flowmeters because flowmeters were found to record spurious revolutions during the deployment (descent) phases of tows in subsequent tests (Grimes⁹). Instead, to calculate the volume of water filtered by the net, it was necessary to use global positioning satellite (GPS) vessel positions, warp length, depth, and current velocities to infer the path of the net (which, because of the ship's drift, would be curved in the vertical dimension during hauling; Appendix 1).

With a curved net trajectory, there was a different correction factor for each combination of plankton tow and egg stage because the different egg stages occupied different depths as they ascended the water column and because the net sampled more water in layers of equal thickness in the upper water column than in the lower column. To calculate egg age and depth range (Table 1), data on egg development rate as a function of temperature, buoyancy by egg stage, and temperature as a function of depth were

⁹ Grimes P. 1996. NIWA, P.O. Box 14-901, Kilbirnie, Wellington, New Zealand. Unpubl. data.

Table 1

Egg age (h) and depth (m) ranges used in calculating correction factors for count standardization for Ritchie Bank plankton samples. Egg stages are described in Grimes et al. (Footnote 3 in the text).

Stage	Min. age	Max. age	Max. depth	Min. depth
0	0.0	0.0	850	725
1	0.0	5.1	850	784
2	5.1	8.2	784	743
3	8.2	11.2	743	704
4	11.2	14.0	704	667
5	14.0	16.7	667	631
6	16.7	19.3	631	596
7	19.3	21.8	596	563
8	21.8	24.1	563	531
9	24.1	26.3	531	500
10	26.3	28.4	500	470
11	28.4	33.4	470	400
12	33.4	40.0	400	301
13	40.0	45.5	301	216
14	45.5	50.2	216	143
15	50.2	54.3	143	78

used with the methods of Zeldis et al. (1995) and the Ritchie Bank CTD temperature profiles described below. Ritchie Bank temperatures were within the range of those observed in Zeldis et al. (1995). Current velocities as a function of depth were calculated from geostrophic velocity profiles (Pond and Pickard, 1978) by using Guildline CTD profiles taken over Ritchie Bank. A reference depth of no motion at 1,000 m was assumed, and geostrophic velocities at 100 m were corrected to match the 100-m velocities measured by a buoy drogued to that depth. This buoy was deployed over Ritchie Hill on 28 June 1993, re-located 20 hours later, and subsequently lost.

Correction factors were to convert egg counts to densities were also calculated (assuming the trajectory of the net was straight) for comparison with those where a curved trajectory was assumed. For this, the volume filtered v (m^3) was estimated by using

$$v = 2\sqrt{p^2 + z^2},$$

where p = the distance the ship drifted from deployment to recovery of the net, determined with GPS;

z = the maximum depth of the net; and

factor 2 = the area (m^2) of the net mouth.

It was assumed that, at the start of hauling, the net was at the position of the vessel when deployment commenced, i.e. the net dropped vertically through the water during deployment.

Estimates of egg abundance by age group in the survey area (N_a) were calculated by multiplying the mean egg density at age in each stratum by stratum area and by summing across strata. In the case of the time strata in the center of the survey area, the egg abundances were averaged before summing with the other strata. The CV of N_a was calculated by using the standard deviation of egg density at age and stratum, weighted by stratum area. The average of the standard deviations was used in the case of the central time strata.

The maximum age of eggs that could be used in estimating daily egg production was the maximum age for which there appeared to be no significant advection out of the survey area owing to water movements (a loss of eggs by advection would cause a negative bias in N_a). Advection was examined by plotting centroids of each age group (Appendix 2) and by using the buoy and CTD data described above.

The daily egg production, N_0 (eggs/day), and instantaneous mortality for eggs, Z (per day), were estimated by maximum likelihood with the mortality model

$$N_a = N_0 e^{-zt},$$

where t = the mean age (days) of age group a (Appendix 3).

The precision of these estimates was estimated by a bootstrap procedure (Appendix 3).

Daily fecundity per female weight

Survey design Female fecundity and ovarian stage samples were taken from trawls from the RV *Tangaroa* on Ritchie Bank from 7 June–6 July and from commercial vessels on 22 June, 11 July, and 13 July (Table 2). Trawling was done during the week before spawning started (8–11 June), to sample total annual fecundity for the AEPM, and from the start of spawning until spent fish were common (20 June–13 July), to sample fecundity reduction for the DFRM. Twenty five of the trawls were from Ritchie Hill (within the area of the central stratum in Fig. 2B) and three were from North Hill, a spur off the north end of Ritchie Bank, about 12 km north of Ritchie Hill (Fig. 2B) where fish were spawning.

Oocyte sampling, ovarian staging, and daily fecundity estimation The oocytes of 569 mature fish (about 35 fish/trawl) in macroscopic ovarian stages 3 (late vitellogenic, prespawning), 4 (hydrated), 5 (ovulated), or 8 (late vitellogenic, partially spent) were counted. Of these, 218 fish were prespawning and used for total annual fecundity analysis. The remainder were used for DFRM analysis. Oocytes were counted by using the automated system described in Appendix 4.

The proportions of females in ovarian stages 3, 4, 5, and 8, and stage 6 (spent) in the trawl samples were estimated by using macroscopic ovarian staging of about 100 randomly chosen females per trawl.

The ovarian stages were further grouped because it was observed that stages 3 and 4 (group 1) had higher fecundities/kg than stages 5 and 8 (group 2); this difference was due to fish in group 2 having started spawning. Therefore, the estimate of fecundity per female weight, R_i , was stratified by these groupings to minimize error. Stage-6 fish (spent) were placed in group 3. Thus, R_i was estimated as the mean number of eggs/kg of all females that would spawn, were spawning, or were spent, for trawl i :

$$R_i = \frac{\sum_{j=1}^2 n_{ij} r_{ij}}{\sum_{j=1}^3 n_{ij}}$$

Table 2

Trawl stations used for estimation of total annual fecundity for the AEPM and fecundity reduction for the DFRM June–July 1993 on Ritchie Hill (R. Hill) and North Hill (N. Hill) (Fig. 2B). Catches taken on 22 June and 11 and 13 July were from commercial tows and catch sizes were unknown. No. staged = number of fish staged; Immat. = immature; Prop. active = proportion of active fish.

Date	Site	Catch (kg)	No. staged	Immat.	Stage 3	Stage 4	Stage 5	Stage 8	Stage 6	Prop. active
AEPM										
8 Jun	R.Hill	67	26	0	24	2	0	0	0	1.00
8 Jun	R.Hill	30	9	0	8	1	0	0	0	1.00
9 Jun	R.Hill	980	95	0	78	15	0	0	2	0.98
9 Jun	R.Hill	980	95	0	78	15	0	0	2	0.98
11 Jun	R.Hill	35	10	0	9	1	0	0	0	1.00
11 Jun	R.Hill	239	88	2	70	11	3	2	0	1.00
11 Jun	N.Hill	7,494	165	2	125	33	4	1	0	1.00
11 Jun	R.Hill	549	81	1	67	13	0	0	0	1.00
14 Jun	R.Hill	122	41	1	28	7	4	1	0	1.00
14 Jun	R.Hill	103	31	3	22	5	0	1	0	1.00
14 Jun	R.Hill	573	75	0	51	17	3	4	0	1.00
15 Jun	R.Hill	1,195	77	0	51	21	1	4	0	1.00
15 Jun	R.Hill	82	23	0	10	8	2	3	0	1.00
16 Jun	R.Hill	47	14	1	9	2	0	2	0	1.00
16 Jun	N.Hill	3,634	63	1	25	23	10	3	1	0.98
17 Jun	R.Hill	21,478	214	0	90	96	24	4	0	1.00
17 Jun	R.Hill	215	63	2	30	21	9	1	0	1.00
DFRM										
20 Jun	R.Hill	23,535	139	0	31	85	22	1	0	1.00
22 Jun	R.Hill	unknown	107	0	19	83	4	1	0	1.00
27 Jun	R.Hill	7,218	83	0	6	26	39	10	2	0.98
27 Jun	R.Hill	33,975	227	0	10	128	78	8	3	0.99
30 Jun	R.Hill	19,405	135	0	3	50	69	8	5	0.96
2 Jul	R.Hill	7,797	45	0	3	12	22	5	3	0.93
4 Jul	R.Hill	2,936	147	0	1	67	50	13	16	0.89
6 Jul	N.Hill	25,400	56	0	0	7	27	10	12	0.79
6 Jul	R.Hill	402	83	0	0	2	57	19	5	0.94
11 Jul	R.Hill	unknown	31	0	0	2	15	3	11	0.65
13 Jul	R.Hill	unknown	77	0	0	6	31	11	29	0.62

where n_{ij} = number of fish of ovarian group j at station i ; and
 r_{ij} = mean fecundity (eggs/kg) of fish of ovarian group j at station i .

The mean fecundities/kg of fish of ovarian groups 1 and 2 (r_{ij}) were estimated as

$$r_{ij} = \frac{\sum_{k=1}^{m_{ij}} e_{ijk}}{\sum_{k=1}^{m_{ij}} w_{ijk}}$$

where e_{ijk} = total fecundity of the k th fish of group j in the fecundity sample from station i (adjusted by the gonad wall proportions of total ovary weight in Appendix 4);

w_{ijk} = body weight (kg) of the k th fish of group j in the fecundity sample from station i ; and
 m_{ij} = number of fish of group j in the fecundity sample from station i .

The R_i 's from the 11 DFRM trawls were fitted with a linear regression against time (weighted by the total number of fish in the ovarian-stage sample for each R_i) to estimate D , which is the mean daily fecundity (eggs/(kg × day)) for mature fish. The CV of D was estimated as the standard error of the slope of the regression, divided by the slope.

Biomass of spawning females

The biomass of spawning females B_{spf} was calculated by using the DFRM model given above. The CV of

B_{spf} was determined from the standard error of 1,000 estimates of B_{spf} , formed by dividing the 1,000 estimates of N_0 (Appendix 2) by 1,000 normally distributed estimates of D , formed from the mean and standard error of D .

Proportions spawning, recruited, and female

The scaling factors needed for converting the biomass estimate of Ritchie Bank spawning females to one for recruited fish (≥ 32 cm SL for both sexes) for the entire mid-east coast stock were estimated from the March–April 1993 wide-area east coast trawl survey (Field et al.²), instead of from the trawl data gathered at the time of the egg survey, for two reasons. First, not all recruited fish spawn each year (and thus may not migrate to Ritchie Hill). Second, a more precise estimate of sex ratio is available from the trawl survey than from the relatively few trawls carried out during spawning (when sex ratios are most variable; Zeldis, 1993). The trawls from the wide-area survey used for the scaling factors were those from over the entire mid-east coast survey area, from just north of Ritchie Bank, south to Banks Peninsula (Fig. 1; quota management areas 2A South, 2B, and 3A, respectively). This is the likely distribution of the stock that migrates to the Ritchie Bank to spawn.¹⁰ No spawning orange roughy have been located in areas 2B or 3A, and genetic data show that orange roughy from these three areas cannot be separated, whereas they are genetically distinct from orange roughy on Chatham Rise (Fig. 1).

Stage-3 (late vitellogenic) females in each trawl in the 1993 wide-area trawl survey were assumed to be those that would spawn that year (Bell et al., 1992). Because ovaries of stage-3 females are indistinguishable macroscopically from ovaries of fish in which massive atresia has occurred (Bell et al., 1992), the macroscopic staging was checked by histological examination of about 20 stage-3 fish collected on each day of the 28-day trawl survey.

Recruited biomass

The scalar (S) was calculated as

$$\frac{\sum_i (P_{rec,i} C_i \frac{A_i}{n_i})}{\sum_i (P_{spf,i} C_i \frac{A_i}{n_i})}$$

where $P_{rec,i}$ and $P_{spf,i}$ = the proportions (by weight) of recruited fish and spawning (stage-3) females, respectively, in the catch from the i th trawl;

C_i = the catch rate (t/nmi) at the i th trawl;

A_i = the stratum area for the stratum containing the i th trawl; and

n_i = the number of trawls for the stratum containing the i th trawl.

The precision of the estimates of S was estimated by using the following bootstrap procedure. For each trawl, the triplet ($X_i, P_{rec,i}, P_{spf,i}$) was calculated, where $X_i = C_i A_i / n_i$. One thousand simulated data sets were generated by drawing triplets at random with replacement. Each simulated survey contained the same number of trawls as the area of the original trawl survey. For each simulated survey a bootstrap estimate of S was calculated as

$$\frac{\sum_i (P_{rec,i} X_i)}{\sum_i (P_{spf,i} X_i)}$$

The bootstrap estimates of S were used to calculate a CV for S .

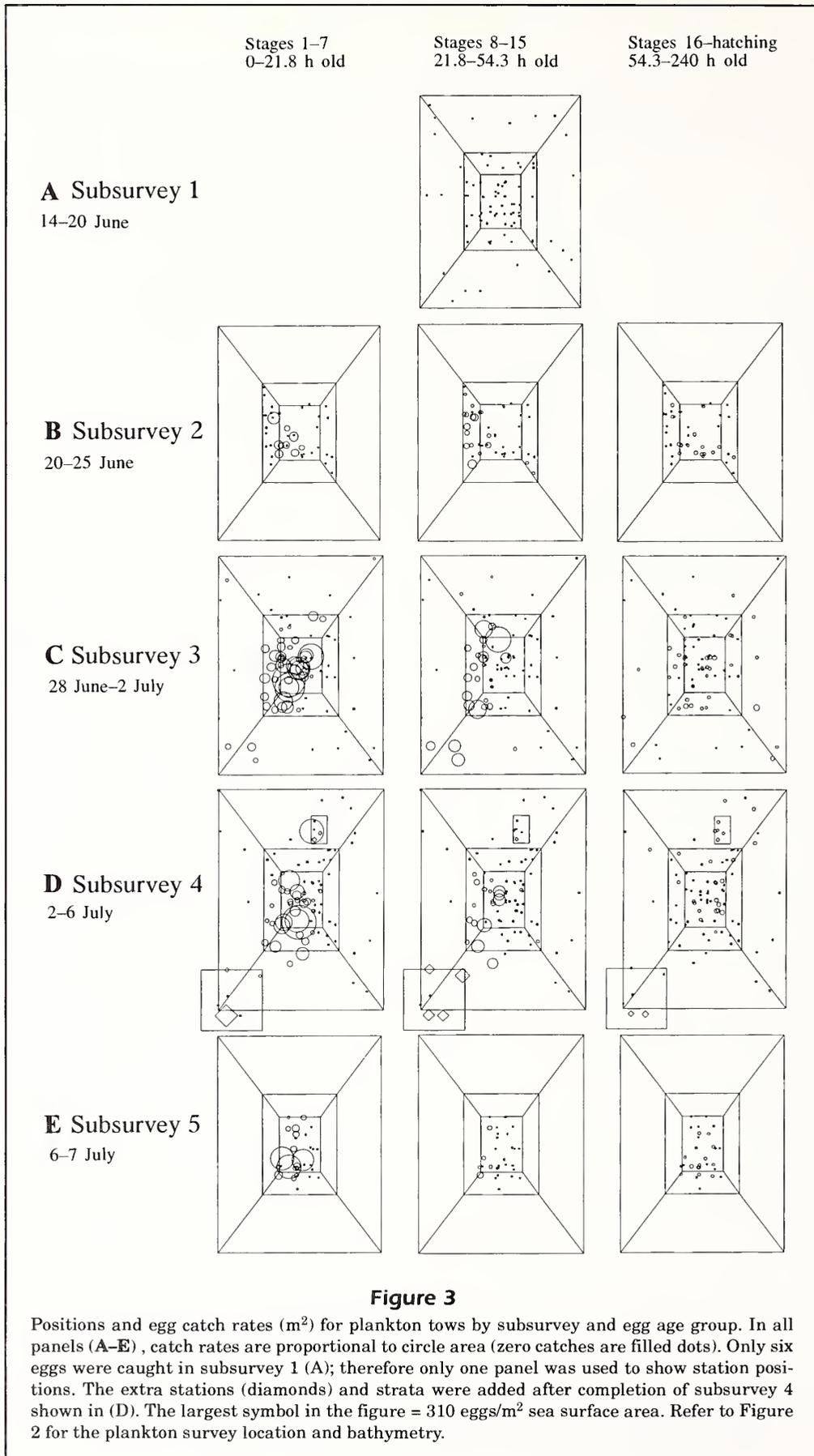
The recruited biomass, B_{rec} , was calculated by using the DFRM biomass model given above. The bootstrap estimates for S were combined with the bootstrap estimates of B_{spf} to obtain a CV for B_{rec} .

Results

Daily planktonic egg production

Planktonic eggs were first captured in very low numbers on 15 June during subsurvey 1 (Fig. 3). Egg abundance remained low until the end of subsurvey 2 (25 June). This subsurvey was prolonged by ship and sampling-equipment breakdowns, and only the central strata, two of the middle strata, and none of the outer strata were sampled. The breakdowns prevented further sampling until the start of subsurvey 3 on 28 June, when large quantities of eggs were captured. Catches then decreased during subsurvey 4 (ending 6 July). Sampling of subsurveys 3 and 4 was completed. In subsurvey 5, only the central stratum and one middle stratum were occupied before the scheduled survey period ended on 7 July. Egg production continued at this time.

¹⁰ Annala, J. H., and K. J. Sullivan (compilers). 1996. Report from the Fishery Assessment Plenary, April–May 1996: stock assessments and yield estimates, 308 p. Unpubl. report held in NIWA Library, Wellington, New Zealand.



Data from the completed subsurveys 3 and 4 showed that egg catches were highest in the central and middle strata (Fig. 3, C and D). These eggs were predominately in the young, grouped-age category (stage 7 or less, ≤ 21.8 h old; Table 1), but many middle-aged and some older eggs were also caught in these strata. A few orange roughly yolk-sac larvae were also caught in the central and middle strata. These high catch rates for eggs were spatially correlated with high research trawl catch rates for adults (Fig. 2, A and B; Table 2). Catches in the outer strata were usually < 10 eggs/tow or zero eggs/tow. However, there was one large catch of young eggs near North Hill (Fig. 3D), on which relatively large catches of spawning adults were made with research trawling (Table 2) and commercial trawling. All of the undamaged eggs in this sample (19% of all eggs) were at the 1-cell stage, indicating that these eggs arose from localized spawning on North Hill. Four additional random tows were then made within an extra stratum created in this area (Fig. 3D) at the end of subsurvey 4. Only 5 additional eggs in total were caught in these tows, indicating that egg production on North Hill was low compared with that on Ritchie Hill.

A few moderate egg catches were also made in the southwestern corner of the survey area (Fig. 3, C and D). Most of these eggs (84%) were $>$ stage 7. Four additional tows were then made within an extra stratum created in this area (Fig. 3D) at the end of subsurvey 4, and in three of these tows, all eggs were $>$ stage 7. The fourth sample had many damaged eggs (\leq stage 7), but it was likely that these were at the older end of the age range of "young" eggs, judging by the stages of undamaged young eggs in that sample (all were \geq stage 5). The bottom in the area where these samples were taken (Fig. 2B) is deeper ($> 1,000$ m) than depths at which orange roughly normally spawn (850–900 m), and trawl catch rates in the area were very low in this survey and in previous surveys (Fig. 2, A and B). This finding indicated that these eggs had not been produced locally, but rather had been advected from the main spawning center on Ritchie Hill.

The positions of the centroids (centers of gravity) of successive egg age groups suggested that advection was initially to the southwest out of the survey area (Fig. 4A) but that older eggs (those of the very-broad-age-group stage 16+, ≥ 54.3 h old; Table 1) re-entered the area, possibly from the east. In interpreting Figure 4, it is important to realize that centroids close to the boundary of the survey area were unlikely because only eggs from within the survey area were used in the calculation of centroid position. An estimate of the average rate of advection, at

the depths of these egg stages, was calculated by dividing the distance between the centroids of stages ≤ 7 and 11 by the difference between the mean ages in these two age groups (Appendix 3) and was found to be 7.4 cm/sec.

The distribution of eggs by age within the survey area (Fig. 4, B and C) confirmed the southwesterly drift pattern. Eggs \geq stage 11 (≥ 28.4 h old) became increasingly centered in the southwestern corner of the survey area (region 1, Fig. 4, B and C). However, the old eggs in the stage 16+ group were most abundant in the eastern and central regions (Fig. 4, B and C).

The advection inferred from egg distributions can be compared with hydrographic results. The drogued buoy was relocated 11.2 km south-southwest (bearing= 207°) of the release site after 20 h at liberty (Fig. 5A), indicating that advection (at 100 m depth) was to the south-southwest, at a rate of 16 cm/sec. Geostrophic analysis of the CTD data (Fig. 5, A–D) indicated that in the northern part of the station grid (in the vicinity of the Ritchie Hill spawning site), current directions turned from south-southeast through south to southwest as depth increased from 100 through 400 to 800 m. The southwestern component of current velocity between 800 and 400 m (the approximate depth range of eggs \leq stage 11; Table 1) in the vicinity of Ritchie Hill averaged about 7 cm/sec (Fig. 5D). Geostrophic current speeds averaged about 12–13 cm/sec in the upper 100 m of the water column, in the vicinity of Ritchie Hill. These speeds were probably underestimates because the velocity profiles showed little evidence of reaching asymptotically low values as the postulated level of no motion (1,000 m) was approached (Fig. 5D), suggesting that some residual velocity existed at that level. This may explain the greater buoy speed than geostrophic speed at 100 m. Current speeds toward the southwest (Fig. 5D) were higher on the northern side of the grid than on the southern side through the upper water column; a significant easterly component was observed in the upper 200 m.

Thus, the advection pattern indicated by egg centroids and stage distributions (Fig. 4, A and C) was consistent with results from the drogued buoy (Fig. 5A) and the geostrophic analysis (Fig. 5, A–D), which indicated that the direction of drift of young eggs in the lower half of the water column was toward the southwest. The geostrophic velocities in the lower half of the water column in the vicinity of Ritchie Hill (at least 7 cm/sec) were consistent with the velocity of egg advection (7.4 cm/sec) from our calculations. The older eggs, which would have spent most of their time in the mixed layer (Zeldis et al., 1995), might have been conveyed into the survey area from

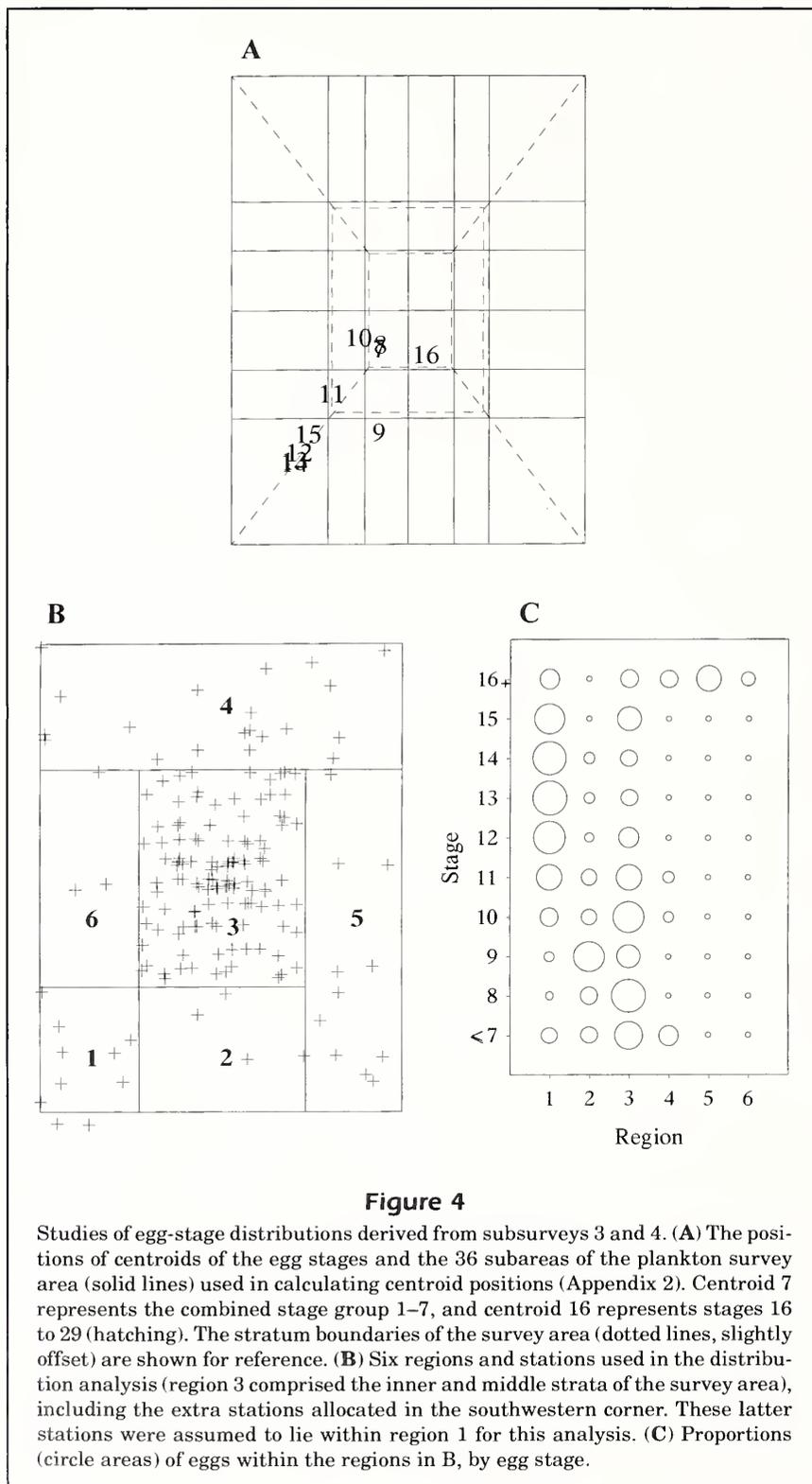
the east by a return flow in the upper water column to the south and east of Ritchie Hill.

Egg abundances over the survey area during subsurveys 3 and 4 were calculated by using the

curved and straight trajectory assumptions (Table 3). The ratios of the curved and straight abundances generally decreased with egg stage. This decrease was expected because the curved trajectory is nearer

to vertical deeper in the water column (where the younger eggs are) than shallower in the column (where the older eggs are). The curved and straight trajectories tended to be nearly parallel in shallower water.

Because eggs were advecting into the southwestern corner of the survey area (region 1, Fig. 4C) by the time they reached stage 11, only stages ≤ 10 were used in the estimation of daily egg production. The criterion used for this cutoff stage was that all stages \geq the first stage to have $>20\%$ of their abundance in region 1 would be excluded from the analysis. This criterion was reached at stage 11. Using the abundance data calculated by assuming a curved net trajectory (Table 3), we estimated that egg production was $N_0 = 10.9 \times 10^9$ eggs/day (CV=0.46) and that the mortality-rate estimate was $Z = 0.70$ /day (CV=0.69) (Fig. 6; Table 4). These calculations used the extra strata at North Hill and in the southwest, and all stations in subsurveys 3 and 4 falling within these strata were considered to have been originally selected within them. The N_0 estimated by assuming a straight trajectory was 8.0×10^9 eggs/day (CV=0.49) with $Z = 0.56$ (CV=0.88). In the remaining analyses, the N_0 value calculated by assuming a curved trajectory was used because this value was likely to be a better approximation to the truth than that obtained by assuming a straight trajectory.



Daily fecundity of females

The proportions of females in each ovarian stage in each DFRM trawl (Fig. 7) showed that the female population was, at first, nearly all in the prespawning state (stage 3). Maxima of hydrated, ovulated, and

spent proportions followed at approximately 10–15 day intervals. Serial spawning was evident in that partially spent, hydrated, and ovulated proportions became fairly constant during a 10-day period (roughly 25 June–5 July) when ovaries of the fish were developing among these stages. Hydration did not appear to be associated with imminent spawning, because significant proportions (0.15) of hydrated fish were present about 5 days before planktonic eggs were first caught on 15 June. However, the first appearance of significant proportions (>0.05) of ovulated fish (14 June) and planktonic eggs (15 June) nearly coincided.

The decline in R_i (Fig. 8) or the daily fecundity per female weight, D , was 787 eggs/(kg × day) (CV = 0.11; Table 4).

Ritchie Bank spawning female biomass

When N_0 was divided by D , the estimate of B_{spf} was 14,000 tons (Table 4), with CV = 0.50.

Biomass of recruited orange roughy in the mid-east coast stock

The factor S was estimated to be 1.77, with CV = 0.03. However, histology showed that for 4.5% of the females identified as spawners in the wide area trawl survey, their entire exogenous vitellogenic oocyte complement was actually in the process of atresia (Bell et al., 1992). These fish were indistinguishable macroscopically from fish that would spawn successfully and did not appear to cluster in any particular area of the trawl survey. The factor S was scaled upward to account for these fish, resulting in $S = 1.85$ (Table 4).

The resulting estimate of B_{rec} was 26,000 t (Table 4), with CV = 0.50. The bootstrap procedure used may have slightly overestimated the CV of S because it did not fully take into account the stratum structure of the wide-area survey. However, this overestimation is of little importance because the CV of S was so much smaller than that of the other components that made up the CV of B_{rec} (Table 4).

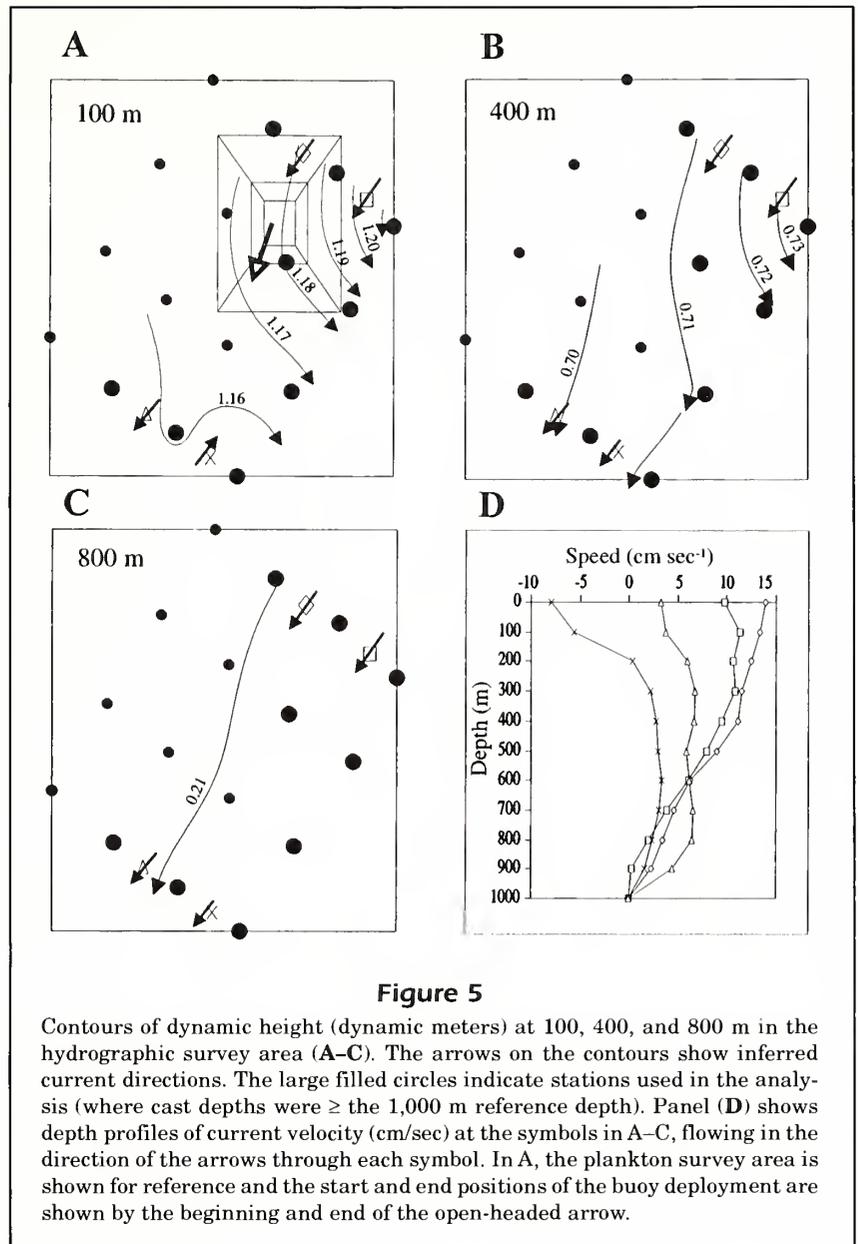


Figure 5
Contours of dynamic height (dynamic meters) at 100, 400, and 800 m in the hydrographic survey area (A–C). The arrows on the contours show inferred current directions. The large filled circles indicate stations used in the analysis (where cast depths were \geq the 1,000 m reference depth). Panel (D) shows depth profiles of current velocity (cm/sec) at the symbols in A–C, flowing in the direction of the arrows through each symbol. In A, the plankton survey area is shown for reference and the start and end positions of the buoy deployment are shown by the beginning and end of the open-headed arrow.

Bias due to turnover

An important potential bias in the DFRM arises from the fact that the method is sensitive to turnover of fish on the spawning ground. For example, if fish arrive, complete spawning, and leave the trawl survey area *before* or *after* the trawl survey period, fecundity will be undetected and biomass will be underestimated. These effects were unlikely, however. Almost no eggs were caught in the first subsurvey (Fig. 3A), and very few spent fish were detected in trawls on Ritchie Hill until 2 July (Fig. 7). This finding suggested that no spawning was completed before the trawl survey began (8 June). In addition,

Table 3

Abundances of eggs ($\times 10^{-6}$) and coefficients of variation (CV) at stage, during DFRM planktonic egg survey, calculated with curved and straight net trajectory assumptions. Also given are the ratios of curved and straight abundances.

Stage	Curved abund.	CV	Straight abund.	CV	Ratios
≤7	7,036	0.26	5,453	0.28	1.29
8	487	0.40	424	0.43	1.15
9	673	0.60	451	0.51	1.49
10	316	0.43	276	0.49	1.15
11	400	0.24	351	0.26	1.14
12	1,420	0.32	1,276	0.32	1.11
13	740	0.23	716	0.24	1.03
14	276	0.38	260	0.37	1.06
15	34	0.42	38	0.38	0.90

proportions of macroscopic stage-3 (vitellogenic) fish declined to 5% by the midpoint of the trawl survey period and to 0% by the end; stage-4 (hydrated) fish showed a similar decreasing trend. Thus no prespawning fish were present at the end of the trawl survey (13 July).

Turnover during the trawl survey period may have biased the biomass estimate if prespawning fish arrived late to the trawl survey area (after trawling for R_i had started), at the beginning of the season. This means that not all prespawning fish would have been sampled by trawls in the spawning area, which would cause an underestimate of R_i , because fish that had started spawning would be over-represented. Similarly, if spent fish departed the trawl survey area early (before trawling for R_i had ended) toward the end of the season, spent fish would be under-represented by trawls in the spawning area. In this case, R_i would be overestimated because fish which had not finished spawning would be over-represented. Both of these effects (late arrivals and early departures) would cause an underestimate of D , which, in turn, would cause an overestimate of biomass, N_0/D .

Was it likely that late arrivals or early departures (or both) of spawners occurred in the present study? The annual fecundity/kg of prespawners, estimated from fish sampled before the R_i sampling period and before any eggs were caught in the plankton (Fig. 8), was 27, 271 eggs/(kg \times yr). If this estimate is divided by the estimated daily fecundity/kg (787 eggs/(kg \times day); Table 4), the period required for the average fish to spawn completely is 35 days. However, the time lag between the first appearance of significant proportions (>0.05) of ovulated and spent fish was about 19 days (from 14 June to 2 July; Fig. 7). If this

Table 4

Parameter estimates for DFRM for Ritchie Hill spawning female biomass and mid-east coast recruited biomass, June–July 1993 (with coefficients of variation in parentheses). N_0 = daily egg production for Ritchie Hill survey area (estimated with curved net trajectory); D = weight specific daily fecundity of females; B_{spf} = biomass of spawning females in Ritchie Hill survey area; S = ratio of recruited biomass to that of spawning females; B_{rec} = biomass of recruited fish. Parameter estimates with subscripts marked "turn" have turnover incorporated (see text); CVs were not estimated in these cases.

Parameter	Estimate
N_0	10.9×10^9 eggs/day (0.46)
D	787 eggs/(kg \times day) (0.11)
B_{spf}	14,000 t (0.50)
S	1.85 (0.03)
B_{rec}	26,000 (0.50)
D_{turn}	1,106 eggs/(kg \times day)
$B_{spf, turn}$	9,900 t
$B_{rec, turn}$	18,200 t

Table 5

Mean abundances (per m^2) of all eggs \leq stage 7 and dates of sampling in the central strata for each subsurvey.

Subsurvey	Date	Mean	CV
1	15–17 June	0.0	0.0
2	20–25 June	3.9	0.34
3	29 June–1 July	49.0	0.29
4	3–5 July	22.6	0.46
5	6–7 July	22.2	0.50
4 and 5	3–7 July	22.4	0.34

lag is interpreted as the duration of spawning in individual fish, D was underestimated by the fecundity reduction trawling.

It would appear, however, that late arrival of prespawners to the trawling area did not contribute greatly to the underestimation of D . The R_i sampling period began on 20 June when prespawner (stage-3) proportions had become low (0.20; Fig. 7) and were decreasing rapidly. At this time the estimated R_i was only about 10% below the prespawning level (Fig. 8). Eggs first appeared in the plankton on 15 June, but catches of young eggs in the central strata were still relatively small (3.9 eggs/ m^2 ; Table 5) during 20–25 June (subsurvey 2). Therefore, only a relatively small reduction in R_i would have been expected by

20 June, in agreement with the reduction actually observed by that date (Fig. 8).

It was likely, however, that early departures caused spent fish to be under-represented in the trawl samples toward the end of the R_i time series. The abundance of young planktonic eggs in the central strata was reduced by more than half between subsurvey 3 (mid-date 30 June) and subsurvey 4 (mid-date 4 July; Table 5). Because subsurvey 3 was done when the spent proportion was virtually zero (Fig. 7), this reduction of planktonic egg abundance implied that about half of the fish had ceased spawning by 4 July (assuming that the spawning rate of remaining active fish was constant). However, only 0.11 of fish were recorded as spent on 4 July (Table 2; Fig. 7); thus this proportion appeared to be underestimated by $0.50 - 0.11 = 0.39$ on 4 July. Commercial catch rates on Ritchie Hill (Fig. 9) also decreased considerably during the last week of June and first week of July, suggesting that fish abundance in the trawling area had declined.

To account for the error in D that the underestimation of spent fish would cause, the proportion of active fish on 4 July was adjusted downward to $0.89 - 0.39 = 0.50$ to estimate a new D value of 1,106 eggs/(kg \times day) (assuming a linear decline between 20 June and 4 July; Fig. 8; Table 4). This adjustment resulted in a period of 25 days for an average fish to spawn completely, which is not greatly different from the 19 days estimated from the time lag between ovulated and spent fish proportions (shown above). This re-estimation of D , to account for turnover, had proportional effects on B_{spf} and B_{rec} (Table 4).

Discussion

This study has used the DFRM to estimate the biomass of recruited individuals in the mid-east coast orange roughy stock, by combining estimates of daily egg production rate, the rate of fecundity reduction, and the proportion of the stock that was spawning females. In this section various sources of error are discussed, and the methods

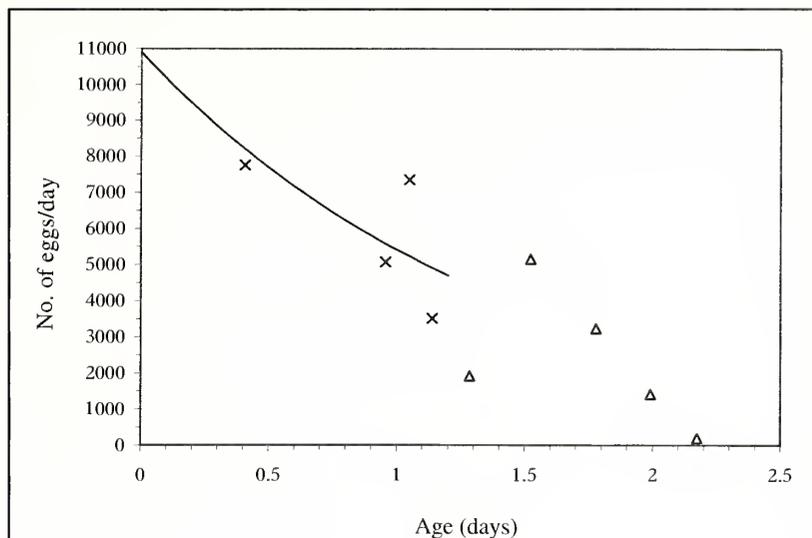


Figure 6

The daily production of eggs as a function of age, calculated by dividing the curved trajectory egg-abundance estimates (Table 3) by the duration of each age group and by plotting against the mean age of eggs in each age group (Appendix 3). The line was fitted by using N_0 and Z (Appendix 3), calculated with only egg stages ≤ 7 to 10 (crosses). Egg stages 11 to 15 (triangles), were not used in the production estimate because they were subject to advection out of the survey area (see text).

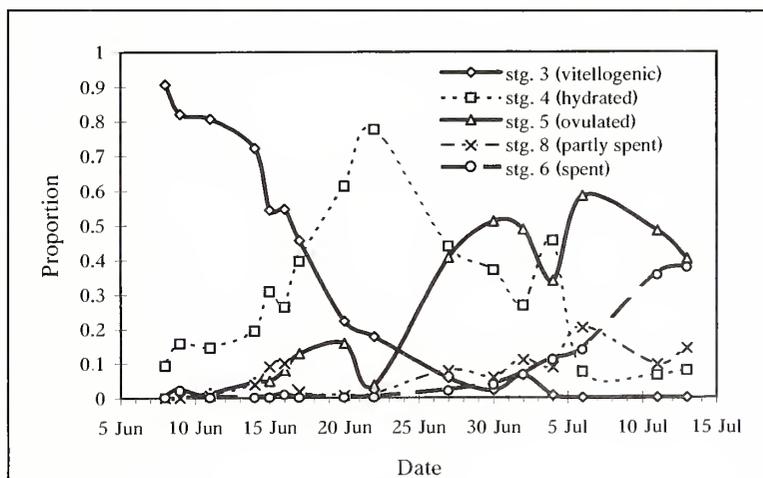


Figure 7

Time series of macroscopic ovarian stages over the survey period. Each point is the proportion of females at that stage, as a proportion of all mature females, averaged for all trawls on that date. Only trawls on Ritchie and North Hills were used (Table 2).

and results of this study are compared with those of other studies. Also, a brief description is made of how the results from this survey have been used in assessing the stock.

Sources of error

In egg-production surveys, the trajectory of the plankton net during deployment and retrieval is usually assumed to be straight (and often, vertical). The analyses presented here (Appendix 1) suggest that, for the present survey, 1) there was significant hori-

zontal movement of the net during deployment owing to drag from the warp (which was caused by ship drift), and 2) the plankton net followed a curved trajectory during hauling. The curved trajectory meant that less water was filtered in deeper than in shallower ocean layers of equal thickness and that larger correction factors were required for younger (deeper) eggs in order to standardize the egg counts to eggs/m². The effect of using curved, rather than straight, trajectories was to increase the estimated production rate by 36% (from 8.0 to 10.9 billion eggs/day). Recent egg-production survey work, using a digitally recording flowmeter system developed at NIWA (Grimes⁹), has shown that 1) there often are spurious revolutions of the flowmeter on the downcast, negating the use of conventional flowmeters and that 2) more water is filtered at shallower depths than at deeper depths, justifying the assumption of a curved net trajectory. Therefore, it is likely that by allowing depth variation in the estimates of the amount of water filtered, a major improvement was made over the assumption of a straight net trajectory.

The precision of the planktonic egg production estimate was influenced by damage to early stage eggs (Zeldis et al., 1995; Grimes et al.³). In the present study, the inability to stage most eggs less than 21.8 h old caused a greater reliance on older egg stages to estimate production. However, the number of older egg stages that could be used for the estimation was limited because eggs older than stage 10 (28.4 h) were subjected to advection toward and through the southwestern boundary of the survey area as they aged. Thus, the original strategy of making the survey area large enough to retain all of the eggs up to 36 h old was defeated, and relatively few stages were available for a mortality estimate. Clearly, the combination of nearly concurrent information on ocean circulation (from CTD and drogued buoy) and on the drift patterns of the eggs themselves provided useful corroborative information for quantitative decisions about the egg-age range available for mortality estimation, when eggs were subject to advection.

Precision estimates for the egg-abundance data may have been biased by potential autocorrelation among the data, which would not bias the esti-

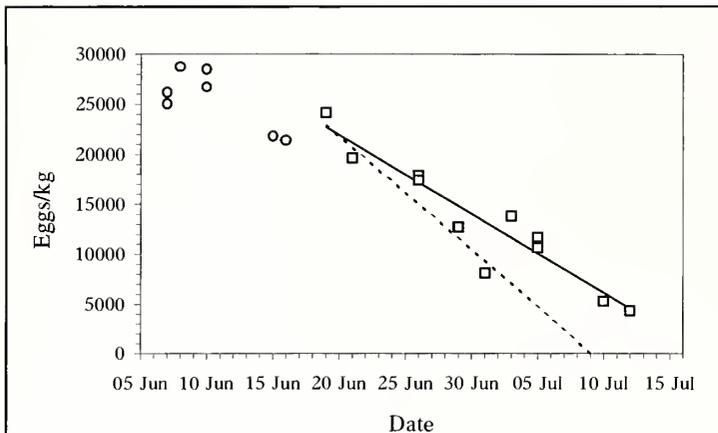


Figure 8

Weight-specific fecundity (eggs/kg spawning female: R_f) from trawls prior and during the DFRM sampling period (circles and squares, respectively, Table 2). Solid line is a weighted linear regression fitted for DFRM trawls. Dotted line is a regression fitted when it was assumed that proportion active was overestimated by 39% on 4 July (see text).

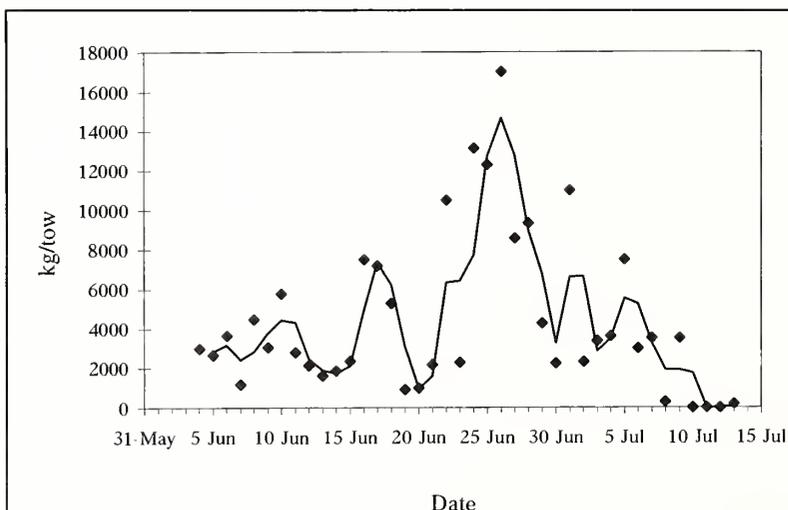


Figure 9

Commercial catch rates of orange roughy, *Hoplostethus atlanticus*, on Ritchie and North Hills, 4 June–13 July 1993. Points are the means of all catches by all vessels on each day (kg/tow), fitted with a moving average (line) with a 2-day period.

mate of egg production but could cause its precision to be overestimated. No attempt was made to correct for this bias because the data were judged to be inadequate to estimate an autocorrelation structure (which would need to have both spatial and temporal terms). Picquelle and Megrey (1993) drew the same conclusion for pollock egg surveys. For the present study, a minimum spacing of 1,000 m was imposed when allocating the stations to the strata. This spacing should have gone some way toward minimizing the effects of spatial autocorrelation. In an explicit study of autocorrelation in anchovy egg catches, Smith and Hewitt (1985) found that spatial autocorrelation diminished rapidly at spatial scales of 2,000 m and that temporal autocorrelation diminished at 0.5 h for 1-day-old eggs. Given that the minimum distances and times between samples for the egg stages used in this study were of this order and that the egg catch rates were highly variable, overestimation of precision was likely to be minor.

Use of the DFRM required the assumption that the 11 trawls used to estimate D representatively sampled spawning females on Ritchie and North Hills. Although it is clear that spawning female biomass is highly aggregated in the Ritchie Hill area (Fig. 2), it is not known to what extent females are randomly distributed within this small area, with respect to ovarian stage. Therefore, it was useful to look at a much larger set of fecundity data collected on these hills in 1995 by N.Z. Ministry of Fisheries (MOF) scientific observers working on commercial vessels (Zeldis, unpubl. data). Samples were taken from 47 trawls made with four vessels (range of 7–16 trawls per vessel) throughout the entire spawning season. These tows were long, typically traversing much of the ridge between North Hill and the south side of Ritchie Hill (Fig. 2) and covering the 850–900 m depth range of orange roughy spawning. The fecundity reduction rate from these 1995 data (uncorrected for turnover) was 965 eggs/(kg \times day) (CV=0.11), which was not significantly different from the uncorrected estimate from 1993 in the present study, 787 eggs/(kg \times day) (CV=0.11; Table 4). This rate showed that widespread and intensive trawling in this area would yield an estimate of D similar to that from the less intensive research trawling of the present study, indicating that the less intensive trawling accurately represented the spawning dynamics of the population.

The reliance of the DFRM on within-spawning season trawl data makes it susceptible to bias due to turnover, which causes an underestimate of fecundity reduction rate. In the present study, it appeared that spent females left the survey area during the period when fecundity reduction was measured, such

that only 0.11 of remaining females were spent 21 days after the start of spawning. A similar pattern of low proportion spent was seen in the 1995 Ritchie Bank scientific observer data described above, with proportion spent < 0.20 about 23 days after the onset of spawning. In contrast, in recent NIWA orange roughy egg production surveys done at East Cape in 1995¹⁰ and at the "Graveyard" area on northern Chatham Rise in 1996¹¹ (Fig. 1), spent proportions were between 0.60 and 0.70 about 20 days after the onset of spawning. This suggested that turnover was less prevalent at these latter sites, an effect which may be related to the fact that although commercial fishing was intensive on Ritchie Bank during the 1993 and 1995 spawning seasons, there was no commercial fishing during the 1995 and 1996 spawning seasons at East Cape and the "Graveyard." Significantly, the value of D at East Cape was 1,036 eggs/(kg \times day), with no correction for turnover, which was similar to the turnover-corrected value for the present study at Ritchie Bank of 1,106 eggs/(kg \times day) (an estimate is not yet available for the "Graveyard"). For this reason, the turnover-corrected fecundity reduction rate estimated for Ritchie Bank in 1993 is considered to be more reliable than the uncorrected estimate and also a reasonably reliable estimate of the true rate of decline in Ritchie Bank population seasonal fecundity.

Comparison with other studies

The first use of the DFRM was by Lo et al. (1992; 1993) to estimate the biomass of a deepwater pleuronectid flatfish, Dover sole (*Microstomus pacificus*), which spawns between 600 and 1,500 m depth on the continental slope of western North America. The model used in the present study to describe the daily fecundity reduction was simpler than that of Lo et al. (1993). It assumed that the fecundity per fish weight was a linear function of time only (fish weight was considered as an additional predictor but did not significantly improve the fit). Lo et al. (1993) assumed that both total fecundity of active females and the fraction of active females (their E_t and G_t) were linear functions of time and fish weight. The former model was used for two reasons. First, in calculating fecundity reduction, there seemed no need to treat active and inactive females separately. Second, in the absence of any evidence of lack of fit, the rule of Occam's razor suggested using the simpler model.

¹¹ Grimes, P. J. 1996. Voyage Report, TAN9608 (Part II). NIWA unpublished voyage report held in NIWA Library, Greta Point, Wellington, New Zealand, 4 p.

A second difference between the DFRM used here and that of Lo et al. (1993) is the way sex ratio and active female proportion were estimated and brought into the biomass model. In the present study, the proportion of all recruited fish that were spawning females was estimated with parameter S , whereas this proportion was estimated within the R and D parameters in the model of Lo et al. (1993). Orange roughy spawning takes place in dense aggregations that form after the spawners have migrated hundreds of km from the nonspawners. Therefore, it is not possible to estimate the proportion of active females to all recruited fish with the trawls done on the spawning ground during the spawning season (which are used to monitor fecundity reduction). This estimation must be done with a separate trawl survey over the whole stock area, preferably before the spawners have aggregated significantly. In contrast, Dover sole spawning appears to be dispersed over a wide latitudinal area of the North American west coast slope (Lo et al., 1993) and takes place over a long spawning season (6 months; Hunter et al., 1992). In Lo et al. (1993), the spawners were assumed to be dispersed in the same geographic region as the nonspawners during spawning, and therefore sex ratio and proportion active components were estimated from the same trawls that were used to estimate fecundity reduction.

There are few other estimates of planktonic egg mortality (Z) in the literature for deepwater spawners that can be compared with the value ($Z=0.7$) obtained for orange roughy in this study. Lo et al. (1993) fitted a Pareto decay function to Dover sole egg abundances, in which mortality was allowed to decrease with egg age. Initial mortality was 0.63 which halved by the age of 1 day. Another western North American slope species, sablefish (*Anoplopoma fimbria*), has been the subject of egg-production studies (Moser et al., 1994) and for this species, Z varied between 0.25 and 0.48, depending on region (it should be noted that counts of 1-day-old and 2-day-old eggs were excluded because these eggs were undersampled). Thus, the few Z estimates that exist for other deepwater species indicate variable mortality rates, but that mortalities can be quite high. Orange roughy egg abundance was estimated by Koslow et al. (1995) in their application of the AEPM to orange roughy biomass estimation on St. Helen's Seamount, Tasmania. These authors assumed that mortality in the first 28 h after spawning was zero and that the mean abundance of 0 to 28 h old eggs equalled N_0 . This assumption was based on their finding no differences in abundance among fertilization or 1-cell eggs (stages 1 and 2 of the present study) and their subsequent two stages which were 2 cell and 4–128 cells (stages 3 and 4–9, respectively, of the present study;

see also Grimes et al.³). As mentioned, the differentiation of stages 1–7 was not possible for the great majority of the samples in the 1993 Ritchie Bank survey because of egg damage. However, the probability that the mortality rate estimated from the grouped stages 1–7 and stages 8, 9, and 10 was zero was low ($P=0.10$).

The procedure used to estimate S , for converting spawning female biomass to recruited biomass, is easily adapted to estimate the proportion of females in the stock area that will spawn in the current year. For the mid-east coast stock in 1993, S was estimated as 0.52 of all mature females (by weight), a result similar to that for orange roughy stocks in southern Australia (0.45, by numbers; Bell et al., 1992). Wide-area trawl surveys of the east coast were also done in March–April of 1992 and 1994,¹⁰ and these yielded similar values for these proportions (0.49 and 0.42 by weight). Also, a low proportion of females with fully atretic ovaries was found (0.045) over the mid-east coast survey area in 1993, again in common with the results of Bell et al. (1992).

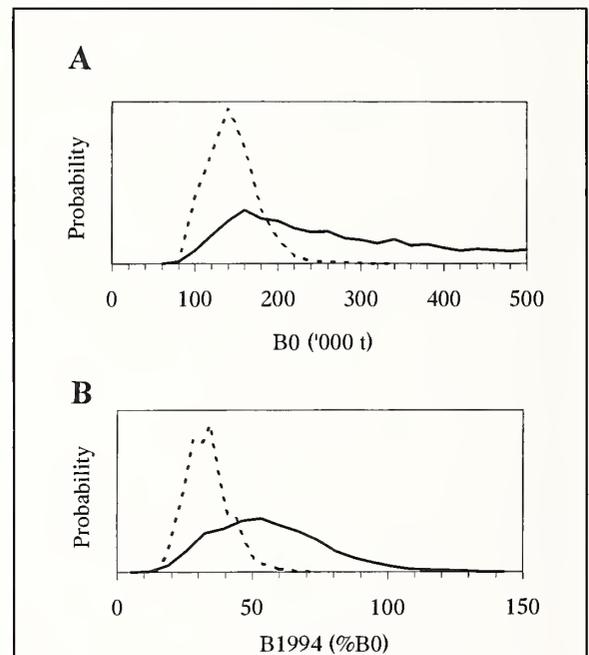


Figure 10

Probability distributions of (A) virgin biomass (B_0) and (B) 1994 biomass as a percentage of B_0 , from the 1994 stock reduction analysis for the mid-east coast orange roughy, *Hoplostethus atlanticus*, fishery (see Footnote 2 in the text). Each panel shows (solid line) the distribution when the analysis was done without the DFRM estimate (with only CPUE, trawl survey indices, and mean fish length data) and (dotted line) the distribution when the DFRM estimate was included.

Use in stock assessment

Although the biomass estimates derived from this DFRM survey were rather imprecise (CV=0.50), they were capable of having a dramatic effect on the assessment of the mid-east coast stock. In 1994, an estimate of 45,000 t recruited biomass (CV=0.40) from a preliminary analysis of these data was used in assessing this stock (Field et al.²; this estimate differs from those given above because some data errors have subsequently been corrected and the analyses have been refined). The inclusion of this estimate greatly improved the precision of the assessment (Fig. 10), which resulted in a 2-year stepped reduction in TACC from 10,333 t in 1993–94 to 2500 t in 1995–96.

Acknowledgments

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Appendix 1: Calculation of "curved" correction factors

This appendix describes, for the case where the path of the net during hauling is assumed to be curved, the calculation of the correction factors that convert egg counts to egg density (eggs/m²).

For each plankton tow, we calculated the following:

- 1 the position of the net at the start of hauling;
- 2 the position of the net at a series of equally spaced times during hauling;
- 3 the flow of water through the net at each of these times; and
- 4 a correction factor for each of these times.

Finally, interpolation was used to calculate the correction factor when the net was at the mid-point of the depth layer associated with each egg stage. This was taken as the correction factor for that egg stage at that plankton tow.

First, the assumptions behind these calculations and some notation are defined.

Assumptions and notation

The calculations required the following assumptions:

- 1 the vessel drifted at a constant velocity while shooting and hauling;
- 2 the net dropped at a constant speed during shooting;
- 3 the warp was always straight and decreased in length at a constant rate during hauling;
- 4 the net mouth was always perpendicular to the warp;
- 5 the water velocity varied only with depth (not with longitude, latitude, or time); and
- 6 the following are known exactly:
 - a) the vessel position at the time of shooting and at the start and finish of hauling,
 - b) the net depth and warp length at the start of hauling, and
 - c) the water velocity profile.

Two further assumptions are described in sections "Calculating P_{n1} " and "Calculating the net path during hauling."

Let $\underline{P}_n(t)$ and $\underline{P}_v(t)$ be 3-dimensional vectors describing the position of the net and the vessel at time t , where time and position are measured in relation to the time and the vessel position when the net was shot, and where the three coordinates give distances, in meters, to the east, north, and downwards, respectively. (In this Appendix, vectors are underlined to distinguish them from scalars.) Let t_1 and t_2 stand for the times at the start and finish of hauling.

Let the water velocity at depth z be described by the vector $\underline{C}(z)$, and the mean water velocity between the surface and depth z by $\underline{C}'(z)$. Denote the net depth and the warp length at time t by $z_n(t)$ and $w(t)$, respectively (note that $z_n(t)$ is the depth coordinate of $\underline{P}_n(t)$).

Where it is convenient, the symbols t_1 and t_2 will be replaced by subscripts 1 and 2, so that, for example, $\underline{P}_n(t_1)$,

$z_n(t_1)$, and $\underline{P}_v(t_2)$ may be written as \underline{P}_{n1} , z_{n1} , and \underline{P}_{v2} , respectively.

From the above assumptions, \underline{P}_{v1} , \underline{P}_{v2} , z_{n1} , and w_1 are known, as are $\underline{C}(z)$ and $\underline{C}'(z)$ for all z . Also, of course, $\underline{P}_{n2} = \underline{P}_{v2}$.

Calculating P_{n1}

In calculating the position of the net at the start of hauling, it was assumed that, while the net was sinking prior to hauling, its horizontal velocity was the sum of the water velocity and some fraction c of the vessel velocity (the latter component being caused by drag from the warp). Thus,

$$\underline{P}_{n1} = c\underline{P}_{v1} + t_1\underline{C}'(z_{n1}) + \underline{Z}_{n1}, \quad (\text{A1})$$

where $0 \leq c \leq 1$, and \underline{Z}_{n1} is the 3-dimensional vector, $(0, 0, z_{n1})$. Also, from assumptions 3 and 6,

$$|\underline{P}_{n1} - \underline{P}_{v1}| = w_1. \quad (\text{A2})$$

The value of c (and thus \underline{P}_{n1}) can be calculated by solving the simultaneous equations A1 and A2. Geometrically, this is equivalent to finding a point of intersection of the horizontal line defined by Equation A1 and the horizontal circle defined by Equation A2 (both are at depth z_{n1}).

Substituting for \underline{P}_{n1} from Equation A1 in Equation A2 and expanding, we get the quadratic equation in $(c-1)$

$$(c-1)^2|\underline{P}_{v1}|^2 + 2(c-1)t_1\underline{P}_{v1} \cdot \underline{C}'(z_{n1}) + t_1^2|\underline{C}'(z_{n1})|^2 + z_{n1}^2 - w_1^2 = 0, \quad (\text{A3})$$

which is solved with the usual formula (\cdot denotes the vector dot product).

Where there were two solutions for c (at all but a few stations), the one using the negative square root was chosen because it was usually the one that satisfied the condition $0 \leq c \leq 1$.

For the few stations where Equation A3 had no real solution (i.e. the line and circle did not intersect), \underline{P}_{n1} was taken to be the point on the circle closest to the line. It may be shown that this \underline{P}_{n1} is given by

$$\underline{P}_{n1} = r \frac{\underline{P}_{cl}}{|\underline{P}_{cl}|} + \underline{P}_{v1} + \underline{Z}_{n1} \quad (\text{A4})$$

where r is the radius of the circle and \underline{P}_{cl} is the point, on the surface vertically above the line, that is closest to the shot position, and is given by

$$\underline{P}_{cl} = t_1\underline{C}'(z_{n1}) - \frac{t_1\underline{C}'(z_{n1}) \cdot \underline{P}_{v1}}{|\underline{P}_{v1}|^2} \underline{P}_{v1}. \quad (\text{A5})$$

Stations where Equation A3 did not have a real solution, or where c did not satisfy $0 \leq c \leq 1$, were assumed to be instances where the above assumptions did not hold.

Another situation in which the assumptions clearly did not hold was at the 13 stations where $z_{n1} > w_1$. For these stations, z_{n1} was set equal to w_1 , and \underline{P}_{n1} was taken to be vertically below \underline{P}_{v1} .

Calculating the net path during hauling

From assumptions 1 and 3, the position of the vessel and length of the warp at any time during hauling was calculated by using

$$\underline{P}_v(t) = \frac{(t_2 - t)\underline{P}_{v1} + (t - t_1)\underline{P}_{v2}}{(t_2 - t_1)} \quad (\text{A6})$$

and

$$w(t) = \underline{P}_v(t) - \underline{P}_n(t) = \frac{(t_2 - t)w_1}{(t_2 - t_1)} \quad (\text{A7})$$

To calculate the position of the net during hauling, we made one further assumption: that the velocity of the net is the sum of the water velocity and a vector in the direction of the warp. With this assumption, an iterative procedure was used to calculate $\underline{P}_n(t)$ at times $t_1 + *t$, $t_1 + 2*t$, etc, for a small time interval $*t$. The basis of this procedure is the ability to calculate $\underline{P}_n(t + *t)$ once $\underline{P}_n(t)$ is known. This is done as follows.

The velocity assumption may be written approximately as

$$\frac{\underline{P}_n(t + \delta t) - \underline{P}_n(t)}{\delta t} = p(t) \frac{\underline{P}_v(t) - \underline{P}_n(t)}{|\underline{P}_v(t) - \underline{P}_n(t)|} + \underline{C}(z_n(t)), \quad (\text{A8})$$

where $p(t)$ is an unknown scalar which varies with t . Replacing t by $t + *t$ in Equation A7, we get

$$|\underline{P}_v(t + \delta t) - \underline{P}_n(t + \delta t)| = \frac{(t_2 - t - \delta t)w_1}{(t_2 - t_1)} \quad (\text{A9})$$

and substituting for $\underline{P}_n(t + *t)$ from Equation A8, Equation A9 may be rewritten as

$$|p(t)\underline{A} + \underline{B}| = \frac{(t_2 - t - \delta t)w_1}{(t_2 - t_1)}, \quad (\text{A10})$$

where

$$\underline{A} = -\frac{(t_2 - t_1)\delta t}{w_1(t_2 - t)}(\underline{P}_v(t) - \underline{P}_n(t)) \quad (\text{A11})$$

and

$$\underline{B} = \underline{P}_v(t + \delta t) - \underline{P}_n(t) - \delta t \underline{C}(z_n(t)). \quad (\text{A12})$$

Expanding Equation A10, we get the quadratic equation

$$\underline{A} \bullet \underline{A} p(t)^2 + 2\underline{A} \bullet \underline{B} p(t) + \underline{B} \bullet \underline{B} = \left[\frac{(t_2 - t - \delta t)w_1}{(t_2 - t_1)} \right]^2, \quad (\text{A13})$$

which may be solved for $p(t)$ in the usual manner.

In solving Equation A13, the solution using the positive square root was ignored because it led to large values of $p(t)$ and large vertical oscillations in the net path.

Flow of water through the net

Because, by assumption 4 above, the net mouth was always perpendicular to the warp, the flow of water through the net at time t (in m³/s) is given by

$$F(t) = 2V_{nw} \bullet \underline{U}_{wp}, \quad (\text{A14})$$

where V_{nw} is the velocity of the net relative to the water, given approximately by

$$\underline{V}_{nw} = \frac{\underline{P}_v(t + \delta t) - \underline{P}_n(t)}{\delta t} - \underline{C}(z_n(t)), \quad (\text{A15})$$

\underline{U}_{wp} is a unit vector in the direction of the warp, given by

$$\underline{U}_{wp} = \frac{\underline{P}_v(t) - \underline{P}_n(t)}{|\underline{P}_v(t) - \underline{P}_n(t)|}, \quad (\text{A16})$$

and factor 2 is the net mouth area in m².

Calculation of correction factors

The correction factor associated with a horizontal layer of water is given by

$$CF = \frac{\text{Thickness of layer}}{\text{Volume of water filtered by net within layer}} \quad (\text{A17})$$

Thus, for the layer of water that the net passed through between times t and $t + *t$, the correction factor is given approximately by

$$\frac{z_n(t) - z_n(t + \delta t)}{F(t)\delta t}$$

which is treated as the correction factor associated with depth $z_n(t)$. Thus, for each plankton tow, correction factors for depths $z_n(t_1)$ ($=z_{n1}$), $z_n(t_1 + *t)$, $z_n(t_1 + 2*t)$, etc. were calculated.

Finally, the correction factor for a given egg stage at a given plankton tow was calculated, by interpolation, as the correction factor at the mid-point of the depth layer associated with that egg stage.

Appendix 2: Calculation of centroids

This appendix describes the procedure for calculating the centroid (= center of gravity) of each age group (plotted in

Fig. 4A). First, the survey area was divided into 36 subareas (Fig. 4A). The longitude of the centroid for age group a , X_a , was estimated by using

$$X_a = \frac{\sum_j x_j M_{aj} A_j}{\sum_j M_{aj} A_j},$$

where $M_{aj} = \frac{1}{n_j} \sum_j C_{aj}$

and C_{aj} = catch rate (eggs/m²) for age group a at the i th station in subarea j ;

M_{aj} = mean catch rate for age group a in subarea j ;

n_j = number of stations in subarea j ;

A_j = area of subarea j ; and

x_j = longitude of center of subarea j .

The latitudes of the centroids were calculated similarly. These calculations use the approximation that, for each age group, the centroid of eggs within a subarea is at the center of the subarea.

Appendix 3: Egg production model and estimation

This appendix describes the calculation of daily egg production, N_0 , and CV given in Table 4 and shown in Figure 6. It is assumed that

- 1 the rate of egg production was constant (both from day to day and within each day) in the period immediately preceding and during the plankton survey,
- 2 egg mortality was constant over the same period and independent of age, and
- 3 the egg abundance estimates, N_a , of Table 3 are unbiased and lognormally distributed with CV's, c_a , as given in Table 3.

Under these assumptions, E_a , the expected value of N_a , is given by

$$E_a = \int_{t_{a-1}}^{t_a} N_0 e^{-zt} dt = \frac{N_0}{Z} (e^{-Zt_{a-1}} - e^{-Zt_a}),$$

where N_0 = the daily egg production (eggs/day);

Z = the daily instantaneous egg mortality (per day); and

(t_{a-1}, t_a) = the range of ages (day) in age group a .

The mean age of eggs of age group a (used in Fig. 6) is given by

$$\frac{1}{E_a} \int_{t_{a-1}}^{t_a} t N_0 e^{-Zt} dt = \frac{1}{Z} + \frac{(t_a e^{-Zt_a} - t_{a-1} e^{-Zt_{a-1}})}{e^{-Zt_a} - e^{-Zt_{a-1}}}.$$

N_0 and Z were estimated by maximum likelihood, ie. by maximizing the likelihood, L , which is given by (ignoring constants)

$$L = \prod_a \left[\frac{1}{N_a} \exp \left(-0.5 \sum_a \left[\frac{1}{\sigma_a} \log \left(\frac{N_a}{E_a} \right) + 0.5 \sigma_a \right]^2 \right) \right],$$

where σ_a is the standard error of $\log(N_a)$, given by

$$\sigma_a = [\log(1 + c_a^2)]^{\frac{1}{2}}.$$

By definition, Z must be positive. However, in the bootstrap procedure described next, it sometimes happened that the maximum likelihood estimate of Z was negative (because, by chance, simulated egg abundance estimates increased with age). When this happened, Z was forced to be zero, so that

$$E_a = N_0(t_a - t_{a-1}).$$

The following bootstrap procedure was used to estimate the degree of uncertainty in the estimates of N_0 and Z .

- 1 the maximum likelihood estimates of N_0 and Z were used to calculate the expected egg abundances, E_a , using the formula above;
- 2 new egg abundance estimates, N_a , were simulated by using lognormal distributions with expected values, E_a , and CV's, c_a ;
- 3 maximum likelihood estimates of N_0 and Z were calculated from the simulated values of N_a , and
- 4 steps 2 and 3 were repeated 1,000 times.

The resulting 1,000 values of N_0 and Z are the bootstrap distributions for these parameters; the 0.025 and 0.975 quantiles of these distributions were taken as bounding the 95% confidence intervals for each parameter. The CV's of these distributions are taken as estimates of the CV's of the maximum likelihood estimates of N_0 and Z .

Appendix 4: Analysis of ovarian samples

Ovaries frozen onboard were thawed in the laboratory, weighed, and then one of the two slit open. A subsample of about 5 g was scraped from the full length of one ovary from each fish, because preliminary analyses had indicated there was some variation in egg density from different parts of the ovary. The subsample was then placed into 1M KOH for a period of 5–15 minutes depending on the ovarian stage. Maturing oocytes (stage 3) were bound more tightly in the matrix than advanced stages, and therefore needed a longer KOH treatment to separate individual oocytes. Stage-3 oocytes generally retained a medium orange color after KOH treatment, and thus needed no further treatment after separation. However, the more transparent stage-4, stage-5, and stage-8 oocytes were stained with Semichon's carmine. The subsample was then washed through a 0.7-mm mesh sieve that was found to be of a suitable mesh size to retain oocytes with a diameter greater than about 1.2 mm. Primary, early vitellogenic, and atretic oocytes, as well as small fragments of matrix and tissue

passed through the mesh. Atretic eggs, in particular, had dimensions of 0.5 to 1.0 mm (from histological observations) and were found to wash through the sieve. The mean size of stage-3 oocytes was 1.56 mm (range 1.30–1.83 mm, SE=0.01). More advanced stages had larger oocytes (stage 4=2.15 mm; stage 5= 2.55 mm; stage 8=2.20 mm) and therefore were fully retained.

Eggs were then counted with an electronic egg counter incorporating a phototransistor (Bycroft, 1986). Eggs were siphoned from a large beaker into a perspex chamber with a vacuum pump attached to the top of the chamber. Water flow was regulated to keep this chamber about three-quarters full, so that any air bubbles rose to the top. Eggs passed from the bottom of the chamber through a small tube past a phototransistor and light source. The reduction in light intensity (caused by the presence of the eggs) was detected by the phototransistor and was recorded on an electronic counter with digital readout. The rate of flow was regulated to avoid large numbers of eggs in the chamber and exit tube at any one time (which could result in multiple eggs passing the counter at the same time and being recorded as only as one egg). A gain control (set very low) was used to alter the sensitivity of the counter so that small fragments of extraneous material that remained after the sieving were not counted.

Checks of the accuracy of the electronic counter were made by comparing manual counts (made with a dissecting microscope) with electronic counts and no significant difference was found (*t*-test, $P < 0.01$, number of comparisons=4). Also, a reference set of a known number of eggs was regularly used to check the calibration. Up to four determinations were made in each trial, which produced CV's of the mean count of generally less than 0.01.

Total fecundity from both ovaries was initially calculated from the number of oocytes/g \times ovarian weight. Although this is common practice in fecundity studies, it may introduce bias because ovary weight includes ovary wall which does not contain eggs. Several comparisons were made between estimated fecundity based on the scaled-up subsample count, and actual counts of all oocytes in an ovary. Scaled-up subsample counts typically overestimated actual fecundity by 10–20%. The proportion of wall weight to total ovary weight (for stages 3, 4, 5, and 8) were estimated by stripping a number of weighed ovaries of all eggs and weighing the remaining wall (Appendix 4, Table 1). The proportions were then used to adjust the total fecundities of each fish in each stage. The higher proportions for stages 5 and 8 are to be expected because some stage-5 fish may be in the act of spawning and stage-8 fish have already spawned some of their eggs; therefore the ovary wall is a greater proportion of total ovary weight.

Table 1

The contribution (percentage) of the ovary wall to ovary weight at each ovarian stage. See text for stage definitions.

Stage	Mean	SE	<i>n</i>
3	9.6	1.2	15
4	6.6	0.4	14
5	13.9	2.7	14
8	29.7	4.4	19

Abstract.—Maturity and total fecundity are reported for arrowtooth flounder, *Atheresthes stomias*, from the Gulf of Alaska. Histological examination of both ovarian and testicular tissues revealed that the maturity state of both sexes could not be determined reliably by macroscopic assessment. Maturity for females ranged from the early perinucleus to the migratory nucleus stage; none of the fish had postovulatory follicles or hydrated oocytes, indicating all samples were collected prior to the spawning season. Condition factor (CF), gonadosomatic index (GSI), and hepatosomatic index (HSI) increased significantly in the later stages of female development. Eyed-side ovarian lobes were significantly heavier than blind-side lobes, but oocyte size and density (oocytes/gram) did not vary between lobes of the ovary or within the individual ovarian lobes. Total fecundity increased exponentially with length ($F=0.0429 \times L^{4.020}$) and linearly with somatic weight ($F=350.4 \times W - 138,482$), with estimates ranging from 250,000 to 2,340,000 oocytes. Histological analysis of tissues indicated that females reach 50% maturity (L_{50}) at 47 cm, males at 42 cm. This estimate of male L_{50} is probably high because no males in this study were ready to spawn, whereas a decrease in CF and an increase in GSI indicate body changes at a size of 30–35 cm.

Maturity and fecundity of arrowtooth flounder, *Atheresthes stomias*, from the Gulf of Alaska

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Arrowtooth flounder, *Atheresthes stomias*, is a large piscivorous flatfish with a range in U.S. waters from California (Allen and Smith, 1988) through the Gulf of Alaska, the Aleutian Islands, and the eastern Bering Sea. Although it is the most abundant groundfish in the Gulf of Alaska and is concentrated in relatively shallow waters (101–200 m, Martin and Clausen, 1995), arrowtooth flounder has experienced only limited commercial harvesting. Arrowtooth flounder flesh softens soon after capture, possibly owing to an enzyme released from a myxosporean parasite (Greene and Babbitt, 1990), greatly reducing its commercial value. Recent advances in food processing, however, have allowed production of marketable quality arrowtooth flounder fillets (Greene and Babbitt, 1990) and surimi (Wasson et al., 1992; Porter et al., 1993; Reppond et al., 1993), which may stimulate further development of a fishery.

Hunter and Macewicz (1985, a and b), Hunter et al. (1992), Morrison (1990), and others have carefully examined many of the assumptions of maturity and fecundity work and have provided histological details that made this project possible. Rickey's (1995) research off the Washington coast has shown that arrowtooth flounders are group-synchronous batch spawners, and researchers generally agree on a fall or winter spawning period (Pert-

seva-Ostroumova, 1961; Shuntov, 1970; Fargo et al., 1981; Rickey, 1995; Hosie and Barss¹). Studies on arrowtooth flounder have calculated length at 50% maturity (L_{50}) for both males and females from different areas, but only by using macroscopic maturity assessment (Hosie and Barss¹ for Oregon; Fargo et al., 1981, for British Columbia, Canada; Rickey, 1995, for Washington). Rickey (1995) included histological analysis and descriptions of different maturity stages of ovarian tissues but did not use histological analysis for calculating L_{50} and did not examine males histologically.

No study has ever reported weight-based or length-based estimates of total fecundity (as defined in Hunter et al., 1992), nor have researchers examined possible differences in oocyte density or oocyte size between or within ovarian lobes, which could bias total fecundity estimation. Researchers also have not reported changes in condition factor, gonadosomatic index, and hepatosomatic index with maturity stage; such information could provide useful information on development.

In this study, I report on the maturity and total fecundity of arrowtooth flounder in the Gulf of Alaska.

¹ Hosie, M. J., and W. H. Barss. 1977. Age and length at maturity of arrowtooth flounder, *Atheresthes stomias*, in Oregon waters. Marine Field Laboratory, Oregon Dep. Fish and Wildlife, P.O. Box 5430, Charleston, OR 97420. Unpubl. manuscr., 9 p.

Histology is used to determine maturity, and detailed descriptions of maturity stages (adapted from Rickey, 1995) are provided for both males and females. Changes in condition factor, gonadosomatic index, and hepatosomatic index are reported for the different maturity stages. Another objective of this study is to assess methods for describing arrowtooth flounder maturity (macroscopic vs. histologic) and for determining total fecundity. The accuracy of macroscopic maturity staging is assessed by comparing histological staging with macroscopic staging for all fish sampled, since Rickey (1995) noted the possibility of misassigning maturity stages by macroscopic means. Comparisons are made between this study and results from arrowtooth flounder maturity studies conducted from the eastern Bering Sea to Oregon.

Materials and methods

Maturity

Arrowtooth flounder were collected from bottom trawl hauls aboard the NOAA vessel *Miller Freeman* (cruise 93-10) on Portlock Bank near the eastern end of Kodiak Island, Alaska. The hauls were made during daylight hours from 6 to 16 September 1993 in depths ranging from 66 to 165 m. Fork lengths (cm) were recorded, and somatic fish weights (less stomach contents) were measured to ± 2 g on an electronic scale. The gonadal tissues were removed from the fish within a few hours of capture and preserved in a 10% formalin solution neutrally buffered with sodium acetate. Eyed-side and blind-side lobes of the ovary were dissected apart and stored separately. Livers were removed and weighed on the vessel (± 2 gm). Specimens less than 20 cm in length were weighed on the vessel and preserved whole in a 10% formalin solution. Preserved fish were later dissected in the laboratory, and liver weights were measured to ± 0.001 gm.

The author assigned a macroscopic maturity stage to males and females (Table 1) based on external appearance of gonads, according to descriptions adapted from Rickey (1995). (The author is an experienced groundfish biologist and prior to this project had examined the appearance of arrowtooth flounder gonadal tissue, through sex determination work, on thousands of arrowtooth flounders). Collections were initially limited to two fish per centimeter for each sex; additional females were collected over the length range where macroscopic maturity stages overlapped.

The accuracy of macroscopic stages assigned to whole ovaries was assessed by histological analysis of the ovarian sections. After being preserved in for-

malin, gonadal tissues were blotted dry and weighed on an electronic scale (± 0.001 g) in the laboratory. Sections for histology were approximately 3 mm thick. For females, the sections were cut perpendicularly through the eyed-side ovarian lobe as near to the posterior end of the lobe in order for the section to fit on a slide. For males, the section was cut perpendicularly through a distal lobe of the testis, or through the entire organ, if small. Histological samples were dehydrated, infiltrated with paraffin, and embedded in blocks of paraffin. Sections were cut from the frozen blocks on a microtome at a thickness of 5 μ , heat-fixed to a glass slide, and stained with hematoxylin and eosin. Under a compound microscope, the ovary samples were assigned one of 11 maturity stages on the basis of the most advanced oocyte seen (Table 2). Atresia of large, yolked oocytes was noted, but not quantified.

The gonadosomatic index (GSI) was calculated to show differences in development of the gonads with respect to body weight:

$$GSI = (\text{gonad weight} \times 100) / \text{somatic weight}.$$

Condition factor (CF) was calculated as an overall measure of robustness of the fish:

$$CF = (\text{somatic weight} \times 100) / \text{length}^3.$$

A hepatosomatic index (HSI) was also calculated to estimate the relative size of the liver to body weight:

$$HSI = (\text{liver weight} \times 100) / (\text{liver} - \text{free somatic weight}).$$

Although HSI is generally not included in maturity studies, the liver plays an important role in sexual maturity of both sexes. Oocyte yolk comes from the manufacture of vitellogenin in the liver (Wallace, 1985), and HSI may be a good predictor of male gonadal development, as was shown for Pacific cod (*Gadus macrocephalus*; Smith et al., 1990).

Significant differences between mean values of length, weight, GSI, CF, and HSI at the different maturity stages were tested with a one-way analysis of variance (ANOVA, $\alpha=0.05$). The mean values were further tested with a Tukey test to reveal which means were significantly different. For purposes of these tests, fish in the late perinucleus stage (stage 4) were combined with those that had atresia of previously vitellogenic oocytes but that did not yet have mature oocytes beyond the late perinucleus stage (stage 11) in the current season.

Females were classified as mature if their oocytes had entered the cortical alveoli stage (stage 5; Rickey,

1995) or showed atresia of vitellogenic oocytes. Males whose testes contained either spermatids or spermatogonia were classified as mature. The proportion mature at each length was calculated by

$$P_x = 1/(1+e^{ax+b}),$$

where P_x is the proportion mature at a given length x , and a and b are constants. Size at fifty percent

Table 1

Macroscopic and histological descriptions of developmental stages used to classify male and female arrowtooth flounder, *Atheresthes stomias* (adapted from Rickey, 1995). Mean oocyte diameter in parentheses.

Macroscopic stage and description	Histological stage and description
Females	
A Immature Ovaries small and pink with no oocytes visible.	1 Oogonia Very small (2.5 μ) and staining dark purple.
	2 Chromatin nucleolus Nucleus large, one nucleolus, cytoplasm layer thin, both staining dark purple (25–75 μ).
	3 Early perinucleus Nuclear material granular, several nucleoli around perimeter of dark-purple-staining nucleus, lighter purple vacuoles (cortical alveoli) forming around nucleus and moving outward in dark-purple-staining cytoplasm. Cytoplasm growing in thickness (37.5–75 μ).
	4 Late perinucleus Material in nucleus often moving to one side leaving much of nucleus clear, becoming fibrous with lampbrush chromosomes. Many nucleoli evenly spaced around perimeter of nucleus, cytoplasm staining less purple, ring of light purple vacuoles (cortical alveoli) still moving outward, sometimes dividing cytoplasm into two zones (150–162.5 μ).
B Developing Ovaries white to yellow, firm, oocytes visible.	5 Cortical alveoli Some lampbrush chromosomes still present, but nuclear material dispersing and nucleus turning light purple, collapsing inward. Vacuoles in cytoplasm (cortical alveoli) near cell wall, clear, one to three layers thick, cytoplasm much lighter purple (325–375 μ).
	6 Early vitellogenesis Nucleus light purple to pink in color, collapsing inward. Cortical alveoli increasing in diameter, on the outer margin of the cell wall. First yolk globules (pink) in cytoplasm, generally closer to the center of the oocyte than the cortical alveoli, sometimes in spokelike configuration. Cytoplasm less than 50% filled with yolk (375–425 μ). Yolk globules 7.5 μ .
	7 Late vitellogenesis Pink-staining yolk globules occupy 50–100% of the cytoplasm. Oocyte diameter 500 μ and yolk globules expanding to 12.5 μ .
	8 Migratory nucleus Yolk globules coalescing and increasing in diameter (25–37.5 μ), nucleus sometimes visible as a crescent shape, cortical alveoli no longer visible near edge of cytoplasm, oocyte large (625–725 μ).
C Gravid Hydrated oocytes present.	9 Hydrated Nucleus no longer visible, yolk coalescing and filling cytoplasm as continuous material.
D Ripe and running Oocytes extruded with light pressure.	10 Spawning Postovulatory follicles present.
E Spent or resting Ovaries bloodshot, flaccid, and dark red to purple.	11 Atretic Atresia of large, previously yolked oocytes, no stages beyond late perinucleus present.
Males	
Immature Testes small and threadlike, pink.	Spermatogonia, primary or secondary. Spermatocytes present.
Mature Testes enlarged, folded, brown or white in color.	Spermatids or spermatogonia present.

maturity was estimated by substituting 0.5 for P_x . The constants a and b were estimated through iterative, nonlinear regression by the StatGraphics Plus (version 6.1 for DOS) program.

Total fecundity

Weighed samples (± 0.0001 g) of whole oocytes from the most mature females (stage 8, Table 1) were counted and measured under a dissecting scope with Optimas image analysis software, and numbers were expanded to the whole ovary by using the gravimetric method. Only yolked oocytes, which were opaque, appeared as dark images on the computer monitor with back lighting. Immature oocytes, which were without yolk, were translucent and not discernible on the screen. The Optimas software automatically measured the area of the oocytes by delimiting the circumference, from which the diameters were derived. Individual measurements of oocyte diameters were normalized with a cubic transform (diameter³) because the distributions were skewed to the left (negatively) (Zar, 1984). Possible differences of oocyte density (oocytes/gram) and mean oocyte diam-

eters between ovary lobes were tested with paired t -tests. Two-way ANOVA's were used in testing for differences in oocyte density and diameter among anterior, medial, and posterior positions within the same ovarian lobe.

Possible differences between the weights of the eyed-side and blind-side ovarian lobes were tested with a paired t -test, and the relation between the lobe weights was described with a linear regression.

Results

Maturity

Gonadal tissue samples were collected from a total of 176 female and 58 male arrowtooth flounder. Damage to the ovarian lobes, or other tissues, and loss of ovarian tissue during dissection and storage were common in the larger, more mature females. This damage or loss of tissue resulted in a lower sample size ($n=158$) for measurements such as GSI and HSI. In addition, the ovarian lobes of three fish were so small that the lobes were not separated during dis-

Table 2
Histological analysis of macroscopic maturity stages.

Macroscopic maturity stage	Microscopic maturity stage	Count	Percent	Number with atresia	Percent per stage with atresia
Stage A (Immature)	3	11	14.5	0	0.0
	4	51	67.1	0	0.0
	5	6	7.9	5	83.3
	11	8	10.5	8	100.0
Subtotal		76		13	17.1
Stage B (Developing)	5	1	2.0	1	100.0
	6	3	6.0	1	33.3
	7	31	62.0	6	19.4
	8	15	30.0	0	0.0
Subtotal		50		8	16.0
Stage E (Spent or resting)	4	2	4.4	0	0.0
	5	13	28.9	6	46.2
	6	11	24.4	2	18.2
	7	11	24.4	1	9.1
	8	4	8.9	0	0.0
11	4	8.9	4	100.0	
Subtotal		45		13	28.9
Stage A or E (Developing, or spent or resting)	7	3	100.0	1	33.3
Unidentified	4	1	50.0	0	0.0
	6	1	50.0	0	0.0
Total		176			

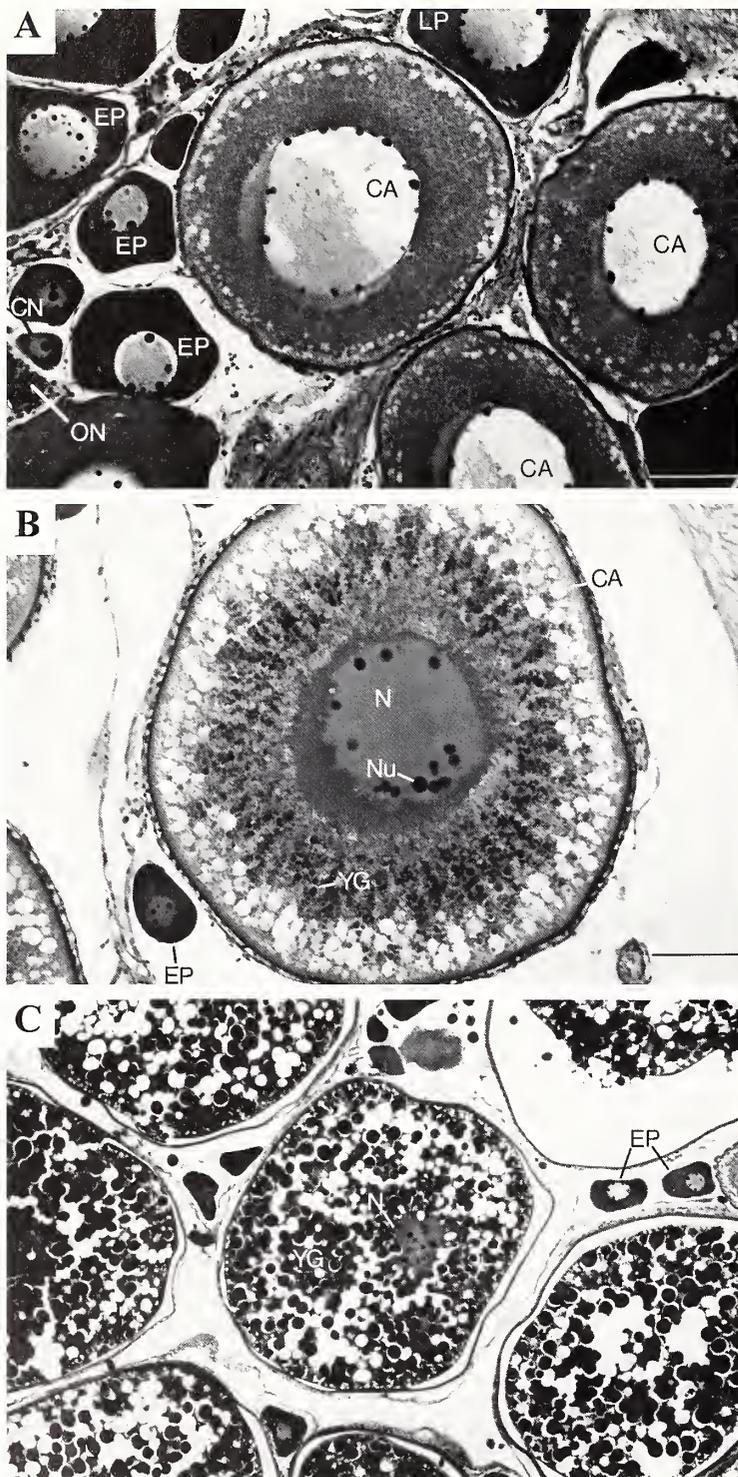


Figure 1

Oocytes in arrowtooth flounder, *Atheresthes stomias*, at different stages of development. (A) Oocytes of a 57-cm-FL female at the cortical alveoli stage as well as less mature oocytes. (B) Oocyte of a 66-cm-FL female at the early vitellogenesis stage. (C) Oocytes of a 82-cm-FL female at the migratory nucleus stage. Bar = 0.1 mm; ON = oogonial nest; CN = chromatin nucleolus; EP = early perinucleus; LP = late perinucleus; CA = either cortical alveoli stage oocytes or cortical alveoli structures (with arrow); N = nucleus; Nu = nucleolus; YG = yolk globule.

section, making them unavailable for the lobe-weight comparison.

In the five-tier macroscopic staging scale for females (Table 1), fish were classified only as "immature" (stage A), "developing" (stage B), or "spent or resting" (stage E). No females were found with hydrated oocytes ("gravid," stage C) or that were "ripe and running" (stage D). The two-tier macroscopic maturity scale for males was abandoned early in the study because of lack of confidence in assigning stages—nearly all males appeared to be "immature."

Histological analysis revealed that all females were in stages 3–8 and stage 11 of oocyte development (from early perinucleus to the migratory nucleus stage, and the atretic stage, Table 2). The lack of hydrated oocytes or post-ovulatory follicles in any of the ovaries indicated that these samples were collected prior to the spawning season. None of the males were ready to spawn but in some specimens, spermatids and spermatozoa were present, indicating that the males were preparing to spawn.

Figure 1 shows photographs of histological sections taken from females at three different stages of maturity. The progression of size increase of oocytes from the oogonial nest stage through the cortical alveoli stage can be seen in Figure 1A. Some specimens in early vitellogenesis, such as shown in Figure 1B, had yolk globules arranged in a spoke-like configuration in the cytoplasm. The increase in oocyte size in the migratory nucleus stage, in comparison with oocyte size in the early perinucleus stage, and the increase in size of yolk globules are shown in Figure 1C.

The categories of maturity stages, based on macroscopic examination, are shown in Table 2. Most of the females classified macroscopically as "immature" (stage A, $n=76$, length range 14–64 cm) were in the early or late perinucleus stage ($n=62$, 81.6%). A total of 18.4% (14 of 76) of these females classified macroscopically as "immature" were either in the process of maturing (cortical alveoli stage) or showed evidence that they had been mature the previous season (atresia of previously yolked oocytes).

Table 3

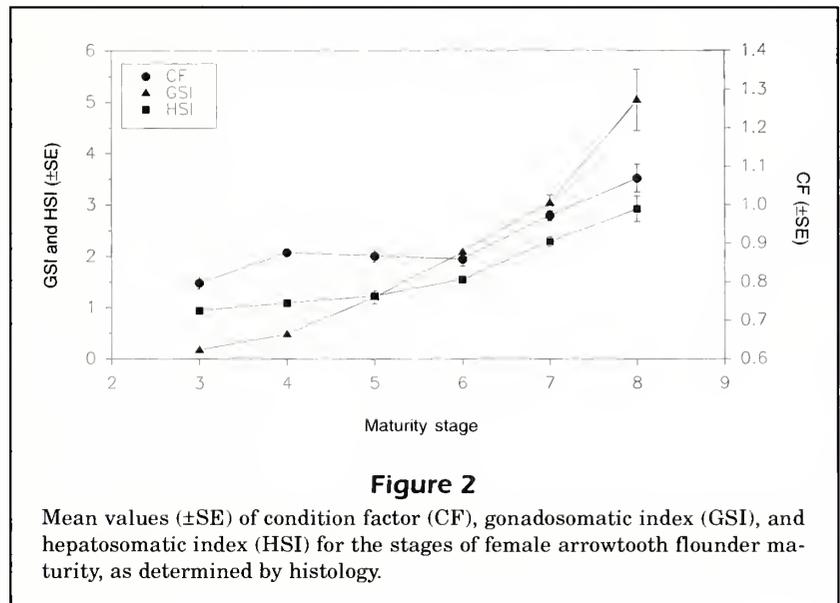
Tukey test results showing significant differences (<) and equalities (—) between arrowtooth flounder (*Atheresthes stomias*) females in different stages of development, as determined by histology (EP = early perinucleus, LP = late perinucleus, CA = cortical alveoli, EV = early vitellogenesis, LV = late vitellogenesis, and MN = migratory nucleus).

Variable	Histological stage										
	EP		LP		CA		EV		LV		MN
Length	EP	<	LP	<	CA		EV		LV		MN
Weight	EP		LP	<	CA		EV		LV		MN
Condition factor	EP		EV		CA		LP	<	LV	<	MN
Gonadosomatic index	EP		LP	<	CA	<	EV	<	LV	<	MN
Hepatosomatic index	EP		LP		CA		EV	<	LV	<	MN

Histological examination of females classified macroscopically as “developing” (stage B, $n=50$, length range 47–83 cm) revealed that they were in vitellogenesis and thus correctly classified. Most of the females had oocytes that were in some phase of yolk acquisition (early vitellogenesis to migratory nucleus stages), and only 2.0% were in the cortical alveoli stage. Sixteen percent of these fish had atretic oocytes.

Most of the females categorized as “spent or resting” (stage E, $n=45$, length range 49–83 cm) were in some stage of vitellogenesis ($n=39$, 86.7%) and should have been classified as “developing.” The percentage of fish with atresia declined with increasing maturity stage, from 46.2% in the cortical alveoli stage to 0.0% in the migratory nucleus stage. Overall, 28.9% of these “spent or resting” fish had atresia, the highest rate of all three macroscopic stages. Only 4 fish out of 45 were correctly determined to be “spent or resting” (late perinucleus with atresia).

Three females were assigned a combined macroscopic classification of “developing” or “spent or resting.” In two of the fish the anterior portion of the ovarian lobes appeared to be “developing” whereas the posterior ends appeared to be “spent or resting.” In the third fish the blind-side ovarian lobe appeared to be “developing” whereas the eyed-side appeared to be “spent or resting.” Histological examination demonstrated that all three of these fish were in late vitellogenesis; even samples taken from the portions of the ovary that were macroscopically classified as

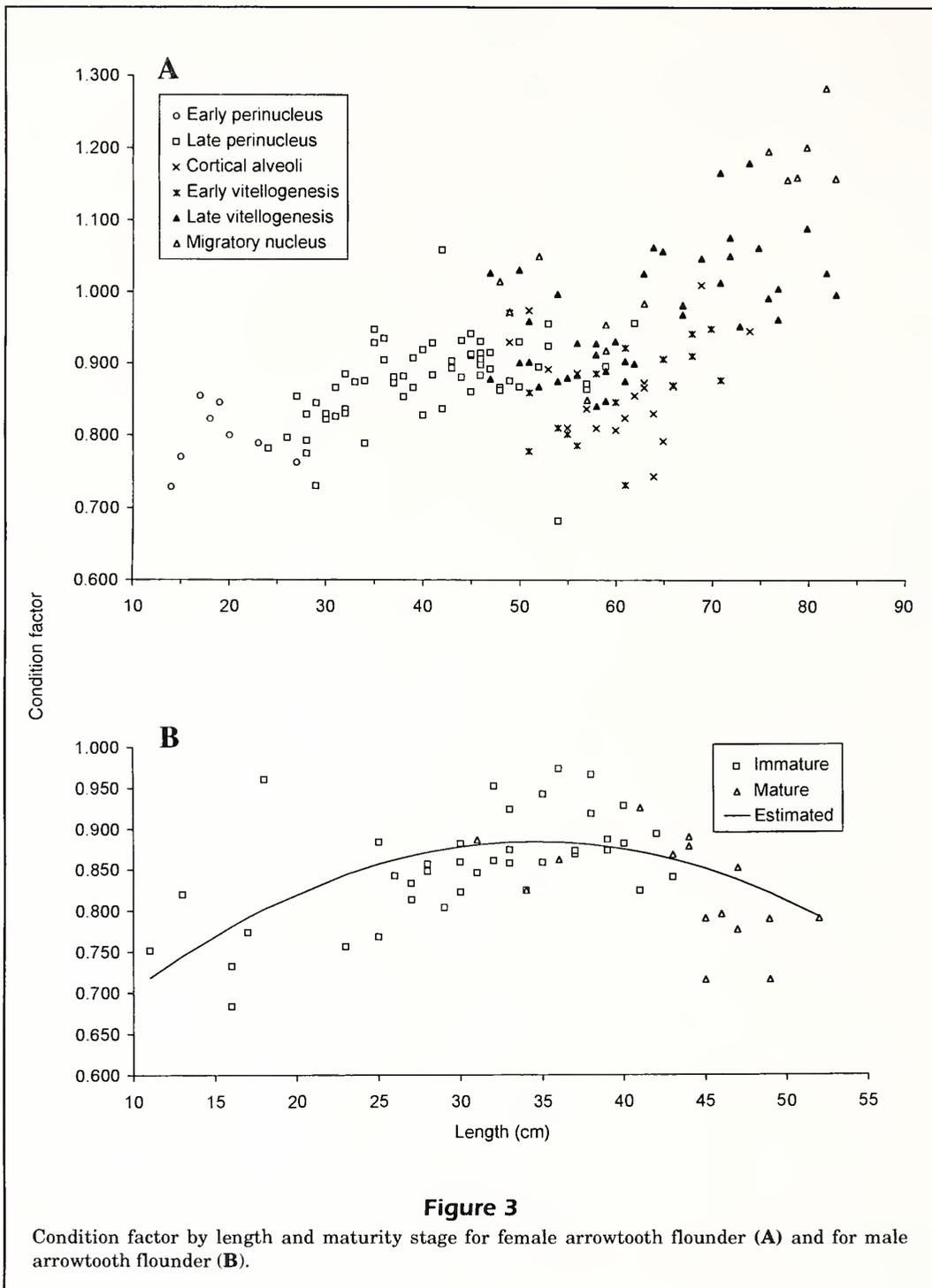
**Figure 2**

Mean values (\pm SE) of condition factor (CF), gonadosomatic index (GSI), and hepatosomatic index (HSI) for the stages of female arrowtooth flounder maturity, as determined by histology.

“spent or resting” demonstrated that the fish were in late vitellogenesis.

I failed to classify two females macroscopically because of size-based bias. A large fish (66 cm), in which the ovary appeared to be “immature,” was actually in the early vitellogenesis stage. A small fish (20 cm), in which the ovary appeared to be “developing,” was in the late perinucleus stage.

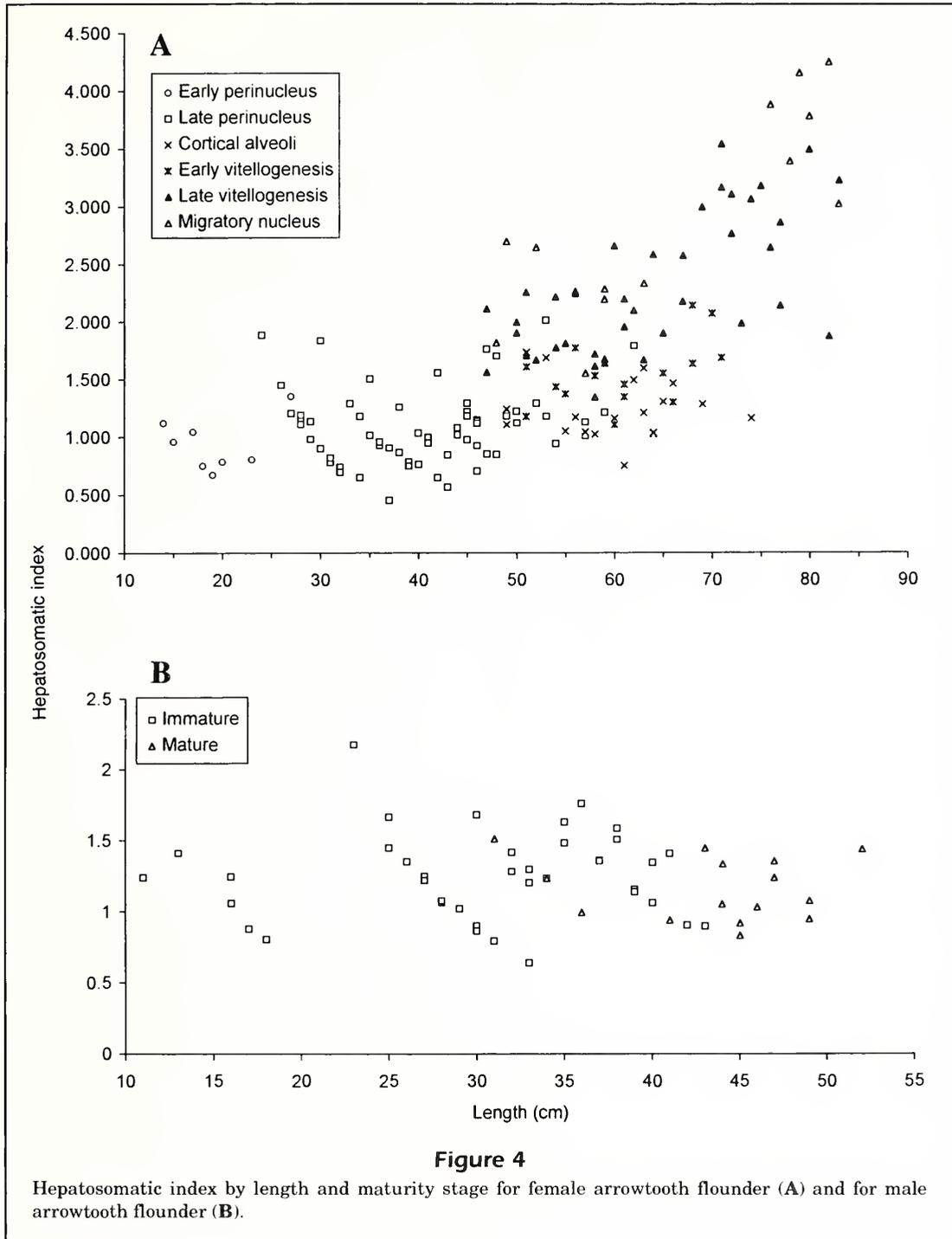
Mean values of CF, HSI, and GSI of the histological stages for females are presented in Figure 2, with significant differences shown in Table 3. Condition factors of the first four stages were not significantly different, but CF was higher in the late vitellogenesis stage and highest in the migratory nucleus stage (Single-factor ANOVA; $df=5$, $F=25.9$, $P<0.001$; Tukey tests). The small decline in mean CF values between



stages 4, 5, and 6 was not significant (Fig. 2), but there was a similar decline in CF in fish between 50 and 60 cm in length (Fig. 3A). Condition factor of immature males (0.854) was not significantly different (t -test; $df=56$, $P>0.05$) from that for mature males (0.822); however, the regression fit of the relationship ($df=55$, $F=4680$, $P<0.001$, $r^2=0.31$) shows that

CF increased with length for small fish, reached a peak at 34.5 cm, and declined in larger fish (Fig. 3B).

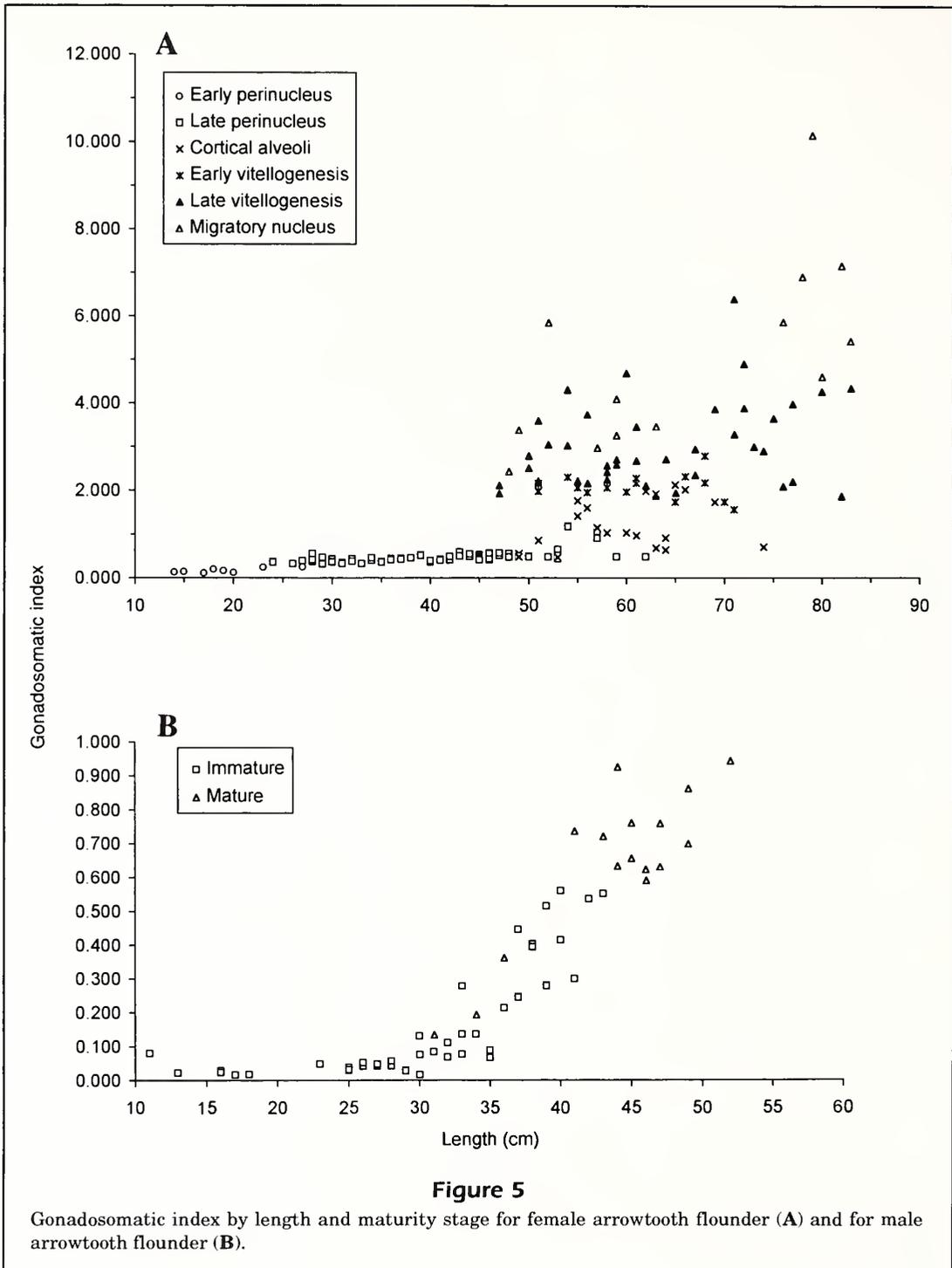
Hepatosomatic index varied significantly among female maturity groups (single-factor ANOVA; $df=5$, $F=59.0$, $P<0.001$) and was significantly greater in both the late vitellogenesis stage (2.281) and migratory nucleus stage (2.921). In general, HSI increased



with increasing female length (Fig. 4A). There was no difference in HSI between mature and immature males (unpaired *t*-test; $df=27$, $P>0.05$), and no trends in the data (Fig. 4B).

Gonadosomatic index varied significantly among female maturity groups (single-factor ANOVA; $df=5$, $F=91.9$, $P<0.001$). The Tukey test revealed that de-

spite more than doubling, the GSI did not change significantly between the early and late perinucleus stages (Table 3). After that, the GSI was significantly greater in each succeeding stage of maturity (Table 3). Figure 5A shows that GSI remained low until fish reached lengths over 45 cm. GSI was significantly greater in mature males than in immature males

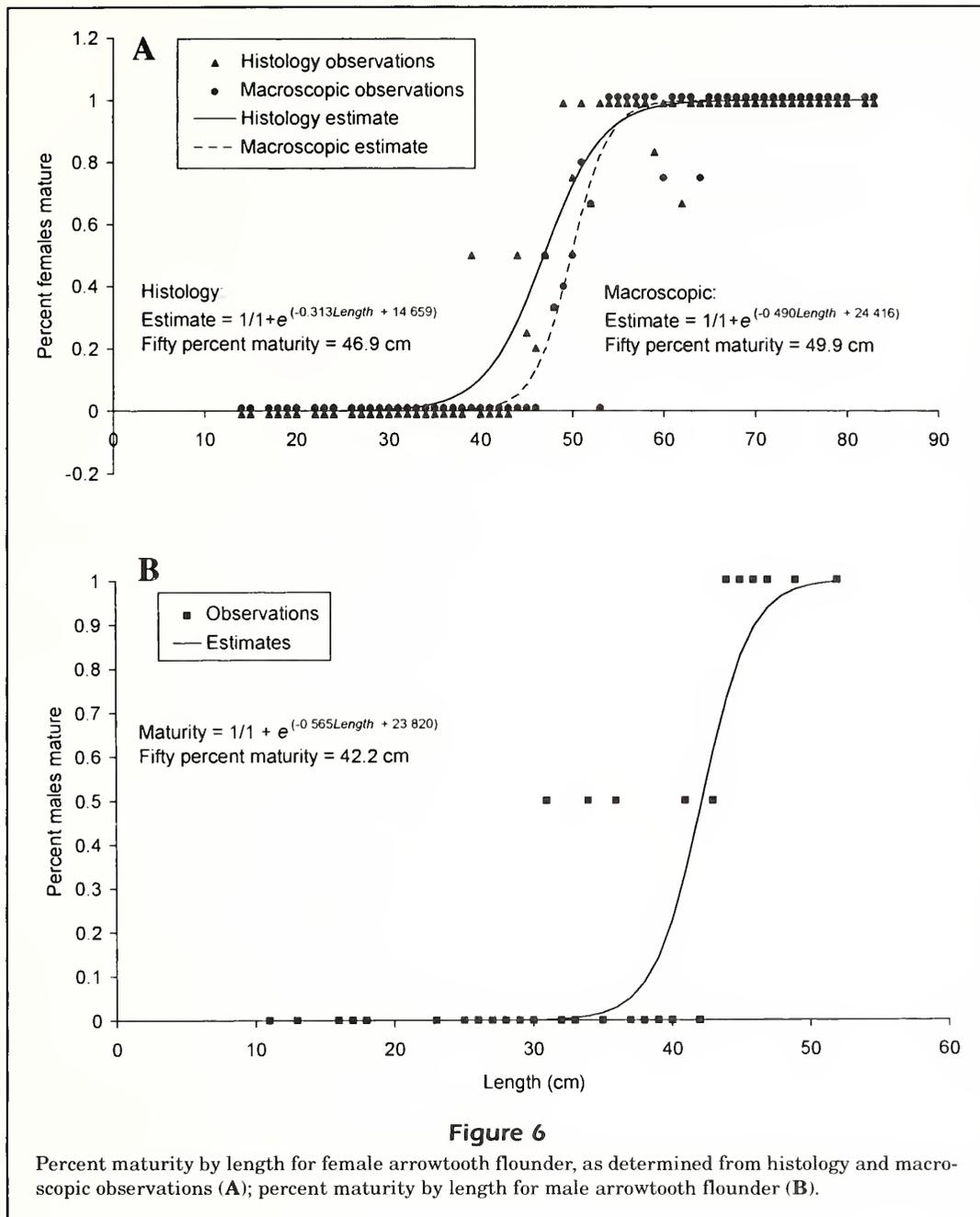


(unpaired *t*-test; *df*=27, $P < 0.001$); the increase began between 30 and 35 cm in length (Fig. 5B).

According to histological analysis, L_{50} for females occurred at 46.9 cm (*df*=174, $F=897$, $r^2=0.76$, Fig. 6A) and at 42.2 cm (*df*=56, $F=69$, $r^2=0.60$, Fig. 6B) for males. According to macroscopic staging, L_{50} for females occurred at 49.9 cm (*df*=172, $F=748$, $r^2=0.76$, Fig. 6A).

Total fecundity

In general, the eyed-side ovary lobes were heavier than the blind-side lobes (paired *t*-test; *df*=154, $t=2.663$, $P=0.009$). Linear regression analysis (*df*=153, $F=2365$, $P < 0.001$, $r^2=0.94$) described the relation between the weight of ovarian lobes as



$$W_B = 0.843(W_E) + 1.398,$$

where W_B = the weight of the blind-side lobe; and
 W_E = the weight of the eyed-side ovary lobe.

All the frequency distributions of the diameter of maturing oocytes were unimodal and had a long tail on the left. A cubic transform (diameter³) normalized the distributions. The transformed values of the mean diameter of oocytes did not vary significantly among positions (anterior, medial, posterior) within

the same ovarian lobe (two-factor ANOVA, $df=2$, $P>0.05$) or between lobes (paired t -test, $df=9$, $P>0.05$). Density of oocytes (count of oocytes per gram of ovarian tissue) also did not vary significantly between positions within ovarian lobes (two-factor ANOVA, $df=2$, $P>0.05$) or among ovarian lobes (paired t -test, $df=9$, $P>0.05$). Thus samples for total fecundity were combined from the different positions and ovarian lobes.

Total fecundity was significantly related to fish length ($df=11$, $F=125.7$, $P<0.001$, $r^2=0.92$) by the equation

$$\ln(F) = 4.020 \ln(L) - 3.149,$$

from which was derived

$$F = 0.0429 (L)^{4.020},$$

where F = total fecundity; and

L = fork length in centimeters (Fig. 7A).

Length-based total fecundity estimates ranged from 246,000 (48 cm) to 2,224,000 (83 cm) oocytes. Total fecundity was also significantly related to somatic fish weight ($df=11, F=264.7, P<0.001, r^2=0.96$):

$$F = 350.4(W) - 138,482,$$

where F = total fecundity; and

W = somatic weight in grams (Fig. 7B).

Weight-based total fecundity estimates ranged from 255,000 (1,122 g) to 2,339,000 (7,070 g) oocytes.

Discussion

Maturity

Histological analyses demonstrated that the assignment of macroscopic maturity stages was not always reliable. Although it was confirmed through histol-

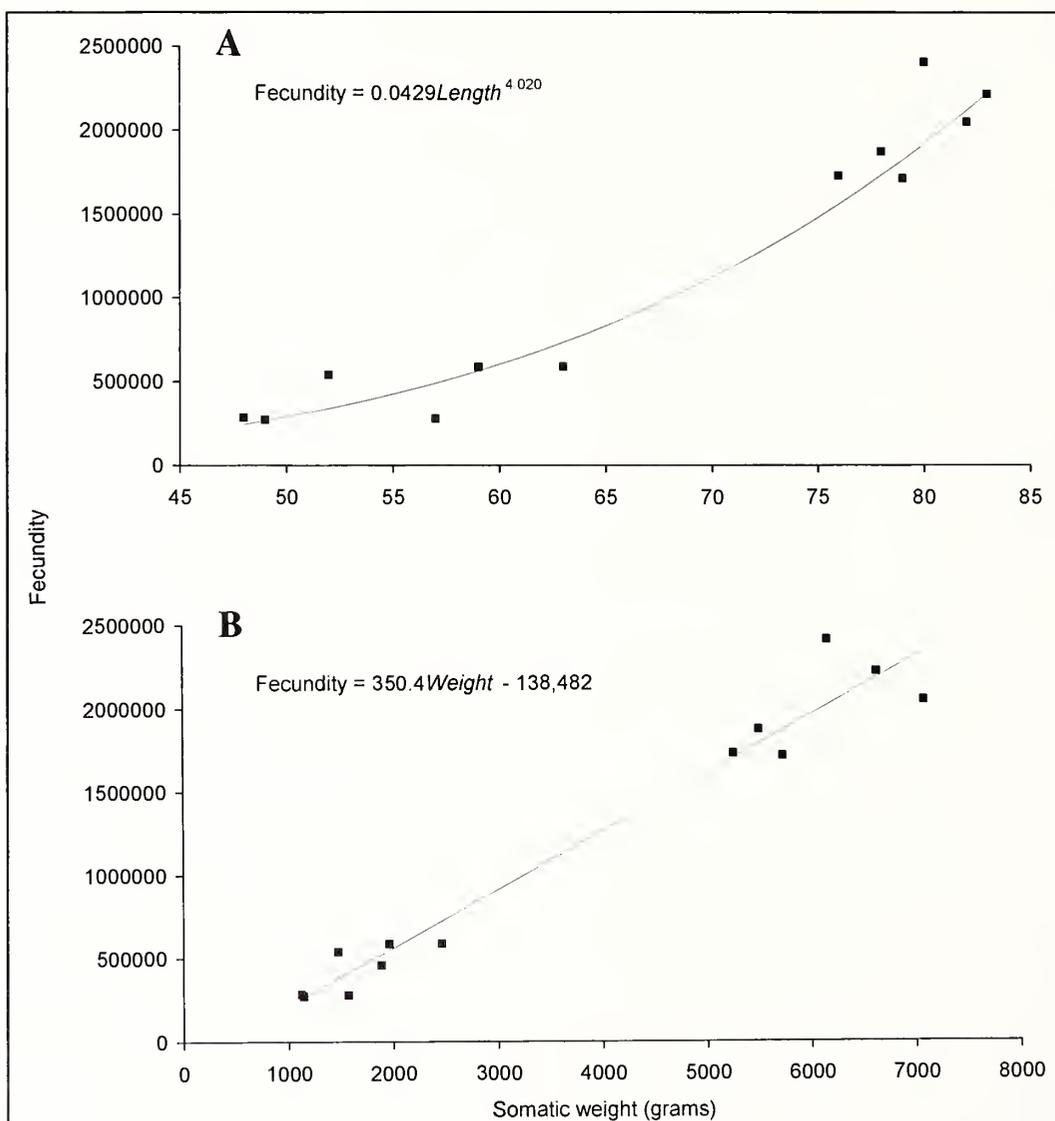


Figure 7

Total fecundity by length for female arrowtooth flounder (A); total fecundity by weight for female arrowtooth flounder (B).

ogy that none of the "immature" females had begun acquiring yolk, some had begun the process of maturing oocytes, and several had atresia of large, previously yolked oocytes, indicating that these females had probably spawned during the previous year. All females classified macroscopically as "developing" had maturing oocytes to spawn, most of them in the later stages of vitellogenesis. Few of the fish classified as "spent or resting" were actually resting: most were in vitellogenesis and should have been classified as "developing." In addition, the author was unable to assign a single maturity stage to ovaries with a mixed appearance and to assign a stage for ovaries from some females.

The several females correctly classified as "spent or resting" deserve some discussion. These fish had oocytes only as advanced as the late perinucleus stage and had degenerating oocytes present, which had previously been yolked. These fish were classified as mature because they had previously contained yolked oocytes, but they were unable to spawn soon, despite the upcoming spawning season, and they did not show signs of recent spawning. Hunter and Macewicz (1985, a and b) have reported histological details on creation and resorption of atretic oocytes and postovulatory follicles in the northern anchovy, *Engraulis mordax*. Their results have shown that the relatively rapid resorption of yolked oocytes (after 23 days of starvation; Hunter and Macewicz, 1985a) and postovulatory follicles (after 3–4 days; Hunter and Macewicz, 1985b) seems to contradict my assertion that atretic vitellogenic oocytes from the previous spawning season were still being resorbed in arrowtooth flounder just prior to the spawning season. A comparison of the reproductive cycle of arrowtooth flounder (which is a determinate-spawning benthic flatfish, dwelling in relatively cold northern waters) with that of the northern anchovy (an indeterminate-spawning pelagic roundfish, occupying much warmer southern waters) is not without merit. It is important to note, however, that significant differences could occur in the rate in which these species cycle between reproductive stages. Hunter and Macewicz (1985b, p. 87) caution that "the duration of postovulatory stages must be newly estimated for each species, and an assumption that the duration of these stages in a new species is similar to the northern anchovy is highly speculative." Perhaps further sampling of this arrowtooth population closer to or during the spawning season could have provided more information on the further development of these "spent or resting" fish.

Macroscopic classification was not successfully applied to the males. Only by histologic work was male maturity confidently assessed. Rickey (1995, p. 130),

in her nearly year-round sampling of arrowtooth flounder, also had difficulty with assigning macroscopic maturity stages to males, stating that males "... did not show grossly apparent developmental changes over time ... no spawning males were seen."

In the present study, females were classified as mature if they had oocytes as advanced as the cortical alveoli stage (Rickey, 1995), or showed atresia of previously vitellogenic oocytes. Significant differences in GSI and HSI occurred between the late perinucleus and cortical alveoli stages, and fish at the cortical alveoli stage were also longer and heavier. The insignificant but noticeable decline in condition factor in the cortical alveoli and early vitellogenic stages also indicates an emphasis in gonad growth over somatic growth. Rickey (1995), in examining Washington coast arrowtooth flounder collected during the spawning season, found that all of the fish had either matured beyond the cortical alveoli stage or had not yet matured that far. This finding supports the idea that fish in the cortical alveoli stage prior to the spawning season will mature during the same spawning season. Histology is regarded as the best method available to assess maturity (Hunter et al., 1992; West, 1990), but Hunter et al. (1992) concluded that even with the broadest criteria defining maturity, some spent fish are not identifiable as post-spawners when sampling is done after spawning has commenced.

Hosie and Barss¹ determined that Oregon arrowtooth flounder males reach L_{50} at 29 cm and females reach L_{50} at 44 cm. Rickey (1995) determined that Washington males reach L_{50} at 28.0 cm and females reach L_{50} at 36.8 cm. Fargo et al. (1981) determined that British Columbia males reach L_{50} at 31 cm and females reach L_{50} at 37 cm. All the above studies determined maturity by using macroscopic classification of arrowtooth flounder gonads.

It was thought that macroscopic observations of maturity would result in a lower L_{50} , as all the other arrowtooth flounder maturity studies showed, but instead the L_{50} based on macroscopic observations was 3 cm higher. This finding is the opposite of that found in a study by Walsh and Bowering (1981) who compared macroscopic and histological staging of Greenland halibut (*Reinhardtius hippoglossoides*) ovaries and demonstrated that L_{50} was 3 cm higher in the maturity ogive derived from histological work.

Time of sampling in relation to the spawning season may have been a factor in determining female L_{50} . Hunter et al. (1992) showed that estimates of L_{50} for female Dover sole (*Microstomus pacificus*) taken during the spawning season were higher than estimates of L_{50} for female Dover sole taken just prior to the spawning season, whereas Rickey (1995) found

the opposite for arrowtooth flounder; her highest L_{50} values were derived from fish taken prior to spawning and her lowest value was derived from fish taken during the spawning season. The Oregon study occurred from September through June (Hosie and Barss¹), the Washington study occurred nearly year-round (Rickey, 1995), and the British Columbia study occurred only in June (Fargo et al., 1981).

Histological examination revealed that most mature males in this study had only a small portion of their testes filled with spermatozoa; and thus they were not yet ready to spawn. It is likely that, as these large males continued to develop sexually during the season, other smaller males would have become sexually mature, thus lowering the male L_{50} . The male L_{50} value of 42.2 cm determined in this study should be viewed as a high estimate. Male GSI values started increasing at around 30 cm in length, and CF values began declining at 34.5 cm; both trends indicate a transition from somatic growth to gonad maturation at a much smaller size than that for the L_{50} reported here.

In general, the largest females were the most mature in this study, indicating that they might spawn the earliest. The high values of CF, GSI, and HSI for these largest, most mature females also show that these fish are best able to support the burden of spawning. The noticeable but insignificant drop in CF for females in the cortical alveoli and early vitellogenesis stages (Fig. 2), at around 50–60 cm in length (Fig. 3A), if real, can be explained by two possibilities. Either these mid-size fish are affected more by vitellogenesis than are the larger fish, or all females suffer losses in CF in the early stages of vitellogenesis and recover during later maturity stages. Gonadosomatic index was also highest in the largest males; thus they appear to mature earlier in the season than smaller males. The largest, most mature males had decreasing CF values that indicated an impact of maturing testes on body composition.

The spawning habits of arrowtooth flounder are not well known. Shuntov (1970) was unable to determine accurate spawning times for arrowtooth flounder in the eastern Bering Sea but nonetheless stated that they were close to those of Kamchatka flounder (*Atheresthes evermanni*), which were found in spawning condition in January and March. Fargo et al. (1981), using macroscopic observations of gonads collected in June from Hecate Strait, concluded that spawning takes place prior to June, probably in spring months. Rickey (1995) showed that spawning occurred off the Washington coast from September through December, and possibly as late as February. Hosie and Barss¹ reported a December–March spawning period for arrowtooth flounder off the Or-

egon coast. Pertseva-Ostroumova (1961) reported arrowtooth flounder spawning in the Bering Sea from January through March. The results presented here, that a spawning season begins after September, are supported by all of the studies mentioned above.

Total fecundity

Both macroscopic and microscopic observations showed that this study was made prior to the spawning season: none of the females were “ripe and running,” had hydrated oocytes, or had postovulatory follicles, and none of the males were ready to spawn. Thus no bias due to loss of oocytes was expected.

Total fecundity estimates for arrowtooth flounder had not been previously reported in the literature. The only other member of the genus, Kamchatka flounder, has an estimated fecundity range of 130,000–500,000 oocytes (Pertseva-Ostroumova, 1961), which is much lower than what is reported here for arrowtooth flounder. As with many other flatfish species, arrowtooth flounder total fecundity increases linearly with fish weight and in a curvilinear fashion with length (Hempel, 1979). The largest arrowtooth flounder in this study had about 10 times as many oocytes as the smallest fish for which total fecundity was estimated. The unimodal frequency distribution of maturing oocyte diameters is supported by Rickey's (1995) determination that arrowtooth flounder is a group-synchronous spawner.

The significant difference in weight between the eyed-side and blind-side lobes has not been previously reported for arrowtooth flounder but has been reported for sole (*Solea solea*, Witthames and Walker, 1995). Nichol² found that blind-side lobes were significantly larger than eyed-side lobes in yellowfin sole (*Pleuronectes asper*). This finding suggests that in flatfish species both ovarian lobes should be considered when calculating GSI or total fecundity. Because there were no significant differences in mean oocyte diameter or mean oocyte density within or between ovarian lobes, total fecundity samples may be taken from any portion of the ovary. In his review paper, West (1990) mentioned that typically there is no difference in oocyte size or diameter frequency distribution between ovarian lobes, but differences along the length of the ovary and in cross sections do occur in some species. Hunter et al. (1992) found no differences in oocyte density between ovarian lobes, along the length of a lobe, or by cross section of a lobe in Dover sole.

² Nichol, D. G. 1995. Resource Assessment and Conservation Engineering Div., Alaska Fish. Sci. Center, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

Although this study provides the first information on total fecundity of arrowtooth flounders, subsampling of ovarian tissue for total fecundity, histology of males, comparison of macroscopic and histological methods, and relation of ancillary body measures such as CF, GSI, and HSI, there is still much that is unknown about this species. The lag of male maturity in comparison to that of females in this study, and the lack of spawning males in Rickey's (1995) study are parts of an interesting riddle. Possible seasonal migrations proposed by Shuntov (1970) and Rickey (1995) need to be thoroughly documented, as well as possible spawning migrations. Differences in size at maturity found in this study, compared with those found in studies conducted in southern waters, need to be explored. A study, in which collections are made at preselected depths and in which age and histological data are collected at regular intervals throughout a year, would answer many questions.

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The reproductive biology and early life stages of *Podothecus sachi* (Pisces: Agonidae)*

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Within the agonids, 20 genera and 50 species are recognized, with most distributed from the bottom of the north Pacific Ocean to the Bering Sea (Nelson, 1984). The agonid body is covered with bony plates and is unusual among teleost fishes. Several taxonomic studies have been conducted (Jordan and Evermann, 1898; Matsubara, 1955; Kanayama, 1991); however, little ecological information on the agonids exists because of their poor commercial value and small population density. Even for the sail-fin poacher, *Podothecus sachi*, the most common of the Japanese agonids, only larvae and juveniles have been reported from the adjacent waters of northern Japan (Maeda and Amaoka, 1988). Past reports concerning the reproductive ecology of agonids have suggested that they have internal fertilization and that females produce small clutches of eggs almost daily (Iioka and Gunji, 1979; Sugimoto, 1987; Aoyama and Onodera, 1989). Recently, eggs of copulating cottids that were thought to undergo internal fertilization were shown to be fertilized by the received spermatozoa only after eggs were deposited (Munehara et al., 1989, 1991, 1994a, in press; Koya et al., 1993), i.e. there is an internal deposition of sperm that do not penetrate the ova or egg until after the latter are spawned and free in the environment. This spawning mode, named the internal gametic association (Munehara

et al., 1989), is characterized by the deposition of unfertilized eggs whose paternity has been fixed before spawning (Munehara et al., 1990; 1994b). This spawning mode is so unique that it is not included in other categories of the parity mode of fishes, as determined on an evolutionary basis (Wourms et al., 1988). A comparative osteological and myological study on Scorpaeniformes indicated that the Agonidae family is most closely related to the Cottidae family (Yabe, 1985). Therefore, it is possible that the internal gametic association mode of spawning that occurs in agonid fishes may provide information concerning the relation of the two families. In this study, I report on the reproductive biology and the early life stages of *P. sachi*, comparing them with those of other agonid fishes.

Materials and methods

Three adult females of *P. sachi* were collected with gill nets from offshore bottom waters (60–80 m depth) at Usujiri, southern Hokkaido, 7 October 1992. After the live fish had been transported to the laboratory, their ovaries were surgically removed, and ripe eggs and ovarian fluid were extracted. Great care was taken to prevent contamination by seawater, urine, and blood. The ovarian fluid was isolated with a pipette for use in the

following test. To determine if egg development began before or after contact with seawater, eggs of each female were placed in separate petri dishes containing either ovarian fluid or seawater at 6°C. After 20 hours, the number of developing eggs were counted on the basis of occurrence of cleavage and formation of the blastodisc, which were regarded as signs of initial fertilization and autoactivation, respectively.

Histological observations were carried out on several eggs before exposure to seawater to determine if internal fertilization occurred. Ovaries were examined to decide their developing mode. The ovaries were fixed in Bouin's fluid. Serial paraffin sections, 5–8 µm, were prepared and stained with Delafield's hematoxylin and eosin. The criteria of the maturing oocytes followed the classification of Yamamoto (1956).

Eggs remaining from the above observations were used for morphological observation of the early life stages of this fish. The eggs not used for artificial insemination were kept in a 1-L glass dish at a mean water temperature of 5°C. No bubbling stone was placed in the dish, but half of the seawater was replaced once a week. Juveniles were fed nauplii of *Artemia salina*. Measurement and observation of embryonic development were conducted once every 1–3 days. Sampling of hatched fish was done at intervals of 1–2 weeks until 93 days after hatching. Specimens were observed under a microscope after fixation in 5% neutral formaldehyde solution. Terminology of the

* Contribution 117 from Usujiri Fisheries Laboratory, Faculty of Fisheries, Hokkaido University, Hokkaido, Japan.

bony plates followed Gruchy (1969) and Maeda and Amaoka (1988).

Results

General anatomy and histology of the ovary

The paired ovary of *P. sachi* was bilobed anteriorly but fused together from the middle region; its posterior end reached beyond the genital duct, which was located at the middle of the abdominal cavity (Fig 1). The anterior part of the genital duct was retractable and could be everted by pressing the fish's belly. The protruded duct was tapered, about 2 cm length in 27.5–29.1 cm standard-length (SL) specimens (Fig. 1A). Blood vessels in the ovary ran radiately in the tunica of the dorsal side. The ovarian cavity passed through the center of the ovary and then directly faced the ovarian wall lined with epithelia near the genital duct. The genital pore opened just behind the pelvic fins. The cavity and the genital duct contained several hundred ripe eggs (Fig. 1B).

Sections of the ovary contained oocytes in various developing stages, including the chromatin-nucleolus, perinucleolus, yolk-vesicle, oil-droplet, yolk-globule, migratory-nucleus, premature, and ripe stages (Fig. 2). In addition, postovulatory follicles in the stage just after ovulation or in the stage of regenerating were also found. These observations indicated that female *P. sachi* produce multiple clutches in a breeding season.

Appearance of eggs

Eggs were demersal, adhesive, and almost spherical in shape. The mean egg size was 1.73 mm in dia-

meter, ranging from 1.70–1.75 mm ($n=30$). The yolk was light pink, and many oil droplets and small, whitish, granular material were observed within the yolk.

Initiation of egg development

Although the eggs from the three females were not artificially inseminated, most eggs placed in seawater had developed to the 2-cell stage after 20 hours (Table 1). In contrast, none of the eggs kept in the ovarian fluid showed any sign of development. When

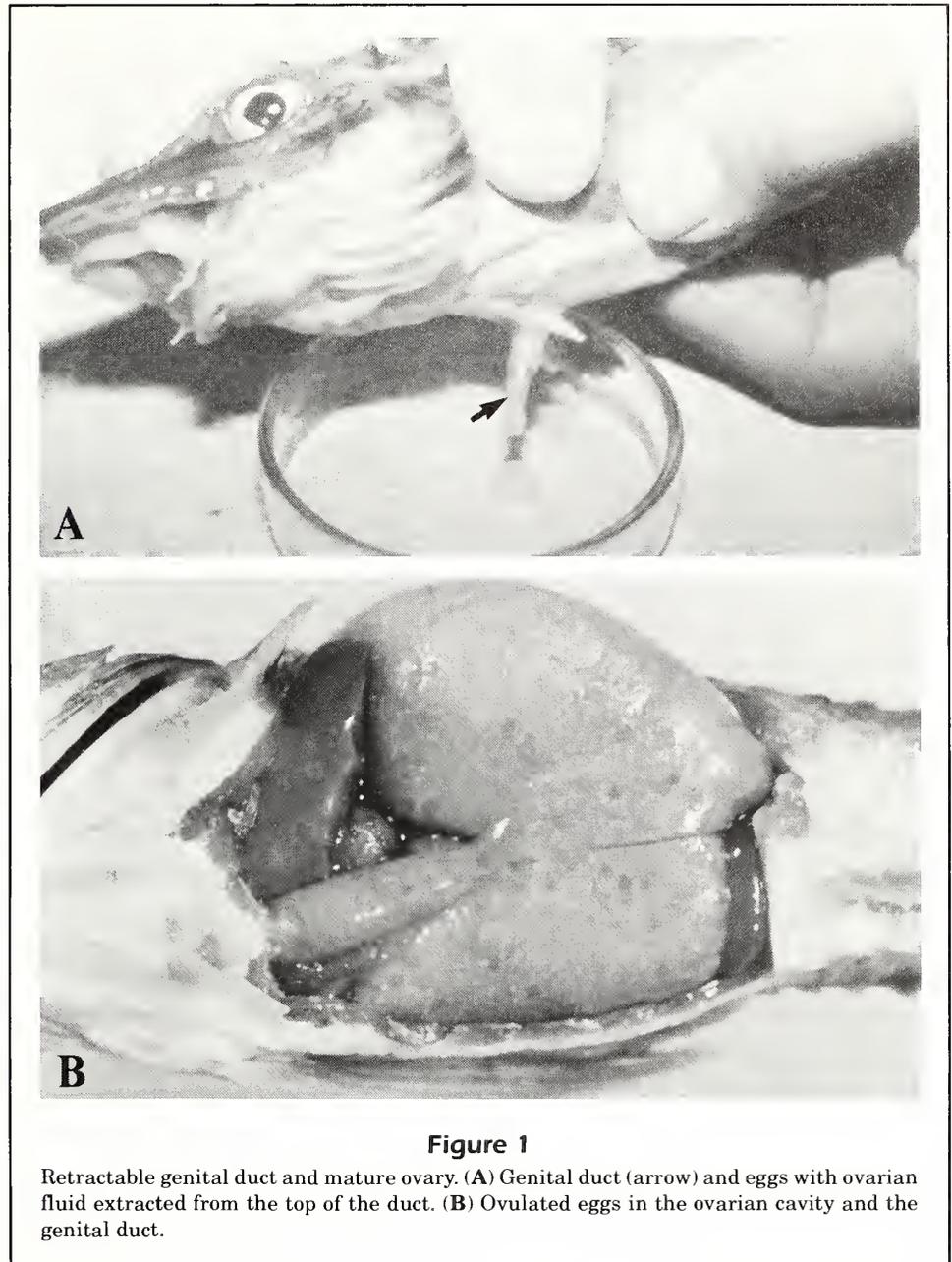


Figure 1

Retractable genital duct and mature ovary. (A) Genital duct (arrow) and eggs with ovarian fluid extracted from the top of the duct. (B) Ovulated eggs in the ovarian cavity and the genital duct.

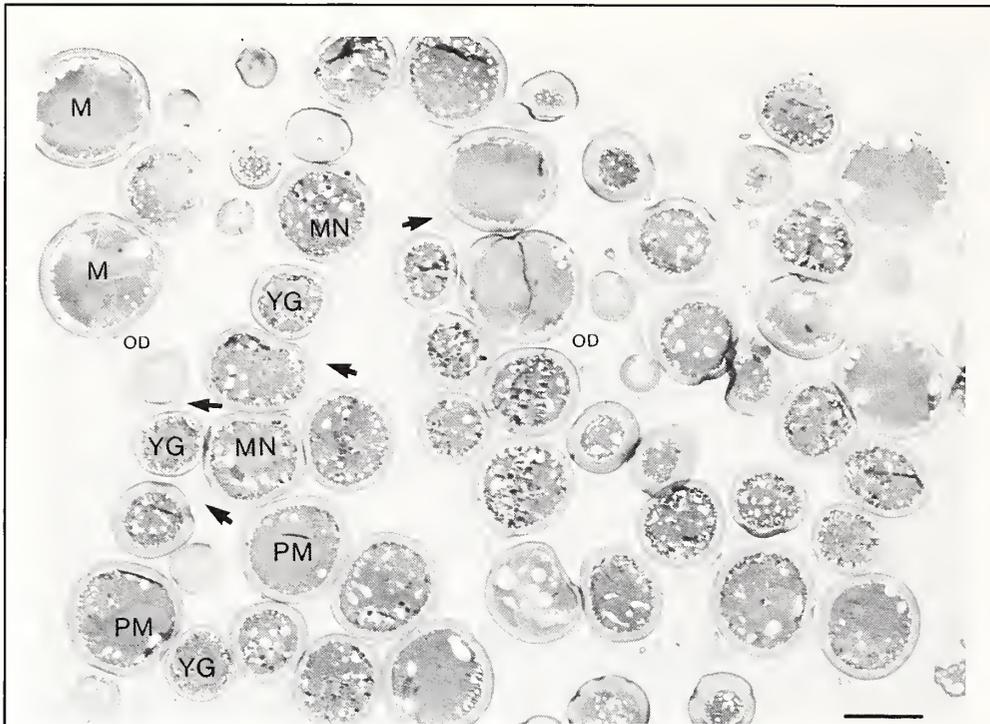


Figure 2

A section of mature ovary. M = mature stage oocytes, PM = premature stage oocytes, MN = migratory nucleus stage oocytes, YG = yolk globule stage oocytes, OD = oil droplet stage oocytes. Arrows indicate postovulatory follicles. Bar indicates 1mm.

Table 1

Embryonic development of *Podothecus sachi* eggs from 3 specimens 20 hours after immersion in seawater or ovarian fluid at 6°C.

Rearing medium	Percent (no.) of 2-cell stage eggs	Percent (no.) of undeveloped eggs	Percent (no.) of dead eggs
Seawater	97.5 (118)	1.7 (2)	0.8 (1)
Ovarian fluid	0 (0)	98.5 (133)	1.5 (2)
24 h after egg transfer from ovarian fluid to seawater	96.3 (130)	1.5 (2)	2.2 (3)
Seawater	95.5 (106)	3.6 (4)	0.9 (1)
Ovarian fluid	0 (0)	98.3 (117)	1.7 (2)
24 h after egg transfer from ovarian fluid to seawater	95.8 (114)	1.7 (2)	2.5 (3)
Seawater	97.2 (141)	1.4 (2)	1.4 (2)
Ovarian fluid	0 (0)	98.4 (124)	1.6 (2)
24 h after egg transfer from ovarian fluid to seawater	93.7 (118)	4.8 (6)	1.6 (2)

such eggs were transferred into seawater, they developed to the 2-cell stage within 24 hours. This finding indicates that egg development was initiated only after the eggs came in contact with seawater. It appeared that every female used in this study had copulated and that spermatozoa had already been transferred into the ovarian cavity.

Histological observation of gametes before exposure to seawater

The micropyle of *P. sachi* eggs consisted of a micropylar vestibule, a funnellike depression about 100 μm across at the level of the egg surface, and a micropylar canal penetrating the approximately 90- μm

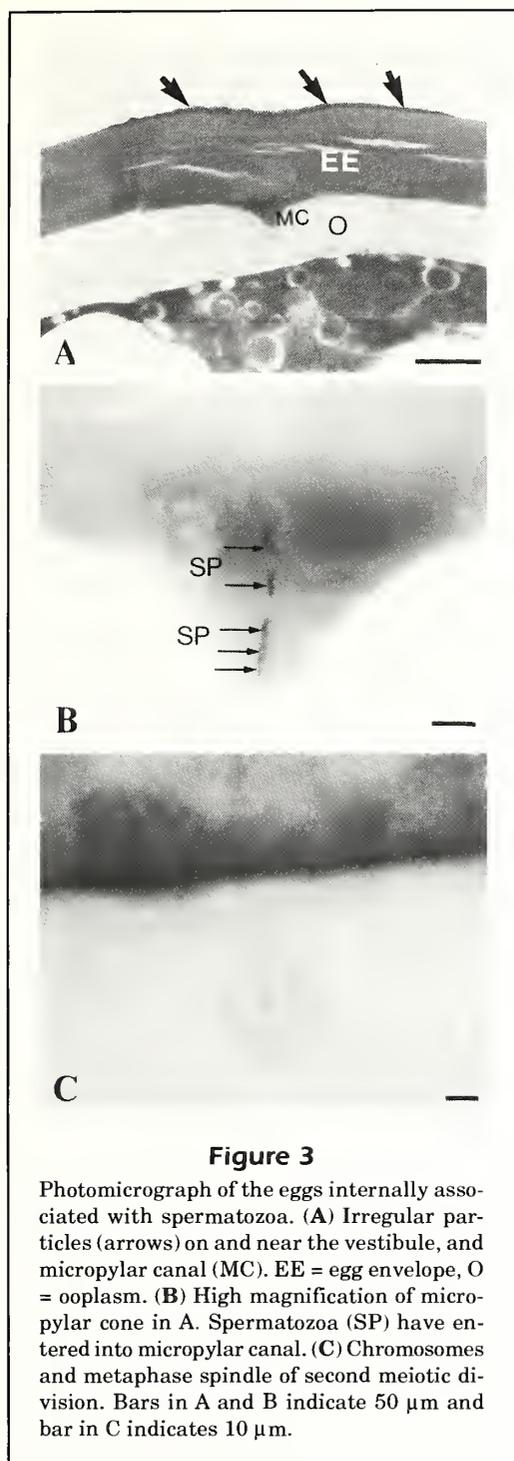


Figure 3

Photomicrograph of the eggs internally associated with spermatozoa. (A) Irregular particles (arrows) on and near the vestibule, and micropylar canal (MC). EE = egg envelope, O = ooplasm. (B) High magnification of micropylar cone in A. Spermatozoa (SP) have entered into micropylar canal. (C) Chromosomes and metaphase spindle of second meiotic division. Bars in A and B indicate 50 μm and bar in C indicates 10 μm .

thick egg envelope (Fig. 3A). The external opening of the canal was centrally located at the bottom of the vestibule. The canal was slightly tapered, and its inner opening was situated at the center of the micropylar cone. The external opening of the canal was about 5 μm in diameter. Many irregular particles stained with hematoxylin were deposited on and near the vestibule (Fig. 3A).

In eggs fixed before exposure to seawater, a number of spermatozoa were found to have entered the micropylar cone (Fig. 3B), but membrane fusion had not yet occurred. Furthermore, in the region of the ooplasm near the micropylar cone, chromosomes and a metaphase spindle of the second meiotic division were detected (Fig. 3C).

Embryonic development

After developing to the 2-cell stage after 20 hours of immersion in seawater, eggs reached the 32-cell, morula, and blastula stages on the 1st, 5th, and 8th days, respectively (Fig. 4A). The embryo became visible on the 13th day. The early embryo was smaller than the egg size, its length approximately 1/5 of the yolk's circumference. A pair of optic vesicles and optic lenses appeared on the 16th and the 21st day, respectively. Myomeres began forming on the 22nd day (Fig. 4B). On the 29th day, the tail of the embryo began to grow free from the yolk. The heart was pulsating and the embryo was moving occasionally on the 31st day. On the 35th day, a pair of otoliths was observed and the eyes began blackening. The embryo elongated to encircle the yolk completely by the 42nd day (Fig. 4C). A pair of pectoral fins began to extend at this time. Melanophores first appeared on the abdominal membrane on the 57th day. They began forming on the side of the trunk on the 62nd day. On the 76th day, the intestine and the liver were differentiated, and blood vessels appeared along the yolk below the thoracic region of the embryo. Just before hatching, the embryo measured 1.5 times the yolk circumference, and some projections of supralateral and infralateral bony plates were observed (Fig. 4D). Hatching began on the 92nd day and ended by the 104th day.

Larvae and juveniles

Newly hatched larvae were 6.9–7.1 mm in notochord length (NL) (Fig. 4E). Their bodies were slender, white, and pigmented on the head, trunk, and finfold. Yolks had not been completely absorbed yet, and an oil droplet remained in each yolk's anterior part. The larvae were weak swimmers and usually lay on the bottom of the tank. Most hatched 101 days after fertilization. On the 3rd day of hatching, not only supralateral and infralateral bony plates, but dorsal and ventral bony plates began to form. The larvae occasionally fed on *Artemia salina*. The urinary bladders of larvae were always swollen with transparent liquid. On the 14th day, the yolk was completely absorbed; a 7.4-mm-NL specimen had melanophores on the lateral sides of the abdomen and two pairs of fronto-

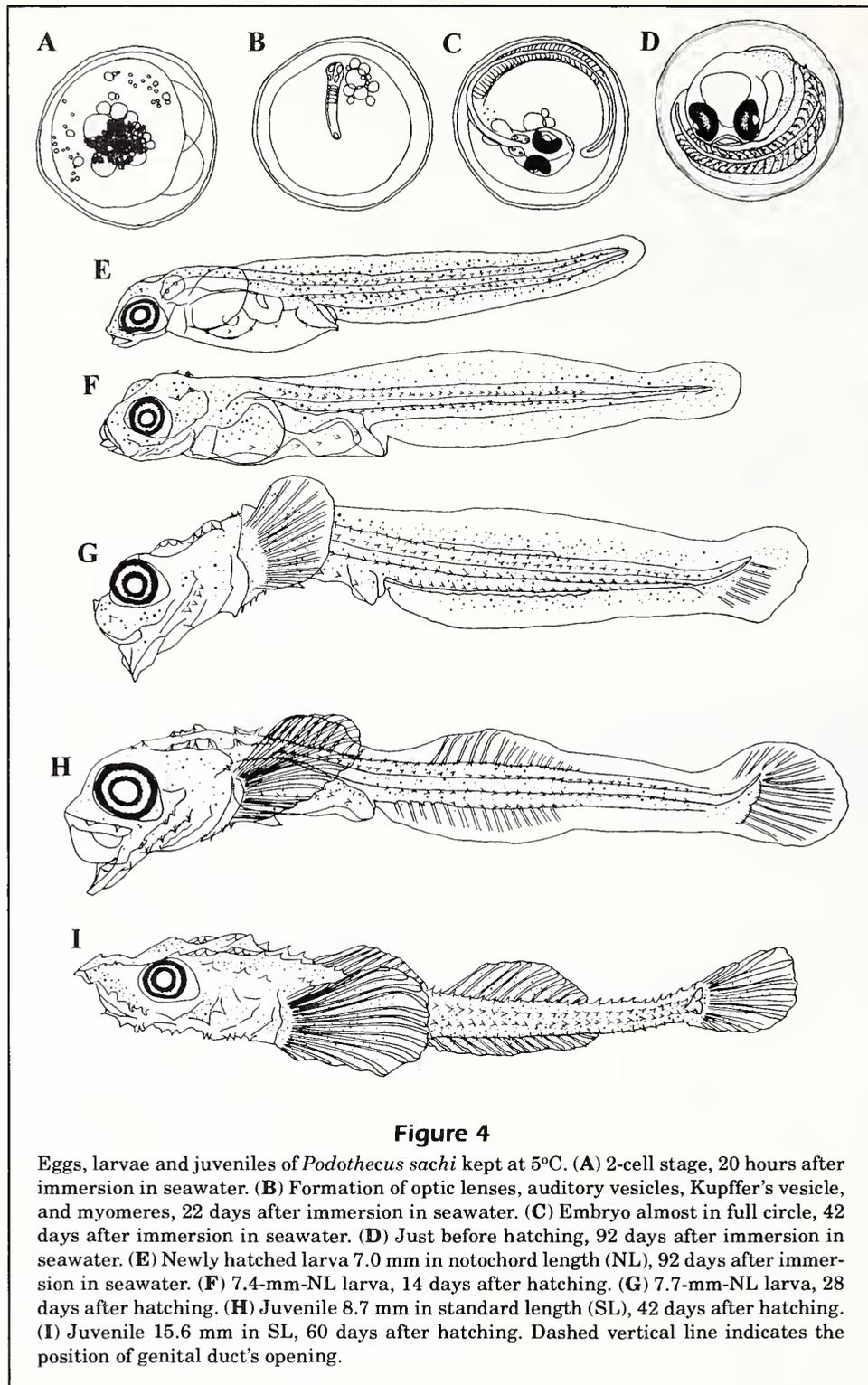


Figure 4

Eggs, larvae and juveniles of *Podotheucus sachi* kept at 5°C. (A) 2-cell stage, 20 hours after immersion in seawater. (B) Formation of optic lenses, auditory vesicles, Kupffer's vesicle, and myomeres, 22 days after immersion in seawater. (C) Embryo almost in full circle, 42 days after immersion in seawater. (D) Just before hatching, 92 days after immersion in seawater. (E) Newly hatched larva 7.0 mm in notochord length (NL), 92 days after immersion in seawater. (F) 7.4-mm-NL larva, 14 days after hatching. (G) 7.7-mm-NL larva, 28 days after hatching. (H) Juvenile 8.7 mm in standard length (SL), 42 days after hatching. (I) Juvenile 15.6 mm in SL, 60 days after hatching. Dashed vertical line indicates the position of genital duct's opening.

parietal ridges with one spinule (Fig. 4F). The pectoral fins began to enlarge, and the larvae spent more time swimming near the surface than lying on the bottom. A 7.7-mm-NL specimen observed on the 28th day had 14 rays in its pectoral fins, melanophores

on the ventral sides of the abdomen, and both jaws protruded slightly (Fig. 4G); four spines on preopercular and 2–4 spinules on each frontoparietal ridge were found. Another specimen measuring 8.3 mm NL on the 28th day was found to be in flexion; the larva

had 13, 16, and 15 rays in its dorsal, anal, and pectoral fins, respectively. On the 42nd day, a specimen measuring 8.7 mm SL had 10 spines and 13 rays on its dorsal fin and 15 and 16 rays on its anal and pectoral fins, respectively, forming a full complement (Fig. 4H). The pelvic fins were still buds. The opening position of the anal and the genital pore began moving from just anterior to the anal fin toward the base of the pelvic fins. Whiskers, a mustache, and pelvic fins first appeared in a 15.6-mm-SL specimen on the 60th day (Fig. 4I) and were completely formed in a 24.6-mm-SL specimen on the 93rd day. Juvenile *P. sachi* almost corresponded to adults in morphological features, but movement of the anal and genital pore openings were only half finished. The 24.6-mm specimen swam, using its elongated pectoral fins, but never used its posterior trunk for propulsion owing to hardened bony plates.

Discussion

Internal gametic association and external fertilization

As noted, *P. sachi* eggs placed in seawater and without artificial insemination began to develop and grow to juveniles, whereas eggs maintained in ovarian fluid showed no signs of development. In addition, histological observations of eggs directly obtained from the ovary showed that spermatozoa had entered the micropyle before contact with seawater, indicating that fertilization was not initiated in the ovarian fluid. This observation demonstrates that the spawning mode of *P. sachi* is of the internal gametic association type, reported in previous studies of copulating cottids (Munehara et al., 1989, 1991, 1994a; Koya et al., 1993). Atlantic wolffish, *Anarichas lupus* (Perciformes, Anarichadidae), is also known to undergo copulation before egg laying, but the spawning mode of this fish is not comparable to that of *P. sachi* because inseminated eggs of Atlantic wolffish develop internally (Pavlov, 1994). This information seems to support Yabe's hypothesis (1985), based on comparative osteological and myological observations, that the family Agonidae may be the most closely related family to the Cottidae.

Early life history

Many larvae and juveniles, 8.3–25.1 mm SL, have been collected by plankton nets (Maeda and Amaoka, 1988). In the present study, the largest specimen took 93 days to grow to 24.6 mm SL after hatching. Thus, *P. sachi* probably inhabits the pelagic ocean during

its first three months. It seems reasonable that whiskers and mustache, which function as sensory organs for detection of benthic prey (Sato, 1977), are completed before juveniles become benthic.

Reproductive style of agonid species

Information on the reproduction of agonids is available for only 6 of 50 species (Table 2). Many common characteristics are recognized among these species.

First, the reproductive behavior of the Agonidae involves copulation. All the agonid species whose reproductive styles are known (*Agonomalus proboscidalis*, *Ocella iburia*, and *Bracdyopsis rostratus*) have been described as internally fertilizing species on the basis of the development of eggs deposited without male involvement (Iioka and Gunji, 1979; Sugimoto, 1987; Aoyama and Onodera, 1989). These agonids probably exhibit external fertilization with internal insemination, as does *P. sachi*, because *B. rostratus* has been determined to be of the internal gametic association type from the same investigations done for *P. sachi*, and information on internal fertilization of the agonids was proposed prior to the first recognition of the internal gametic association in teleost fishes (Munehara et al., 1989).

A second characteristic of the reproductive style is that agonids have a long embryonic period, ranging from 100 days to 1 year. In addition to the Agonidae, such extraordinarily long embryonic periods in teleost fishes are known for only a few trichodontids and cottid species (Okiyama, 1990; Munehara and Shimazaki, 1991).

The third and fourth characteristics are egg deposition in concealed sites and lack of parental care. Naturally deposited egg masses of *Agonus caphractus* were collected from the roots of kelp (Breder and Rosen, 1966). Spawning of captive *Agonomalus mozinoi* and *A. proboscidalis* was performed by concealing eggs in the exoskeletons of invertebrates or between rocks (Marliave, 1978; Aoyama and Onodera, 1989). Egg masses of *B. rostratus* were found deposited on the bottom of a tank, but the spawner was kept in a bare tank with no suitable substrate (Sugimoto, 1987). It is still unknown where *P. sachi* spawns its eggs. However, it is probable that the spawning of this fish involves brood hiding and lack of parental care because this species has a retractable genital duct and a long incubating period, similar to other copulating cottids that deposit their eggs into sponges, polychaete tube colonies, and narrow fissures (Gomelyuk and Markevich, 1986; Munehara, 1991, 1992, 1996). Deposition of egg masses on such spawning substrates limits predation on the eggs. In addition, flagellar movements of

Table 2
Comparison of reproductive characteristics in some agonid fishes.

Species name	Spawning mode	Embryonic period and egg diameter	Spawning substrate	Parental care	Spawning system	References
<i>Agonomalus mozinoi</i>	unknown	unknown 1 mm	barnacle, tube worm ²	without	remarkable iteroparity of small clutches	Marliave, 1978
<i>A. proboscidalis</i>	internal fertilization ¹	110–114 days 2.05–2.30 mm	between rocks and sand on bottom	without	remarkable iteroparity of small clutches	Iioka and Gunji, 1979 Aoyama and Onodera, 1989
<i>Agonus cataphractus</i>	unknown	1 year 1.76–2.23 mm	on roots of kelp	unknown	remarkable iteroparity of small clutches	Eherenbaum, 1936 in Breder and Rosen, 1966
<i>Brachyopsis rostaratus</i>	internal gametic association ¹	287–324 days 2.1 mm	on bottom ²	without	remarkable iteroparity of small clutches	Sugimoto, 1987; this study
<i>Ocella iburia</i>	internal fertilization ¹	unknown unknown	unknown	unknown	unknown	Sugimoto, 1987
<i>Podothecus sachi</i> ¹	internal gametic association ¹	92–104 days 1.70–1.75 mm	unknown	unknown	remarkable iteroparity of small clutches	this study

¹ The studies had been reported before publication of internal gametic association (Munehara et al., 1989).
² The findings were observed in aquaria.

host invertebrates, for aspiration and filtration, incidentally supply oxygen to eggs deposited inside or on the invertebrates (Munehara, 1991). The protracted period of incubation may have promoted egg deposition in any safe cradle for embryos rather than parental care.

Multiple clutches are produced by agonid species during a breeding season, as demonstrated by histological observation of the ovary of *P. sachi*; moreover, observations of *A. mozinoi*, *A. proboscidalis*, and *B. ostratus* indicate that females spawn small clutches almost daily in aquaria (Marliave, 1978; Iioka and Gunji, 1979; Sugimoto, 1987; Aoyama and Onodera, 1989). The fifth characteristic is the remarkable iteroparity of small clutches, which may have evolved in association with the laying of eggs, both into narrow spaces and without male involvement.

In summary, it is suggested that five common characteristics, i.e. copulation, a protracted period of incubation, concealment of deposited eggs, lack of parental care, and remarkable iteroparity of the reproductive ecology of agonids have been closely correlated with each other through evolutionary construction of their distinctive reproductive style. Copulation enabling impregnated females to spawn eggs without subsequent involvement of male fish seems to be a principal element of these characteristics.

Acknowledgments

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Age and growth of totoaba, *Totoaba macdonaldi* (Sciaenidae), in the upper Gulf of California

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The totoaba, *Totoaba macdonaldi* (Gilbert), also known as Mexican giant bass, is found only in the Gulf of California. This species during 1934–45 supported one of the most important sport and commercial fisheries in the Gulf, with total annual landings exceeding 2,000 metric tons (Rosales-Juárez and Ramírez-González¹). At present, it is considered endangered (Flanagan and Hendrickson, 1976; NMFS²) as a result of 1) a high mortality of juveniles in shrimp trawl nets, 2) past overexploitation, 3) current illegal fishing during its reproductive season (early February to early May), and 4) ecological alterations of its spawning and nursery grounds. Flanagan and Hendrickson (1976) suggested that there was a high probability that this species would become extinct by 2000 AD. In 1975 the Mexican government declared a moratorium on fishing totoaba.

This paper reports on the age and growth of totoaba as determined from sectioned-otolith readings and contrasts current population age composition with what was known about the early population. Previous studies have reported ages based on nonvalidated scale readings (Nakashima, 1916; Berdegué, 1955; Molina et al.³).

Materials and methods

Totoaba were sampled in 1986–91 from the northern part of the upper Gulf of California between 31° and 32° N Lat. and 114° and 115° W Long. (Fig. 1). In 1989–91, juveniles were collected from shrimp trawl nets. Adults were sampled with gill nets during their reproductive season (Feb–Apr) of 1986, 1987, and 1989–91.

After determining individual standard (SL) and total length (TL) in millimeters and weight in grams, we extracted otolith (sagittal) pairs from 118 fish and embedded them in epoxy resin. For comparison with other age studies of totoaba, a linear regression was performed for converting total length into standard length. Lowerre-Barbieri et al. (1994) reported that sectioned otoliths were the best structure for ageing weakfish, *Cynoscion regalis*.

To permit data recovery when only severed heads were available, 118 otoliths were weighed (OW; ± 0.001 g) and measured to determine their relation with SL (Pauly, 1984); only whole individuals were used in the present study. Maximum otolith length (OL; ± 0.05 mm) was measured from rostrum to postrostrum margins (anterior–

posterior), and maximum otolith thickness (OT; ± 0.05 mm) from the dorsal to ventral margins (distal–proximal plane).

A transverse section was made from 101 otoliths with an Isomet low speed saw following a technique described by Beckman et al. (1990), Lowerre-Barbieri et al. (1994), and Secor et al.⁴ and the otolith ring counts were read to determine age. Each thin section was read three times with transmitted light in a bright field by the same person. Following the criteria of Beamish and Fournier (1981), we calculated an index of average percent error for the single reader.

Three different axes (Fig. 2) were explored to measure the otolith radius (OR) of 94 thin sections. Annuli were most clearly counted and measured along axis 1; thus otolith radius (OR) was defined as the distance from the center of the core to the otolith outer edge along the ven-

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¹ Rosales-Juárez, F., and E. Ramírez-González. 1987. Estado Actual del Conocimiento Sobre la Totoaba (*Cynoscion macdonaldi*), Gilbert 1890. Secretaría de Pesca, México, 41 p. ISBN 968-817-086-0. [In Spanish; available at CICESE library.]

² NMFS (National Marine Fisheries Service). 1991. Endangered Species Act Status Review, totoaba (*Cynoscion macdonaldi*). Prot. Spec. Manage. Admin. Rep. SWR-91-01, 9 p.

³ Molina, D., M.A. Cisneros-Mata, R. Urias, C. Cervantes y M. A. Márquez. 1988. Prospección y evaluación de la totoaba (*Totoaba macdonaldi*) en el Golfo de California. Tech. Report, 18 p. [In Spanish, available from Cisneros-Mata, CRIP-Guaymas, Calle 20, No. 605 Sur, Guaymas, Sonora, Mexico c.p. 85400.]

⁴ Secor, D. H., J. M. Dean, and E. H. Laban. 1990. Manual for otolith removal and preparation for microstructural examination. Electric Power Research Inst., The Belle W. Baruch Inst. for Marine Biology and Coastal Research, 85 p.

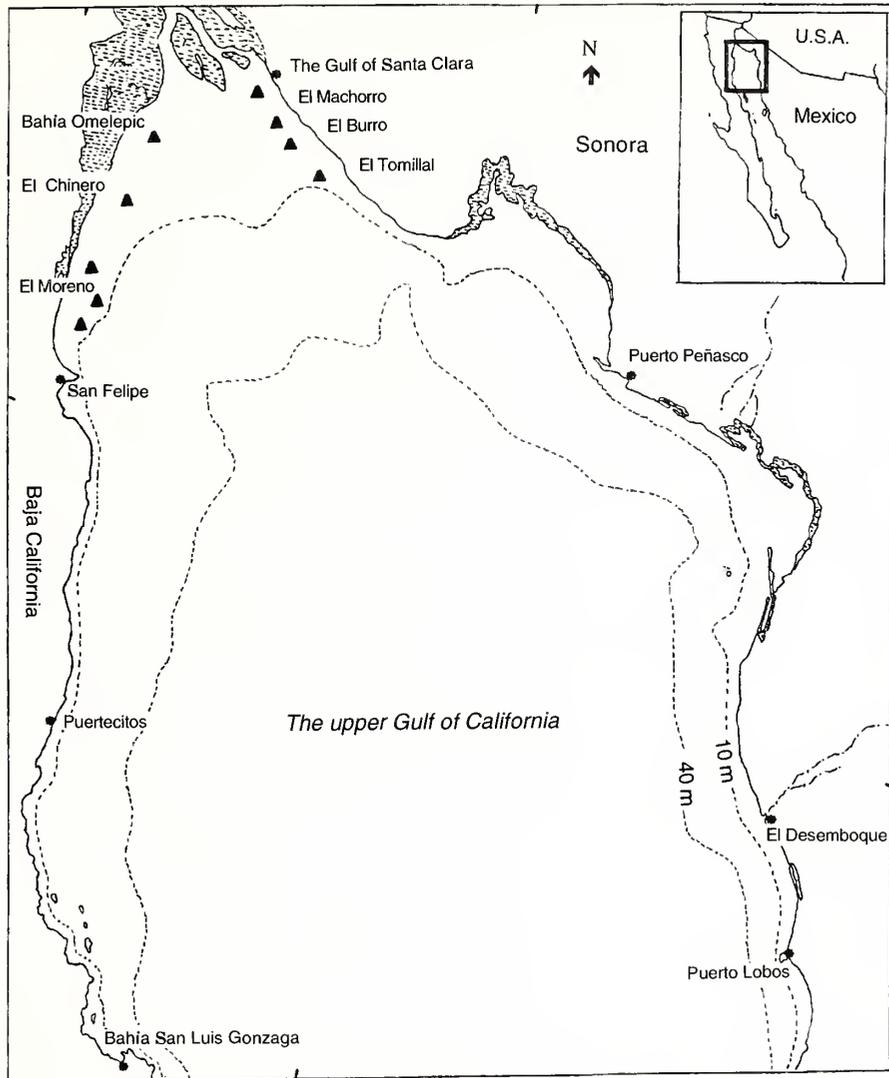


Figure 1

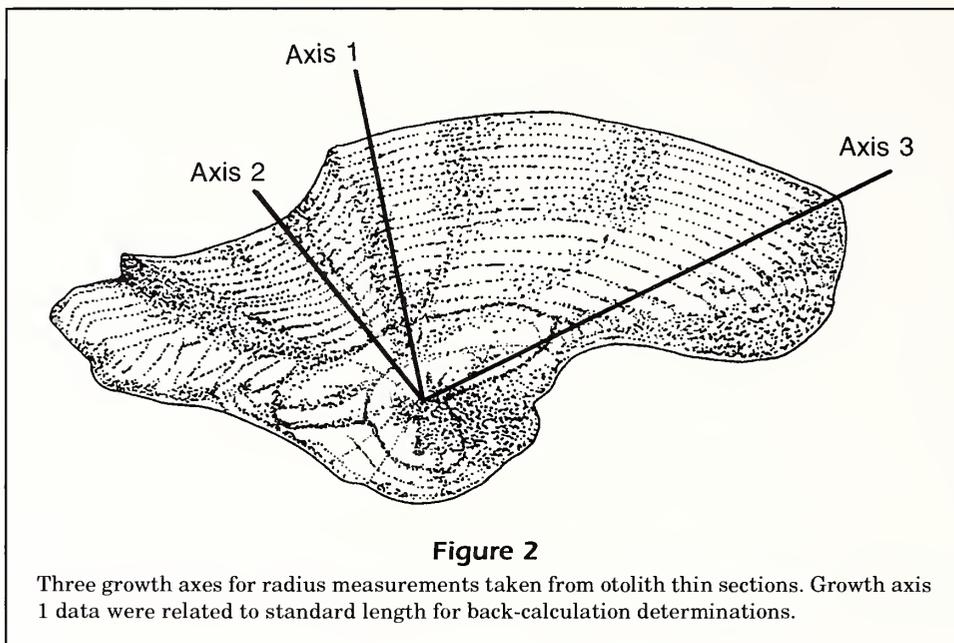
Location of sampling sites in the northern upper Gulf of California. (▲) = adults; juveniles were collected within the 40-m depth contour.

tral arm of the sulcal groove. The relation between otolith radius and fish length was fitted by using the Gompertz function (Ricker, 1979) and the computer program Fishparm 3.0 (Prager et al., 1989). To determine size at ages that were not collected, we backcalculated past ages following Bagenal and Tesch (1978) and Jerald (1983), using the Gompertz relation between OR and SL, not the otolith length to fish length regression.

A von Bertalanffy growth model (VBGM) was fitted to the observed SL at the midpoint of each age group represented in our sample ($n=101$) and also to the back-calculated sizes ($n=346$) determined from 81 otolith thin sections, by using the computer program Fishparm 3.0 (Prager et al., 1989). The growth

equation was calculated for pooled sexes because juveniles can be sexed only by using histological techniques; age and length differences between males and females have not been reported in the literature.

Three juveniles captured in trawl nets during July and August 1989 were kept alive and transferred to the Centro Ecológico de Sonora Research Aquarium (Hermosillo, Sonora, Mexico); (see Almeida Paz et al. [1990] for more details). One fish died after almost 12 months of captivity; the other two were sacrificed 24 months after capture. Lengths and weights of these fish were taken every month beginning five months after capture. These lengths and the ring counts found in the otoliths of these fish were used to validate annual otolith ring deposition.

**Table 1**

Meristic relations between totoaba standard length (SL) and total length (TL), otolith length (OL), otolith thickness (OT), and otolith weight (OW). For otolith measurements, $n = 118$.

Parameter	Equation	r^2
Fish total length (TL)	$SL = 0.917TL - 26.34$ ($n=951$)	0.99
Otolith length (OL)	$SL = 16.91 \exp(4.7(1 - \exp(-0.96 \times OL)))$	0.99
Otolith thickness (OT)	$SL = 8.53 \exp(5.4(1 - \exp(-0.17 \times OT)))$	0.98
Otolith weight (OW)	$SL = 788.8 \times OW^{0.4518}$	0.99

Results

From shrimp trawl nets, 1,125 juvenile totoaba (100–600 mm SL, mean=223, SD=65 mm SL) and 157 adults were collected (600–1,850 mm SL, mean=1,360, SD=89 mm SL). Figure 3 shows the length-frequency distribution for the specimens collected.

Totoaba sagittal otoliths are large and beanlike, as are most sciaenid otoliths (Secor et al.⁴). Table 1 shows the linear equation describing the relation between SL and TL, the Gompertz relations between SL and otolith length (OL), otolith thickness (OT), and the allometric equation for the SL and otolith weight (OW) relation (Fig. 4). Otolith growth in weight changes in relation to fish growth in length and is an allometric, not isometric relation ($b=2.176$, $H_0: b=3.00$, student's t -test ($_{0.025, 111}$) =21.41).

Transverse sections of the totoaba otolith (Fig. 5) typically showed clear, opaque, and translucent zones and when the otolith is sectioned exactly through the focus, the core appears as a dense opaque zone, next to which the first annulus is found. The distance between the core and the first annulus is variable but is typically greater than increment sizes between the remaining annuli. The relation between otolith radius (OR) along radius 1 and SL (Fig. 6) was fitted to a Gompertz function:

$$SL = 30.92 \times \exp(3.86(1 - \exp(0.99 \times OR))),$$

$$[r^2=0.98, n=94].$$

We found specimens representing 15 year classes between 0 and 24 years (Table 2). Of the 101 readable otolith sections, 66 fish were young-of-the-year (110–377 mm SL). Ten juveniles were of age class 2

(378–620 mm SL), and one was of age class 3 (740 mm SL). The remaining specimens were adults between age classes 4 and 24. The index of average percent error was 16.10% for the single reader.

Observed lengths and otolith ring counts were used to fit the von Bertalanffy model to obtain the growth curve for the totoaba population in the Gulf of California (Fig. 7); the fit was good ($r^2=0.98$, $n=101$). Past ages ($n=346$) were backcalculated from the thin-section otolith radius (OR) to fish length relation of 81 fish, and the von Bertalanffy growth model was also determined (Fig. 7). Table 2 compares the observed standard lengths with those calculated from both growth models. Figure 8 shows the relation between maximum whole otolith length and age as an exponential function.

In the case of the fish that died after a year of captivity (11 mo 21 d), its otoliths showed only one ring; the second fish held for two years, had two rings. The otoliths from the third specimen were decalcified and readings, unfortunately, were not possible. Fish held in captivity were captured in the same trawls as the rest of the juveniles used for age determination in this study. Otoliths of juveniles sacrificed at the time of capture did not present any rings or marks similar to those detected in otoliths of the individuals kept in captivity.

Discussion

The relation between otolith dimensions and fish length can be used to obtain data from the totoaba heads commonly found on the beaches of the northern Gulf. This relation is particularly important when one considers the restrictions and the potential impact of sampling an endangered species. Otolith growth and fish growth are proportional regardless of how growth rate changes with time; in early stages, both fish and otoliths increase faster than in adult stages after maturity is reached. Barbieri et al. (1994) reported for Atlantic croaker (*Micropogonias undulatus*) that age has an important effect on the otolith dimension to fish length relation. For totoaba, however, fish length alone described over 98% of the variability in otolith size. This growth pattern is common for other sciaenid species (Ross, 1988; Murphy and Taylor, 1989).

The relation between standard length and otolith radius in sciaenids has been fitted to several growth equations. Maceina et al. (1987) and Blake and Blake

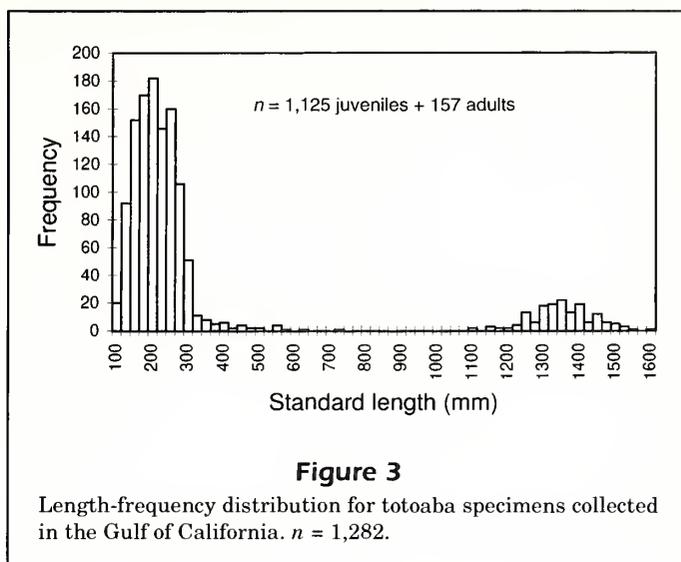


Figure 3

Length-frequency distribution for totoaba specimens collected in the Gulf of California. $n = 1,282$.

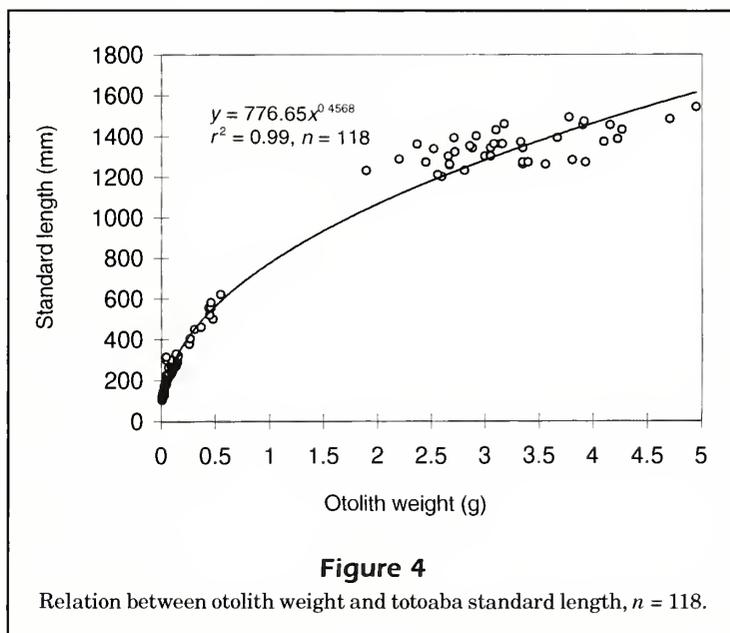


Figure 4

Relation between otolith weight and totoaba standard length, $n = 118$.

(1981) found good fit with a linear model, but Barger (1985) found the best fit with a power function. For totoaba in our study, the best fit was found with a Gompertz model for radius along axis 1. The wide range of radii at the maximum fish length (shown in Fig. 6), supports our assumption that annuli are formed throughout the life of the fish, as is also suggested by the power function fitted to the otolith length and age relationship (shown in Fig. 8). Barbieri et al. (1994) also reported the formation of annuli throughout the life of the Atlantic croaker. Although the otolith length to age relation could be used to estimate fish age, the fit is not as good as that between standard length and

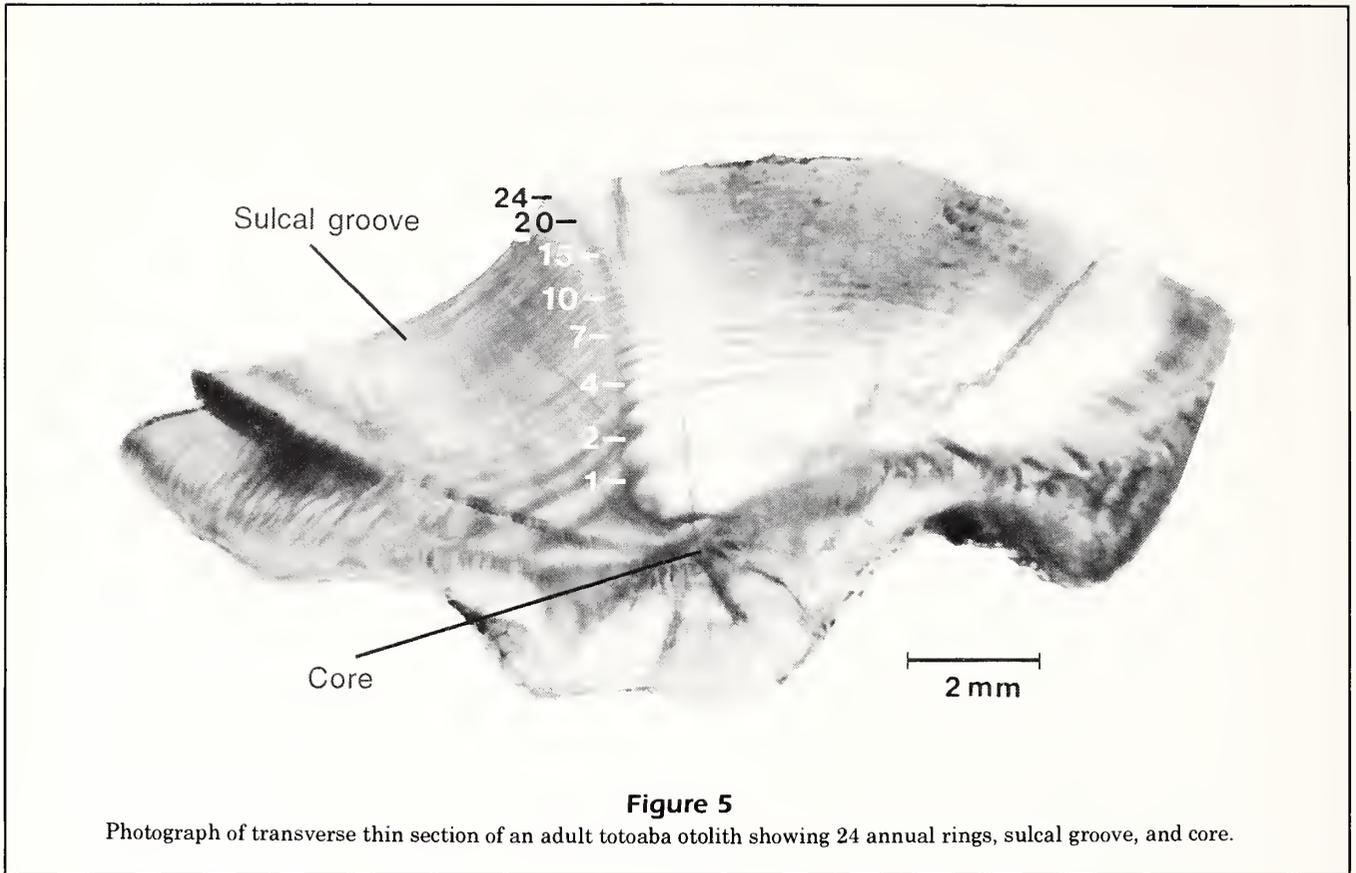


Figure 5

Photograph of transverse thin section of an adult totoaba otolith showing 24 annual rings, sulcal groove, and core.

age. No "Lee's phenomenon" (Ricker, 1969) was observed, and the von Bertalanffy growth model resulting from back-calculated data was very similar to that derived from observed data (Fig. 7 ; Table 2).

Gauldie and Nelson (1990) commented that otolith growth is typically repressed on the ventral plane because this part of the otolith is in direct contact with the skull, which restricts otolith growth; although otolith growth ceases in the ventral plane, it continues to grow in the sulcular region. For totoaba, otolith growth seems to continue on the proximal side along the sulcal groove. The ventral arm of the sulcal groove has been reported as the best area for otolith reading in other sciaenids (Beckman et al., 1990; Lowerre-Barbieri et al., 1994).

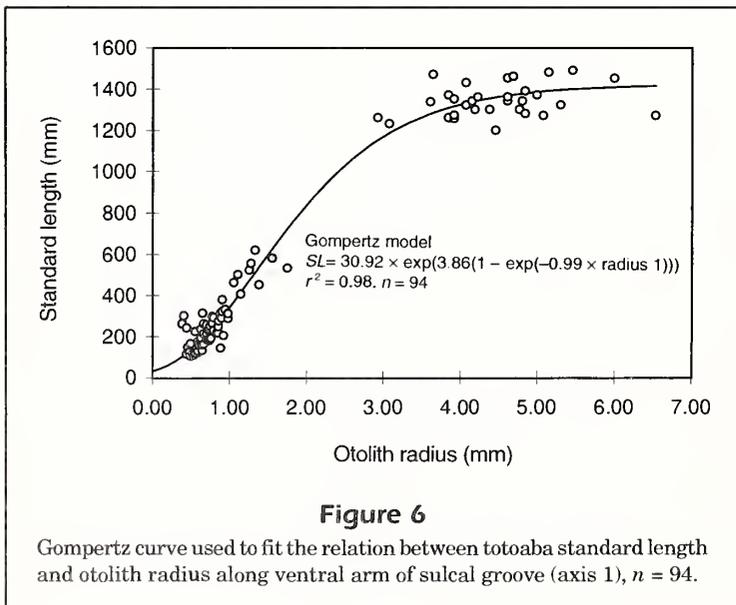


Figure 6

Gompertz curve used to fit the relation between totoaba standard length and otolith radius along ventral arm of sulcal groove (axis 1), $n = 94$.

Major increases in length occur during the first and second years, diminishing once totoaba reach their sixth or seventh year, the age at first maturity. After this stage, the growth curve reaches an asymptote from about the twelfth to fourteenth year. The observed adult mean standard lengths at age in our study are very close to those calculated by VBGM from observed data and also from back-calculated data.

In a comparison of age determinations with scales (Nakashima, 1916; Berdegué, 1955;

Table 2

Observed and predicted mean standard length at year-class midpoints. n = sample size. SD = standard deviation. VBGM = von Bertalanffy growth model. BC = back-calculated model.

Year class midpoint (yr)	n	Observed SL: mean (mm)	Observed SD	Predicted VBGM (mm)	Predicted VBGM BC (mm)
0.5	66	218	66	216	319 ¹
1.5	10	503	75	525	595
2.5	1	740	—	750	797
3.5	1	1,080	—	914	945
4.5	0	—	—	1,034	1,053
5.5	0	—	—	1,121	1,133
6.5	0	—	—	1,184	1,192
7.5	1	1,260	—	1,231	1,234
8.5	0	—	—	1,264	1,266
9.5	0	—	—	1,289	1,289
10.5	1	1,271	—	1,307	1,306
11.5	0	—	—	1,320	1,318
12.5	2	1,363	38	1,329	1,327
13.5	5	1,318	88	1,336	1,334
14.5	4	1,309	102	1,341	1,339
15.5	5	1,340	24	1,345	1,342
16.5	1	1,390	—	1,348	1,345
17.5	1	1,300	—	1,350	1,347
18.5	0	—	—	1,351	1,348
19.5	1	1,280	—	1,352	1,349
20.5	0	—	—	1,353	1,350
21.5	1	1,490	—	1,354	1,350
22.5	0	—	—	1,354	1,351
23.5	0	—	—	1,354	1,351
24.5	1	1,453	—	1,354	1,351
Total	101				

¹ Otolith core to margin measurements along ventral arm of sulcal groove were used for year-class 0, and predicted lengths were derived from the resulting equation.

Flanagan, 1973; Molina et al.¹), versus otoliths, as used in our study (Table 3), the greatest difference is found with Nakashima (1916). He estimated the maximum age for a fish of 1,980 mm (SL) to be nine years; our study shows that this fish could be older than 24 years. The von Bertalanffy parameters we estimated are very similar to those reported by Berdegué (1955) and Flanagan (1973). In the Molina et al.¹ study there was a large underestimation of maximum age in comparison with our results, reflected in the K value. This difference could be due to our use of a greater range of year classes from young-of-the-year to adults, whereas Molina et al.¹ used only adult fish. Juveniles or young-of-the-year should be included to fit the von Bertalanffy growth

curve because if only adults are used, there is a tendency to obtain low K values (Beckman et al., 1990).

Scales often result in the underestimation of age (Beamish and McFarlane, 1987) owing to difficulty in reading, especially in the outer rings which are very close. Furthermore, there is a possibility of using regenerated scales in which the first rings that were formed are not included. Authors working with sciaenids have mentioned that reading scales is easier for short-lived species, like some species of *Cynoscion* (Villamar, 1972; De Vries and Chittenden, 1982).

On the basis of growth and otolith marks observed in two juveniles held in captivity, we suggest that ring formation in totoaba from the Gulf of California is annual; annual deposition patterns have been re-

ported for other sciaenids (Beckman et al. 1990, Murphy and Taylor 1991), including species of *Cynoscion*, a closely related genus (González, 1977; Blake and Blake, 1981; Shlossman and Chittenden, 1982; Barbieri et al., 1994; Lowerre-Barbieri et al., 1994). The well-defined seasonality in temperature in the Gulf of California (Alvarez Borrego et al., 1973; Paden et al., 1991) also suggests that the marks seen in totoaba otoliths are annual because such temperature changes are an important factor in ring deposi-

tion (Brothers, 1978; Beckman et al., 1990). Berdegué (1955) considered scale rings to be annual on the basis of the migratory pattern and reproductive period of totoaba.

The recent creation of the Upper Gulf of California and Colorado River Delta Biosphere Reserve will enhance conservation efforts for totoaba by protecting important spawning and nursery habitat. Furthermore, fishing pressure from commercial shrimp trawls and gill nets will be greatly decreased.

Barrera-Guevara (1990) reported that 92% of young-of-the-year totoabas were killed in the commercial shrimp fishery. In our study we were not able to sample organisms between ages 5 and 11 because they were not available to trawls and gill nets and because we did not sample in areas where prerecruit totoaba concentrate. These areas are difficult to sample because of their depth; the Guaymas basin reaches more than 200 m depth. It has been suggested that the summer migration of totoaba is toward deep waters in the central Gulf of California (Berdegué, 1955; Arvizu and Chavez, 1972; Flanagan and Hendrickson, 1976). These fish, however, are accessible to hook and line fishing, and "catch and release" sport fishing practices should be encouraged.

It is clear that the current available habitat for totoaba will not allow significant population increase. Nevertheless, we found a population age-structure similar to that existing during the early 1890's (assuming that fish of ages 3–11 years exist but were unavailable to our sampling as previously described), and we suggest that continued conservation efforts should allow for the survival of a stable but small population of totoaba in the Gulf of California. Estimates of adult survival proposed by Cisneros-Mata et al. (1995) before and after the 1975 moratorium also support evidence of stability in the current population age-structure.

Acknowledgments

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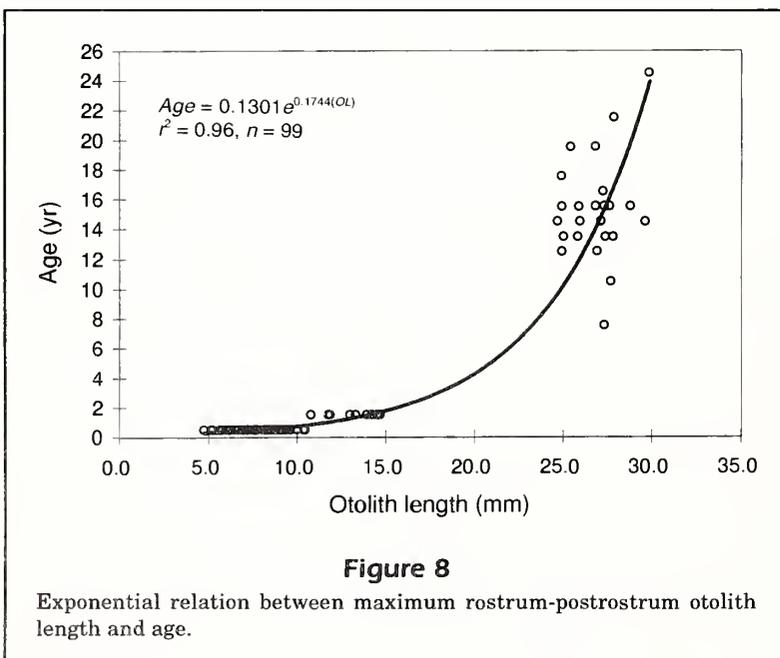
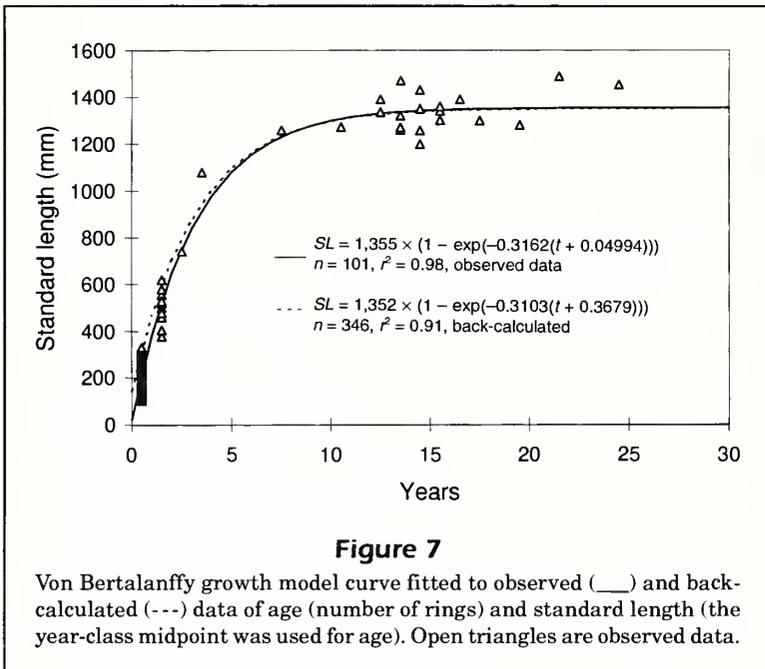


Table 3

Comparison of von Bertalanffy growth parameters for different studies of totoaba.

Author	K	L_{∞}	t_0	Max. age (yr)
Present observed data	0.3162	1,355	-0.0499	24
Present back-calculated data	0.3103	1,352	-0.3679	24
Nakashima (1916)	—	1,980	—	9
Berdegúe (1955)	—	1,330	—	15
Flanagan (1973)	0.16	1,467	—	20
Molina et al. ¹	0.271	1,373	-2.264	19

¹ See Footnote 1 in the text.

gación Pesquera en Guaymas for assistance in the field with sampling juveniles. The Fish and Wildlife Foundation is acknowledged for support of field work during 1989. Sampling was carried out under Fisheries Research Permit No. 1229, Secretary of Fisheries, Mexico. We acknowledge the valuable suggestions of two anonymous reviewers.

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Mark retention and growth of jet-injected juvenile marine fish

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The type of mark or tag used for a particular study depends on the objectives of the study. Retention and recognition of a mark are critical to the success and reliability of a study. External tags have been the most common fish tags used (McFarlane et al., 1990), but they may affect survival, behavior, and growth of fish (Andersen and Bagge, 1963; McFarlane and Beamish, 1990). Each tag type has limitations and capabilities, but ideally external tags should be easily and rapidly applied to many fish, be inexpensive, easily identified, not easily lost or entangled, and not be stressful enough to alter fish survival, behavior, or growth. Studies that require such characteristics, therefore, are restricted in the type of tag that can be used and thus must rely on internal marks or dyes to identify fish. Identification of internal marks, however, generally requires that fish be killed, thus eliminating any possibility of repeated measurements of individual fish. Choice of mark is further restricted when marking juveniles that are of small size and that exhibit rapid growth.

Jet injection is a method of applying external marks to fish (Hart and Pitcher, 1969) that is relatively fast and can apply a variety of colors for either batch or individual marking. Jet injection does not affect survival or growth of juvenile

salmonids in the laboratory (Cane, 1981; Herbinger et al., 1990; Thedinga and Johnson, 1995) but may contribute to increased mortality in field situations (Thedinga et al., 1994). Injection by Panjet has been used primarily on freshwater fish species (Hart and Pitcher, 1969) in addition to salmonids (Cane, 1981; Pauley and Troutt, 1988; Laufle et al., 1990). Juvenile flatfish have been marked with needle-injected latex (Riley, 1966) as well as by freeze branding (Dando and Ling, 1980), but not by jet injection. To our knowledge, juvenile sablefish have been marked only with Floy anchor tags (Rutecki and Meyers, 1992). Our objectives were to evaluate retention of jet-injected marks and their effect on growth of four marine fish species, as well as their effect on the tissue structure of three marine species held in the laboratory.

Methods

We tested the retention of jet-injected marks and effects of marks on growth of four species of marine fish and histological effects on three species of marine flatfish. We injected two substances into juvenile sablefish, *Anoplopoma fimbria*, and one substance into juvenile yellowfin sole, *Pleuronectes asper*, rock sole, *Pleuronectes bilineatus*, and

Pacific halibut, *Hippoglossus stenolepis*. Sablefish were captured by hand-jigging in St. John Baptist Bay near Sitka, Alaska, September 1993 (Rutecki and Meyers, 1992). Sole were captured by beach seining in Auke Bay, Alaska, May to July 1994, and halibut were collected by trawling in Sitkinak Strait and Ugak Bay near Kodiak Island, Alaska, August 1994.

A total of 28 sablefish and 30 flatfish were injected with a Panjet in 1993–94. Sablefish were marked with alcian blue dye (65 mg/mL aqueous solution) and fluorescent orange acrylic paint (Liquitex, 50% aqueous solution); 10 of each flatfish species were marked with alcian blue dye. All sablefish were marked on the abdomen between the pelvic fins (Fig. 1). Flatfish, however, were marked with individual identifying marks on the ventral surface at one to four locations along the lateral margin and on the caudal peduncle (Fig. 2); 12 sablefish and 10 of each flatfish species were left unmarked as controls.

The Panjet was held about 25 mm from the fish's skin during marking. Sablefish were anesthetized with tricaine methanesulfonate (MS-222) before marking but flatfish were not. After marking, excess dye or paint was rinsed off with water to check mark quality. If a mark was good, the fish was put in a recovery tank; if poor, the fish was remarked.

Sablefish and flatfish were held in different environments. After being marked, sablefish were held in 600-L flow-through tanks for 238 days. Because of space restrictions, blue-marked and control fish were held in one tank, but each group was kept in separate compartments. Orange-marked fish were held in another tank but died prematurely in a laboratory accident

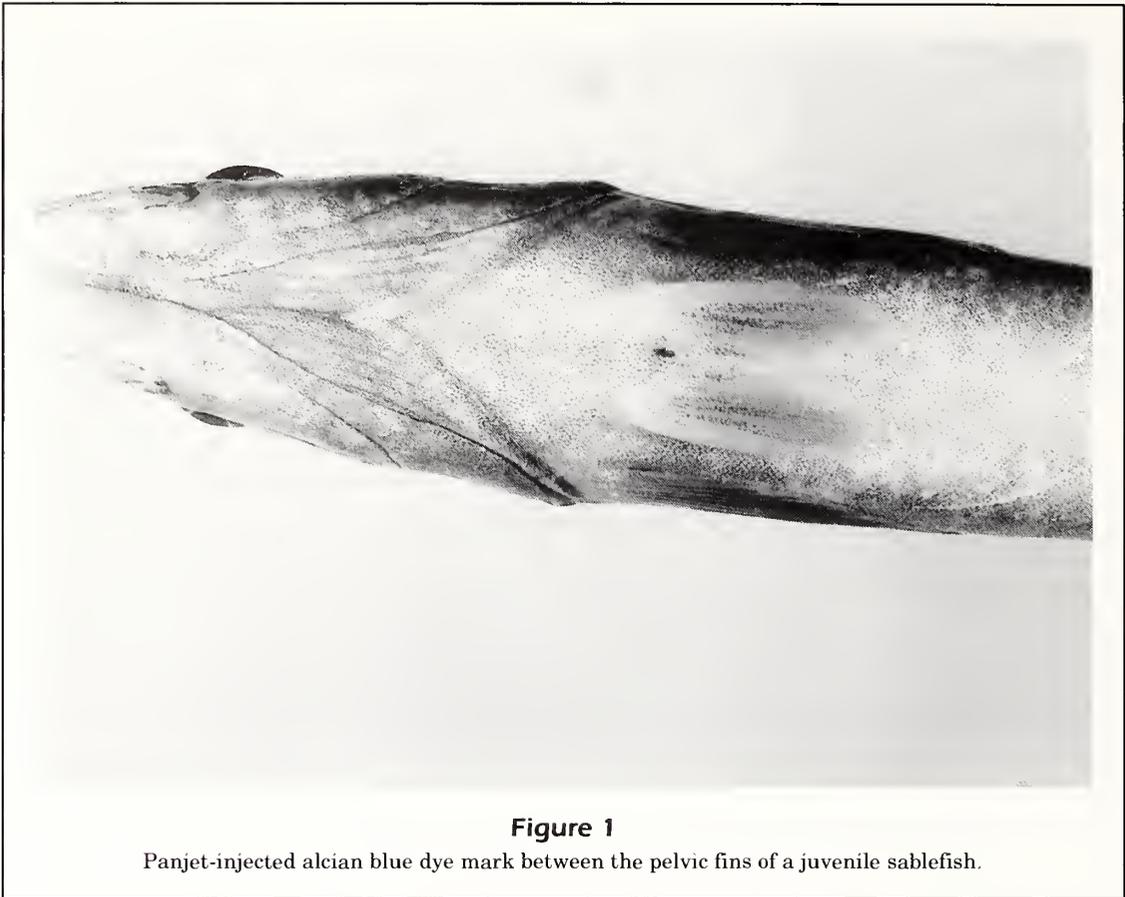


Figure 1

Panjet-injected alcian blue dye mark between the pelvic fins of a juvenile sablefish.

after 189 days and were frozen prior to analysis. Flatfish were held for 90 d in six 70-L flow-through tanks on their preferred bottom type (mud substrate for soles [Moles and Norcross, 1995], sand substrate for halibut). For each flatfish species, control and marked fish were held in separate tanks. Sablefish were held indoors and were provided about 8 h of fluorescent light daily, whereas flatfish were held outdoors under an awning with 12 h of fluorescent light daily. Sablefish were fed ad libitum, and flatfish were fed 10% of their initial body weight per day throughout the study. The substrates in the flatfish tanks were initially frozen three days to kill meiofauna and macrofauna. Mark recognition for sablefish was checked about every 3 weeks, flatfish about every 4 weeks. Blue marks were viewed under fluorescent light, orange marks under fluorescent and ultraviolet (UV) light. Mark retention was rated subjectively as acceptable (retained) or unacceptable (not retained) by the same person each time the fish were checked. Fish lengths were recorded at the beginning and end of the study: fork length (FL) for sablefish, total length (TL) for flatfish. Because we were obtaining additional data (histological) from flatfish, we also recorded flatfish weights when we recorded

their lengths. Differences in acceptable mark retention were tested with a chi-square test, and differences in fish size and growth rate were tested with a *t*-test.

Absolute growth rate in length of flatfish was calculated as

$$L = TL_2 - (TL_1/90)(10),$$

where L = absolute growth in length;
 TL_2 = total length at 90 days; and
 TL_1 = total length at day 1 (beginning of the study).

Instantaneous growth rate in weight of flatfish was calculated as

$$W = (\log_e W_2 - \log_e W_1)/90,$$

where W = instantaneous rate of increase in weight;
 W_2 = weight at 90 days; and
 W_1 = weight at day 1 (beginning of the study).

All flatfish were examined for histological changes. Fish were examined for gross pathology at 50× with a dissecting microscope. Gill and liver tissues were

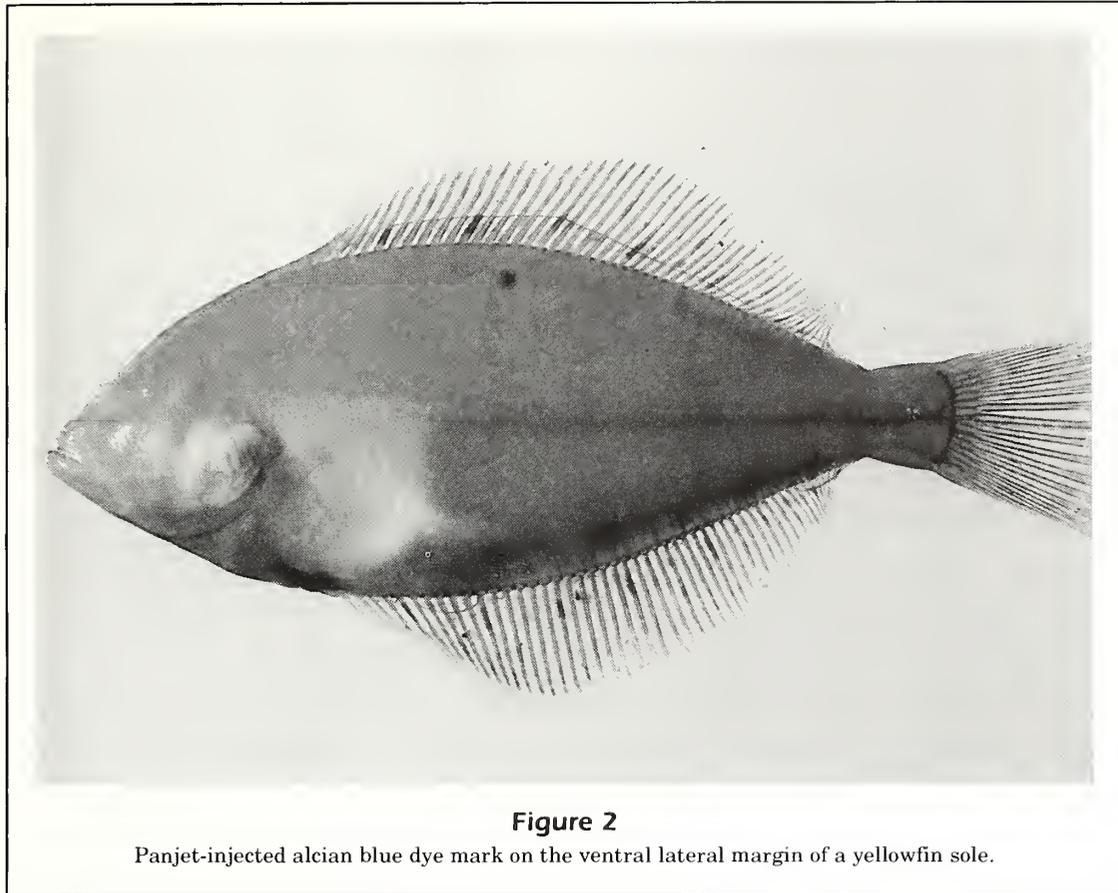


Figure 2

Panjet-injected alcian blue dye mark on the ventral lateral margin of a yellowfin sole.

excised and fixed in 10% buffered seawater. Tissues were then placed in 70% ethanol for two days, dehydrated in a graded ethanol series, cleared in xylene, embedded in paraffin, and sectioned at 6 μ . Sections were stained with hematoxylin and eosin and examined for lesions and evidence of wound healing.

Results

For sablefish, mark retention varied with mark color and method of detection. Retention of marks was significantly higher ($P < 0.001$) for alcian blue dye (100%) than for fluorescent orange acrylic paint when orange marks were viewed under fluorescent light but was similar ($P = 0.99$) when orange marks were viewed under UV light (Fig. 3). Retention of orange marks viewed under fluorescent light was 100% after 21 days but decreased to less than 20% after 84 days. Retention of orange marks viewed under UV light, however, decreased only to 92% after 84 days and remained at that level throughout the remainder of the study.

Mean length at the end of the study was similar ($P = 0.24$) between blue-marked sablefish (280 mm)

Table 1

Mean fork length of jet-injected and control juvenile sablefish at time of injection and after 33 weeks. Fish were injected with alcian blue dye and fluorescent orange acrylic paint. Standard error is in parentheses.

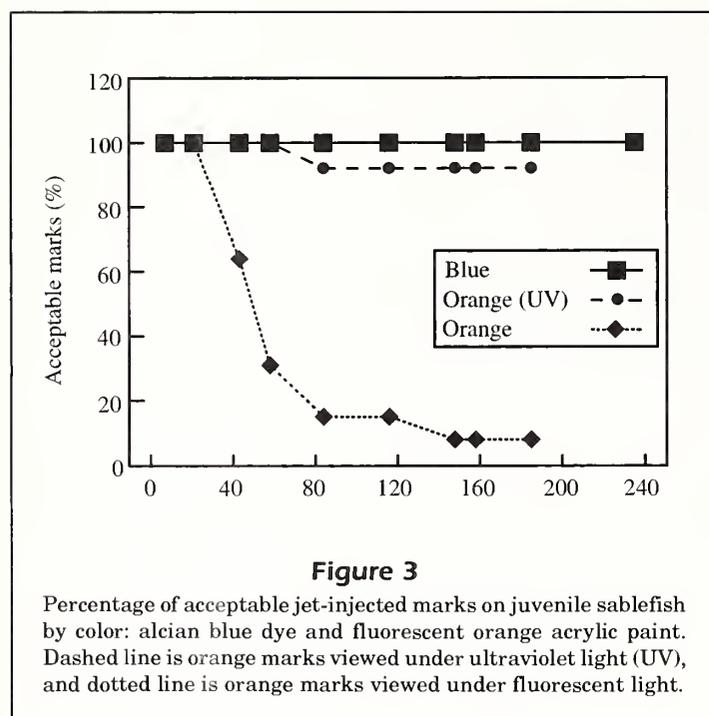
	Mean fork length (mm)	
	Initial	After 33 weeks
Blue	212 (0.80)	280 (1.07)
Orange	212 (0.96)	270 (1.18)
Control	218 (1.16)	288 (1.48)

and controls (288 mm) (Table 1). Despite the potential for tank-linked effect due to holding the marked fish in a separate tank, mean length of the orange-marked sablefish (270 mm) was not significantly different from that of the controls (288 mm) ($P = 0.06$) (Table 1). Mortality was zero.

For all flatfish, mark retention was 100% throughout the study, and growth was similar between marked and control fish (Table 2). The instantaneous rate of increase in length and weight at the end of

the study was similar ($P \geq 0.10$) for marked and control fish, indicating that marking did not affect growth. Again, mortality was zero.

Histological examination of flatfish indicated that the marks were nonirritating and nontoxic. Necropsy of the flatfish revealed no evidence of damage to skin or musculature and no alteration in the structure of dyed tissue. All liver hepatocytes were normal, indicating no toxic exposure. There was no evidence of increased macrophage aggregations in the liver or hyperplasia in the gills to suggest cellular responses to dyes.



Discussion

Marine fish can be jet injected rapidly with many individual marks, often without anesthesia. For example, in this study we marked several nonanesthetized flatfish per minute. Jet-injected alcian blue dye produced a highly visible intradermal mark that was retained for at least 8 months by juvenile sablefish, 3 months by juvenile flatfish. Detection of alcian blue dye marks on flatfish is easy and requires minimal handling. Usually marks can be detected without anesthesia and without turning fish over. Increased visibility of jet-injected marks, however, could make fish more conspicuous to predators. Fluorescent orange acrylic paint marks, however, faded rapidly, making marks less visible to predators but necessitating the use of UV light for detection.

Mark retention was similar to that reported for other species. Thedinga and Johnson (1995) reported 96% retention of alcian blue dye and fluorescent orange acrylic paint marks on the caudal fin of juvenile coho salmon, *Oncorhynchus kisutch*, and sockeye salmon, *O. nerka*, after nearly 4 months, and Herbinger et al. (1990) reported 96% retention of alcian blue dye-marked Atlantic salmon, *Salmo salar*, after 6 months. Few studies have been published that used marked juvenile sablefish or flatfish, and only one used a dye mark. Kelly (1967) injected Fast Blue 8GX and hydrated chromium oxide by needle into the heads of juvenile winter flounder, *Pleuronectes americanus*, and had 100% retention after 4 months.

Jet-injected marks did not affect growth or mortality. Unlike Petersen disc and roll tags, which depressed growth rates (Andersen and

Table 2

Mean initial total length (mm) and weight (g) and mean absolute growth rate in length and instantaneous growth rate in weight of marked (jet-injected with alcian blue dye) and control juvenile yellowfin sole, rock sole, and halibut 90 d after marking. Standard error is in parentheses.

	Initial size		Growth rate after 90 d	
	Marked	Control	Marked	Control
Length				
Yellowfin sole	67.9 (1.04)	74.2 (1.45)	0.198 (0.067)	0.196 (0.054)
Rock sole	59.7 (0.92)	71.6 (1.56)	0.161 (0.068)	0.137 (0.073)
Halibut	72.3 (0.81)	71.8 (0.88)	0.228 (0.059)	0.241 (0.050)
Weight				
Yellowfin sole	3.5 (0.49)	5.2 (0.64)	0.823 (0.144)	0.841 (0.120)
Rock sole	2.3 (0.32)	5.2 (0.68)	0.610 (0.171)	0.817 (0.153)
Halibut	4.1 (0.36)	4.1 (0.36)	1.193 (0.109)	1.175 (0.111)

Bagge, 1963) and resulted in increased mortality in sablefish (McFarlane and Beamish, 1990), jet-injected marks did not affect flatfish and sablefish growth or survival. Marks, however, may not be retained as long under natural conditions where growth is faster: sablefish in their natural habitat average 31–33 cm FL in spring (McFarlane and Beamish, 1983) in contrast with 28 cm FL recorded at the end of our laboratory study in spring.

Jet-injected marks did not affect fish histology. There was no evidence of lesions in skin or musculature and no alterations in either the cells or the structure of dyed tissues. Changes in liver hepatocytes occur when fish have been exposed to toxicants (Hinton et al., 1992) but test hepatocytes in our preparations were normal.

Jet-injection of either alcian blue dye or fluorescent orange acrylic paint is a good method for mass marking or individually marking juvenile marine fish and meets most criteria for an effective external marker (Kelly, 1967). The marks are effectively retained and nontoxic and nonirritating; they do not affect mortality, can be used rapidly, and are inexpensive, readily visible, and permit numerous different mark combinations (Thedinga et al., 1994). Their application requires minimal training and equipment. Most importantly, jet injection does not alter the growth or tissue structure of fish. A limitation of jet-injection marking is the nonpermanent nature of the mark (Thedinga and Johnson, 1995). As a moderate-lasting marking method of juvenile marine fish, it is superior to most available external marking methods.

Acknowledgments

We thank Mike Murphy and Scott Johnson for reviewing the manuscript and Mark Carls for photographing jet-injected sablefish and yellowfin sole.

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Erratum

Erratum: Fishery Bulletin 95(1):11–24.

Crockford, Susan J.

Archeological evidence of large northern bluefin tuna, *Thunnus thynnus*, in coastal waters of British Columbia and northern Washington

Correction: Susan Crockford has brought to our attention an error in the last column of data in her original Table 4 (page 18). The correct data for estimated FL (cm) should read as follows:

Table 4

Archeological bluefin tuna vertebrae measurements and fork length estimates, by vertebrae number. All specimens. Measurements are defined in Figure 2.

Vertebra no.	Centrum GL (mm)	Centrum GB(p) (mm)	Estimated FL (cm)	Vertebra no.	Centrum GL (mm)	Centrum GB(p) (mm)	Estimated FL (cm)
01	27.0	44.4	198.7	21	38.3	45.1	189.6
02	26.3	48.2	191.5	22	39.2	44.8	188.6
04	22.5	39.6	164.7	22	39.2	46.5	193.5
04	31.6	65.1	224.9	24	39.4	47.5	195.3
05	27.1	58.7	212.4	24	45.1		209.8
06	30.8	58.9	218.2	25	40.8	48.3	194.8
09	25.6	34.4	168.2	26	40.1	47.6	190.7
(09)		48.7	220.8	(28)	30.2	35.9	159.3
(09)	22.3	30.5	153.6	29	33.7	36.3	155.3
(10)	33.4	45.0	206.7	29	45.3	49.5	201.1
11	24.4	34.6	165.5	29	50.3	58.2	221.1
(11)	31.0	37.8	177.5	30	28.1	32.0	138.5
(12)	35.0		200.5	30	36.7		167.1
(12)	36.7	46.5	206.9	30	38.3	44.0	172.3
(12)	34.9	41.9	192.0	30	46.7		199.2
14	33.5		187.0	30	47.3	50.0	201.1
(14)	33.9	40.9	185.4	30	47.5	51.2	201.7
(14)	34.1	42.0	189.3	31	48.6	52.8	201.3
(14)	32.5	42.1	189.7	31	52.7	53.8	215.3
(14)	27.7	32.8	157.8	32	41.7	45.6	179.3
15	35.4	42.5	188.4	32	43.7		185.6
(15)	31.4	42.5	188.4	32	49.7	54.4	204.4
16	35.9	45.6	191.2	33	26.6	27.0	122.4
16	36.1	42.9	191.9	33	43.8	44.8	178.9
(16)	31.3	35.4	175.0	33	44.5	47.2	186.5
(16)	33.8	40.9	183.9	33	44.7	45.6	181.4
(16)	40.2	47.2	206.0	33	47.9	53.9	207.3
(16)	41.2	51.8	209.4	33	52.2	53.7	206.7
17	36.0	42.8	187.3	33	53.7	55.2	211.3
17	37.5	47.3	200.2	34	48.1		202.4
(17)	37.0	43.9	190.4	34	48.2		202.6
(17)	38.2	44.2	191.3	35	41.2	42.0	200.8
18	37.2	46.5	195.4	36	30.5		198.9
(18)	26.8	32.4	153.5	38	11.9	28.2	210.3
19	39.4	47.2	196.0	38	16.5	31.8	243.2
(19)	27.2	32.7	151.9	39		23.0	198.3
20	35.5	44.5	182.4	39		19.5	174.3
(20)	38.0	45.0	191.3				
(20)	44.3	54.0	213.4				

Fishery Bulletin

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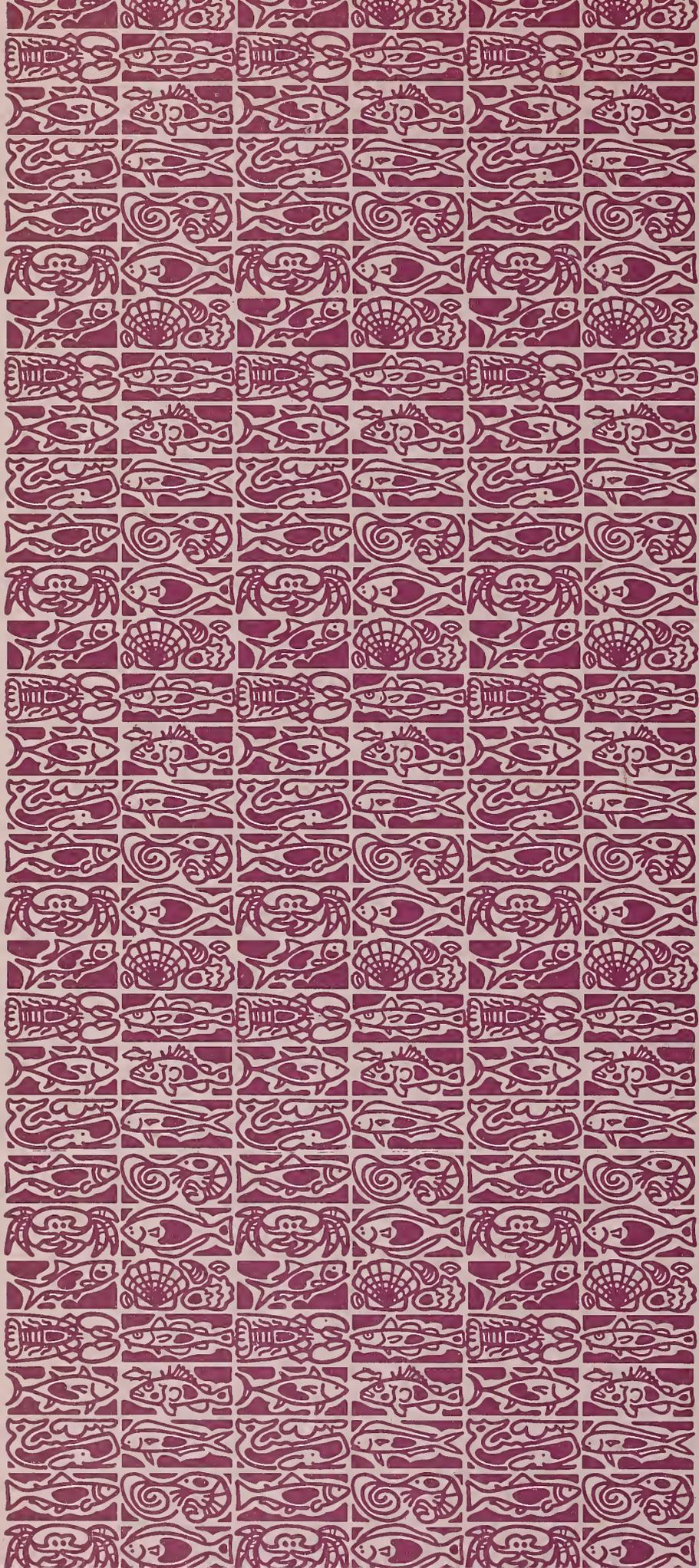
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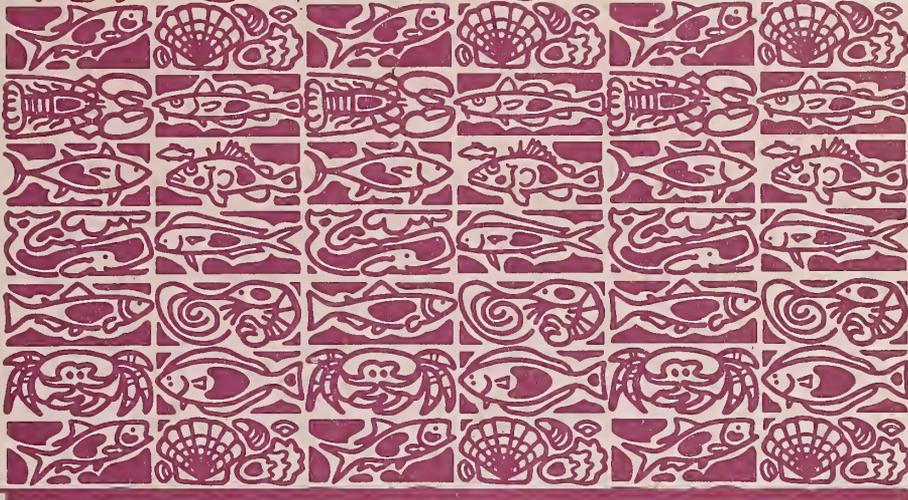
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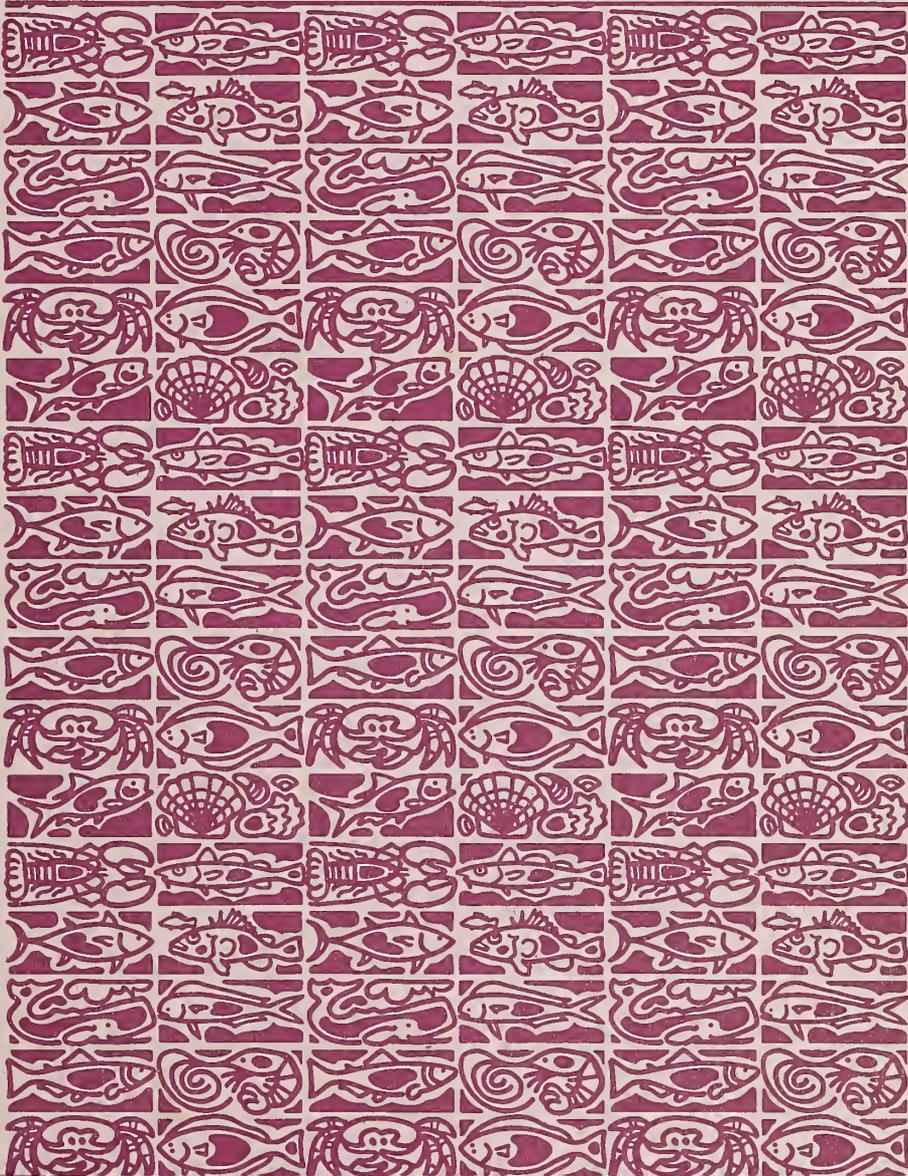


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Abstract.—The effect of different fishing mortality (F) and natural mortality (M), and age at first capture (t_c) on yield-per-recruit of Atlantic croaker, *Micropogonias undulatus*, in the lower Chesapeake Bay and North Carolina were evaluated with the Beverton-Holt model. Independent of the level of M (0.20–0.35) or F (0.01–2.0) used in simulations, yield-per-recruit values for Chesapeake Bay were consistently higher at $t_c = 1$ and decreased continuously with increases in t_c (2–5). Although maximum yield-per-recruit always occurred at the maximum level of F ($F=2.0$), marginal increases in yield beyond $F = 0.50$ – 0.75 were negligible. Current F (F_{CUR}) is estimated to be below the level that produces maximum potential yield-per-recruit (F_{MAX}) and at or below the level of $F_{0.1}$ if $M \geq 0.25$. Although modeling results indicated yield-per-recruit could be maximized by reducing the current level of t_c ($t_c=2$), the resultant gains were small and did not appear to justify such management measures. Instead, it is suggested that regulatory measures be directed at maintaining the current level of t_c in the lower Chesapeake Bay. Simulation results for North Carolina showed a pattern opposite to that shown for Chesapeake Bay, with yield-per-recruit curves increasing consistently with increases in t_c . Estimates of F_{CUR} for $t_c = 1$ were consistently higher than $F_{0.1}$ as well as F_{MAX} , indicating that during the period 1979–81 Atlantic croaker were being growth-overfished in North Carolina. However, differences between Chesapeake Bay and North Carolina seem to reflect temporal rather than spatial differences in Atlantic croaker population dynamics, because data for North Carolina came from a period coinciding with the occurrence of unusually large Atlantic croaker along the east coast of the United States.

Manuscript accepted 11 March 1997.
Fishery Bulletin 95:637–645 (1997).

Yield-per-recruit analysis and management strategies for Atlantic croaker, *Micropogonias undulatus*, in the Middle Atlantic Bight*

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The Atlantic croaker, *Micropogonias undulatus* (Linnaeus), is one of the most important commercial and recreational fishery resources of the southeastern coast of the United States (Wilk, 1981; Schmied and Burgess, 1987; Mercer¹). Along the Atlantic coast, commercial fisheries for Atlantic croaker are centered in Chesapeake Bay and in North Carolina waters (Joseph, 1972; Rothschild et al., 1981; Ross, 1988; Mercer¹); both inshore and offshore catches are distributed according to the seasonal migratory patterns of Atlantic croaker. From late spring to early fall Atlantic croaker are caught in estuarine areas, primarily by haul-seine, pound-net, and gill-net fisheries (Ross, 1988; Chittenden, 1991; Barbieri et al., 1994a). From late fall through winter, after adults have moved out of estuaries, they are caught in continental shelf waters by otter-trawl and gill-net fisheries (Wilk, 1981; Ross, 1988; Mercer¹).

Commercial landings of Atlantic croaker have fluctuated widely over

the past 50–60 years (Joseph, 1972; Rothschild et al., 1981; Wilk, 1981). Landings exceeded 20,000 metric tons (t) between 1937 and 1940, peaked at ca. 29,000 t in 1945 and dropped to less than 1,000 t between 1967 and 1971 (Wilk, 1981; McHugh and Conover, 1986). The most recent peak in landings occurred in 1977 and 1978 at just over 13,000 t annually (Mercer¹). Recreational catches in the mid-Atlantic and South Atlantic regions during 1979–93 have also fluctuated, although they do not reflect fluctuations in commercial landings for the same period. Commercial landings from Virginia and North Carolina—the

* Contribution 2057 from Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062.

¹ Mercer, L. P. 1987. Fishery management plan for Atlantic croaker (*Micropogonias undulatus*). North Carolina Dep. Nat. Res. Comm. Dev., Div. Mar. Fish., Spec. Sci. Rep. 48, 90 p. [Available from North Carolina Department of Environment, Health, and Natural Resources, Div. Marine Fisheries, PO Box 769, Morehead City, NC 28557-0769.]

two states with 98% of the Atlantic catch—have declined since 1987, whereas recreational catches peaked in 1991 with an estimated 21 million fish (Newlin, 1992; Speir et al., 1994).

A lack of accurate catch and effort data from both the commercial and recreational fisheries makes it difficult to evaluate to what extent these long-term fluctuations represent natural changes in population abundance or reflect historic changes in Atlantic croaker exploitation. There has been a growing concern, however, that recent low landings may be related to the large numbers of young fish killed as bycatch in the southern shrimp fishery and as part of the scrap catch in pound-net, haul-seine, and trawl fisheries (Speir et al., 1994; Mercer¹). In response to these concerns, the 1993 review of the Atlantic States Marine Fisheries Commission Fishery Management Plan for Atlantic croaker (Speir et al., 1994) has recommended the use of bycatch reduction devices and the establishment of a coast-wide minimum size limit that would maximize Atlantic croaker yield-per-recruit.

Yield-per-recruit models, widely used in fish population dynamics studies (Beverton and Holt, 1957; Ricker, 1975; Gulland, 1983), can be a useful tool in defining routine fisheries management measures such as minimum size limits, closed seasons, etc. (Gulland, 1983; Deriso, 1987). However, the only published application of yield-per-recruit models to Atlantic croaker is based on data from the northwestern Gulf of Mexico (Chittenden, 1977) and points out that results may or may not apply to other areas. In this paper we use stock assessment data from the Chesapeake Bay (years 1988–91; Barbieri et al., 1994a) and from North Carolina (years 1979–81; Ross, 1988) to evaluate the effect of different fishing (-induced) and natural mortality, and age-at-first-capture schedules on Atlantic croaker yield-per-recruit. Implications of this analysis for management of Atlantic croaker are discussed.

Methods

Yield-per-recruit analysis

Yield-per-recruit curves were calculated with the Beverton-Holt yield-per-recruit model (Beverton and Holt, 1957):

$$Y/R = F e^{-M(t_c - t_r)} W_\infty \sum_{n=0}^3 \frac{U_n e^{-nK(t_c - t_0)}}{F + M + nK}, \quad (1)$$

where Y/R = yield-per-recruit in weight (g);

- F = instantaneous fishing mortality coefficient;
- M = instantaneous natural mortality coefficient;
- W_∞ = asymptotic weight (von Bertalanffy growth parameter);
- U_n = summation parameter ($U_0=1$, $U_1=-3$, $U_2=3$, $U_3=-1$);
- t_c = mean age at first capture;
- t_r = mean age (years) at recruitment to the fishing area;
- t_0 = hypothetical age at which fish would have been zero length (von Bertalanffy growth parameter); and
- K = the Brody growth coefficient (von Bertalanffy growth parameter).

Computations were performed with the computer program B-H3 available in the Basic Fisheries Science Programs package (Saila et al., 1988).

Parameter values used in simulations are summarized in Table 1. Estimates of growth parameters (W_∞ , K , and t_0) for Chesapeake Bay and North Carolina were obtained from Barbieri et al. (1994a) and Ross (1988), respectively. For both areas, W_∞ was converted from L_∞ by using an allometric length-weight relation ($b=3.23$; Ross, 1988; and $b=3.30$; Barbieri et al., 1994a). One of the assumptions of the Beverton-Holt yield-per-recruit model is that growth is isometric—i.e. the coefficient b in the length-weight relation is equal to 3 (Beverton and Holt, 1957; Ricker, 1975). We, however, considered that departure from the assumption of isometric growth did not affect interpretation of our modeling results because the factor of interest in these simulations is the relative difference in yield resulting from varying t_c and F at different levels of M . The relative error in such differences, when using an incorrect b , tends to be much less than that in absolute levels (Ricker, 1975).

Estimates of t_r , the mean age at recruitment to the fishing area, were based on Atlantic croaker life history information (Chao and Musick, 1977; Ross, 1988). Estimates of current t_c , the mean age at first capture, was based on Atlantic croaker age compositions reported for the pound-net, haul-seine, and gill-net catches in the lower Chesapeake Bay for the period 1988–91 (t_c =age 2; Barbieri et al., 1994a) and from age compositions reported for the haul-seine fishery in North Carolina for the period 1979–81 (t_c =age 1; Ross, 1988). Because of the uncertainty associated with estimates of M in fish populations (Vetter, 1988), simulations for both areas were conducted over a range of M values (0.20–0.35; Table 1).

The instantaneous total annual mortality rate, Z , for fully recruited Atlantic croaker in North Carolina is 1.3 (Ross, 1988) and ranges from 0.55 to 0.63, with a mean value of 0.59 for the lower Chesapeake

Table 1

Parameter estimates or range of values used in yield-per-recruit simulations for Atlantic croaker, *Micropogonias undulatus*, in the lower Chesapeake Bay (period 1988–91) and North Carolina (period 1979–81). See Equation 1 for definitions of parameter variables.

Parameter	Chesapeake Bay	North Carolina
K	0.36	0.20
W_{∞}	409.9 g	3,814 g
t_0	-3.26 yr	-0.60 yr
t_r	0 yr	0 yr
t_c	1–5 yr	1–5 yr
F	0.01–2.0	0.01–2.0
M	0.20–0.35	0.20–0.35

Bay (Barbieri et al., 1994a). To estimate current levels of fishing mortality (F_{CUR}) for different values of M , we used $Z = 0.60$ for Chesapeake Bay and $Z = 1.3$ for North Carolina, as

$$F_{CUR} = Z - M_i, \quad (2)$$

where $i = 0.20, 0.25, 0.30$, and 0.35 .

The value of $F_{0.1}$ (the level of F for which the marginal increase in yield-per-recruit due to a small increase in F is 10% of the marginal yield-per-recruit in a lightly-exploited fishery [Gulland and Boerema, 1973; Anthony²]), was estimated for Chesapeake Bay with $F = 0.01$ and $t_c = 2$ (Barbieri et al., 1994a) and for North Carolina with $F = 0.01$ and $t_c = 1$ (Ross, 1988).

Cohort biomass and harvesting time

In general, the maximum possible yield for a given year class occurs at the critical age t_{CRITIC} , the age where biomass of a cohort is maximum in the absence of fishing. For comparison with the Beverton-Holt yield-per-recruit modeling results, we estimated t_{CRITIC} for Atlantic croaker following Alverson and Carney (1975) and Deriso (1987) as

$$t_{CRITIC} = t_0 + \frac{1}{K} \ln(3K/M + 1), \quad (3)$$

where t_0 , K , and M are defined as in Equation 1. Parameter estimates or the range of values used in calculations are listed in Table 1.

To evaluate the proportion of the potential growth span (P_g) remaining when Atlantic croaker enter the exploited phase of life (Beverton and Holt, 1957), we used the quantity (Beverton, 1963):

$$P_g = (1 - l_c / L_{\infty}), \quad (4)$$

where L_{∞} , the asymptotic length, was obtained from Barbieri et al. (1994a) and Ross (1988) and l_c , the average length at first capture, was obtained by converting t_c to length with the von Bertalanffy growth curve reported for Atlantic croaker in Chesapeake Bay (Barbieri et al., 1994a) and North Carolina (Ross, 1988). Both parameters are based on total length (TL) in mm.

Results

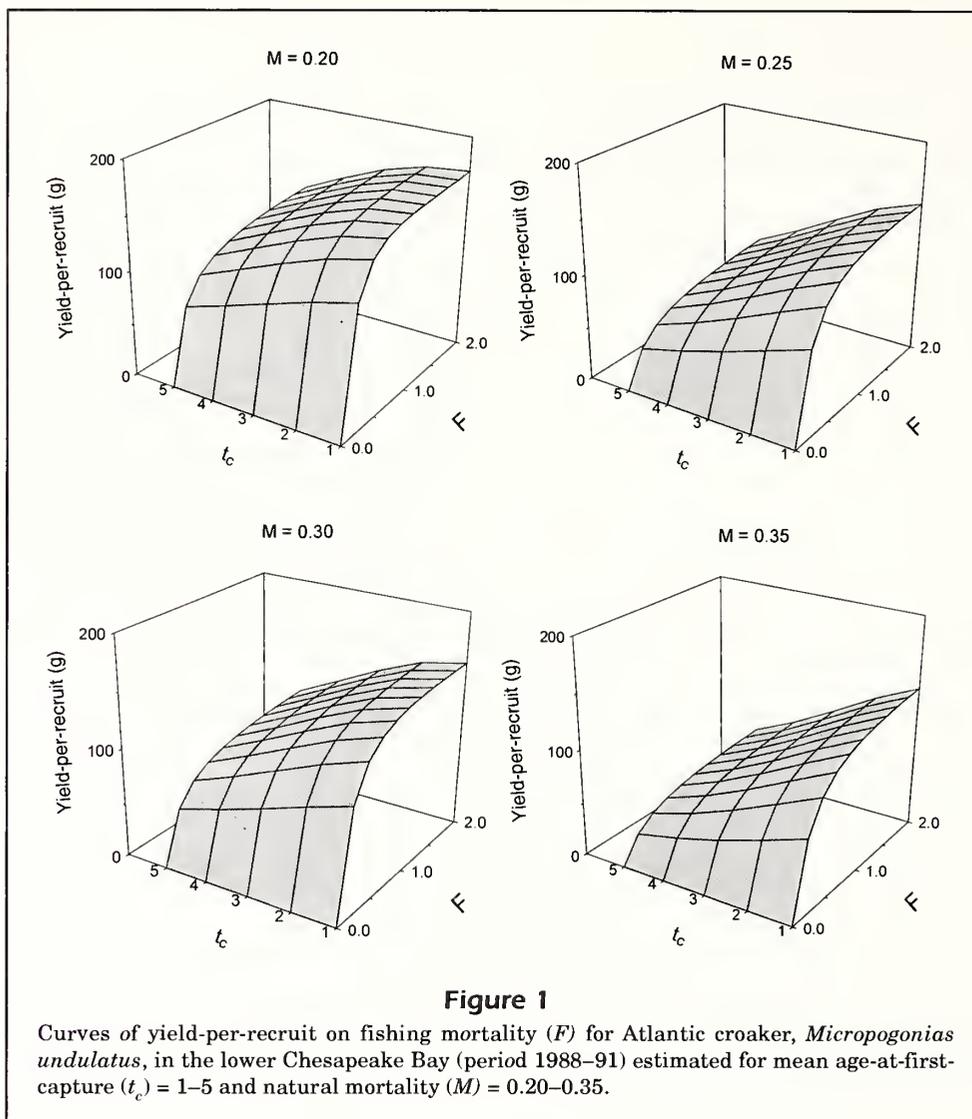
Chesapeake Bay

Curves of yield-per-recruit on F (Fig. 1) showed that the yield of Atlantic croaker in Chesapeake Bay could be maximized by decreasing the current level of $t_c = 2$ (265 mm TL) to $t_c = 1$ (245 mm TL). Independent of the level of M or F used in simulations, yield-per-recruit values were consistently higher at $t_c = 1$ and decreased continuously with increasing t_c . However, increases in yield from $t_c = 2$ to $t_c = 1$ were generally small and gradually increased with increases in M . For example, at the estimated current levels of fishing mortality for Atlantic croaker in the Chesapeake Bay (F_{CUR}), increases in yield between $t_c = 2$ and $t_c = 1$ would be 7.1% at $M = 2.0$, 12.6% at $M = 0.25$, 18.4% at $M = 0.30$, and 24.6% at $M = 0.35$.

The curves of yield-per-recruit for Atlantic croaker on F for different levels of M and t_c showed no clearly defined peaks. Although the magnitude of yield curves was dependent on the level of M used in simulations, relative changes in yield as a function of F and t_c were very similar, regardless of M (Fig. 1). For all levels of M and t_c , yield curves increased rapidly in the range of F between 0 and 0.50–0.75, and remained relatively flat thereafter. Although yield values increased continuously with F , i.e. maximum yield-per-recruit always occurred at the maximum value of F used in simulations ($F=2.0$), increases in yield beyond $F = 0.50$ – 0.75 were very small. For example, increases in yield from $F = 0.75$ to F_{MAX} ranged from 5.3% to 22.7%, depending on the level of M and t_c used in the model (Table 2). However, this relatively small gain in yield corresponds to an increase in F of 166.7%.

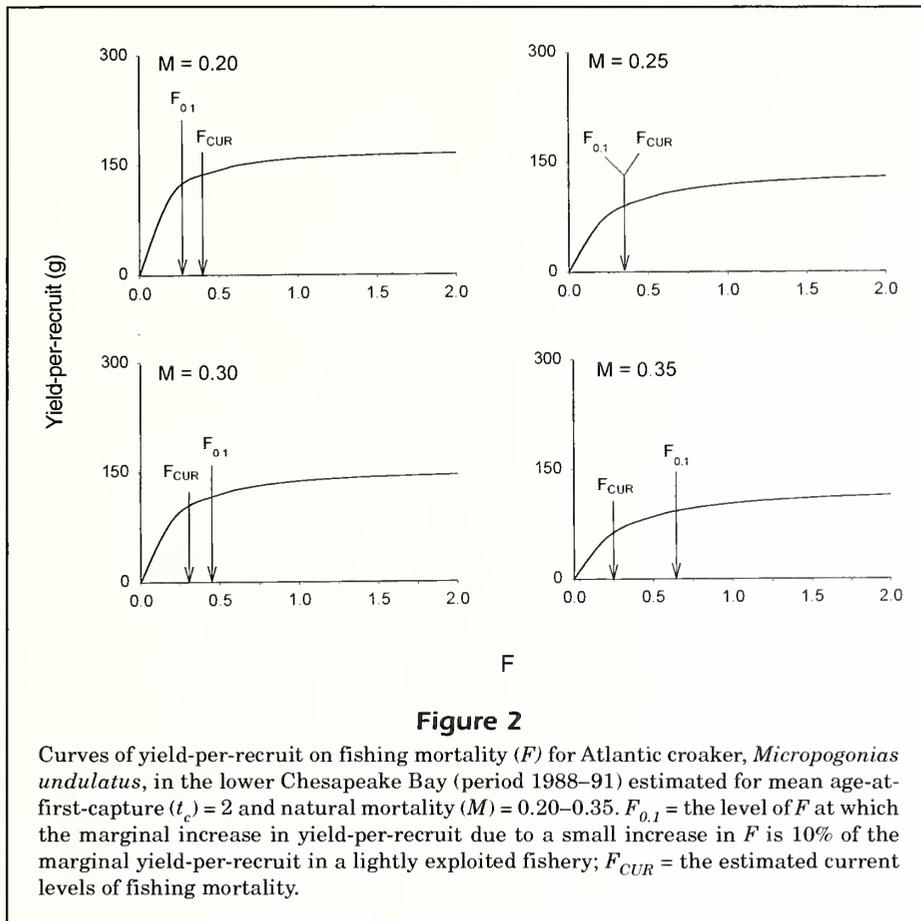
For the range of M used in our study, estimates of F_{CUR} are below the levels that give maximum potential yield-per-recruit (F_{MAX}) and, for $M \geq 0.3$, below

² Anthony, V. 1982. The calculation of $F_{0.1}$: a plea for standardization. Northwest Atlantic Fisheries Organization, SCR Doc. 82/VI/64 Ser. No. N557, 15 p. NAFO, PO Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

**Table 2**

Percent increase in yield-per-recruit of Atlantic croaker, *Micropogonias undulatus*, from fishing mortality (F) = 0.75 to fishing mortality at the level that gives maximum potential yield-per-recruit (F_{MAX}) for mean age-at-first-capture (t_c) = 1–5 and natural mortality (M) = 0.20–0.35 for Chesapeake Bay.

M	t_c	Yield-per-recruit (g)			M	t_c	Yield-per-recruit (g)		
		$F = 0.75$	F_{MAX}	% increase			$F = 0.75$	F_{MAX}	% increase
0.20	1	160.4	168.9	5.3	0.30	1	129.2	142.5	10.3
	2	153.9	165.1	7.3		2	112.8	128.9	14.3
	3	140.3	154.1	9.8		3	93.4	109.0	16.7
	4	123.5	137.8	11.6		4	74.6	88.2	18.2
	5	106.3	119.8	12.7		5	58.2	69.4	19.2
0.25	1	143.7	153.5	6.8	0.35	1	116.5	132.4	13.6
	2	131.6	145.8	10.8		2	97.0	114.0	17.5
	3	114.3	129.5	13.3		3	76.5	91.7	19.9
	4	95.8	110.3	15.1		4	58.1	70.7	21.7
	5	78.5	91.2	16.2		5	43.1	52.9	22.7



the level of $F_{0.1}$ (Fig. 2; Table 3). For $M = 0.20$, F_{CUR} is higher than $F_{0.1}$, indicating that, although it produces slightly higher yield values, current fishing mortality is not at its most economically efficient level. For example, for $t_c = 1$ and $t_c = 2$, over 90% of the yield obtained at F_{CUR} can be achieved by lowering fishing mortality to the level of $F_{0.1}$. For $M = 0.25$, both F_{CUR} and $F_{0.1}$ equal 0.35, indicating that, although below the maximum potential yield-per-recruit, estimated current levels of harvest probably correspond to the most efficient level of F . In contrast, if M ranges from 0.30 to 0.35, $F_{0.1}$ is higher than F_{CUR} (Table 3), suggesting there would still be room to increase yield efficiently with increases in F . However, at these higher levels of M , increases in F necessary to achieve the yields at $F_{0.1}$ may be unrealistically high (Table 3).

Values of t_{CRITIC} estimated with different values of M were relatively low for Atlantic croaker in Chesapeake Bay. For M equal to 0.20, 0.25, 0.30, and 0.35, values of t_{CRITIC} were 1.9, 1.4, 1.0, and 0.6 years, respectively. These values indicate that, for the range of M considered herein, maximum theoretical cohort biomass in the absence of fishing would be achieved before Atlantic croaker reach age 2 (years).

Table 3

Estimated value of current levels of fishing mortality (F_{CUR}) and level of fishing mortality at which the marginal increase in yield-per-recruit due to a small increase in F is 10% of the marginal yield-per-recruit in a lightly exploited fishery ($F_{0.1}$) for Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay region for a range of fishing mortality (M) = 0.20–0.35, and the percent increase or decrease in F_{CUR} necessary to make it equal to $F_{0.1}$.

M	F_{CUR}	$F_{0.1}$	% Difference
0.20	0.40	0.27	-48
0.25	0.35	0.35	0
0.30	0.30	0.45	+50
0.35	0.25	0.64	+156

Estimated values of P_g for Atlantic croaker in Chesapeake Bay were also relatively low. For $L_\infty = 312$ mm, and the current estimated level of l_c (265 mm, corresponding to $t_c = 2$), $P_g = 0.15$, i.e., on the average, only 15% of their potential growth still remains when Atlantic croaker in Chesapeake Bay enter the exploited phase at age 2. For alternative values of t_c

equal to 1, 3, 4 and 5 years, values of P_g are 0.21, 0.10, 0.07, and 0.05, respectively.

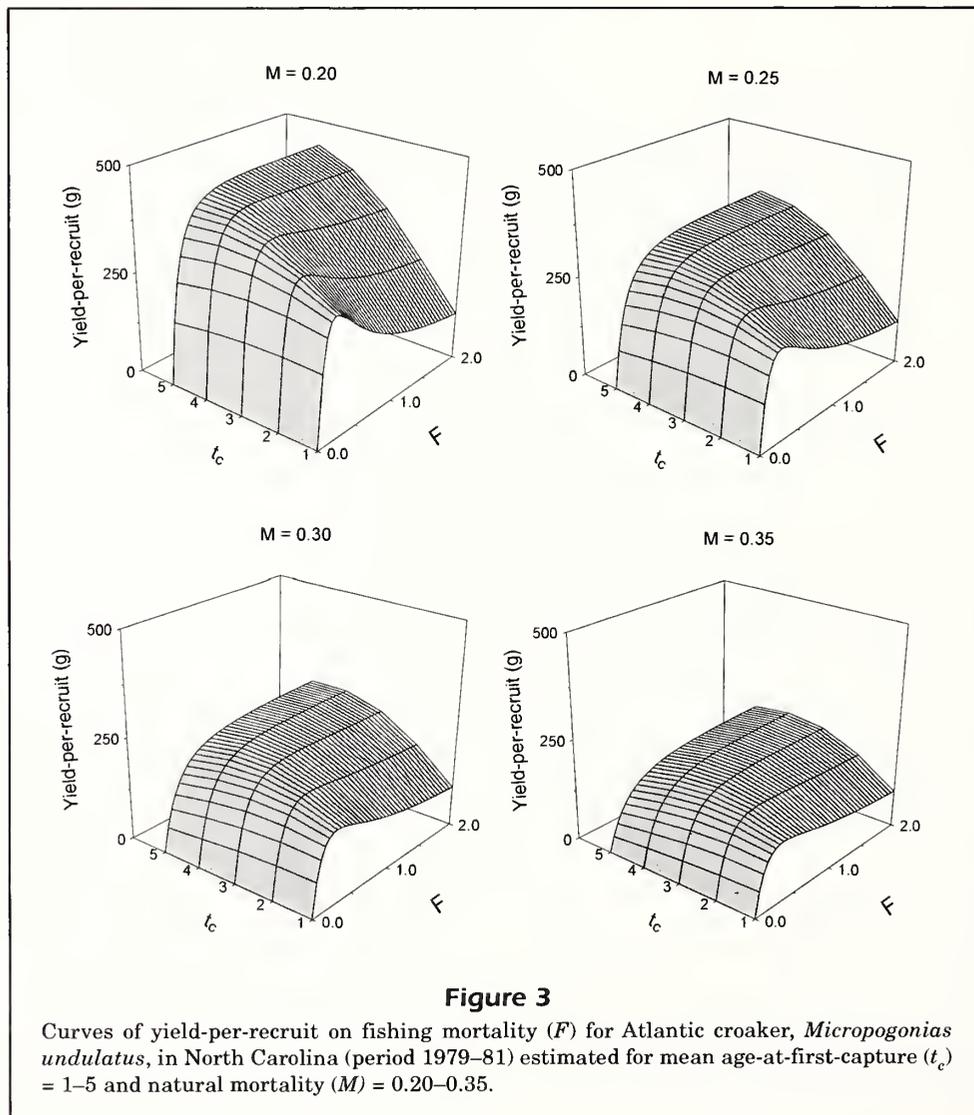
North Carolina

Curves of yield-per-recruit on F for Atlantic croaker in North Carolina (Fig. 3) showed an opposite trend from that shown in Chesapeake Bay. For all levels of F or M used in simulations, yield values continuously increased from $t_c = 1$ (177 mm TL) to $t_c = 5$ (434 mm TL), indicating that yield could be maximized by increasing t_c . However, the shape of yield-per-recruit curves differed among different levels of M and t_c (Fig. 3). For $M = 0.20$ and 0.25 , curves for $t_c = 1-3$ peaked at low to intermediate levels of F ($F_{MAX} = 0.20-0.60$) and gradually decreased after that, whereas for $t_c = 4-5$ they increased rapidly in the range of F between 0 and 0.35-0.60 and remained

relatively flat thereafter. For $M = 0.30-0.35$, the peaks in yield at low to intermediate levels of F occurred only for $t_c = 1-2$ and were a lot less pronounced than those at lower levels of M .

For the range of M used in our simulations, estimates of F_{CUR} (Fig. 4) indicated that during the period 1979-81 the level of fishing mortality for Atlantic croaker in North Carolina was well above the levels of $F_{0.1}$ and F_{MAX} . At $t_c = 1$, estimated losses in potential yield-per-recruit from F_{MAX} to F_{CUR} were equal to 45%, 35%, 25%, and 4% for $M = 0.20, 0.25, 0.30,$ and 0.35 , respectively. Estimated losses if fishing mortality were kept at the level of $F_{0.1}$ would be 44%, 22%, 20%, and 14%, respectively.

Estimated values of t_{CRITIC} and P_g for Atlantic croaker in North Carolina were much higher than those estimated for Chesapeake Bay. For M equal to 0.20, 0.25, 0.30, and 0.35, values of t_{CRITIC} were 7.5,



6.7, 6.1, and 5.6 years, respectively. For $L_\infty = 645$ mm and the estimated level of l_c for the period 1979–81 (177 mm, corresponding to $t_c=1$), $P_g = 0.72$, i.e., on the average, 72% of their potential growth still remained when Atlantic croaker in North Carolina entered the exploited phase at age 1 during the period 1979–81. For alternative values of $t_c = 2$ –5 years, values of P_g were 0.59, 0.49, 0.39, and 0.33, respectively.

Discussion

Our modeling results indicate that, for the range of M and F used in simulations, yield-per-recruit of Atlantic croaker in the lower Chesapeake Bay could be maximized by a management strategy that incorporates early age at first capture ($t_c=1$) and high rates of fishing mortality ($F=2.0$). However, the analysis for Chesapeake Bay also showed this is probably not the most efficient management option for this species. Because of the essentially asymptotic relation between yield-per-recruit and F , harvesting Atlantic croaker at or near their maximum potential yield (i.e.

at F_{MAX}) would require a disproportionate increase in fishing mortality making it an economically inefficient management option. In addition, given the multispecies nature of the main fisheries for Atlantic croaker in Chesapeake Bay (Austin, 1987; Chittenden, 1991), raising current levels of F would greatly increase overall rates of exploitation and probably interfere with management of other species such as weakfish, *Cynoscion regalis*, and spot, *Leiostomus xanthurus*.

Decreasing the current level of t_c for Atlantic croaker in Chesapeake Bay would not be recommended for two reasons. First, for the range of M used in simulations, gains in yield-per-recruit from $t_c = 2$ to $t_c = 1$ were relatively small at F_{CUR} . Second, because of the magnitude of the scrap catch of Atlantic croaker in Chesapeake Bay (Mercer¹), it is likely that this species is already entering the exploited phase at age 1 or younger. The current estimate of t_c ($t_c=2$; Barbieri et al., 1994a) may be an overestimate because it was based on arbitrarily defined commercial market grades instead of overall catches—including the scrap. Because the market accepts only fish above a certain size, a reduction in mesh sizes to attempt

to increase the proportion of age-1 Atlantic croaker in the catches would probably only increase the number of fish sold as scrap and have little or no effect on commercial market grades.

Nevertheless, the analysis showed no indication that fully recruited Atlantic croaker in Chesapeake Bay are being growth-overfished (i.e. that the fish were being caught before they had a chance to grow to their ideal size). Yield-per-recruit modeling results and estimated values of F_{CUR} indicated that, over a likely range of M , current levels of harvest are below the levels at F_{MAX} and, under most scenarios, at or below the levels at $F_{0.1}$. In addition, yield-per-recruit curves showed no signs of decrease at higher levels of F , even if M is as low as 0.20. This pattern suggests that stocks of Atlantic croaker in the Chesapeake Bay region show the same great biologi-

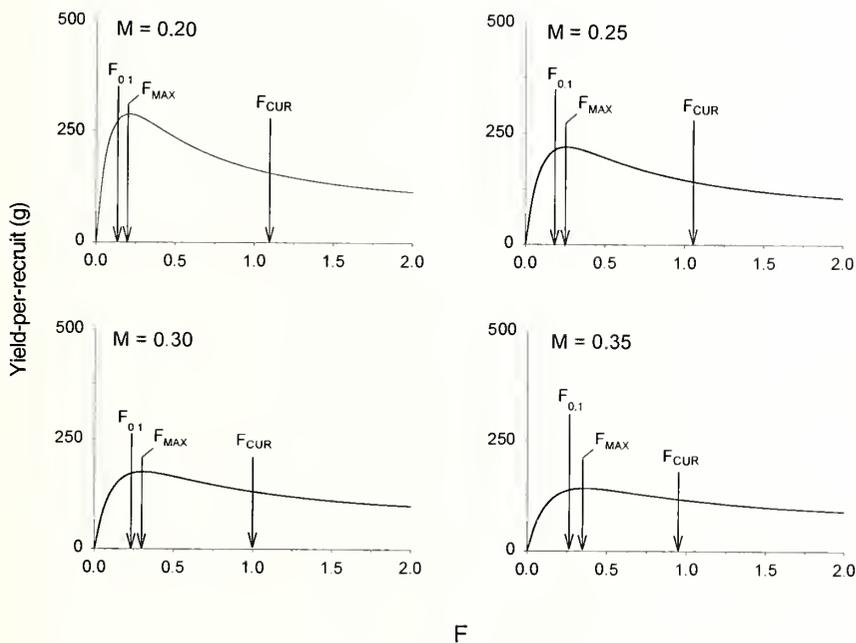


Figure 4

Curves of yield-per-recruit on fishing mortality (F) for Atlantic croaker, *Micropogonias undulatus*, in North Carolina (period 1979–81) estimated for mean age-at-first-capture (t_c) = 1 and natural mortality (M) = 0.20–0.35. $F_{0.1}$ = the level of F at which the marginal increase in yield-per-recruit due to a small increase in F is 10% of the marginal yield-per-recruit in a lightly exploited fishery; F_{CUR} = the estimated current levels of fishing mortality.

cal capacity to resist growth overfishing as those stocks in the northwestern Gulf of Mexico (Chittenden, 1977). The low values of t_{CRITIC} and P_g agree with yield-per-recruit modeling results and indicate that 1) for a reported maximum longevity of 8 years in Chesapeake Bay (Barbieri et al., 1994a), maximum theoretical biomass is achieved very early in life, before fish reach age 2; and 2) very little potential for a growth span still remains when fish enter the exploited phase at age 2. As a precaution against future problems—especially considering that annual recruitment is reported to be highly variable and strongly density independent—we suggest that regulatory measures for Atlantic croaker in the lower Chesapeake Bay be directed at maintaining the apparent current level of t_c (age 2; $l_c=265$ mm TL; Barbieri et al., 1994a). In addition, the magnitude and composition of the scrap catch for the main fisheries in this area need to be estimated, and their effect on estimates of F_{CUR} and t_c need to be assessed more precisely before any definite conclusion on Atlantic croaker yield-per-recruit can be reached.

In contrast to what we found for the lower Chesapeake Bay, results for North Carolina indicated that Atlantic croaker were being severely growth-overfished. First, independent of the level of F or M used in simulations, yield-per-recruit values were consistently higher at higher levels of t_c , indicating that age and size limits during the period 1979–81 ($t_c=1$, $l_c=177$ mm TL; Ross, 1988) were unrealistically low. Second, estimates of F_{CUR} for $t_c=1$ were not just consistently higher than $F_{0.1}$ but were also well above F_{MAX} . The pattern of declining yield-per-recruit values with increasing F at lower levels of t_c agrees well with the high estimates of t_{CRITIC} and P_g and indicates that, contrary to the pattern shown in Chesapeake Bay, maximum cohort biomass is attained later in life (ages 5–7).

However, differences in yield-per-recruit modeling results between Chesapeake Bay and North Carolina seem to reflect temporal rather than spatial differences in Atlantic croaker population dynamics. Parameters used in simulations for North Carolina were obtained from a study (Ross, 1988) conducted during a period (1979–81) that coincides with the occurrence of unusually large Atlantic croaker (350–520 mm TL; Ross, 1988) along the east coast of the United States (Barbieri et al., 1994a). However, since 1982, Atlantic croaker catches in North Carolina have been dominated by smaller fish. Modal lengths of Atlantic croaker in the long haul-seine fishery during 1982–92 ranged from 215 to 245 mm TL; in the winter trawl fishery, they ranged from 215 to 240 mm TL. In both fisheries, less than 10% of the fish were older than age 3 (Wilson, 1993). Therefore, yield-per-recruit modeling results presented here for

North Carolina should not reflect current conditions, but rather be considered representative of temporal changes in Atlantic croaker population dynamics.

The specific value of M used in our simulations had no effect on the levels of F or t_c that produce maximum yield-per-recruit values and would not change conclusions for either Chesapeake Bay or North Carolina. However, these conclusions are still critically dependent on how realistic is the range of M used in these simulations. Methods currently used to estimate M have strong limitations and disadvantages (Vetter, 1988), and the method used here is no exception. However, we feel comfortable with the range of M used in this study because it agrees with values of M reported for other sciaenids with similar life spans, e.g. spotted seatrout, *Cynoscion nebulosus* (Rutherford et al., 1989).

Yield-per-recruit analysis is only part of a fishery management strategy (Beverton and Holt, 1957; Gulland, 1983; Deriso, 1987). It must be applied in conjunction with eggs-per-recruit (Prager et al., 1987) and spawning stock biomass per recruit models (Gabriel et al., 1989; Goodyear, 1993; Schirripa and Goodyear, 1994) to allow managers to examine the effects of different policies on both reproduction (i.e. egg production) and biomass yield. The pattern of early maturation, multiple spawning, long spawning season, and indeterminate fecundity in Atlantic croaker (Barbieri et al., 1994b) suggest that reproduction would be compromised only at extremely high levels of fishing. However, eggs-per-recruit and spawning stock biomass models must be applied before this issue can be properly evaluated.

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Abstract.—Eight female cunners, *Tautogolabrus adspersus*, were tagged externally with ultrasonic transmitters in Newfoundland, and their activity pattern was recorded. They were active diurnally, commencing activity, on average, 55 minutes after sunrise and ceasing activity about 50 minutes after sunset. The diurnal activity period was interrupted by periods of inactivity usually lasting 5–15 minutes. Levels of activity varied daily and seasonally; seasonal changes were the most dramatic. On average, female cunners were active for more than 12.5 h/day in June–July and for only 3 h/day in October–November. Decrease in activity reflected decreasing day length; as photoperiod became shorter, cunners spent a much larger portion of the daylight period inactive (22.9% in June–July compared with 71.8% in October–November). Decrease in cunner activity in the fall occurred while water temperature was as high as that in June and July and is speculated to be controlled by an endogenous rhythm.

Daily and seasonal activity patterns of female cunner, *Tautogolabrus adspersus* (Labridae), in Newfoundland

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Cunner, *Tautogolabrus adspersus*, is the most northerly distributed labrid fish in the western North Atlantic, reaching the northern extent of its range in waters off Newfoundland. A member of a large, essentially tropical, family, it is well known for its annual state of prolonged physiological torpor, which in Newfoundland may last for more than 6 months (Green and Farwell, 1971). The ability of cunners to undergo a long period of torpor is apparently one of the factors that have enabled this species to flourish in a low temperature environment (Curran, 1992). In waters off Newfoundland, cunners are abundant and inhabit sites where summer maximum water temperature is less than 11°C and the winter minimum is below -1°C. Newfoundland cunners enter and remain in torpor when seawater temperature is below about 5°C (Green and Farwell, 1971).

Throughout their range, Chesapeake Bay to the Strait of Belle Isle, cunners are associated with inshore habitats that provide shelter during nocturnal quiescence (a characteristic of labrids) as well as during

overwintering torpor (Pottle and Green, 1979a). Rather than migrating to deeper, warmer water as the temperature declines in the fall, Newfoundland cunners take shelter under boulders and rocks at their summer feeding and reproductive sites. There they remain until the seawater temperature approaches 5°C the following year, usually in early June (Green and Farwell, 1971). In Conception Bay, Newfoundland, territorial males establish territories within a week of emerging from winter torpor and maintain them until just prior to reentering winter torpor, usually in late November or early December (Pottle and Green, 1979a). Spawning commences in mid to late July, depending upon water temperature, and lasts for 2–3 weeks. All spawning activity occurs within male territories (Pottle and Green, 1979b; Martel and Green, 1987).

We recently reported on a home-range size for adult female cunners in Conception Bay, Newfoundland, that was based on telemetry data

from fish tagged with ultrasonic transmitters (Bradbury et al., 1995). Female cunners occupy small home ranges (300–2,353 m²) and exhibit seasonal variation in the size of their home range. The largest home ranges occur during June and July, a time when cunners are replacing energy stores depleted during winter torpor (Bradbury et al., 1995). This is also the time of year with the longest photoperiod and hence with the maximum potential foraging period for a diurnal species.

In this study, we report on the daily activity patterns of the female cunners in Conception Bay. Cunners at the northern extent of their range are of interest because their prolonged winter torpor may reduce annual foraging time. We expected that as the photoperiod decreased, female cunners would be active for more of the diurnal period, both to maximize growth and increase energy stores in preparation for six months of winter torpor.

Methods

Tracking

A fixed hydrophone array tracking system (Bradbury et al., 1995) was used to monitor the activity of eight female cunners tagged with ultrasonic transmitters in Broad Cove, Conception Bay. The system provided positional information (fixes) on a tagged fish once every 15 seconds. The change in the quality of the transmitter signal when a tagged cunner sought shelter by going under a boulder or into a crevice between two rocks enabled us to monitor activity-inactivity patterns accurately in much the same way as Chapman et al. (1975) had done with Norway lobster (*Nephrops norvegicus*). For a description of the tracking system, tagging procedure, and study site see Bradbury et al. (1995). With our tagging procedure, a tag holder and dummy tag were initially attached to fish in the field. After a week (minimum period), a fish with a tag holder and dummy tag was recaptured by a diver, and the dummy transmitter was replaced with a functional one. The latter procedure involved handling the fish for 1–2 min, from capture to release.

Tagged cunners were from 194 to 250 mm in total length (Table 1). At this size female cunners in Conception Bay are sexually mature (Pottle and Green, 1979a). Fish were tracked from June until November, i.e. during most of the period between the end and start of winter torpor. Lightning damage to the tracking system limited the amount of tracking that could be done in August. Individual fish were tracked for 4 to 32 days during which they all remained in the area encompassed by the hydrophone array. For

Table 1

Total length and tracking dates for female cunner tagged with ultrasonic transmitters in Broad Cove, Conception Bay, Newfoundland.

Fish identification	Total length (mm)	Tracking dates	Track duration (days)
A	194	17 Jun–30 Jun 5 Jul–6 Jul	14 2
B	215	18 Jun–4 Jul	17
C	250	28 Jun–21 Jul	24
D	235	12 Jul–21 Jul	10
E	195	15 Aug–18 Aug	4
F	225	30 Aug–22 Sep	16
G	245	23 Sep–20 Oct	22
H	240	21 Oct–24 Nov	32

the duration of the tracking period, information on water temperature, sea state, tidal phase, and cloud cover was available on a daily basis, as described by Bradbury et al. (1995).

Activity-inactivity

A tagged cunner was determined to be active or inactive based on information from the tracking system. If a strong transmitter signal was received, and positional information was obtained, the subject was considered active. If, on the other hand, signals were weak and no positional fix could be determined for more than 3 min (12 possible fixes), the fish was considered inactive. With scuba or snorkel equipment, divers documented over a period of >20 h that cunners had retreated into cracks and crevices or underneath objects when transmitter reception was poor. These observations also showed that female cunners do not “rest” on the substrate in open sites.

During the night, cunners seek shelter and undergo a period of nocturnal quiescence during which positional fixes cannot be obtained. The first and last positional fixes of the day therefore marked the beginning and end of diurnal activity. Onset of diurnal activity was expressed as the number of minutes before or after sunrise, whereas cessation of diurnal activity was expressed as the number of minutes before or after sunset. The duration of diurnal activity for an individual was defined as the total elapsed time between the onset and cessation of its daily activity.

Cunners also entered shelter (became inactive) at various times throughout the day; sites where cunners were inactive are termed day-rest sites. The duration of each inactive period (the time between

the initiation and the end of a poor transmitter signal) was recorded. On the basis of these data, the portion of the diurnal activity period spent inactive was calculated and expressed as a percentage.

In describing the activity-inactivity patterns of female cunners, five parameters were used: 1) onset of activity, 2) cessation of activity, 3) duration of diurnal activity, 4) length of inactivity bouts, and 5) percent of diurnal activity period spent inactive.

Analysis of data

Although a fish was handled for only 1–2 min when a transmitter was inserted into its tag holder and although field observations did not detect any changes in the behavior of fish following this procedure, nonparametric paired *t*-tests were used to examine whether female cunners showed similar activity on the first complete day of tracking (day 2) compared with the following day of tracking (day 3). All five activity parameters were tested.

A nonparametric analysis (Wilcoxon matched-pairs signed-ranks test) was used to compare inter-individual differences in activity between the two pairs of subjects tracked during the same periods (Table 1). Comparisons were made between fish A and fish B for a total of 11 days (i.e. June 18, 19, 20, 21, 22, 24, 25, 27, 28, 29, and 30) and between fish C and fish D for a total of 9 days (i.e. July 13–21 inclusive) for all five activity parameters.

A least-squares multiple regression analysis was used to determine whether date, time of day (i.e. morning vs. afternoon), or environmental variables (water temperature, cloud cover, and sea state) had a significant effect on activity. All activity parameters were tested. Because the activity data were normally distributed, no transformations were carried out. Although there were 141 tracking days, some days could not be used for certain activity parameters. For example, there were only 72 tracking days during which both the time of onset and cessation of activity were known for any given fish, both of which are required to calculate the duration of diurnal activity.

The tidal cycle was divided into four phases: low-tide, flood-tide, high-tide, and ebb-tide as described by Bradbury et al. (1995). For fish A, B, C, and D, mean activity parameters (i.e. percentage of time spent inactive and length of inactivity bouts) were determined for each tidal phase for the duration of the tracking period. An analysis of variance with three factors was used to test for intra- and inter-individual differences in activity during the tidal phases. We included only the fish by tide interaction term in our analyses because we did not expect any temporal variation in tide (tide \times date) or activity

Table 2

Mean number of minutes before sunrise and after sunset when tracked female cunners began and ceased their diurnal activity. Because the data for onset of activity for fish E consisted of a single point, no standard deviation is given.

Fish identification	Onset (minutes before sunrise)			Cessation (minutes after sunset)		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
A	57.6	10.02	9	57.6	26.70	9
B	40.2	23.95	12	63.6	18.10	12
C	48.7	10.93	18	74.3	19.64	22
D	31.7	18.48	6	43.0	43.59	4
E	45.0	—	1	50.3	34.46	4
F	52.0	21.28	3	36.5	41.16	4
G	49.4	32.69	14	54.1	20.33	17
H	72.4	52.54	28	18.9	39.12	27
All	54.7	36.63	91	49.1	36.15	99

(fish \times date), given the relatively short time (i.e. 11 and 9 days) over which observations were made.

Paired comparison *t*-tests were used to examine whether the one female cunner tracked during both the prespawning and spawning period had the same activity patterns during both periods. All activity parameters were tested.

Statistical analyses were performed with Minitab (Minitab, Inc., 1992) or SPSSX (SPSS Inc., 1990) statistical software packages.

Results

There were no significant differences ($P > 0.05$, non-parametric paired *t*-test) in activity parameters between the first complete day of tracking (day 2) and the following day.

All tagged fish were active during the day, inactive at night. Activity commenced, on average, 55 minutes (SD=36.6) before sunrise and ceased 49 minutes (SD=36.2) after sunset; however, there was considerable daily variation among individuals (Table 2). Throughout the day, activity was interrupted by periods of inactivity, usually lasting 5–15 minutes. Among those fish tracked on the same day, there were no significant differences between subjects for any of the activity parameters (Table 3).

When water temperature was below 5°C, cunners were inactive. On 23 and 24 June, for example, strong northwesterly winds forced cold water into the study area causing the water temperature to drop from 6°C to 3°C and the cunners to be inactive for two days. On the morning of 26 June the water temperature

Table 3

Results of the Wilcoxon matched-pairs signed-ranks test (*t*-value) used to compare interindividual differences in activity between pairs of cunners tracked during the same periods (*n* represents the number of days during which comparisons were made). Critical values of *t* are derived from Rohlf and Sokal (1969). There were no significant differences between fish for any of the activity parameters tested.

Behavioral parameter	Comparisons between fish A and fish B			Comparison between fish C and fish D		
	<i>n</i>	<i>t</i> -value	Critical <i>t</i> -value (significance level)	<i>n</i>	<i>t</i> -value	Critical <i>t</i> -value (significance level)
Percent of time inactive	11	26	13 (0.0415)	9	11	8 (0.0488)
			14 (0.0508)			9 (0.0645)
Length of inactivity bout	11	26	13 (0.0415)	9	14	8 (0.0488)
			14 (0.0508)			9 (0.0645)
Onset of activity	9	15	8 (0.0488)	7	6	3 (0.0391)
			9 (0.0645)			4 (0.0547)
Cessation of activity	8	10	5 (0.0391)	7	5	3 (0.0391)
			6 (0.0547)			4 (0.0547)
Duration of diurnal activity	8	13	5 (0.0391)	7	7	3 (0.0391)
			6 (0.0547)			4 (0.0547)

Table 4

Summary of multiple regression analysis on the effects of time of day (prior to 1200 h vs. after 1200 h), date, and environmental variables on activity of female cunner. A minimum of 62 days and a maximum of 89 days were incorporated in the regression analysis for the last three behavioral parameters. Percentage of variation accounted for by each variable is given. * = significant at 0.05 level; ** = significant at 0.01 level; and *** = significant at 0.001 level.

Behavioral parameter	<i>n</i>	Time of day	Date	Water temperature >5°C	Sea state	Cloud cover	Combined variables
Percent of time inactive	205	0.6	58.7***	0.2	0.3	0.1	59.9***
Length of inactivity bout	229	0.1	12.7***	2.8**	1.7*	0.2	17.5***
Onset of activity	75	NA	6.6*	1.9	0.0	0.1	8.6
Cessation of activity	83	NA	22.3***	0.2	0.0	0.5	23.0***
Duration of diurnal activity	62	NA	92.3***	0.9**	0.1	0.1	93.4***

again dropped to 3°C, resulting in cunners being inactive for the remainder of the day. Temperatures above 5°C had small but significant effects on length of inactivity bouts and duration of diurnal activity (Table 4). Length of bouts of inactivity tended to decrease with increasing water temperature, whereas the trend was reversed for the duration of diurnal activity. Water temperatures above 5°C had no significant effect on the onset or cessation of activity or on the percentage of time spent inactive.

Sea state had a significant ($P < 0.05$) effect on length of cunner inactivity bouts (Table 4), with bouts of inactivity tending to be longer on days with high surface waves. Sea state did not have a significant effect on other activity parameters. Cloud cover had no significant effect on any of the activity param-

eters. There was a trend, however, for females to remain inactive for longer periods (i.e. percentage of time spent inactive increased as well as length of inactivity bouts) as cloud cover increased. There was also a tendency for the duration of diurnal activity to decrease with increasing cloud cover. Neither percentage of diurnal activity period spent inactive or length of inactivity bouts differed between morning and afternoon (Table 4).

There was no significant difference in fish behavior owing to tides (Table 5), indicating that both fish A and fish B responded similarly to the tidal cycle. Furthermore, there was no significant difference in activity (i.e. percentage of time spent inactive) between the various tidal phases for fish A or fish B (Table 5). Finally, there were no significant differ-

Table 5

Results of analysis of variance performed on the percentage of time spent inactive by fish A and fish B during the four phases of the tidal cycle. df = degrees of freedom; SS = sum of squares; MS = mean of squares.

Source	df	SS	MS	F-value	Probability value P
Date	10	5,492.5	549.3	1.74	0.089
Fish	1	33.1	33.1	0.10	0.747
Tide	3	1,320.8	440.3	1.39	0.252
Fish × tide	3	771.5	257.2	0.81	0.490
Error	70	22,117.3	316.0		
Total	87	29,735.3			

ences between the tidal phases for the length of inactivity bouts of fish A and fish B ($F_{3,70}=1.57$, $P=0.204$; $F_{1,3}=0.4$, $P=0.756$), percent of time spent inactive by fish C and fish D ($F_{3,56}=0.50$, $P=0.685$; $F_{1,3}=0.79$, $P=0.505$) and length of inactivity bouts of fish C and fish D ($F_{3,56}=0.82$, $P=0.4986$; $F_{1,3}=1.94$, $P=0.134$).

Time of year, i.e. seasonal factors, accounted for 58.7% of the variation in the percentage of the diurnal activity period spent inactive, i.e. the amount of time spent in shelter between the commencement and cessation of daily activity (Table 4). Cunners spent an increasing proportion of the diurnal period inactive from June through November. This factor accounted

for 12.7% of the variation in length of inactivity bouts (which increased over time as well) and for 6.6% and 22.3% of the variance in onset and cessation of activity, respectively (Table 4). The trend was for activity to begin later in the morning and to end earlier in the evening (in relation to sunrise and sunset) as the season progressed. Time of year accounted for 92.3% of the variation in duration of diurnal activity. As the seasons progressed and the photoperiod became progressively shorter, there was a corresponding decrease in the duration of diurnal activity (Fig. 1).

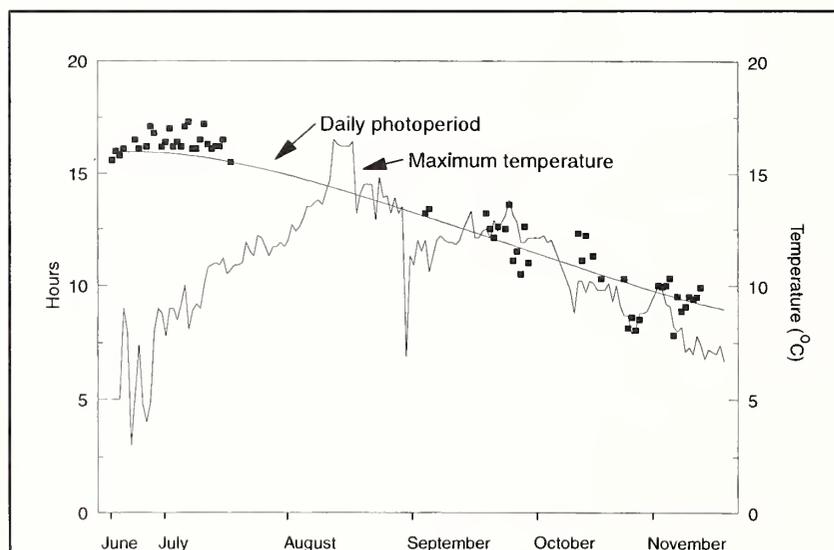
Thus the duration of cunner diurnal activity, percentage of time inactive, and length of inactivity bouts were all closely related to day length. By combining data from all subjects, the average elapsed time between onset and cessation of activity (i.e. duration of diurnal activity) was 16.5 h ($n=38$, $SE=0.10$) during June–July, 13.5 h ($n=8$, $SE=0.19$) during August–September, and 11.0 h ($n=27$, $SE=0.25$) during October–November. Cunner spent 22.9% ($n=35$, $SE=15.5$) of the diurnal period inactive between June and July, 47.0% ($n=13$, $SE=24.3$) of the diurnal period inactive in August–September, and 71.8% ($n=30$, $SE=13.2$) of the diurnal period inactive during October–November; length of inactivity bouts, on the other hand, increased from an average of 6.4 min ($n=64$, $SE=0.75$) in June–July to 9.3 min ($n=15$, $SE=1.56$) in August–September, to 12.7 min ($n=41$, $SE=1.14$) in October–November.

These data were used to calculate the number of hours a female cunner spent out of its shelter per day. On average, during June–July, female cunners were active for 12.5 h/day, during August–September 7 h/day, and during October–November only 3 h/day. The remainder of the year was spent in winter torpor.

There were no significant differences ($P>0.05$, paired comparison t -test) in any of the activity parameters for the single female cunner tracked during both the prespawning and spawning periods.

Discussion

Pottle (1979) reported that in Newfoundland territorial male cunners undergo periods of daylight quiescence under cover. Whoriskey (1983) also observed cunners in Massachusetts underneath boulders at those times during the day when they were

**Figure 1**

Relation between length of daily photoperiod and duration of diurnal activity (■) for eight female cunners tracked in Conception Bay, Newfoundland, between June 17 and November 24. Maximum daily seawater temperature at the study site is also shown.

not foraging. The female cunners we studied exhibited similar behavior, seeking shelter beneath rocks or in crevices during the day.

Some workers have assumed that temperate wrasses use cover to avoid predation (Olla et al., 1979; Hobson et al., 1981), although threat of predation has not been well documented as a factor. Whoriskey (1983) interpreted the diurnal use of shelter by cunners in Massachusetts as predator avoidance. Although he may have been correct, our field observations in Newfoundland do not support this hypothesis. Predation on adult cunners in Conception Bay is very low as judged by over 400 hours of diving observations during which no predation, or attempted predation, on adults was observed.

Females may seek shelter to avoid conspecifics with courting and chasing behaviors, especially territorial males. This explanation, however, is inadequate in elucidating why males exhibit the same behavior or why the behavior occurs so frequently outside the spawning period.

A reduction in energy expenditure may be associated with such behavior because cunners probably require less energy to maintain a position in a shelter than in the water column, even when water movement from currents and waves is minimal, and because the length of inactivity bouts increased with increased water turbulence. However, such an explanation is weak unless it can be shown that continued foraging would result in a net loss of energy.

In many diurnal fishes, including cunners, the onset and cessation of daily activity coincides closely with the rising and setting of the sun (e.g. Hobson, 1972, 1973; Hawkins et al., 1974; Olla et al., 1974, 1975; Clark and Green, 1990). As expected, females exhibited a marked seasonal decrease in the duration of their diurnal activity (from 16.5 h in June–July to 11.0 h in October–November) as day length decreased. Light intensity at sunrise and sunset was affected seasonally by the surrounding topography at the study site (e.g. in the fall the sun “set” behind a range of hills rather than at sea level), and this topography may have accounted for some of the seasonal change in the onset and cessation of diurnal activity. However, the considerable variation in the onset and cessation of daily activity among cunners suggests that this variation is not simply a response to a threshold light intensity.

Contrary to the expectation that female cunners would maximize foraging opportunities prior to entering winter torpor, they spent a larger percentage of the diurnal period inactive as the length of the photoperiod decreased. Why cunners should significantly reduce their foraging activity, at a time when food is still available and they could acquire more

energy for somatic growth and winter torpor, is not clear. Although water temperature is decreasing during this period, our analyses show that above $\sim 5^{\circ}\text{C}$, temperature has little direct effect in determining the ratio of activity to inactivity. Mean daily water temperatures during June–July and October–November were approximately the same (8.2°C and 9.2°C , respectively) (Fig. 1), yet there were large differences in the amount of time cunners spent in shelter. During June and July, females were outside their shelter for about 12.5 hours of the day, whereas from October to November cunners were active, on average, only 3 hours of the 11-h sunrise to sunset period.

Fall or winter decreases in the activity or feeding behavior (or both) of fishes in the absence of changes in water temperature are common, although the mechanisms underlying these decreases are not understood. Smith et al. (1993) for example found that in Atlantic salmon (*Salmo salar*), seasonal reductions in swimming activity and feeding were more closely related to day length and changes in day length than to other environmental variables, including water temperature. This also seems to be true for cunners. Presumably their temporal pattern of activity is adaptive and important to their success at northern latitudes. Cunners survive six months or more of torpor that can begin at a time not predictable by exogenous cues in the marine environment. At our study site, the date at which winter torpor commences (i.e. when seawater temperature remains below $\sim 5^{\circ}\text{C}$) can vary year to year by at least four weeks. Perhaps an endogenous mechanism sensitive to changes in day length, or to some other environmental cue, regulates the physiological processes associated with successful winter torpor. Although such a mechanism may exist in cunners, the identification of endogenous rhythms in fishes is difficult (Boujard and Leatherland, 1992).

Our findings concerning seasonal changes in the activity patterns of cunners have implications for estimating the size of their populations. For example, population estimates based on visual surveys by divers should take into account that, depending on when the survey is conducted, a significant and variable proportion of the population will be out of sight, under cover. Significant errors in estimates of population size are likely, and errors will not be consistent for different times of the year. This caution may apply to other species with similar behavior patterns.

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Abstract.—The effectiveness of a new bycatch reduction device (BRD) was tested across a wide geographical range to determine its use in the NSW oceanic prawn-trawl fishery. Using four commercial trawlers, each from a different port located in the fishery, we compared the catches and bycatches from conventional trawls with those from trawls containing composite panels of netting (60 mm and 40 mm) hung on the bar and inserted into the top anterior section of the codend (termed the composite-panel codend). This panel was designed so that the 40-mm mesh 1) would allow some small fish to escape and 2) would distribute the load anterior and lateral to the 60-mm mesh (which was located in an area where waterflow was thought to be greatest), allowing the 60-mm mesh to remain open and thus facilitate the removal of larger fish. Simultaneous comparisons against a control codend showed that the composite-panel codend significantly reduced the weights of discarded bycatch at all four locations (means reduced by 23.5% to 41%) and the numbers of juveniles of commercially important species, such as whiting, *Sillago* sp. (by up to 70%). At three of the locations the composite-panel significantly increased the catches of the prawn *Penaeus plebejus* (5.5% to 14%) and, although not statistically significant, showed a similar trend at the fourth location (mean increase of 4%). As a result of this study, the composite-panel codend has been adopted and voluntarily used by fishermen throughout the New South Wales oceanic prawn-trawl fishery.

The composite square-mesh panel: a modification to codends for reducing unwanted bycatch and increasing catches of prawns throughout the New South Wales oceanic prawn-trawl fishery

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In New South Wales (NSW), Australia, oceanic prawn-trawling involves over 300 vessels operating from 11 major ports along 1,000 km of coastline and is valued at approximately A\$17 million per annum. Vessels operating in this fishery primarily target the eastern king prawn, *Penaeus plebejus*, although a significant portion of the total value in the fishery is derived from the sale of legally retained bycatch (termed "by-product")—comprising several species of fish, crustaceans, and cephalopods. As in the majority of the world's prawn-trawl fisheries, however, significant numbers of nontarget organisms are also captured and discarded in this fishery (for reviews see Saila, 1983; Andrew and Pepperell, 1992; Alverson et al., 1994; Kennelly, 1995). In NSW, this discarded bycatch includes individuals of byproduct species that are smaller than the minimum commercial size and a large assemblage of noncommercial species (see Kennelly, 1995).

Unwanted bycatch has been reduced in several of the world's prawn-trawl fisheries by means of modifications to codends that contain bycatch reduction devices (BRD's) (e.g. Watson et al., 1986; Matsuoka and Kan, 1991; Isaksen et al., 1992; Rulifson

et al., 1992; Renaud et al., 1993; Christian and Harrington¹). In general, these modifications have involved either 1) some form of rigid structure that functions by mechanically separating larger unwanted individuals or 2) a strategically placed escape "window" made of netting that works by exploiting behavioral differences between prawns and smaller finfish. Although many of these modifications have proven effective in reducing bycatch from prawn trawls, sometimes they have not been favored by commercial fishermen (see Kendall, 1990; Renaud et al., 1993) because of their size (in relation to the codend), their often complex design (e.g. Mounsey et al., 1995), and, in some cases, their failure to maintain prawn catches at the same levels as conventional trawls (e.g. Rulifson et al., 1992; Robins-Troeger et al., 1995; Christian and Harrington¹).

One modification that has been successfully tested and adopted in

¹ Christian, P., and D. Harrington. 1987. Loggerhead turtle, finfish and shrimp retention studies on four excluder devices (TEDs). In Proceedings of the nongame and endangered wildlife symposium; 8–10 September 1987, Georgia, p. 114–127. Dep. Nat. Resources, Social Circle, GA.

several trawl fisheries in the North Atlantic involves inserting large panels of square-mesh in codends (Robertson and Stewart, 1988; Carr, 1989; Briggs, 1992; Isaksen and Valdemarsen²; Suuronen³). These studies have shown that square-mesh panels often reduce the bycatch of juvenile roundfish while retaining a large proportion of the targeted catch. In previous experiments (Broadhurst and Kennelly, 1994, 1995, 1996; Broadhurst et al., 1996), we have shown that relatively small panels of square-mesh, inserted into the top anterior sections of penaeid prawn-trawl codends, allowed large numbers of small fish to escape without any losses of prawns. In these experiments, the majority of fish were thought to have been herded together in the narrow anterior section of the codend, immediately in front of the catch (see also Wardle, 1983). This concentration of fish was thought to upset the balance of the school and to initiate a response in the fish to escape by swimming towards the sides and top of the net and out through the open square-meshes. In addition, we showed that codend circumference and differences in hydrodynamic pressure had significant effects on the rates of movement of these fish through the square-mesh panel. The reaction of prawns to these stimuli was considered to be fairly limited, given their inability to maintain an escape response to trawls (see Lochhead, 1961; Main and Sangster, 1985).

In a recent experiment (Broadhurst and Kennelly, 1996) in one location in NSW, we tested a new design of codend, comprising composite panels of square-shaped mesh (referred to as the composite-panel codend), designed for and located in the codend, to take advantage of the theory discussed above. The results showed that this design was effective in reducing up to 40% of the total unwanted bycatch and

up to 70% of the numbers of juveniles of commercially important species with no significant reduction in the catches of prawns and other commercially important species. Although not validated statistically, there was also some evidence to suggest that the trawls with the composite square-mesh panel retained, on average, slightly more prawns than a conventional trawl (means increased by up to 3%). This latter result, in particular, led numerous local fishermen to install the composite-panel voluntarily in their trawls and use it as part of normal commercial operations.

To assess the performance of this design throughout the full geographic range of this fishery (encompassing the range of fishing conditions and catches) and to promote its voluntary acceptance, our specific goals in the present study were to investigate the effectiveness of the composite-panel under normal commercial operations at four major ports along the NSW coast in 1) reducing unwanted bycatch, 2) maintaining catches of commercially important byproduct, and 3) increasing catches of prawns.

Materials and methods

This study was performed between December 1995 and February 1996 with four commercial vessels (see Table 1 for details) on prawn-trawl grounds offshore from four ports (Port Stephens, Southwest Rocks, Yamba, and Ballina) in New South Wales, Australia (Fig. 1). Each vessel was rigged with three Florida flyers (mesh size=42 mm) in a standard triple gear configuration (see Kennelly et al., 1993 for details), towed at 2.5 knots. Each of the identical outside nets on each vessel were rigged with zippers (no. 10 nylon open-ended auto-lock plastic slides) to facilitate removal and attachment of the codends. Because each of the middle nets were not rigged in exactly the same way as the outside nets, their catches were excluded from any analysis.

The codends used in the study measured 58 meshes long (2.3 m) and were constructed from 40-mm mesh

² Isaksen, B., and J. W. Valdemarsen. 1986. Selectivity experiments with square mesh codends in bottom trawl. Int. Coun. Explor. Sea council meeting 1986/B: 28, 18 p.

³ Suuronen, P. 1990. Preliminary trials with a square mesh codend in herring trawls. Int. Coun. Explor. Sea, council meeting 1990/B: 28, 14 p.

Table 1
Summary of vessels, trawl headline lengths, and depths trawled for each of the four ports.

Port	Vessel and (length in m)	Trawl headline length for each net (m)	Depth trawled (m)
Port Stephens	<i>Fairwind</i> (16)	16.45	75-88
Southwest Rocks	<i>Shelley-Anne</i> (13.7)	10.97	47-53
Yamba	<i>L-Margo</i> (15.93)	12.8	20-49
Ballina	<i>New Avalon</i> (18.5)	14.63	29-55

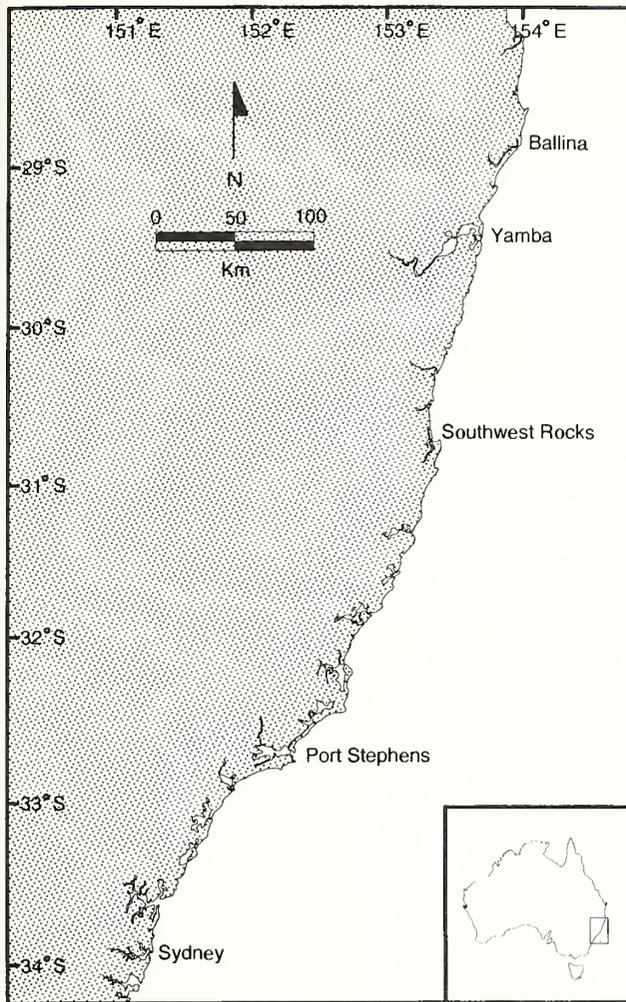


Figure 1

Map of New South Wales showing locations of the four ports that were sampled (Ballina, Yamba, Southwest Rocks, and Port Stephens).

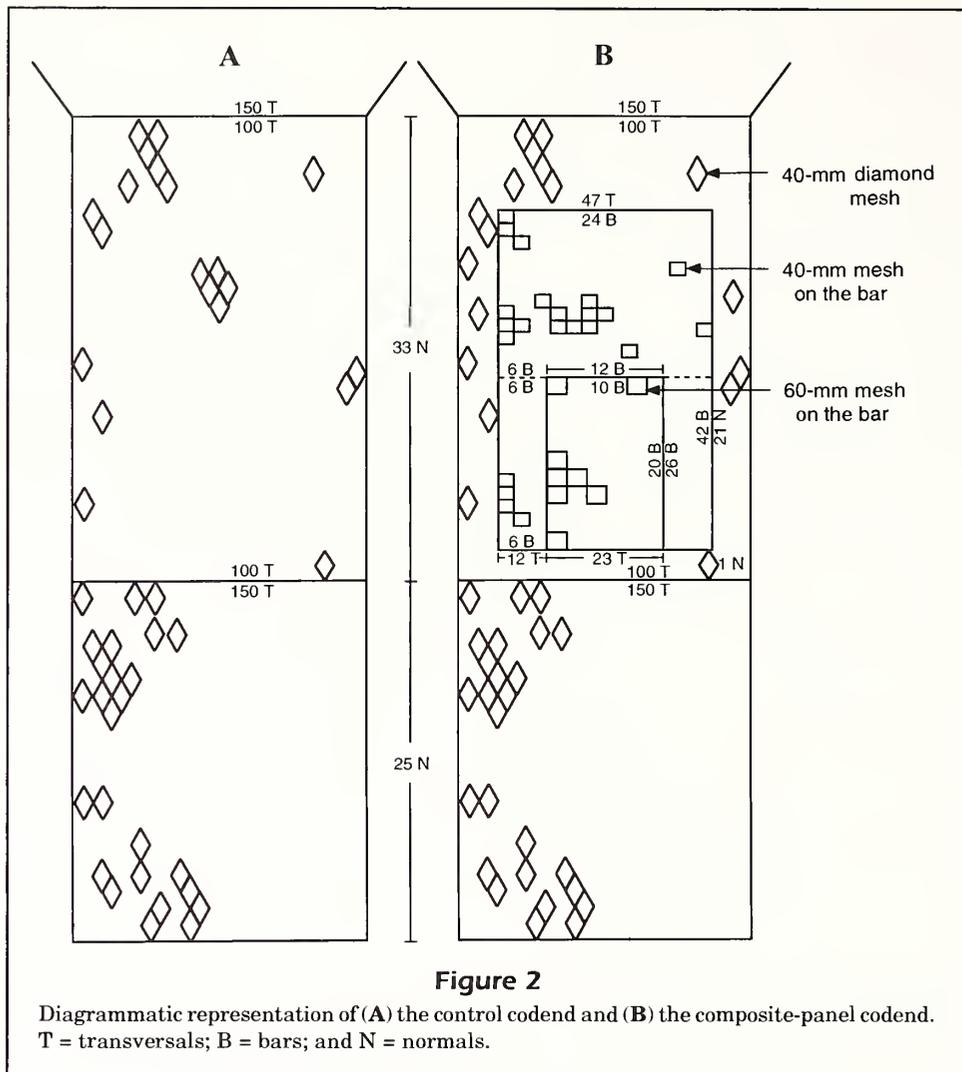
netting and 48-ply twine (Fig. 2). They comprised two sections: the anterior section was 100 meshes in circumference, 33 meshes in length, and attached to a zipper; the posterior section was 150 meshes in circumference and 25 meshes in length. Two designs of codend were compared. The control codend was made entirely of diamond-shaped meshes (Fig. 2A). The second codend (termed the composite-panel codend) was similar to the control but had composite panels made of 60-mm and 40-mm netting cut on the bar and inserted into the top of the anterior section (Fig. 2B—see also Broadhurst and Kennelly, 1996). The composite-panel codend was designed so that the load was distributed anteriorly and laterally to the panel of 60-mm square-mesh, allowing this 60-mm panel to remain open. We predicted that 1) large numbers of fish would escape through this panel, located at the point where waterflow was thought to be great-

est and that 2) in addition to reducing load on the 60-mm panel, the 40-mm square-mesh would also facilitate the escape of smaller fish.

The two codends were compared with each other in independent, paired trials, with the two outside nets of each vessel at each location. The codends were used in normal commercial tows of 90-min duration and alternated after each shot (to eliminate biases between different trawls and sides of the vessels). Because some significant effects of a delay in haul-back (the period between slowing the vessel and engaging the winch to haul the trawl) were detected in a previous experiment (Broadhurst et al., 1996), all tows were performed with no delay in haulback. The location of each tow was randomly selected from the available prawn-trawl locations that were possible under the fishing conditions. During a period of four nights at locations offshore from each of the four ports, we completed a total of 16 replicate tows (i.e. four separate paired comparisons of 16 replicate tows each throughout the fishery).

After each tow, the two codends were emptied onto a partitioned tray. Prawns and all commercially important species larger than the minimum legal size (retained commercials) were separated. The remaining bycatch (termed "discarded by-catch") was then sorted. This included individuals of commercially important species that were smaller than the minimum legal size ("discarded commercials"). Data collected from each tow were as follows: the total weight of king prawns and a subsample (50 prawns from each codend) of their sizes (to the nearest 1-mm carapace length); the weight of the discarded bycatch; the weights, numbers, and sizes (to the nearest 0.5 cm) of retained and discarded commercial species; the weights and the numbers of the most commonly occurring noncommercial species; and the total numbers of discarded commercial species. Several species (commercial and noncommercial) were caught in sufficient numbers to enable meaningful comparisons (see Table 2).

Data at each port for all replicates that had sufficient numbers of each variable (defined as >2 individuals in at least 8 replicates) were analyzed with one-tailed, paired *t*-tests (i.e. four separate analyses). Because a previous experiment had shown that trawls with the composite-panel have the potential to retain more prawns than conventional trawls (Broadhurst and Kennelly, 1996), we tested the hypothesis that the composite-panel codend caught more prawns but less total bycatch than the control codend. Where analyses provided similar results for weights and numbers of taxa, only data about numbers were included in the figures to conserve space. Size frequencies of prawns, as well as discarded stout



whiting, red spot whiting, and retained red mullet (where there were sufficient numbers) were plotted for each port and compared with two-sample Kolmogorov-Smirnov tests ($P=0.05$).

Results

Compared with the control codend, the composite-panel codend significantly reduced the weights of discarded bycatch (means reduced from 23.5% to 41%) at all four ports and significantly increased the catches of prawns at Port Stephens, Yamba, and Ballina (means increased by 14%, 5.5%, and 6%, respectively) (Fig. 3, A and B; Table 3). Although not to a significant degree (4%), the composite-panel codend used at Southwest Rocks also retained, on average, more prawns than the control codend (Fig. 3A). There were no significant reductions detected in the numbers and weights of commercial species retained by

the composite-panel codend at any of the four ports (Fig. 3; Table 3).

The mean numbers and weights of discarded red spot whiting and stout whiting were reduced by the composite-panel codend at all locations where there were sufficient numbers to enable meaningful analysis (means reduced by up to 73%) (Fig. 3, F–G; Table 3). At Port Stephens, the composite-panel codend significantly reduced the numbers and weights of discarded john dory (by 50% and 57%, respectively) and blackeyes (by 45%) (Fig. 3, H and M; Table 3). There was a significant reduction in the numbers and weights of flutefish at Southwest Rocks (by 37% and 34%, respectively) and in the numbers and weights of red bigeye at Yamba (by 38.5% and 44%, respectively) and Ballina (by 35%) (Fig. 3, L and K; Table 3). There was also a significant reduction in the numbers and weights of leatherjacket (by 17% and 31%, respectively) and gurnard (by 41.5%) with the composite-panel codend at Ballina (Fig. 3, J and N; Table 3).

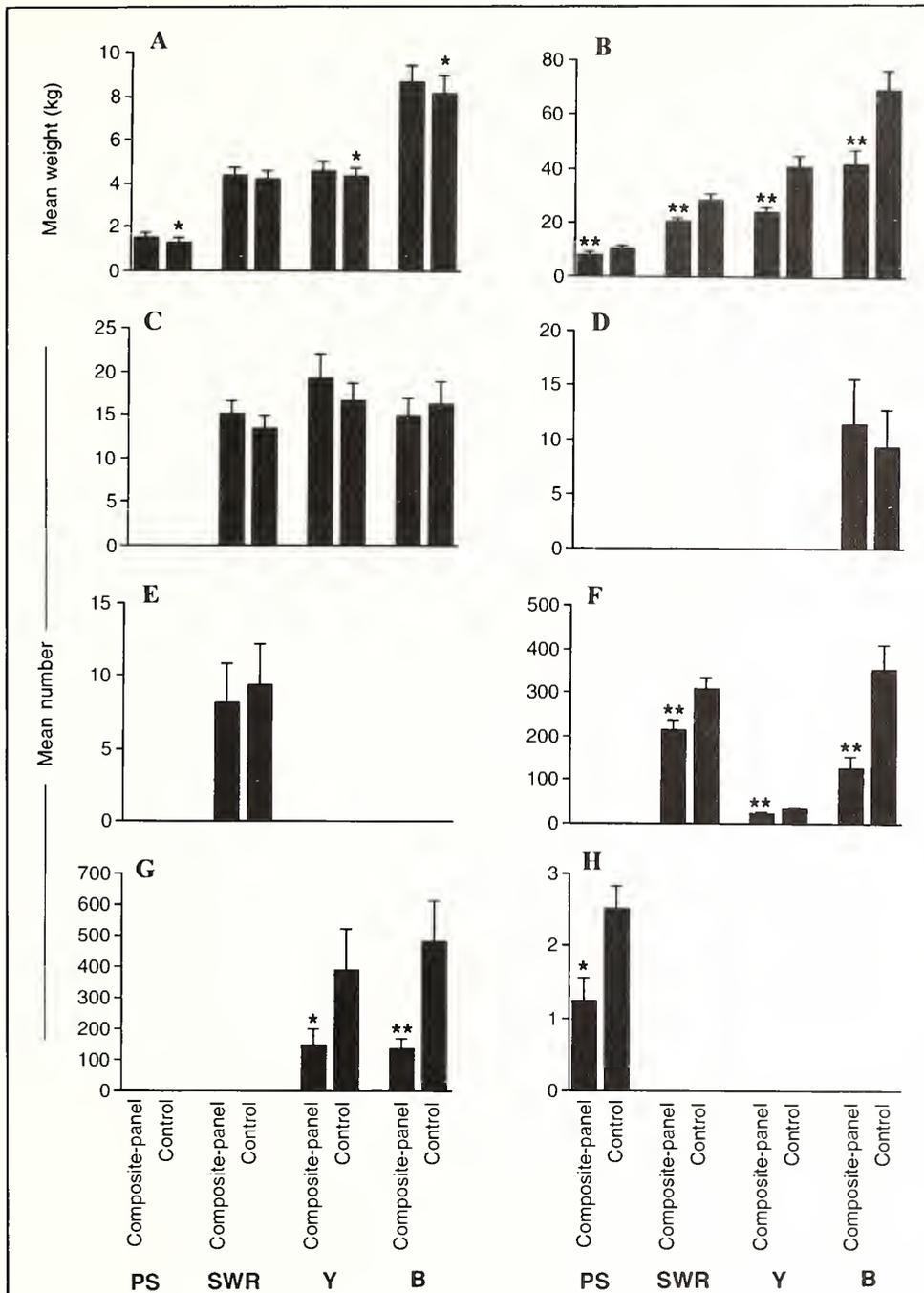


Figure 3

Differences in mean catches (\pm SE) between the control and composite-panel codends at each of the four ports: the weights of (A) prawns and (B) discarded bycatch; and the numbers of (C) retained octopus, (D) retained red mullet, (E) retained red spot whiting, (F) discarded red spot whiting, (G) discarded stout whiting, (H) discarded john dory, (I) discarded eastern blue spot flathead, (J) discarded leather jacket, (K) discarded red bigeye, (L) discarded fluke fish, (M) discarded blackeyes, and (N) discarded gurnard. ** = significant ($P < 0.01$); * = significant ($P < 0.05$); PS = Port Stephens; SWR = Southwest Rocks; Y = Yamba; and B = Ballina.

Two-sample Kolmogorov-Smirnov tests, comparing the size-frequency distributions for prawns, discarded red spot whiting, and retained red mullet measured

from each sample at each site showed no differences in the relative size compositions of fish retained by the two codends (Figs. 4, 5, and 6C). There were no signifi-

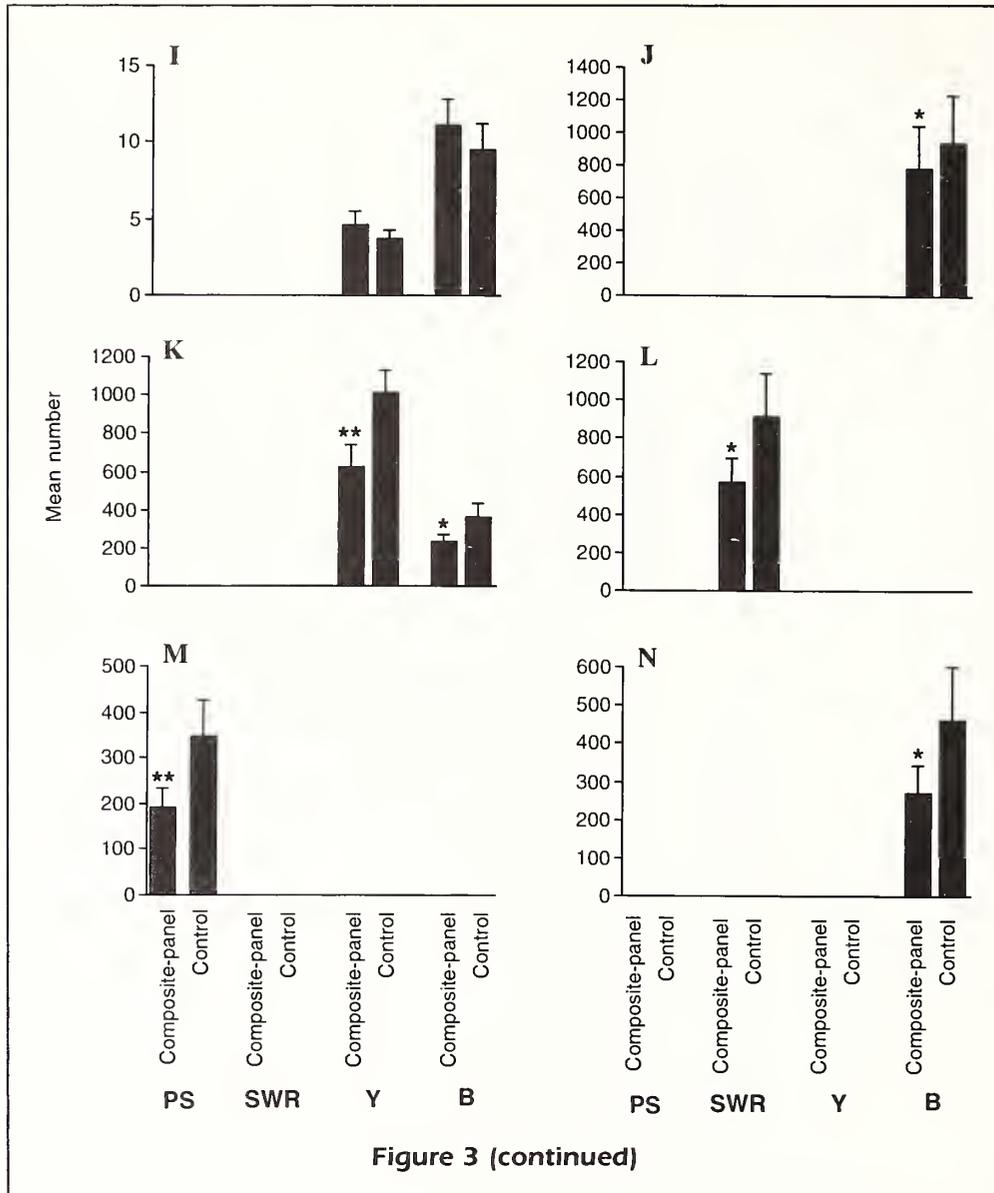


Figure 3 (continued)

Table 2
List of species caught in sufficient quantities to permit analyses.

Scientific name	Common name	Scientific name	Common name
<i>Penaeus plebejus</i>	eastern king prawn	<i>Platycephalus caeruleopunctatus</i>	eastern blue spot flathead
<i>Octopus</i> spp.	octopus	<i>Platycephalus richardsoni</i>	tiger flathead
<i>Sepia</i> spp.	cuttlefish	<i>Centroberyx affinis</i>	redfish
<i>Sepioteuthis australis</i>	southern calamary	<i>Paramonacantus filicauda</i>	threadfin leatherjacket ¹
<i>Ibacus</i> sp.	smooth bug	<i>Priacanthus macracanthus</i>	big redevye ¹
<i>Pecten fumatus</i>	scallop	<i>Macrorhamphosus scolopax</i>	flute fish ¹
<i>Upeneichthys lineates</i>	red mullet	<i>Apogonops anomalus</i>	blackeye ¹
<i>Sillago flindersi</i>	red spot whiting	<i>Lepidotrigla argus</i>	gurnard ¹
<i>Sillago robusta</i>	stout whiting		
<i>Zeus faber</i>	john dory		

¹ Denotes noncommercial species

Table 3

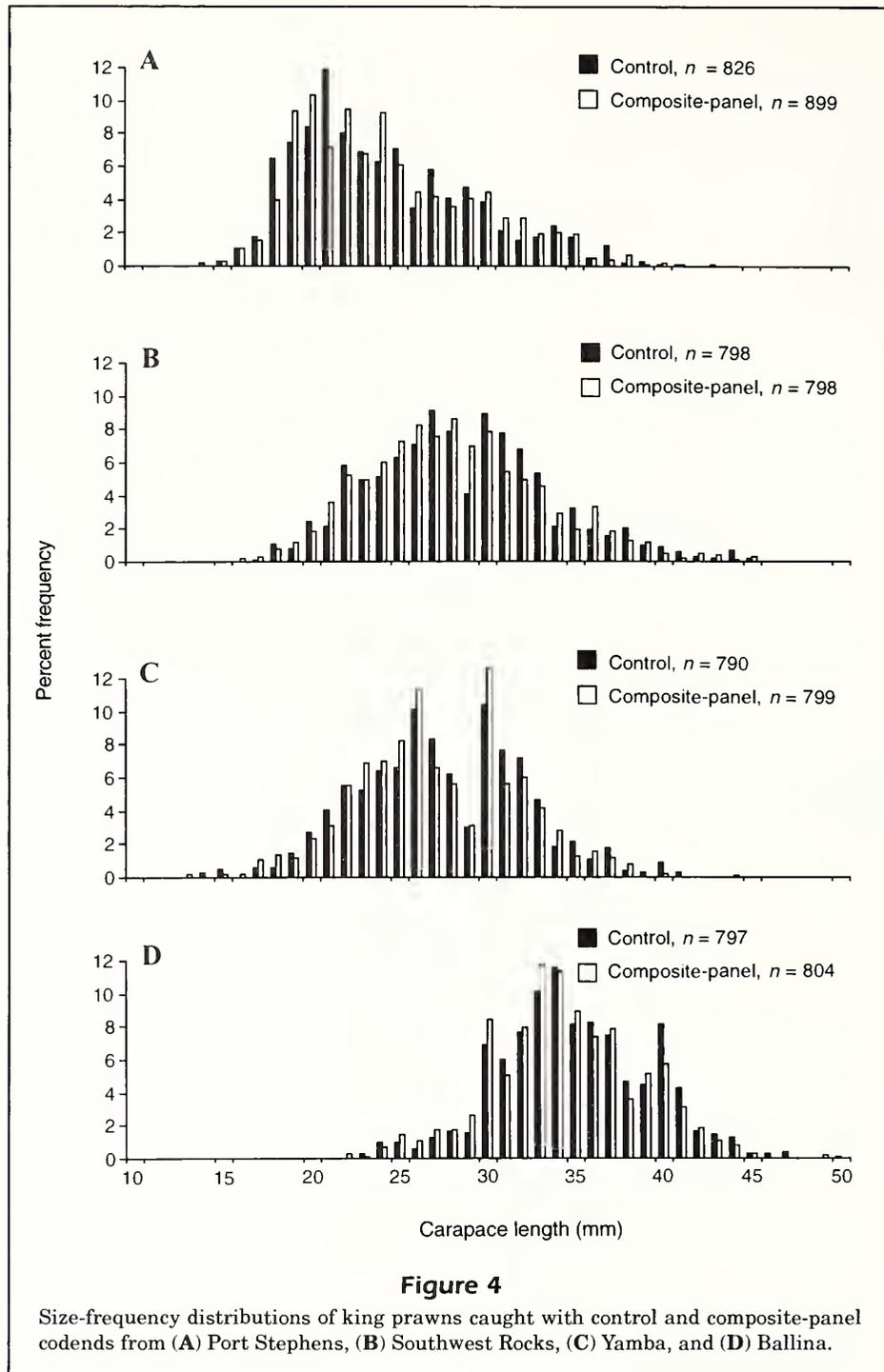
Summaries of one-tailed paired *t*-tests comparing the composite-panel and control codends. pt-v = paired *t*-value; *n* = number of replicates; all weights are in kilograms. disc = discarded; ret = retained; s. calamari = southern calamari; s. bug = smooth bug; rsw = red spot whiting; sw = stout whiting; ebs = eastern bluespot flathead; and comm. sp. = commercial species. Significant *P*-values are in bold; insufficient data are marked by a dash.

	Port Stephens			Southwest Rocks			Yamba			Ballina		
	pt-v	<i>P</i>	<i>n</i>	pt-v	<i>P</i>	<i>n</i>	pt-v	<i>P</i>	<i>n</i>	pt-v	<i>P</i>	<i>n</i>
Wt of prawns	2.139	0.024	16	1.366	0.090	16	2.104	0.026	16	1.963	0.034	16
Wt of disc bycatch	4.467	0.0002	16	2.930	0.0001	16	5.518	0.0001	16	8.254	0.0001	16
No. of ret octopus	—	—	—	-0.913	0.812	16	-1.959	0.964	15	0.904	0.190	16
Wt of ret octopus	—	—	—	-0.868	0.800	16	-0.298	0.615	15	-0.341	0.631	16
No. of disc octopus	—	—	—	0.000	•	10	—	—	—	—	—	—
Wt of disc octopus	—	—	—	-0.171	0.566	10	—	—	—	—	—	—
No. of ret cuttlefish	—	—	—	-0.324	0.624	13	—	—	—	—	—	—
Wt of ret cuttlefish	—	—	—	-0.434	0.664	13	—	—	—	—	—	—
No. of disc cuttlefish	0.631	0.272	10	0.500	0.312	16	—	—	—	—	—	—
Wt of disc cuttlefish	0.165	0.436	10	0.995	0.167	16	—	—	—	—	—	—
No. of ret s. calamari	—	—	—	1.011	0.166	13	—	—	—	—	—	—
Wt of ret s. calamari	—	—	—	1.532	0.075	13	—	—	—	—	—	—
No. of disc s. calamari	—	—	—	0.703	0.248	12	—	—	—	—	—	—
Wt of disc s. calamari	—	—	—	0.887	0.197	12	—	—	—	—	—	—
No. of ret s. bug	0.452	0.329	13	—	—	—	—	—	—	—	—	—
Wt of ret s. bug	1.214	0.124	13	—	—	—	—	—	—	—	—	—
No. of disc s. bug	—	—	—	-0.254	0.597	8	-0.541	0.701	15	—	—	—
Wt of disc s. bug	—	—	—	0.344	0.371	8	-0.593	0.718	15	—	—	—
No. of disc scollop	—	—	—	-0.377	0.644	16	-1.109	0.542	9	—	—	—
Wt of disc scollop	—	—	—	0.501	0.312	16	0.348	0.368	9	—	—	—
No. of ret red mullet	—	—	—	—	—	—	—	—	—	-1.012	0.833	12
Wt of ret red mullet	—	—	—	—	—	—	—	—	—	-0.345	0.632	12
No. of ret rsw	—	—	—	0.893	0.194	14	—	—	—	—	—	—
Wt of ret rsw	—	—	—	1.270	0.113	14	—	—	—	—	—	—
No. of disc rsw	—	—	—	4.911	0.0001	16	3.593	0.004	8	3.704	0.001	15
Wt of disc rsw	—	—	—	4.574	0.0002	16	2.554	0.019	8	3.979	0.0007	15
No. of disc sw	—	—	—	—	—	—	2.776	0.011	10	2.958	0.005	16
Wt of disc sw	—	—	—	—	—	—	2.566	0.015	10	3.077	0.004	16
No. of disc john dory	2.611	0.012	12	—	—	—	—	—	—	—	—	—
Wt of disc john dory	3.174	0.004	12	—	—	—	—	—	—	—	—	—
No. of disc ebs	—	—	—	—	—	—	-1.139	0.862	14	-1.037	0.842	16
Wt of disc ebs	—	—	—	—	—	—	-0.919	0.812	14	-0.971	0.826	16
No. of ret tiger flathead	-0.349	0.634	13	—	—	—	—	—	—	—	—	—
Wt of ret tiger flathead	-0.602	0.721	13	—	—	—	—	—	—	—	—	—
No. of disc tiger flathead	1.282	0.111	14	—	—	—	—	—	—	—	—	—
Wt of disc tiger flathead	1.71	0.055	14	—	—	—	—	—	—	—	—	—
No. of disc redfish	0.947	0.179	15	—	—	—	—	—	—	—	—	—
Wt of disc redfish	-0.131	0.551	15	—	—	—	—	—	—	—	—	—
No. of leatherjacket	—	—	—	—	—	—	—	—	—	2.404	0.014	16
Wt of leather jacket	—	—	—	—	—	—	—	—	—	2.15	0.024	16
No. of red bigeye	—	—	—	—	—	—	3.344	0.002	16	2.528	0.012	15
Wt of red bigeye	—	—	—	—	—	—	4.122	0.0004	16	2.548	0.012	15
No. of flutefish	—	—	—	1.841	0.045	13	—	—	—	—	—	—
Wt of flutefish	—	—	—	1.851	0.044	13	—	—	—	—	—	—
No. of blackeyes	4.364	0.0003	16	—	—	—	—	—	—	—	—	—
Wt of blackeyes	5.459	0.0001	16	—	—	—	—	—	—	—	—	—
No. of gurnard	—	—	—	—	—	—	—	—	—	2.392	0.018	15
Wt of gurnard	—	—	—	—	—	—	—	—	—	2.034	0.033	15
No. of disc comm sp	1.168	0.1306	16	-2.282	0.981	16	0.436	0.334	16	-0.674	0.744	16

cant differences detected in the size-compositions of stout whiting at Yamba (Fig. 6A); however, at Ballina, the control codend caught proportionally more small stout whiting than the composite-panel codend (Fig. 6B).

Discussion

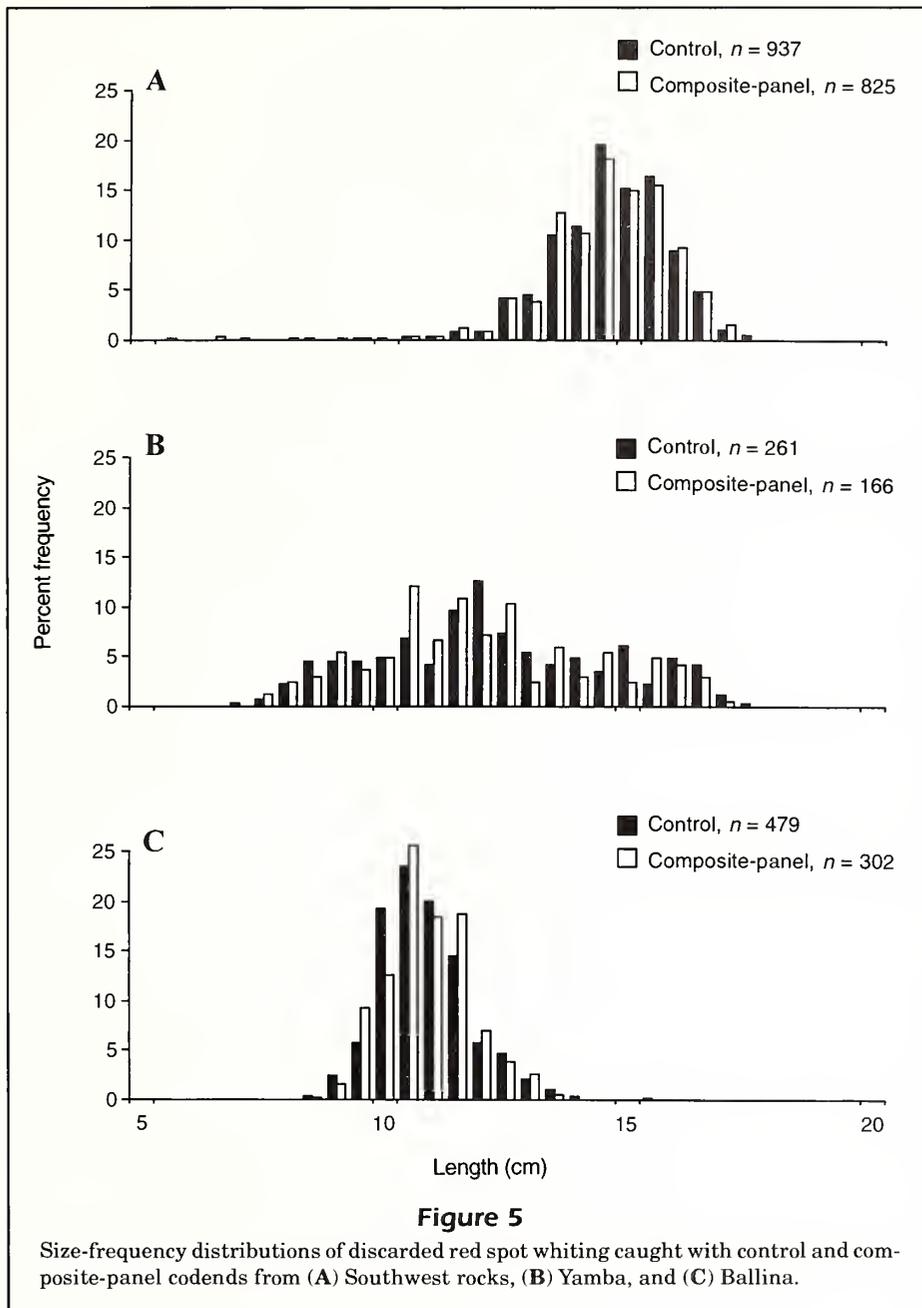
This study has shown the effectiveness of square-mesh panels in allowing nontarget organisms to es-



cape trawls (see also Briggs, 1992; Fonteyne and M'Rabet, 1992; Broadhurst and Kennelly, 1994, 1995, 1996; Broadhurst et al., 1996) while maintaining catches of commercially important species. By conducting independent experiments on different vessels across four ports over a range of fishing conditions and catches, we have also provided information on the relative performance of the composite-

panel throughout the full operational range of the NSW oceanic prawn-trawl fishery and have documented, for the first time, a significant increase in the catch of targeted prawns with this design.

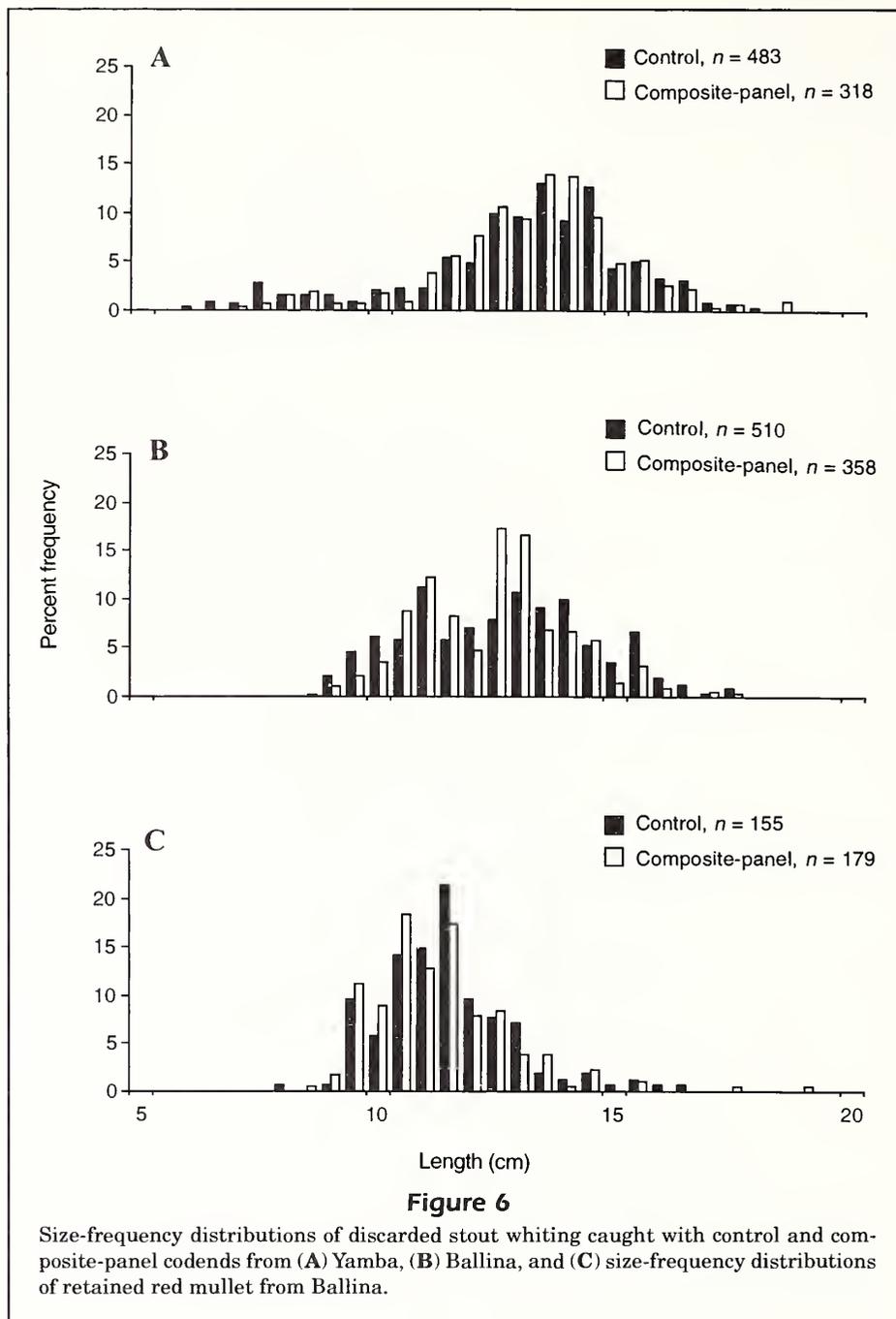
The composite-panel codend was most effective in excluding large quantities of those discarded species that are relatively fusiform and of a size small enough to pass through the square-meshes. Species such as



blackeyes, flute fish, red bigeye, and, in particular, stout and red spot whiting, were all significantly reduced by the composite-panel, which contributed towards a reduction in the mean weight of discarded bycatch at all locations from 23.5% to 41% (Fig. 3). Assuming minimal differences between the various vessels and their gear, the relative availability of these fusiform species throughout waters off New South Wales may explain the variations in the mean reductions of total discarded bycatch at each of the ports and across the fishery. For example, there were no red spot or stout whiting captured at Port

Stephens (Fig. 3, E–G), and there was only a 23.5% reduction in total discarded bycatch by the composite-panel at that location (Fig. 3B). In contrast, the discarded bycatch at Yamba and Ballina included large numbers of whiting and red bigeye (up to 500 fish and 1,000 fish, respectively, from each tow in the control net) (Fig. 3, E–F and K) and correspondingly large percentage reductions in total discarded bycatch (41% and 39.5%, respectively) (Fig. 3B).

The above reductions in total discarded bycatch with the composite-panel provide a possible explanation for the significant increase in catches of



prawns at Port Stephens, Yamba, and Ballina (by 14%, 5.5%, and 6%, respectively) and for the nonsignificant increase of 4% at Southwest Rocks (Fig. 3A). By reducing the amount of total discarded bycatch and therefore the weight and drag in the codend, the trawl with the composite-panel may have achieved greater spreads between the otter boards (i.e. an increased swept area) than did the control, thereby covering more of the seabed and capturing more prawns. These prawns were probably the same sizes as those that we sampled, because Kolmogorov-

Smirnov tests failed to detect any significant differences in prawn sizes between the codends for any of the ports (Fig. 4).

In support of the theory discussed above, there was also an increase (although not statistically significant) in the mean numbers of retained octopus at Southwest Rocks and Yamba (by 11% and 14%, respectively), retained red mullet (by 17%) at Ballina, and discarded eastern blue spot flathead at Yamba and Ballina (by 19.5% and 14.5%, respectively) with the composite-panel (Fig. 3, C-D, and I; Table 1).

Given the physical profile of these individuals and their large size, it is unlikely that once captured by the trawl, they would have been able to fit through the small square-meshes of the composite-panel. In a previous study (Broadhurst and Kennelly, 1996), we showed that large quantities of small individuals of long spined flathead, *Platycephalus longispinis*, escaped through the square-meshes in the composite-panel (62% reduction compared with a conventional codend). Because the tiger and eastern blue spot flathead captured in the present study are physically similar to this species, it may be possible to facilitate their escape simply by increasing the size of mesh in the panel (assuming they display similar responses to stimuli from the trawl). Such a modification, however, would likely result in less retention of smaller individuals of commercially important species such as red spot and stout whiting (see Figs. 5 and 6, A–B), cuttlefish, and southern calamari. In addition, the composite-panel has been designed so that the load is distributed across the many bars of the 40-mm square-shaped mesh. Any major increase in this mesh size would result in the distribution of load across fewer bars, possibly altering the geometry of the codend and its overall performance.

In the present study, we have shown that the composite-panel codend consistently increased catches of prawns over a range of operational conditions while removing large quantities of unwanted bycatch throughout the entire geographic range of the NSW oceanic prawn-trawl fishery. In another study in Australia, Robins-Troeger et al. (1995) tested a large and comparatively complex BRD (termed the "AustTED") off northern Australia and, despite reports of significant losses of prawns, concluded that "the AustTED system has the potential to be developed to suit trawling conditions encountered in different Australian prawn fisheries." It is unlikely, however, that any design of a BRD would be accepted and endorsed by fishermen if it did not consistently maintain catches of the target species throughout the range of the fishery—as is shown to be the case in the present paper for the composite-panel codend (see also Kendall, 1990; Renaud et al., 1992).

In terms of promoting a large-scale voluntary adoption of BRD's, like the composite-panel described in the present paper, it is useful to provide industry not only with evidence of catch rates similar to those obtained with conventional gear but also with evidence of additional benefits, such as a potential for increasing duration of tows, improving quality of catches (due to less damage from bycatch in the codend), increasing savings in labor and fuel, reducing sorting times, and reducing conflicts with other user groups (e.g. recreational and commercial fish-

ermen targeting stocks of bycatch species). The realization of these incentives, along with the results from the present study, have resulted in many commercial fishermen using the composite-panel throughout the entire NSW oceanic prawn-trawl fishery.

Acknowledgments

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Abstract.—Young-of-the-year (YOY) bluefish, *Pomatomus saltatrix*, were collected during the summers of 1992 and 1993 in the Hudson River estuary with beach seine, surface trawl, and gill nets. The temporal and spatial patterns of catch-per-unit-of-effort (CPUE) and gut-fullness values were used to infer bluefish movement and feeding periods, respectively. Estimates of daily ration were made from gut-fullness values and previously published estimates of gastric evacuation rate. Nearshore beach-seine CPUE was highest during day collections and lowest at night. Offshore gill-net CPUE was highest during crepuscular or night periods and lowest during day sets. Hence, YOY bluefish appear to occupy nearshore environments during the day and move away from shore at night. Gut-fullness values for bluefish captured with beach seines were highest at diurnal and crepuscular periods and declined at night; however, there were indications of night feeding on some dates. The magnitude and pattern of daily ration estimates of YOY bluefish in the Hudson River estuary were similar to values measured in previous studies with other methods. Interannual differences in the magnitude of daily ration were observed and may be a result of day-to-day variation in feeding or differences in available prey type and size. Clupeids, striped bass, and bay anchovy were important prey in 1992, whereas striped bass, bay anchovy, and Atlantic silversides were the dominant prey of YOY bluefish in 1993. Improved understanding of the spatial and temporal patterns of bluefish feeding, as well as fine-scale temporal resolution of estimates of bluefish consumption rates, will aid in assessing the impact of YOY bluefish predation on fish populations within the Hudson River estuary.

Movements, feeding periods, and daily ration of piscivorous young-of-the-year bluefish, *Pomatomus saltatrix*, in the Hudson River estuary*

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The movements of fishes are controlled by both biotic and abiotic phenomena. In estuaries, fish may move in relation to the availability of prey and to reduce the risk of predation, as well as in response to fluctuations in light, tide, salinity, temperature, and dissolved oxygen levels (Miller and Dunn, 1980). Fish distribution is often controlled by the interacting effects of these factors (Miller and Dunn, 1980; Gibson et al., 1996). An understanding of the factors that govern the movements and distributions of predators and prey is prerequisite to quantifying predator-prey interactions.

The bluefish, *Pomatomus saltatrix*, is a marine piscivorous predator of circumglobal distribution. On the U.S. east coast, spawning occurs offshore over the continental shelf, but young-of-the-year (YOY) migrate abruptly into estuaries at ~60 mm fork length (Kendall and Walford, 1979; Nyman and Conover, 1988; McBride and Conover, 1991; Juanes and Conover, 1995). Bluefish spawned in the South Atlantic Bight in the spring (spring-spawned) are advected northward in waters associated with the Gulf Stream (Hare and Cowen, 1996) and move

into New York-New Jersey estuaries in June (Nyman and Conover, 1988; McBride and Conover, 1991). A second wave of recruits made up of summer-spawned fish (spawned in the Middle Atlantic Bight) appear in nearshore waters in mid- to late-summer. The habitat shift from oceanic waters to estuarine areas coincides with a shift from feeding that is zooplanktivorous to one that is piscivorous (Marks and Conover, 1993).

This study is part of a larger project designed to estimate the predatory impact that YOY bluefish have on their piscine prey populations in the Hudson River estuary. Young-of-the-year bluefish are known to prey on larval and juvenile fishes in marine embayments and estuaries along the U.S. east coast (Grant, 1962; Friedland et al., 1988; Juanes et al., 1993; Creaser and Perkins, 1994; Hartman and Brandt, 1995a; Juanes and Conover, 1995). In the Hudson River estuary, YOY bluefish prey include the young of several resource species such as striped bass, *Morone sax-*

atilis, and American shad, *Alosa sapidissima* (Juanes et al., 1993; 1994). Mortality caused by YOY bluefish predation may be intense given the relatively high consumption rates of this species (Juanes and Conover, 1994; Buckel et al., 1995). In order to assess the effect of YOY bluefish predation, an understanding of the location and timing of bluefish prey interactions, as well as accurate and fine-scale temporal measurements of bluefish consumption rates, are needed.

Consumption rates of fish are measured with direct methods (laboratory- or field-based) and indirect methods. The field-based method requires measurements of gut fullness over a diel cycle coupled with estimates of gastric evacuation rate (Elliott and Persson, 1978; Eggers, 1979). The indirect method most widely used is a bioenergetic approach that requires knowledge of the predator's growth trajectory, physiological parameters, and environmental data (Kitchell et al., 1977). Because all of these methods have their drawbacks and their use is controversial (Hewett et al., 1991; Boisclair and Leggett, 1991), we used a combination of different techniques in order to compare methods and cross-validate results.

Juanes and Conover (1994) and Buckel et al. (1995) measured YOY bluefish consumption rates in the laboratory. Steinberg (1994) estimated daily ration of Hudson River YOY bluefish with a bioenergetics modeling approach. However, the only two field estimates of bluefish consumption rates that exist were made in Great South Bay, NY (Juanes and Conover, 1994), an environment that differs from the Hudson River estuary.

Here we report on the results of diel field collections of YOY bluefish during the summers of 1992 and 1993 in the Hudson River estuary. These collections allowed us to determine temporal and spatial (e.g. inshore vs. offshore) patterns of YOY bluefish movements and feeding. Gut-fullness values were coupled with previously determined estimates of gastric evacuation rates (Buckel and Conover, 1996) to estimate YOY bluefish daily ration.

Methods

Diel collections—beach seine

Spring- and summer-spawned YOY bluefish (cohorts easily identified by size) and their prey were collected from the lower Hudson River estuary in 1992 and

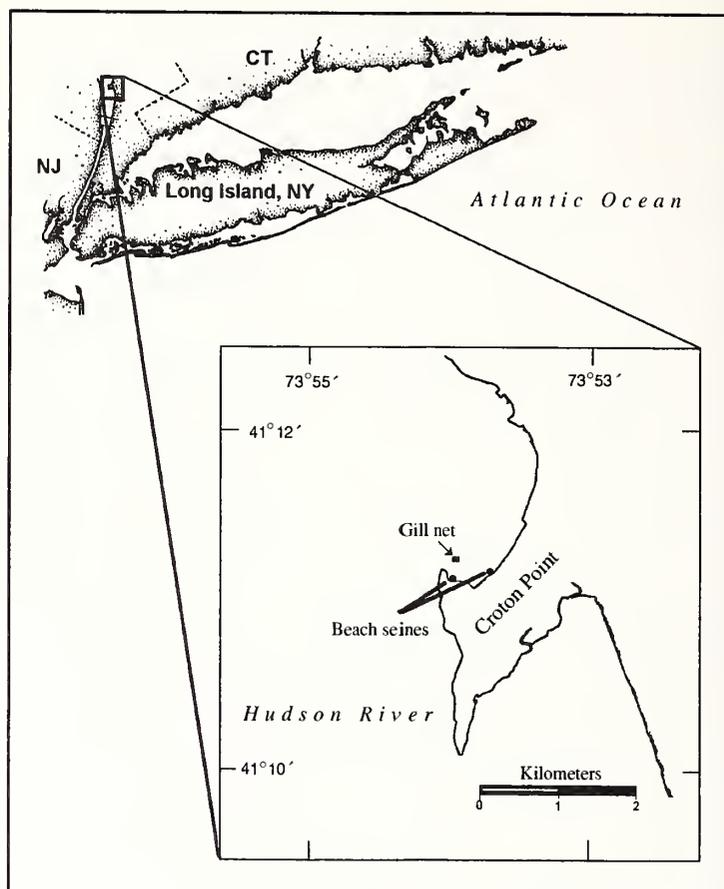


Figure 1

Locations where beach seines and gill nets were used at Croton Point, New York, in the lower Hudson River estuary.

1993 on the north shore of Croton Point (41°11'N, 73°54'W; Fig. 1). Ten diel beach-seine collections were made: five in 1992 (16–17 July, 28–29 July, 13–14 August, 26–27 August, and 19–20 September) and five in 1993 (7–8 July, 20–21 July, 4–5 August, 18–19 August, and 11–12 September). Collections were made every three hours beginning at 1200 h and ending at 1200 h the following day. Sampling began 30 min before and ended 30 min after each time point (e.g. sampling for the 1200 time point began at 1130 and ended at 1230). A 60 × 3 m beach seine (13-mm-mesh wings, 6-mm-mesh bag) and a 30 × 2 m beach seine (6-mm-mesh wings, 3-mm-mesh bag) were used for nearshore sampling. The 60-m seine was set by boat. A minimum of two 60-m seine hauls were made during each one-hour sampling period. Additional seine hauls were sometimes made to increase bluefish sample size. Bluefish and samples of prey were immediately preserved in 10% formalin. Catch-per-unit-of-effort (CPUE) of bluefish was calculated as the number of fish caught per seine haul in the first two 60-m seine hauls. Potential prey were counted

from one haul of each of the 60- and 30-m seines in 1993. Temperature (thermometer), salinity (refractometer), and dissolved oxygen (modified Winkler's method) were measured at each time point. Periodic functions were used to obtain quantitative values of tide and light levels for statistical analyses. Tides at the study site are semidiurnal and the tidal amplitude is ~1.5 m. The state of tide (T) for any given time point was calculated from the following equation:

$$T = \cos(((2\pi / 12.42) \times \text{time of day}) - \theta),$$

where θ = the time of high tide in radians.

A value for illumination (watts/cm²) was calculated for each time point on each specific date (Kuo-Nan, 1980).

The effects of light, tide, salinity, dissolved oxygen, and temperature on CPUE of spring-spawned bluefish were examined with a forward step-wise multiple regression. Data from 1992 and 1993 were analyzed separately and $\log_e(x+1)$ transformed to remove heterogeneity of variances.

Diel collections—gill net and surface trawl

A 90 × 2 m (4-cm-stretch, 2-cm-square) monofilament surface gill net was used to collect spring-spawned YOY bluefish from offshore shoal areas. One end of the gill net was anchored approximately 30 m east of the northernmost tip of Croton Point at a depth of ~3 m (low tide) and set parallel to the north shore of Croton Point (see Fig. 1). The nearest beach-seine site was ~200 m away in the cove just south of the gill-net set location. Gill-net collections were made concurrently with diel beach-seine collections on 20–21 July (approximate mid-set times were 1500, 2100, 0600), 4–5 August (2100, 0130, 0600), and 18–19 August (1500, 2100, 0130, 0600) in 1993. Soak times always lasted two hours. After net retrieval, bluefish were removed and immediately frozen on dry ice. Fish from gill-net collections were not used in the calculation of daily ration. Relative abundances of bluefish were calculated as the number of fish caught per hour of soak time (CPUE).

A surface trawl collection (8.2-m head-rope, 6.7-m foot-rope, 0.9-m-opening height, 2.5-cm-mesh net, 0.6-cm-mesh codend) towed between two boats was made on 15–16 July 1993. It was conducted 1) to supplement night beach-seine collections, 2) to determine YOY bluefish movement patterns, and 3) to estimate daily ration. Collections were made every three hours beginning at 1230 and ending at 1230 the following day. Two to three ten-minute tows were made at each time point. Tow speed was approxi-

mately 4 knots. Bluefish and prey were immediately preserved in 10% formalin. Relative abundances of bluefish were calculated as the number of fish caught per trawl (CPUE).

Diel collections—"movement collection"

A combination gill-net and beach-seine collection was made on 11–12 August 1993 with the sole purpose of examining bluefish movement at crepuscular periods. Fish from these collections were not used in the calculation of daily ration. Collections with beach seines were performed at 1200, 2400, and one hour before and after sunrise (0520 and 0720) and sunset (1900 and 2100). The temporal resolution of this sampling scheme with respect to sunrise and sunset was higher than that of evenly spaced intervals of beach seining described above (every three hours). Gill-net collections lasted two hours and were made throughout the diel cycle.

Feeding period

Values of gut fullness were used to examine the feeding periods of beach-seine-collected YOY bluefish. Gut-fullness values (F) were calculated as

$$F = G/W,$$

where G = prey wet weight; and

W = bluefish wet weight (total weight minus prey wet weight; see "Diet analysis" below).

Arc-sin square root and $\log_e(x+1)$ transformations of individual gut-fullness values did not remove heteroscedasticity; therefore, the effect of time on gut-fullness values from beach-seine data (excluding 11–12 Aug and 11–12 Sep 1993) was examined with a nonparametric Kruskal-Wallis ANOVA. If treatment effects were significant, a nonparametric multiple comparison test for unequal sample sizes (Zar, 1984) was used to compare means.

Daily ration estimates

Values of gut fullness for spring-spawned bluefish from beach-seine (five dates in 1992 and four dates in 1993) and surface trawl (15–16 July 1993) collections were used in estimating daily ration. Daily ration was also estimated for summer-spawned bluefish captured during beach-seine collections (19–20 Sept. 1992). The Elliott and Persson (1978) food consumption model was used to estimate bluefish daily ration:

$$C_{\Delta t} = \frac{(\bar{F}_{t_2} - \bar{F}_{t_1} \cdot e^{-R_e t}) \cdot R_e t}{1 - e^{-R_e t}}$$

where $C_{\Delta t}$ = food consumption between sampling periods at time t_2 and t_1 ;

\bar{F}_{t_2} and \bar{F}_{t_1} = the geometric mean gut-fullness values (back-transformed from $\log_e(x+1)$) at these time points (time points with $n < 3$ fish were not used in daily ration calculation);

R_e = the exponential gastric evacuation rate; and

$t = t_2 - t_1$.

Daily ration was calculated by summing estimates of $C_{\Delta t}$.

The method of Boisclair and Marchand (1993) and Trudel and Boisclair (1993) was used to estimate 95% confidence intervals for daily ration estimates. There were four steps in the analysis. First, an estimate of exponential evacuation rate (R_e) was made from the average water temperature during a given sampling period. Estimates of R_e were calculated from the equation

$$R_e = 0.015e^{(0.103T)},$$

where T = water temperature ($^{\circ}\text{C}$) from Buckel and Conover (1996).

Periods of declining gut fullness can be used as a validation of laboratory-based gastric evacuation rates (see Parrish and Margraf, 1990) and were used for seven out of ten diel beach-seine collections with the same data analysis techniques as those described in Buckel and Conover (1996). The mean field-derived estimate of R_e for these dates was 0.241/h, and the laboratory-derived estimate was 0.201/h (± 0.038 SE).

Second, a normal distribution of 1,000 pseudo values of R_e were calculated as

$$R_e^* = R_e + (SE_{R_e} \times RN),$$

where R_e^* = the pseudo value of evacuation rate;

R_e = the estimated mean evacuation rate;

SE_{R_e} = the standard error of R_e (Buckel and Conover 1996); and

RN = a random number (different for each calculation) from a normal distribution with a mean of 0 and standard deviation of 1.

Third, a normal distribution of 1,000 pseudo values of gut fullness (F) were calculated for each time point as

$$F_t^* = F_t + (SE_{F_t} \times RN),$$

where F_t^* = the pseudo value of gut fullness;

F_t = the mean $\log_e(F+1)$ transformed gut fullness;

SE_{F_t} = the standard error of F_t ; and

RN = a random number (different for each calculation) from a normal distribution with a mean of 0 and standard deviation of 1.

Fourth, Monte-Carlo simulations were used to estimate $C_{\Delta t}$ from the above equations by randomly choosing values of R_e^* , $F_{t_1}^*$, and $F_{t_2}^*$ from the distributions of 1,000 pseudo values (values of $F_{t_1}^*$ and $F_{t_2}^*$ were back-transformed before calculation of $C_{\Delta t}$). Simulated values of $C_{\Delta t}$ were generated for each of the eight time intervals (nine sampling points; less if a time point had $n < 3$ fish) and summed to estimate a daily ration. This calculation was repeated 1,000 times. The 2.5 and 97.5 percentiles of these daily ration estimates were taken as the 95% confidence intervals.

Diet analysis

Diets of bluefish captured with beach seines, surface trawls, and gill nets were quantified. In the laboratory, bluefish were measured for total length (TL, ± 1.0 mm), weighed (± 0.01 g), and their stomachs were extracted. Stomach contents of bluefish were identified to the lowest possible taxon, enumerated, blotted dry, weighed (± 0.01 g), and measured (TL, ± 1.0 mm; eye diameter, ± 0.1 mm; caudal peduncle depth, ± 0.1 mm). Regressions relating prey eye-diameter and caudal peduncle depth to TL were used to estimate prey TL from prey pieces (see Scharf et al., 1997). A reference collection of Hudson River fish species (whole fish, scales, and bones) was used to aid in identification of digested prey. Two indices were computed to describe diets (see Hyslop, 1980). The indices were 1) number of stomachs in which a taxon was found, expressed as a percentage of the total number of stomachs containing food (%F=percent frequency of occurrence), and 2) weight of taxon, expressed as a percentage of the total weight of food items (%W=percent weight).

Results

Diel collections—beach seine

A total of 1,204 spring-spawned and 64 summer-spawned bluefish were collected during diel beach-seine collections. There were five successful diel col-

lections in 1992 (571 spring- and 64 summer-spawned) and four in 1993 (633 spring-spawned fish). The sample size of bluefish from the 11–12 September 1993 beach-seine collection was too small ($n=23$) for all analyses except diet.

In the forward stepwise multiple-regression analysis, illumination of the surface waters was the only factor that explained a significant amount of the variation in spring-spawned bluefish CPUE for both 1992 ($P=0.006$) and 1993 ($P<0.001$). The influence of illumination on CPUE of spring-spawned bluefish was positive in both 1992 and 1993 (Fig. 2, A and B): more bluefish were captured by day than by night but daytime CPUE was more variable. The CPUE pattern was also seen with summer-spawned bluefish (Fig. 2A).

The number of prey captured in the 60- and 30-m seine hauls at each time point ranged from 1 to 1,910 in 1993. On three out of the four dates examined, the relation between numbers of prey and bluefish (from identical seine hauls) was positive; however, none of these correlations were significant.

Diel collections—gill net and surface trawl

A total of 154 bluefish were captured in gill-net sets on three diel collections in 1993. Mean CPUE was highest during sunset and midnight collections and lowest during afternoon and sunrise sets (Fig. 2C). A total of 94 bluefish were captured during surface trawl collections on 15–16 July 1993. Bluefish surface trawl CPUE was highest during the day (1500) and lowest at sunset (2100) (Fig. 2D).

Diel collections—"movement collection"

Gill nets and beach seines captured 29 and 47 bluefish on 11–12 August 1993, respectively. Gill-net CPUE was low during midday, increased through the evening to a peak at midnight (Fig. 2E), and then declined to zero by morning. Beach-seine CPUE was high during the day and low at night: the drop and increase in CPUE corresponded with sunset and sunrise, respectively.

Feeding period

Time of collection had a highly significant (Kruskal-Wallis ANOVA, $P<0.001$) effect on the gut-fullness values of spring-spawned bluefish in 1992 and 1993 (Figs. 3, A–F, and 4, A–E). Mean gut-fullness patterns from seine-collected bluefish in 1992 increased throughout the afternoon, peaked in late afternoon or evening, decreased throughout the night, and increased during the morning hours (Fig. 3A).

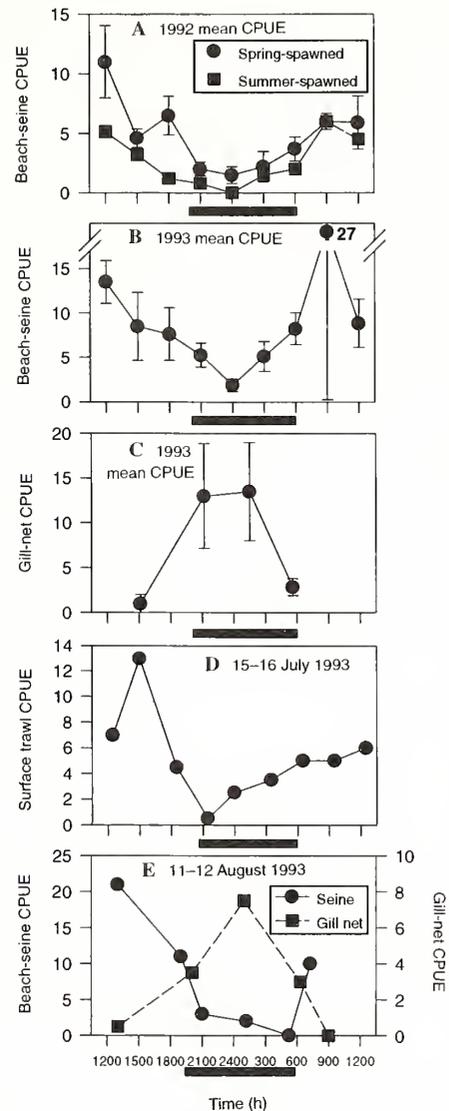


Figure 2

Catch-per-unit-of-effort (CPUE) of bluefish, *Pomatomus saltatrix*, versus time of capture during 1992 and 1993 diel collections. (A) Mean 1992 beach-seine CPUE (circles; \pm SE) of spring-spawned bluefish averaged over all dates of collection (16–17 July, 28–29 July, 13–14 August, 26–27 August, and 19–20 September) and summer-spawned bluefish CPUE (squares) on 19–20 September. (B) Mean 1993 beach-seine CPUE (\pm SE) of spring-spawned bluefish averaged over all dates of collection (7–8 July, 20–21 July, 4–5 August, and 18–19 August). (C) Mean 1993 gill-net CPUE averaged over all dates of collection (20–21 July, 4–5 August, and 18–19 August). (D) Surface trawl CPUE on 15–16 July 1993. (E) CPUE of spring-spawned bluefish during the beach-seine (circles, solid line) and gill-net (squares, broken line) "movement collection" on 11–12 August 1993. The time periods from sunset to sunrise are indicated by dark horizontal bars.

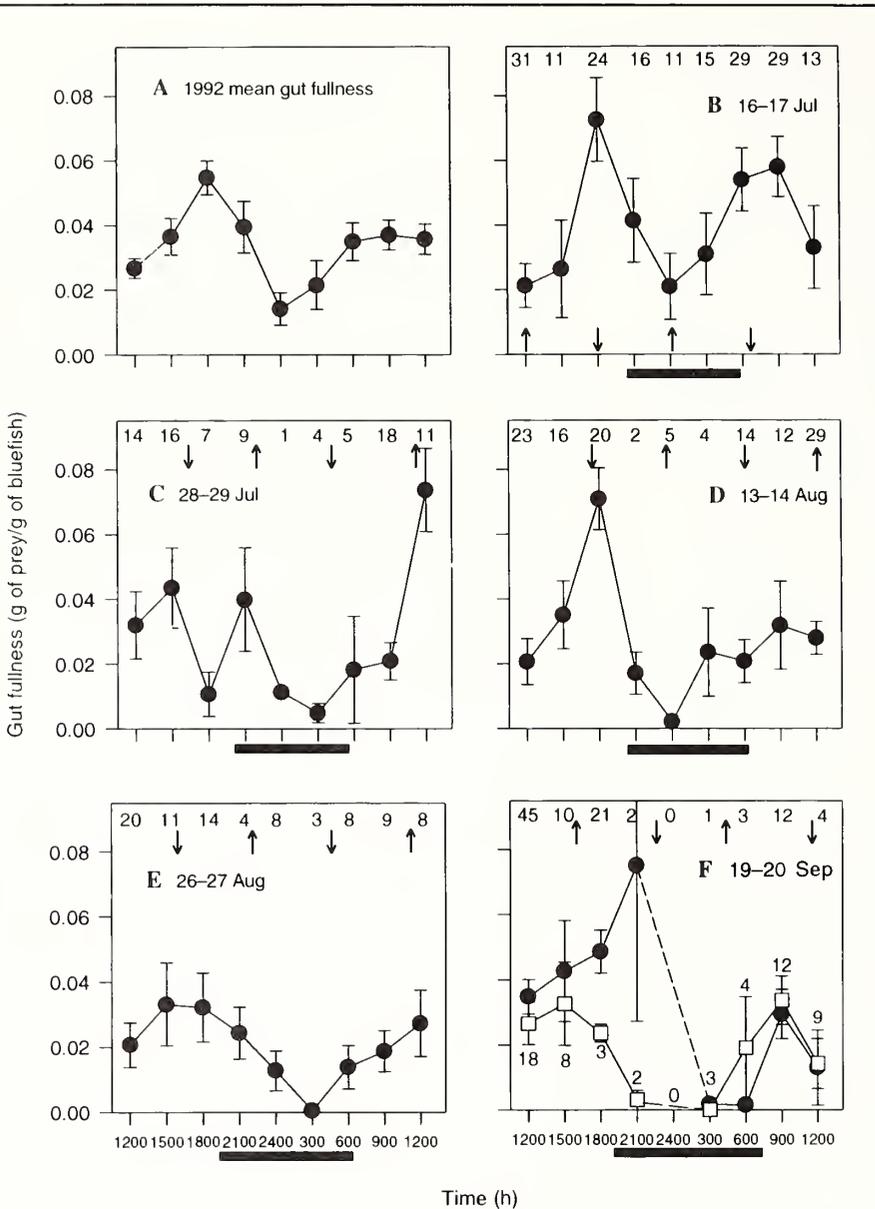


Figure 3

Gut-fullness values (mean \pm SE) of spring-spawned bluefish, *Pomatomus saltatrix*, versus time of capture during 1992 diel beach-seine collections. (A) Mean gut fullness (\pm SE) averaged across all dates of collection: (B) 16–17 July, (C) 28–29 July, (D) 13–14 August, (E) 26–27 August, and (F) spring-spawned (closed circles) and summer-spawned (open squares) bluefish versus time of capture during diel beach-seine collections on 19–20 September. The time periods from sunset to sunrise are indicated by dark horizontal bars. Numbers above (or near, for summer-spawned) each gut-fullness estimate represent bluefish sample size. Upward and downward facing arrows represent the time of high and low tide, respectively.

One potential problem in the above analysis is the potential lack of independence of gut-fullness estimates between time points. This lack of independence is mainly a concern with adjacent time points (spaced 3 hours apart) because gastric evacuation in bluefish is ~6–8 hours (Juanes and Conover, 1994; Buckel

and Conover, 1996). Therefore, gut-fullness estimates at time points that are separated by at least six hours are more likely to be independent of each other. We used post-hoc comparisons to examine for statistical differences between such pairs.

The gut-fullness value at 1800 was significantly higher (nonparametric multiple-comparison test, $P < 0.001$) than the gut-fullness value at 1200, 2400, and 0300. A similar pattern was seen for summer-spawned fish (Fig. 3F). The gut-fullness values of 1993 beach-seine-collected bluefish differed from those seen in 1992 (Fig. 4A); decline in gut fullness at night was not as dramatic. Gut-fullness values at 1200 were significantly lower ($P < 0.01$) than values from morning (0600 and 0900) and evening (2100) collections. However, the lowest night gut-fullness value (0300) was not significantly different from the highest day (0600) gut-fullness value ($P > 0.05$).

Daily ration estimates

Daily ration estimates for YOY spring-spawned bluefish during 1992 beach-seine collections were highest on our first sampling date 16–17 July at 22.2% body weight/d (95% confidence interval (CI) 13.3–32.3) and dropped to 7.3% body weight/d (1.7–13.6) by 19–20 September (Fig. 5A). Although there was a decline in daily ration, these values had overlapping CI's and were therefore not statistically different. In 1993, daily ration values from

beach-seine-captured spring-spawned bluefish were highest on 20–21 July at 14.7% body weight/d (8.5–21.6) and lowest on 7–8 July at 10.1% body weight/d (6.7–14.0) (Fig. 5B). The diel collection made with surface trawls on 15–16 July 1993 yielded a daily ration estimate of 8.6% body weight/d (4.7–12.8).

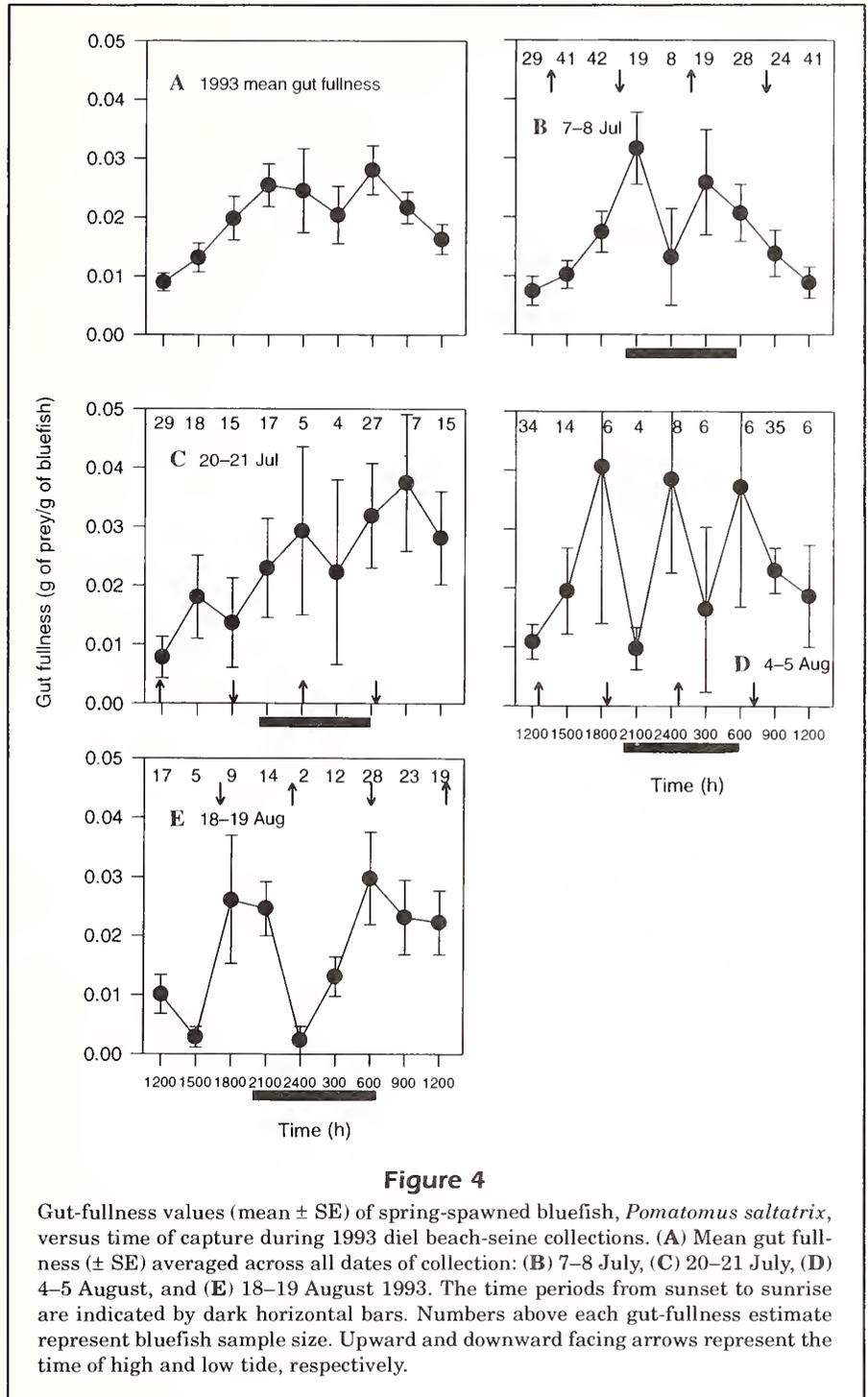
Estimates of daily ration in 1993 were not statistically different from each other. Daily ration of summer-spawned fish on 19–20 September 1992 was 5.7% body weight/d (2.6–9.4).

Diet analysis

Diets of YOY bluefish collected with beach seines during 1992 and 1993 were dominated by fish. Fish prey represented 97–100% of bluefish diet by weight (Table 1 and 2).

In 1992, the diet of YOY bluefish was dominated by clupeids, moronids, and bay anchovy *Anchoa mitchilli* (Table 1). Clupeids (American shad, blueback herring [*Alosa aestivalis*], alewife [*Alosa pseudoharengus*], and *Alosa* spp.—clupeids that could not be identified to species) were the dominant prey of 1992 bluefish collected by beach seine and were found in 30% of stomachs containing prey and represented 27% of bluefish prey weight (Table 1). Striped bass, white perch, *Morone americana*, and *Morone* spp. (moronids that could not be identified to species) were found in 19% of bluefish stomachs and made up 27% of their diet by weight. Bay anchovy were an important component of the diet on 19–20 Sept, representing 47% of the diet by weight (41%F). Atlantic silversides, *Menidia menidia*, and Atlantic tomcod, *Microgadus tomcod*, were found in bluefish diets during August and September. Invertebrates (zoaeae, copepods, and sand shrimp) were a small component of bluefish diet (Table 1).

In 1993, the diet of YOY bluefish was dominated by striped bass, bay anchovy, and Atlantic silversides (Table 2). Striped bass was the dominant prey of YOY bluefish in 1993 beach-seine collections, i.e. in 22% of bluefish stomachs and accounting for 37% of their diet by weight. Bay anchovy was also a major prey of bluefish in 1993 (11%F, 22%W), particularly during



the July collections. The Atlantic silverside became an important prey in August (Table 2). As in 1992, invertebrates were a small component of bluefish diet.

Striped bass (17%F, 35%W) and Atlantic silversides (24%F, 27%W) were dominant prey items of YOY bluefish captured with the gill net in 1993 (Table 3).

Clupeids and bay anchovy were also important prey items of YOY bluefish captured in the gill net. Diets of YOY bluefish captured in the surface trawl on 15–16 July 1993 were dominated by bay anchovy (56%F, 52%W) and striped bass (7%F, 20%W) (Table 3).

Discussion

Diel movements

We found large differences in the CPUE of bluefish with the diel cycle in beach-seine, gill-net, and surface trawl collections. There are several mechanisms

that could account for these patterns. Rountree and Able (1993) distinguished two types of diel sampling bias: 1) direct avoidance of the gear or 2) a change in fish behavior. They further divided the second bias into diel movement between habitats (into or away from the gear sampling area) and diel changes in local activity (e.g. foraging).

Catch-per-unit-of-effort of YOY bluefish (both spring- and summer-spawned cohorts) was higher during day beach-seine collections than during night collections in both 1992 and 1993 (Fig. 2, A–B). Fish would more likely detect and avoid beach-seine gear during the day than at night. Additionally, we used a boat to set the seine, which helped to standardize set time so that there were probably limited avoidance biases between diurnal and nocturnal collections due to “operator” efficiency. We therefore rule out direct avoidance of the gear (bias one) and accept a diel behavioral change (bias two) as an explanation for low night CPUE.

The surface trawl CPUE in 1993 was also highest during daylight hours (Fig. 2D). Because the pattern of CPUE in 1993 was not that expected if fish were visually avoiding the gear (bias one), we propose that a behavioral change that increases the susceptibility of bluefish to the surface trawl gear during the day is most likely responsible for the pattern.

Bluefish CPUE with the gill net was highest at sunset and night sets in 1993 (Fig. 2C). The pattern of gill-net CPUE was the opposite of what we saw with the 1993 beach-seine and surface trawl CPUE data. During the gill-net and beach-seine “movement collection” on 11–12 August 1993, beach-seine catches were higher an hour before sunset than an hour after (Fig. 2E). The opposite pattern was seen at sunrise. On this date, gill-net catches were low during the day and increased to a midnight peak before declining to zero after sunrise (Fig. 2E). We attempted to determine the direction of bluefish movement from the orientation of individual bluefish in the gill net; however, data were inconclusive.

According to beach-seine, surface trawl, and gill-net collections, bluefish occupy nearshore and surface waters during the day and then move offshore and below surface waters at night. Although we cannot rule out avoidance of gill-net gear (bias one) as a possible explanation of low day gill-net CPUE's, concomitant declines in beach-seine CPUE of bluefish in nearshore areas suggest that increased gill-net catches are at least partly a result of bluefish moving offshore. Support for our findings comes from field collections in other estuaries. Pristas and Trent (1977) found significantly higher catches of adult bluefish at night with monofilament and multifilament gill nets in shallow-water (0.7–1.1 m), mid-

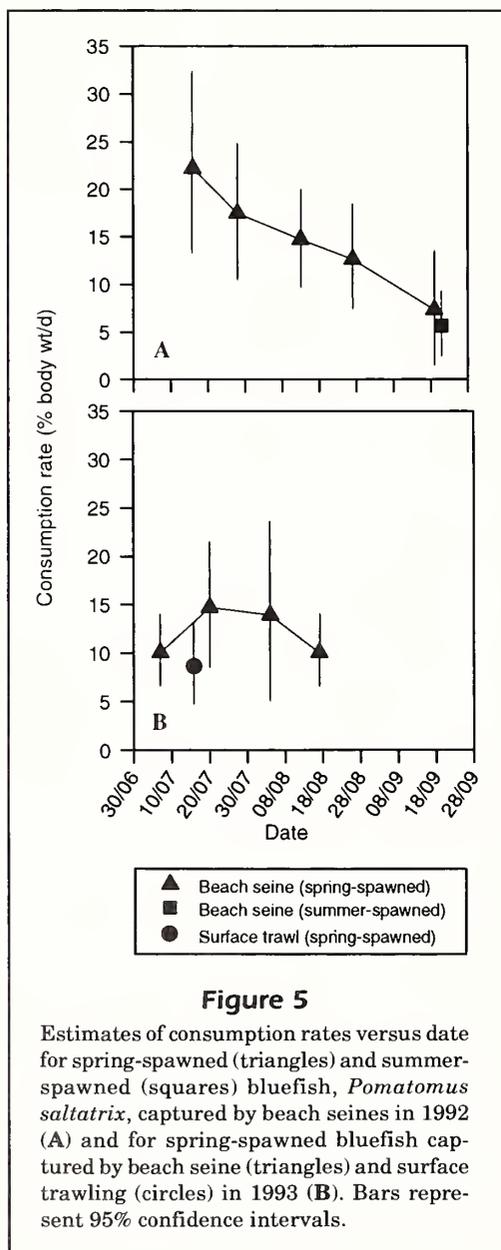


Table 1

Stomach contents of spring- and summer-spawned bluefish, *Pomatomus saltatrix*, captured during diel beach-seine collections in the Hudson River estuary in 1992. %F = frequency of occurrence, %W = percent wet weight.

Prey type	Species	Common name	Spring-spawned										Summer-spawned		Spring-spawned	
			16-17 July		28-29 July		13-14 Aug.		26-27 Aug.		19-20 Sept.		19-20 Sept.		Total	
			%F	%W	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W
	<i>Anchoa mitchilli</i>	bay anchovy	13.5	11.0	5.1	1.9	3.0	0.7	10.3	1.1	41.4	47.1	19.2	18.5	15.0	18.4
	<i>Morone saxatilis</i>	striped bass	17.5	24.4	5.1	3.9	15.2	23.7	11.8	39.0	4.6	9.5			11.8	19.6
	<i>Morone americana</i>	white perch	2.4	1.8	6.8	5.6	6.1	10.6	1.5	1.7	1.2	2.6			3.4	4.8
	<i>Morone</i> spp.		5.6	2.3	3.4	1.5	5.1	4.3	2.9	1.9	1.2	1.0			3.9	2.2
	<i>Alosa sapidissima</i>	American shad	6.4	15.6	15.3	24.1	5.1	7.3	7.4	6.6	9.2	9.7	2.1	9.3	8.0	10.5
	<i>Alosa aestivalis</i>	blueback herring	3.2	4.9	15.3	12.7	1.0	1.4							3.2	2.1
	<i>Alosa pseudoharengus</i>	alewife			3.4	7.1	1.0	3.0							0.7	1.5
	<i>Alosa</i> spp.		21.4	22.9	25.4	26.1	18.2	17.4	17.7	8.7	10.3	5.4	14.9	26.4	18.5	13.0
	<i>Menidia menidia</i>	Atlantic silverside	2.3	2.3			7.1	8.6	13.2	13.8	2.3	5.2	2.1	7.7	4.8	6.9
	<i>Microgadus tomcod</i>	Atlantic tomcod	0.8	0.4			1.0	2.2	2.9	13.4	2.3	2.5			1.4	4.0
	Other fish ¹						1.0	0.1	1.5	3.0					0.4	0.5
	Unidentified fish remains		38.9	12.9	52.5	16.9	49.5	20.5	41.2	10.8	39.1	14.2	55.3	33.6	43.5	15.3
	Total fish			98.5		99.8		99.8		99.5		97.2		95.5		98.8
	<i>Crangon</i> spp.	sand shrimp							1.5	0.2	4.6	1.0	8.5	4.0	1.1	0.2
	Zoeae and copepods		0.8	0.5	1.7	<0.1	2.0	<0.1	2.9	0.3	1.2	1.3			3.6	0.7
	Other ²				3.4	0.2	9.1	0.2	1.5	<0.1	8.0	0.5	14.9	0.8	4.9	0.3
	Total stomachs analyzed			179		83		125		85		99		64		571
	Number containing prey			126		59		99		68		87		47		439
	Mean bluefish size (g) (SE)			4.48		11.30		25.04		41.16		43.71		10.29		
				(0.18)		(0.69)		(1.27)		(2.78)		(2.01)		(1.29)		

¹ "Other fish" include Atlantic menhaden, *Brevoortia tyrannus*, and bluefish, *Pomatomus saltatrix*.

² "Other" includes vegetation, gravel, sand, and rope fibers.

water (2.2–2.6 m), and deep-water (5.2–5.6 m) zones of a Florida estuary. Using a subtidal weir in a polyhaline marsh creek in New Jersey, Rountree and Able (1993) captured a significantly higher number of YOY bluefish during day sampling than during night sampling. They concluded that this CPUE pattern was a result of diurnal foraging or increased activity (or both). Juanes and Conover (1994) made two diel beach-seine collections in Great South Bay, NY. Although they made no comparison between night and day abundance, their mean diurnal catch was two to three times higher than their mean nocturnal catch. These field studies confirm that bluefish activity patterns are influenced by light and dark cycles and that this pattern exists in diverse environments beyond the Hudson River estuary.

Factors that may be responsible for changes in diel activity or movements of fishes include foraging (Sciarrotta and Nelson, 1977; Wurtsbaugh and Li, 1985), reduction in predation risk (Clark and Levy,

1988; see Hobson, 1991), spawning (Conover and Kynard, 1984), and thermoregulation (Caulton, 1978; Rountree and Able 1993; Neverman and Wurtsbaugh, 1994). These factors may be interdependent. For example, Neverman and Wurtsbaugh (1994) found that Bear Lake (Utah-Idaho) YOY sculpin were able to digest their gut contents in a short period (overnight) by moving into warm surface waters at night. By digesting their food overnight, these fish were able to feed the following day. Clark and Levy (1988) showed that the vertical migration of juvenile sockeye salmon in an Alaskan lake during the day could be explained as a tradeoff between foraging and predation risk. For juvenile estuarine fishes, Miller and Dunn (1980) considered foraging as the primary cause of diel movements.

If bluefish movements are directly related to foraging, we might expect a strong correlation between the abundance of bluefish and their prey. Bluefish may congregate where prey density is high, or prey

Table 2

Stomach contents of spring-spawned bluefish, *Pomatomus saltatrix*, captured during diel beach-seine collections in the Hudson River estuary in 1993. %F = frequency of occurrence, %W = percent wet weight.

Prey type		Date													
		7-8 July		20-21 July		4-5 Aug		11-12 Aug ¹		18-19 Aug		11-12 Sept ¹		Total	
Species	Common name	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W
<i>Anchoa mitchilli</i>	bay anchovy	27.9	13.5	30.2	27.3	15.1	8.9	15.4	5.9	12.2	7.8	12.5	3.2	21.7	9.9
<i>Morone saxatilis</i>	striped bass	32.0	67.8	17.4	41.2	16.3	37.0	7.7	13.8	13.0	28.9	12.5	23.9	20.7	32.2
<i>Alosa sapidissima</i>	American shad					2.3	8.5			1.0	1.4			0.6	2.4
<i>Alosa</i> spp.				2.3	5.8	5.8	5.0	2.6	0.5	4.1	4.0			2.5	3.3
<i>Menidia menidia</i>	Atlantic silverside	1.2	1.2	1.2	2.5	16.3	23.1	41.0	69.7	22.5	35.9	12.5	21.0	11.5	32.8
Other fish ²						3.5	1.7			4.1	9.0	12.5	13.2	3.4	4.3
Unidentified fish remains		40.1	14.8	48.8	21.8	40.7	10.8	25.6	7.5	45.0	12.0	75.0	37.1	42.1	13.2
Total Fish			97.3		98.6		95.0		97.4		99.0		98.4		98.0
<i>Crangon</i> and <i>Palaemonetes</i> spp.	sand and grass shrimp					14.0	4.6	10.3	2.6	3.1	0.3	12.5	1.6	4.1	1.6
Zoeae and copepods		6.4	2.4	1.2	0.2					2.0	0.4				
Other ³		5.2	0.3	11.0	1.2	7.0	0.4			10.2	0.3			7.0	0.4
Total stomachs analyzed			248		137		119		47		129		23		703
Number containing prey			172		86		86		39		98		8		489
Mean bluefish size (g) (SE)			4.96 (0.10)		8.96 (0.51)		19.84 (0.94)		23.29 (1.41)		33.41 (1.59)		75.67 (8.79)		

¹ Bluefish that were captured on 11-12 Aug and 11-12 September were not used to calculate daily ration.

² "Other fish" includes killifish, *Fundulus* spp., American eel, *Anguilla rostrata*, white perch, *Morone americana*, *Morone* spp., Atlantic menhaden, and unidentifiable sciaenids.

³ "Other" includes vegetation, gravel, sand, and rope fibers.

may leave an area of high bluefish densities. However, we found no evidence of a correlation between prey and predator abundance; although positive relations between bluefish and prey abundance were found on three out of four dates in 1993, these correlations were nonsignificant.

Sea-surface illumination was the only environmental factor describing a significant amount of the variation in nearshore CPUE of YOY bluefish. Young-of-the-year fish of several shallow-water marine fishes move inshore at night (Keats, 1990; Burrows et al., 1994). We, however, observed an opposite pattern for bluefish in our study. Given that bluefish are visual predators, diurnal schooling and foraging in the nearshore zone is a possible explanation for relatively high and variable daytime beach-seine CPUE. Olla and Studholme (1972) found that adult bluefish in the laboratory had higher activity (swimming speed) and a larger schooling group size during the day than at night. The difference in diel activity was also seen in YOY bluefish and shown to be endogenous (Olla and Studholme, 1978). Olla and Marchioni (1968) found that

photomechanical changes in the retina of YOY bluefish were also internally controlled and thus lessened the time required for light and dark adaptation. Such diurnal rhythms would offer a selective advantage for a predator dependent on vision for prey capture.

Feeding period

During 1992 and 1993, gut-fullness values from bluefish caught in beach seines were highest during day, evening, and morning collections. However, there were dates in 1993 when bluefish gut-fullness levels indicated nocturnal feeding; these dates occurred with a recent full moon (7-8 July, 4-5 August) and a new moon (20-21 July). Therefore, moonlight is not entirely responsible for the nocturnal feeding seen in 1993. In laboratory tanks, YOY bluefish are capable of feeding in complete darkness (Juanes and Conover, 1994). Tide may also influence the timing of feeding; however, the timing of low and high tide had no consistent influence on peaks in gut-fullness levels (Fig. 3-4).

Table 3

Stomach contents of spring-spawned bluefish captured during surface trawl and gill-net collections in the Hudson River estuary in 1993. %F = frequency of occurrence, %W = percent wet weight.

Prey type		Date							
		Surface trawl		Gill net					
		15–16 July		20 July–4 Aug		11–12 Aug		18–19 Aug	
Species	Common name	%F	%W	%F	%W	%F	%W	%F	%W
<i>Anchoa mitchilli</i>	bay anchovy	56.3	51.7	3.0	5.9	6.3	10.1	2.6	0.6
<i>Morone saxatilis</i>	striped bass	7.0	20.4	18.2	47.6	25.0	33.9	18.4	33.3
<i>Morone</i> spp.				6.1	5.1				
<i>Alosa sapidissima</i>	American shad			3.0	5.1	12.5	19.8		
<i>Alosa aestivalis</i>	blueback herring							2.6	3.5
<i>Alosa pseudoharengus</i>	alewife					6.3	8.7		
<i>Alosa</i> spp.		1.4	2.5	15.2	8.5			5.3	2.8
<i>Menidia menidia</i>	Atlantic silverside			6.1	2.9	18.8	9.0	31.6	39.1
Other fish ¹		1.4	10.2	3.0	8.7	6.3	15.2	2.6	1.2
Unidentified fish remains		43.7	13.9	51.5	15.3	25.0	1.4	44.7	19.2
Total fish			98.7		99.2		97.9		99.7
<i>Crangon</i> spp.	sand shrimp			3.0	0.8	12.5	2.1	2.6	0.3
Zoeae and copepods		4.2	0.5						
Total stomachs analyzed			94		83		29		71
Number containing prey			71		33		16		38
Mean bluefish size (g) (SE)			6.83 (0.65)		50.93 (1.81)		55.25 (3.68)		52.95 (2.44)

¹ "Other fish" are bluefish, Atlantic menhaden, unidentified sciaenid, and American eel.

Declining gut-fullness values probably represent periods when fish do not feed. In 1992, these periods occurred mostly after sunset during nocturnal hours for both spring- and summer-spawned bluefish (Fig. 3, B–F). In 1993, declining gut-fullness values were more variable and followed sunset or sunrise peaks in gut fullness, or else not at all (Fig. 4, B–E). Bluefish that Juanes and Conover (1994) captured during diel sampling showed peaks in gut-fullness values during crepuscular periods and a subsequent decline in gut-fullness values and a higher percentage of empty guts at night.

Many freshwater, estuarine, and marine fish species show periodicity in their daily feeding (Helfman, 1979; Miller and Dunn, 1980; Reis and Dean, 1981; Popova and Sierra, 1985; Wurtsbaugh and Li, 1985; Nico, 1990; Jansen and Mackay, 1992). This periodicity is exhibited in fish that feed either diurnally, nocturnally, or during crepuscular periods. Young-of-the-year bluefish appear to be mainly diurnal and crepuscular foragers but are also able to feed at night.

Daily ration estimates

Daily ration estimates from this study are consistent with prior laboratory and field studies in which YOY bluefish were shown to have relatively high consumption rates for a temperate fish (Juanes and Conover, 1994; Buckel et al., 1995). Field estimates of bluefish consumption rates in the Hudson River estuary in early 1992 approached 25% body wt/d. In 1992, daily rations declined as fish grew. Largest values for consumption-rate rations occurred in mid-July (22.2%) and dropped to a low in mid-September (7.3%) (Fig. 5A). The pattern and magnitude of field estimates of consumption rate were similar to values of consumption rate from laboratory-mesocosm experiments made at the same time on similar-size fish (Buckel et al., 1995). In 1993, however, the early (10.1%) and mid-July (8.6%) estimates of daily ration from 24-hour collections made with beach seines (7–8 July) and surface trawls (15–16 July) were lower than the mid-July beach-seine estimate in 1992 (16–17 July). The last three daily ration estimates in 1993

were similar to those estimated for similar dates in 1992 (Fig. 5, A and B). A comparison of these field consumption rate estimates with estimates from bioenergetic models (Steinberg, 1994; Hartman and Brandt, 1995b) is dealt with elsewhere (Steinberg and Conover¹).

There are several possible explanations for the relatively low estimates of daily ration in early July 1993. First, these are point estimates of feeding rate that may not reflect average daily feeding over longer periods (see Smagula and Adleman, 1982; Trudel and Boisclair, 1993). Although Trudel and Boisclair (1993) found low day-to-day variation (7.0–16.3%) of daily ration for minnows in a field study, Smagula and Adelman (1982) found large day-to-day variation (30–40%) in daily ration estimates of piscivorous large-mouth bass in the laboratory.

Alternatively, other factors known to affect fish consumption rates include temperature, fish size, prey availability, prey biomass, prey type and size composition, and risk of predation. Both temperatures and bluefish sizes were similar in 1992 and 1993 (Tables 1–4). Prey abundance was not recorded during diel collections in 1992 and thus cannot be compared, but there were differences in the types and sizes of prey consumed by bluefish in these years (Table 4). The much larger clupeid species were a dominant part of bluefish diet in 1992 but were not a dominant prey in 1993. This finding reflects riverwide relative abundance estimates from a sepa-

rate beach-seine study (Buckel, 1997). In July 1992, clupeids, striped bass, and bay anchovy represented 90% of the available forage fish. Striped bass alone represented 63% of the available forage fish at this time in 1993. Moreover, striped bass and bay anchovy were larger for a given bluefish size in 1992 than in 1993. A combination of the size and type of prey available, along with the possible behavior differences between the prey (e.g. clupeids are more pelagic and less refuge oriented), may have caused the large differences in daily ration in July. We have no information on relative abundances of predators of juvenile bluefish in July 1992 and 1993 and therefore cannot discount predation risk as a potential mechanism explaining differences in daily ration in July.

Diet analysis

Diets of YOY bluefish in 1992 and 1993 were dominated by fish prey, confirming past studies in the Hudson River estuary that have shown YOY bluefish to be largely piscivorous (Texas Instruments, 1976; Juanes et al., 1993). Diets of YOY bluefish were dominated by important anadromous resource species: clupeids in 1992 and striped bass in 1993. Interannual variation in diet was also observed by Friedland et al. (1988) in their study of YOY bluefish in a New Jersey marine embayment. Because YOY bluefish are believed to be opportunistic predators (Friedland et al., 1988; Juanes et al., 1993), the diet differences we observed appear to be a result of the availability of different prey types in 1992 and 1993 (see riverwide abundances above). However, our diet data may be biased because spatial coverage was limited to the Croton Point region of the Hudson River.

¹ Steinberg, N. D., and D. O. Conover. 1997. Young-of-the-year bluefish (*Pomatomus saltatrix*) consumption in the Hudson River estuary: a bioenergetic modeling approach. Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000. Manuscr. in prep.

Table 4

Percentages of fish with empty stomachs, prey types, mean prey size, and mean values of temperature and gut fullness for diel collections in 1992 and 1993 (beach-seine and the 15–16 July 1993 surface trawl collection (ST)). Prey types are C = clupeids; SB = striped bass; BA = bay anchovy; and AS = Atlantic silversides. Prey types are listed in their order of importance in bluefish diet on each date. Mean prey sizes follow the order of prey type.

Year	Date	% with empty stomach	Prey type	Mean prey size (mm)	Mean temp (°C)	Mean gut fullness (g of prey/g of bluefish) (%)
1992	16–17 June	29.6	C, SB, BA	42.9, 32.9, 27.3	25.6	4.31
	28–29 July	28.9	C	45.7	25.3	3.40
	13–14 Aug	20.8	C, SB, AS	50.9, 56.1, 68.3	25.0	3.26
	26–27 Aug	20.0	SB, C, AS	68, 52, 45.2	26.7	2.27
	19–20 Sept	12.1	BA, C	43.2, 60.2	22.4	3.62
1993	7–8 July	30.6	SB, BA	26.3, 16.5	26.9	1.52
	15–16 July (ST)	24.5	BA	20.4	25.6	1.69
	20–21 July	37.2	SB, BA	39.4, 24.5	26.1	2.13
	4–5 Aug	27.7	SB, AS, C, BA	52.5, 47.0, 57.3, 35.7	25.9	2.08
	18–19 Aug	24.0	SB, AS, BA	68.3, 61.5, 40.4	24.8	2.10

Bluefish collected by gill net and surface trawls had diets that were similar to those of bluefish captured with beach seines (Table 1–3). This finding suggests that YOY bluefish feed nearshore and then move offshore or that prey types in offshore shoal feeding areas do not differ from prey nearshore (or both). However, bluefish captured by surface trawls in 1993 had a larger amount of bay anchovy in their diet than did bluefish captured with beach seines during the previous week. This finding may reflect increased availability of bay anchovy in offshore surface waters than in nearshore environments.

Implications

This study provides an improved understanding of the temporal and spatial patterns of bluefish feeding ecology in the Hudson River estuary. Knowledge of the temporal and spatial scales at which predators forage is required for a variety of predator-prey studies. Densities of predator and prey at scales relevant to predator foraging should be used for calculations of prey-type selectivity (O'Brien and Vinyard, 1974), in encounter rate models (see Brandt and Mason, 1994), in functional and numerical response calculations (Peterman and Gatto, 1978), and in calculations of a predator's growth or impact (Brandt and Kirsch, 1993; Petersen, 1994).

Empirical data on the diel changes in spatial overlap of fish and their prey and the timing of foraging activity is often lacking from spatially explicit models of fish feeding and growth. For example, Brandt and Kirsch (1993) used estimates of prey density from offshore nighttime collections. If the sampling design for estimating the densities of YOY bluefish and their prey in the Hudson River were constrained to only offshore or night (or both), the peaks in feeding activity that occur during day and crepuscular periods in the nearshore would be missed. Clearly, a detailed understanding of the spatiotemporal movement and feeding patterns of predators and prey are necessary to produce realistic models of feeding and growth (Mason and Patrick, 1993).

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Abstract.—The herbivorous blue-banded surgeonfish, *Acanthurus lineatus*, was a major species harvested on coral reefs in American Samoa, accounting for 39% by weight of artisanal catches in 1994. Spawning occurred year-round but peaked during the austral spring and summer (October–February). A dense pulse of recruits (0.4–0.6 recruits/m²) settled onto the outer reef flat in March–April. Apparent survival was low during the first year but increased thereafter (80%/year). The fish were strongly site-attached on a daily basis, but an estimated 60% of the adults switched territories at least once during a 3-year period, thereby negating attempts to estimate mortality through attrition rates of marked individuals. Estimates of fish condition changed through the year, generally paralleling seasonal changes in a suite of environmental factors. The fish grew rapidly, attaining 70–80% of their total growth during their first year, followed by slow growth and long life (up to 18 years), characteristics that confounded standard growth analyses by producing age-specific growth parameters. Growth was best described by a two-phase von Bertalanffy growth curve for ages 0–3 ($K=1.1$) and ages 4–18 ($K=0.12$, $L_{\infty}=22.1$ cm), with the separation based on the age at which 50% of the population reached maturity. Indicators of fishing pressure over a 9-year period were equivocal but did not point to significant overfishing.

Population biology and harvest of the coral reef surgeonfish *Acanthurus lineatus* in American Samoa

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Coral reef fishes are harvested for food throughout the South Pacific islands (Wright, 1993; Dalzell et al.¹). In American Samoa, well over 100 species are caught in artisanal and subsistence fisheries, but biological information about these species and their responses to exploitation is sparse. Moreover, these fish are often treated as taxonomic groupings rather than as individual species, and the information that is available often pertains to geographic areas distant from and dissimilar to isolated oceanic islands such as American Samoa.

The purposes of this study were to examine life history characteristics and harvest of one of the most abundant species caught in Samoa, the bluebanded surgeonfish, *Acanthurus lineatus*. This species is one component of a multispecies subsistence fishery that has declined in total catch in recent years for unclear reasons (Craig et al., 1993; Ponwith²; Saucerman³). Thus, we

also examined whether overfishing accounted for declines in catches.

The herbivorous *A. lineatus* is broadly distributed throughout the Indo-Pacific and Indian Ocean regions and has been the subject of several studies on behavioral ecology (Robertson et al., 1979; Robertson and Polunin, 1981; Robertson, 1983 and 1985; Choat and Bellwood, 1985; Polunin and Klumpp, 1989; Choat, 1991; Craig, 1996). On the Great Barrier Reef of Australia, this species is long-lived; some fish live

¹ Dalzell, P., T. Adams, and N. Polunin. 1995. Coastal fisheries of the South Pacific. Workshop on management of South Pacific Inshore Fisheries, New Caledonia, 26 June–7 July 1995. Joint Forum Fisheries Agency—South Pacific Commission, Biol. Paper 30, 151 p.

² Ponwith, B. 1991. The shoreline fishery of American Samoa: a 12-year comparison. Dep. Mar. and Wildl. Res., American Samoa, Biol. Rep. Ser. 23, 51 p.

³ Saucerman, S. 1995. The inshore fishery of American Samoa, 1991 to 1994. Dep. Mar. and Wildl. Res., American Samoa, Biol. Rep. Ser. 77, 45 p.

as long as 44 years (Choat and Axe, 1996). In Samoa, *A. lineatus* occurs in high densities on coral reefs (0.4 fish/m²; Craig, 1996). It maintains feeding territories in shallow waters during the daytime but spends nights in deeper-water crevices where it is harvested by spear fishermen.

The fisheries

American Samoa has several small-scale fisheries for nearshore and offshore fishes and invertebrates (Craig et al., 1993). In 1994, the first year when all components of these fisheries were monitored, *A. lineatus* ranked second only to skipjack tuna (*Kat. vonus pelamis*) among all species harvested, accounting for 10% of the total catch of 295 metric tons (t) (DMWR⁴).

Acanthurus lineatus, a small fish averaging 18 cm fork length (FL) and 170 g, was caught in two inter-related coral reef fisheries: artisanal and subsistence harvests. Multispecies landings in these two fisheries were 76 and 86 t, respectively, in 1994 (Saucerman³). The artisanal fishery consisted of 56 nighttime spear divers, among whom 15 fished regularly (about 15 days per month) by free diving and scuba diving. At 28 t, *A. lineatus* accounted for 39% by weight of artisanal catches (Fig. 1). The subsistence fishery was more diverse: fish were captured by gill nets, throw nets, rod-and-reels, handlines, and by spear fishing; invertebrates were captured by hand picking and spearing. Many species were taken; *A. lineatus*

accounted for only 1–3% of subsistence catches. In both artisanal and subsistence fisheries, use of destructive fishing practices (dynamite, poison) was infrequent.

Materials and methods

Tutuila Island in American Samoa (14°S, 171°W) is a steep volcanic island (142 km²) with 55 km of fringing coral reef. It has two seasons, a wet summer (Oct–May) and a slightly drier and cooler season (Jun–Sep) characterized by 2.5°C cooler nearshore water temperatures and increased SE trade winds. Nearshore water temperature (taken seaward of the reef flat at 0.3 m depth) ranged from 27°C to 31°C (n=295 daily measurements). Additional details about physical variables are presented below as they relate to changes in fish condition. Rainfall and wind data were obtained from NOAA.⁵

Data were collected from 1) field studies conducted by snorkeling in shallow waters (1–4 m) on the coral reefs fronting the villages of Afao, Leone, and Matu'u (Fig. 2) and from 2) market samples of the artisanal fishery. Reef flats at the study sites were narrow (100–250 m), dropped abruptly to a depth of 3–6 m, and descended gradually thereafter to 20 m. The outer reef flat inhabited by *A. lineatus* consisted of consolidated limestone, encrusting coralline algae,

⁵ NOAA (National Oceanic and Atmospheric Administration). 1994. Local climatological data, annual summary with comparative data, Pago Pago, American Samoa. National Climatic Data Center, Asheville, North Carolina, ISSN 0198-4357, 8 p.

⁴ DMWR (Dep. Marine and Wildlife Resources), PO Box 3730, Pago Pago, American Samoa 96799. Unpubl. data.

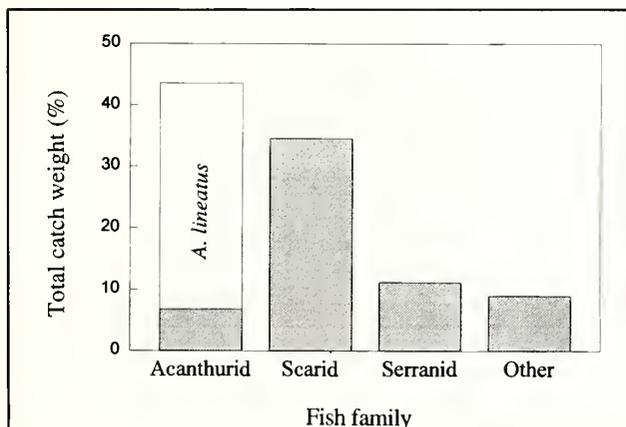


Figure 1

Catch composition (by weight) of fish families in the 1994 artisanal fishery in American Samoa. Redrawn from Saucerman (see Footnote 3 in the text).

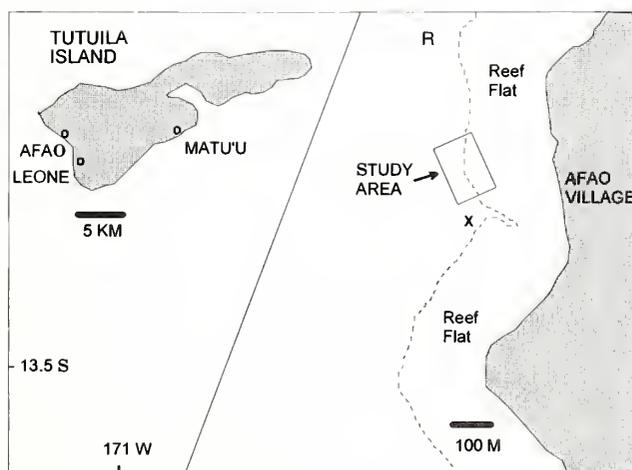


Figure 2

Tutuila Island, showing locations of study sites at the villages of Afao, Leone, and Matu'u. The main study reef at Afao (see enlargement at right) shows the spawning site of *A. lineatus* in the outer reef channel (x), the nighttime rest region (R) for *A. lineatus* using the study area, and the reef flat edge (dashed line).

and only 3.5% live coral cover (Craig, 1996). Spawning and nocturnal rest sites at Afao are shown in Figure 2 for those *A. lineatus* that maintained daytime feeding territories in the study area.

Length, weight, sex, and maturity

Length frequencies of fish in the artisanal catch were measured at 54 occasional intervals from 1987 to 1995. During 1991–94, fish were purchased at local markets to determine fork length (to the nearest mm), weight (to 0.1 g), sex, and maturity. Pooled monthly samples for these years consisted of 18–33 mature females, 18–49 mature males, and 9–116 immature fish, for a total of 1,139 fish. Maturity was assessed by visual inspection of gonads and by gonadosomatic index ($GSI = 10^2 \times \text{gonad weight} / \text{whole body weight}$). To determine maturity-at-size, immature fish whose sex could not be determined (13% of total sample) were assigned in equal proportions to numbers of identified males and females because the sex ratio of identified males and females was equal. Limited samples of rotenone-treated fish were collected at several nearshore sites in August 1990 to compare with sizes of fish taken in the artisanal fishery.

Spawning

Seasonal spawning patterns were determined from GSI trends and by conducting monthly visual surveys in the outer reef channel at the Afao site, 1993–94. Confirmation of spawning was determined by an upward rush of fish with the production of visible milt clouds.

Settlement of young onto reef

At each of the three study sites, newly settled fish in five 2×20 m permanent transects along the outer edge of the reef flat were censused monthly, approximately one week after the new moon. A repeated-measures multivariate analysis-of-variance (MANOVA with Pillai's trace test statistic) was used to test for significant differences in settlement time among the three sites and to accommodate autocorrelation of counts among observed times (Tabachnick and Fidell, 1989).

Condition factor (CF)

We used two measures of fish condition: 1) as $10^5 \times \text{body weight} / \text{length}^3$, and 2) as the weight of the paired postabdominal fat bodies found in surgeonfishes (Fishelson et al., 1985). To examine seasonal changes, monthly mean CF values and fat body

weights were compared with trends in five environmental factors that might affect fish growth: 1) nearshore water temperature, 2) available feeding hours, 3) calm surf conditions, 4) rainfall, and 5) daylength. Available feeding hours were calculated as the number of feeding hours per month during the fish's daily peak feeding period (1000–1800; Craig, 1996), minus losses of feeding time during the cooler season due to earlier sunsets and increased occurrence of spring low tides that prevented access to the fish's intertidal feeding territories. An index of calm surf conditions was calculated as the inverse of wind speed, because seasonally strong winds increase turbulence in the surf zone, thereby decreasing feeding opportunities for *A. lineatus* (Craig, 1996). Rainfall was used as a possible indicator of the amount of nutrient input into coastal waters that might, in turn, enhance growth of the algae that the fish eat. Similarly, daylength might affect algal production. Monthly means of these five factors were calculated for the years 1991–94 and presented as percentages of the maximum monthly value that occurred during this period, which were water temperature (29.6°C), available feeding period (225 h), wind speed (27 km/h), rainfall (72 cm), and daylength (13.0 h).

Growth

Growth data were fitted to the von Bertalanffy growth function (VBGF):

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

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

Two independent estimates of fish growth were made. In the first method, sagittal otoliths were used to estimate ages of 94 fish selected to span the widest size range possible (5.3–22.9 cm FL from pooled locations) with the methods described by Choat and Axe (1996), who aged the same species (by including tetracycline verification) from the Great Barrier Reef. Estimates of L_∞ and K were derived from a Ford-Walford regression of the age-length relation (Pauly, 1983). Estimates of t_0 were made with Pauly's (1979) empirical equation:

$$\log(-t_0) = -0.392 - 0.275 \log L_\infty - 1.038 \log K.$$

Additionally, one of each otolith pair was weighed to 10^{-4} g for comparison with fish age.

In the second method, individual growth rates were calculated for a subset of the naturally marked fish described in the field mortality study (see next section). The 57 fish selected were those for whom a time series of 4–20 size estimates was available for each fish. Lengths were estimated visually underwater; a comparison of visual estimates with actual sizes of the same fish when caught by spear indicated that the average error was $8.1 \pm 1.5\%$ (mean and SE throughout text, $n=19$, 6–20 cm FL).

The fish were initially selected from three general size classes according to their size at settlement onto the reef (2.5–5 cm) and approximate state of maturity based on dissection data (juveniles 6–14 cm, adults 15–23 cm). Sample sizes were 11 newly settled fish (monitored 1.7 ± 0.3 mo), 28 juveniles (5.2 ± 0.6 mo), and 18 adults (14.1 ± 1.0 mo). These fish were grouped into eight size classes of 2.5-cm intervals on the basis of their initial sizes. By using the mean growth rate of each size class, we calculated the time needed to grow to the next size class. These growth increments were plotted sequentially, forming a single growth curve for the population. A Gulland-Holt (1959) plot of growth increments of individual fish produced estimates of L_∞ and K .

Mortality

Total mortality (Z), which equals natural mortality (M) plus mortality caused by fishing (F), was estimated by monitoring the gradual loss of 145 marked fish for three years at the Afao site and by analyzing the length and age composition of fish taken in the artisanal fishery.

Field mortality Earlier work had shown that *A. lineatus* was highly site-attached (Craig, 1996); thus we initially assumed that a fish had died if it failed to re-occupy its territory or nearby area. Individual adults ($n=45$) and juveniles ($n=50$) were recognized by distinctive line patterns behind the eye and on the cheek. Sexual dimorphism was not apparent, thus males and females were not distinguished in the field. Newly settled fish ($n=50$) were identified by a combination of their specific location, size, color phase,⁶ and line pattern when discernible. Because newly settled fish were selected on the basis of identifiability rather than first appearance in the study area, the time elapsed since settlement was not known.

However, surveys were conducted frequently; therefore most newly settled fish had probably arrived within the previous week or two.

On average, about 35 fish were monitored at any one time; new individuals were added when others either outgrew their size class or were not relocated after three successive surveys. Small fish were inspected at least twice each week, larger fish about once per week. All three size groups were intermixed on the outer reef flat.

To calculate mortality, all fish within a size group were aligned to a common starting date. For each size class, mortality at any given time equalled $1 - (\text{no. fish alive} + \text{no. fish outgrowing size class}) / (\text{initial no. fish in that size class})$. This approach 1) underestimated mortality for newly settled fish if there had been high mortality during the first days of settlement before observations began, or 2) overestimated mortality if observed fish emigrated from the study area. Total mortality (Z) was calculated as the slope of the descending limb of the “catch curve” (a plot of the natural logarithm of fish remaining each year versus relative age). Annual mortality was estimated as $1 - e^{-Z}$ (Ricker, 1975).

Total mortality Total mortality for harvested fish was estimated in several ways: 1) length-converted catch curves (Pauly, 1983); 2) the relation between Z and mean length of fish in the catch:

$$Z = K(L_\infty - L_c) / (L_c - L'),$$

where L_c = the average length of fish greater than length L' ; and

L' = the size at which fish are assumed to be fully recruited to the fishery (Beverton and Holt, 1957);

and 3) Hoenig's (1983) empirical relation between Z and a population's longevity:

$$\ln(Z) = 1.46 - 1.01 \ln(t_{max}),$$

where t_{max} = maximum age.

Natural mortality Natural mortality (M) was estimated with two empirical equations:

$$\log M = 0.007 - 0.279 \log L_\infty + 0.654 \log K + 0.463 \log T \text{ (Pauly, 1980),} \quad (1)$$

where T = the average monthly water temperature in the study area (28.6°C), and

$$\ln(M/K) = 0.30 \ln(T) - 0.22 \text{ (Longhurst and Pauly, 1987).} \quad (2)$$

⁶ Color phases of newly settled *A. lineatus* are not described in the literature. The “light” phase is that of adult coloration; the “dark” phase is light-to-dark gray (overlying a faint adult color pattern) and the caudal fin is orange (differentiated from dark newly settled *Ctenochaetus striatus* which have orange only on caudal fin tips).

Biological characteristics of harvest

Length-based estimates of maturity and age were calculated for artisanal catches. Additionally, in 1994–95 we measured the catches of 19 groups of 1–4 fishermen ($n=43$) who had fished together, to determine their average catch per unit of effort (CPUE: kg/h per person). The principal method was spear fishing by free diving; data are presented for that gear only.

Results

Length, weight, sex, and maturity

A complete size range of newly settled, juvenile and adult *A. lineatus* was present in rotenone-treated samples from shallow nearshore waters <2 m deep (Fig. 3), but large fish were underrepresented because some avoided capture. Night spear fishermen harvested the larger fish, generally 15–21 cm FL.

Males and females taken in the fishery were of similar length ($t=0.26$, $df=993$, $P=0.8$) and the sex ratio was nearly equal (1 male:1.1 females, $n=995$). Length-weight relations for the sexes did not differ significantly (ANOVA, $F=0.07$, $P=0.79$); thus all fish were pooled, including smaller unsexed fish: $\log \text{ weight (g)} = -1.60 + 3.03 \log \text{ length (FL in cm)}$ ($r^2=0.99$, $n=1,047$). The relation between FL and standard length in cm was $SL=0.86(FL) - 0.38$ ($r^2=0.99$, $n=94$).

Mature fish of both sexes generally had well-developed gonads (6.2 ± 0.2 g, $n=529$) or gonads that appeared to be partly or wholly spawned out ($1.2 \pm$

0.1 g, $n=108$). Immature fish had little gonad development (0.2 ± 0.01 g, $n=502$). Fish reached sexual maturity at 15–21 cm FL (Fig. 4), with males maturing at a slightly smaller size than females. Half of both sexes were mature at about 18 cm, i.e. at approximately 4 years of age.

Spawning

The gonadosomatic index (GSI) was highest during October–February (Fig. 5) and was strongly correlated with daylength and feeding hours (Table 1). Spawning also occurred throughout the year. During all months, groups of 50–200 fish were observed spawning at dawn in the outer portion of the outer reef channel at Afao (see Fig. 2). Additional details are provided elsewhere (Craig, in press).

Settlement of young onto reef

Newly settled fish ($n=575$) exhibited both light (79%) and dark (21%) color phases.⁶ Settlement peaked in March–April with densities of 0.4–0.6 recruits/m² on

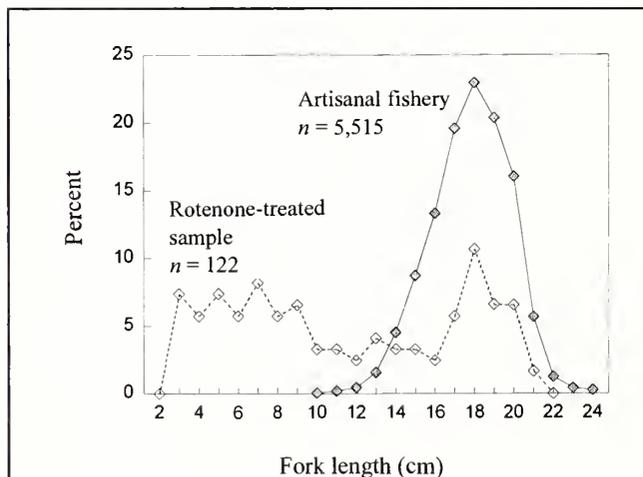


Figure 3

Sizes of *A. lineatus* in the artisanal fishery, all years combined (1987–95), and those collected in rotenone-treated shallow waters.

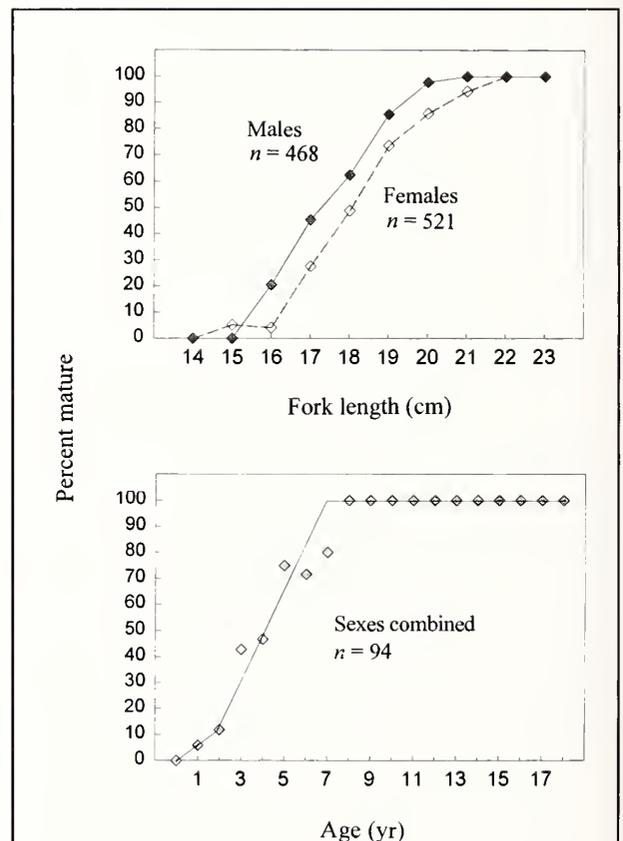


Figure 4

Length and age at maturity for *A. lineatus*.

the outer reef flat (Fig. 6). The settlement pulse occurred one month earlier at Matu'u as indicated by the significant site-time interaction detected by the repeated-measures MANOVA ($P=0.03$, $F=4.67$, numerator $df=22$, denominator $df=6$). In previous years, similar large pulses occurred in earlier months (Nov-Mar; senior author, pers. obs.).

Seasonal changes in fish condition

Fish condition factor (CF) peaked in summer and declined rapidly thereafter (Fig. 7). For mature fish, a decline in CF after the spawning season was expected, but a similar decline was evident among immature fish. Postabdominal fat bodies also declined

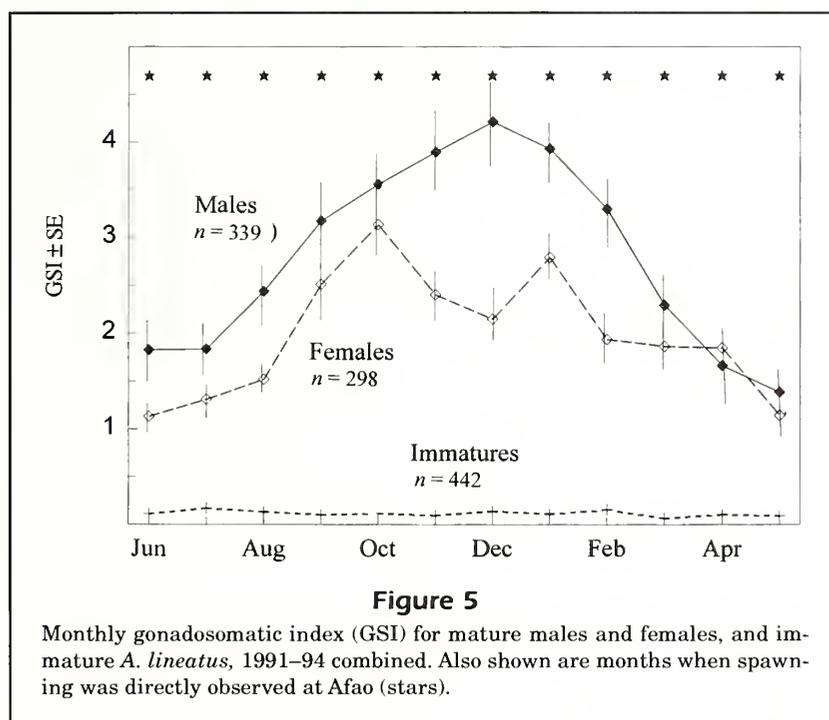
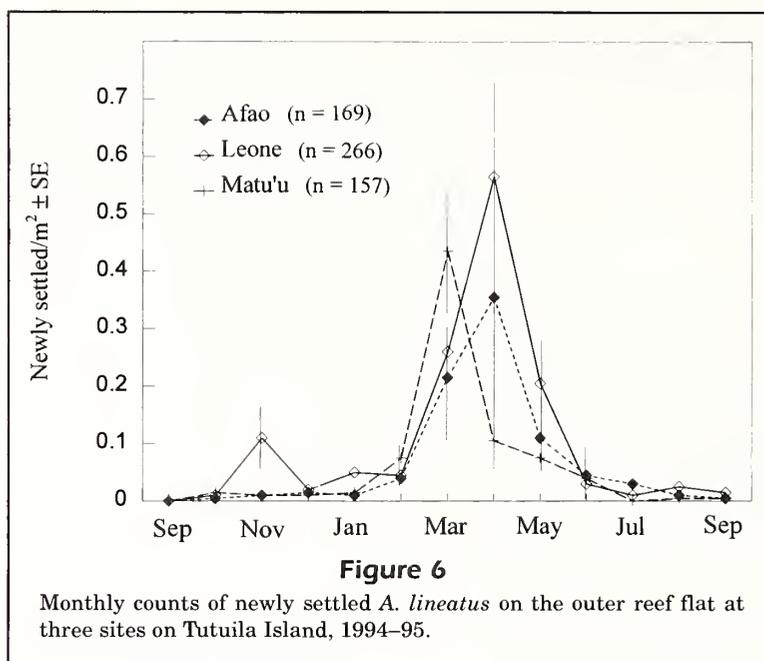


Table 1

Correlation coefficients between monthly averages for physical and biological variables: gonadosomatic index (GSI), condition factor (CF), and paired fat bodies of *A. lineatus*. P = probability value.

	Water temperature	Daylength	Calm surf index	Rainfall	Feeding hours
GSI: mature fish	0.034 $P>0.1$	0.906 $P<0.001$	0.418 $P>0.1$	0.36 $P>0.1$	0.817 $P<0.01$
GSI: immature fish	0.347 $P>0.1$	0.129 $P>0.1$	0.252 $P>0.1$	0.335 $P>0.1$	0.311 $P>0.1$
CF: mature fish	0.495 $P>0.1$	0.703 $P<0.02$	0.65 $P<0.05$	0.667 $P<0.02$	0.511 $P<0.1$
CF: immature fish	0.846 $P<0.001$	0.546 $P<0.1$	0.925 $P<0.001$	0.706 $P<0.02$	0.343 $P>0.1$
Fat bodies: mature fish	0.77 $P<0.01$	0.228 $P>0.1$	0.702 $P<0.02$	0.491 $P>0.1$	0.036 $P>0.1$



steadily from early summer through the cooler season (Fig. 8). These losses resulted in CF values that were about 10% below peak summer levels and in fat bodies that were about two thirds below peak levels.

Seasonal changes in five environmental factors paralleled changes in fish condition (Fig. 8). During the cooler season, nearshore water temperatures dropped below maximum summer values (-9%), as did available feeding hours (-14%), calm water conditions (-44%), rainfall (-76%), and daylength (-13%). Most physical factors were significantly autocorrelated (7 out of 10 comparisons), indicating that there is a distinctive seasonal signal in the nearshore environment, despite Samoa's open-ocean location near the equator. Monthly CF values for immature and mature fish were significantly correlated with 3 of the 5 physical factors (Table 1). It seems clear that the fish were responding to a seasonal change, but causative factors are not known.

Growth

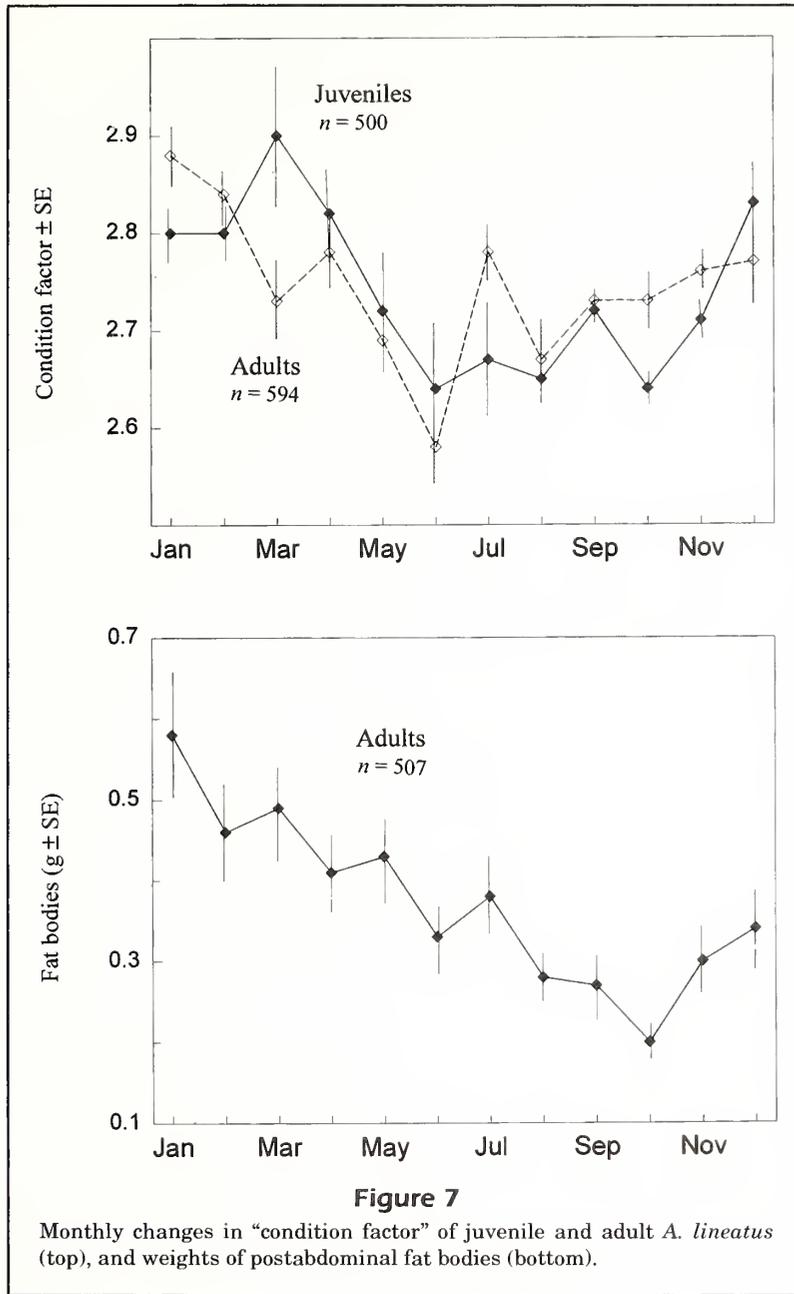
Otolith-based ages and size determinations of naturally marked fish provided two estimates of *A. lineatus* growth. Otolith weight was highly correlated with the number of annular bands in an otolith (Fig. 9). The fish grew rapidly, attaining 70-80% of their total growth by the end of their first year, and they were long-lived—up to 18 years (Fig. 10). Field estimates of fish growth confirmed the rapid early growth but underestimated later growth in comparison with the otolith-based determinations. Similar values of K and L_{∞} were derived

from both the otolith-based age-length relation (Ford-Walford regression: $K=0.7$, $L_{\infty}=20.3$ cm, $r^2=0.93$) and from size increments of marked fish (Gulland-Holt plot: $K=0.8$, $L_{\infty}=21.0$ cm, $r^2=0.58$).

However, L_{∞} and K were highly dependent on the age range of fishes examined (Fig. 11). Iterative Ford-Walford regressions of the smoothed mean size at age showed that K dropped progressively from 0.8 for the whole sample (ages 0-12) to 0.1 when juvenile fish ages 0-3 were excluded. Asymptotic length (L_{∞}) increased in a similarly systematic manner from about 20 cm to 22 cm. Therefore, separate VBGF growth curves were generated for the juvenile phase (ages 0-3, $K=1.1$, $t_0=-0.2$, [$L_{\infty}=18.3$ cm]) and adult phase (ages 4-12, $K=0.12$, $L_{\infty}=22.1$ cm, $t_0=-15.6$), a separation based on the age at which 50% of the population was mature (age 4, Fig. 4). The two-phase curve captured the precocious growth and attained a larger, more realistic L_{∞} that approached the maximum size of fish taken in the fishery (see Fig. 3). Using the relation that longevity is approximated by $3/K$ (Pauly, 1983) and the adult K -value derived for ages 4-12, we predicted that the maximum age would be 25 years, which compared favorably with the observed maximum age of 18 years.

Mortality

Mortality indices differed among the three size classes of naturally marked fish at the Afao site (Fig. 12). Only 2% of the newly settled fish and 34% of the juveniles appeared to survive and grow into the next



larger size class. At these rates, only 1% ($2\% \times 34\%$) of the population would survive their first year on the reef. Thereafter numbers of marked adults declined rapidly at a loss of 48%/yr ($Z=0.65$). At these rates, the life span of combined life history stages would only be about 4–5 years. However, longevity, as revealed by otolith analysis, indicated that field mortality of marked fish was greatly overestimated. Mean ages of artisanal catches were 4–6 years (see below) and some fish lived up to 18 years. It is therefore likely that some marked fish emigrated from the study area rather than died (see "Discussion" section).

To obtain a more realistic estimate of adult mortality, the annual loss of fish in each age class of the 1994–95 fishery was examined by length-converted catch curves calculated in two ways: 1) after conversion with the VBGF parameters for adult fish (Pauly, 1983), and 2) after graphical conversion of lengths to ages based on the weighted length-age relation derived by otolith analysis. The latter was included because of the variability of the VBGF parameters shown in Figure 11. For fish that were assumed to be fully recruited to the fishery, total mortality was low in both cases ($Z=0.24$ and 0.23 ; Fig. 13), equat-

ing to an annual loss of about 20%. Similar values were obtained with Hoenig's equation ($Z=0.23$) and Beverton and Holts' relation between Z and mean length of fish in the catch ($Z=0.19$, $K=0.12$, $L_{\infty}=22.1$ cm, $L_c=19.6$, $L'=18$ cm).

Natural mortality (M) was estimated to be 0.2 and 0.45 with the empirical equations of Longhurst and Pauly (1987) and Pauly (1980), respectively, and with the adult values of K and L_{∞} . The lower value indicated that M is equivalent to Z ; the latter value was spurious given that it exceeded Z .

Biological characteristics of harvest

The flattened growth curve exhibited by older *A. lineatus* limited analyses based on length-converted ages, but the conversion did indicate that most fish taken in the fishery were relatively young (Fig. 14). During the 9-year period 1987–95, annual catches varied moderately in mean age (3.6–6.2 years), mean length (17.5–19.3 cm FL), proportions of immature fish taken (29–60%), and total mortality (0.16–0.31)(Table 2). No trends in these variables were apparent, with one exception: the maximum size of fish decreased. Maximum sizes of fish in 1987–88, however, seem unrealistically high (Fig. 14), and in any case, mean sizes in later years (1994–95) were significantly larger than in earlier years (1987–88)($t=9.7$, $df=5088$, $P<0.001$).

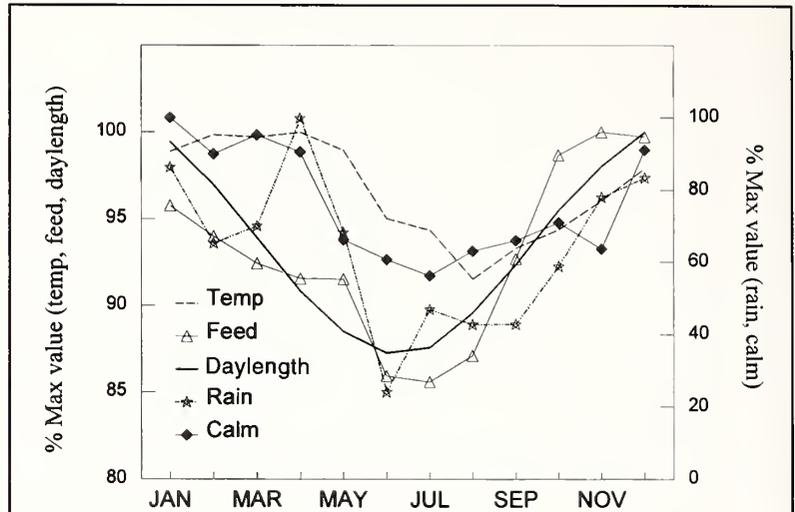


Figure 8
Relative seasonal changes in five environmental variables in the study area (see text for definitions): water temperature, feeding hours, daylength, rainfall, and calm surf. Note different y-axes.

Although the more detailed 1994–95 market data spanned a relatively short period (Fig. 15), available data indicated no decrease in fish size ($r=0.28$, $df=17$, $P>0.1$) or CPUE over time ($r=0.41$, $df=17$, $P=0.085$), and no relation between fish size and CPUE at various island-wide fishing sites, i.e. sites with low CPUE did not have smaller fish ($r=0.28$, $df=17$ $P>0.1$).

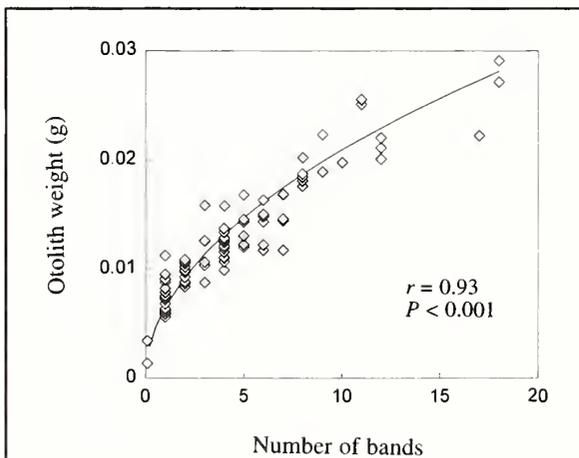


Figure 9
Relation between otolith bands and otolith weight: $\log(\text{age}) = 4.34 + 1.99 \log(\text{otolith wt.})$, $n=88$.

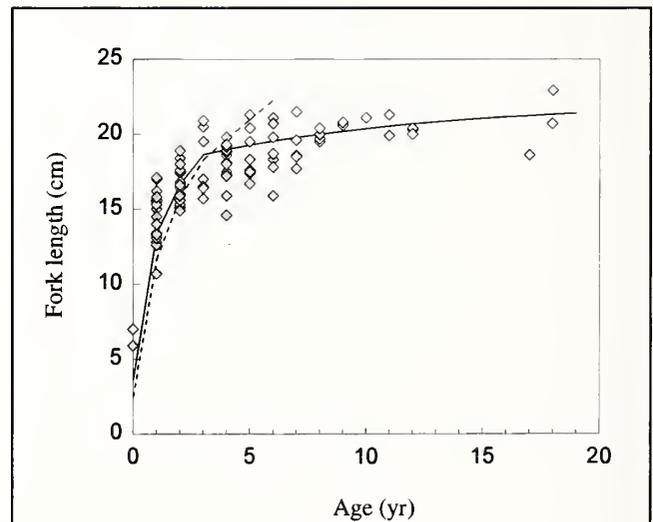


Figure 10
Age-length relations for *A. lineatus*. The solid line indicates a two-phase von Bertalanffy curve for ages 0–3 and 4–18; the dashed line indicates the growth of naturally marked fish based on visual estimates of fish size over time.

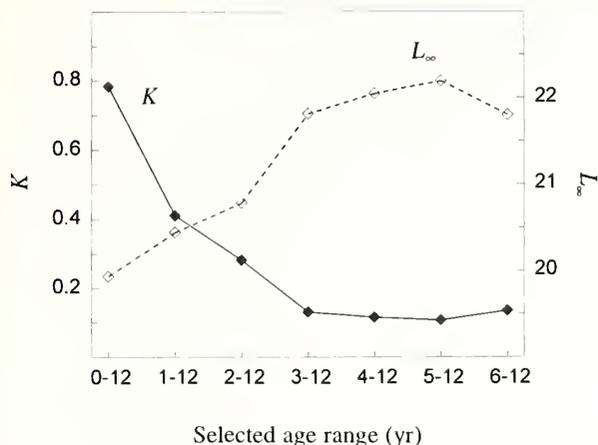


Figure 11

Changes in K and L_{∞} based on iterative Ford-Walford regressions that progressively excluded age classes of younger fish. Age-length data used in this calculation were derived from a smoothed line of mean size at age.

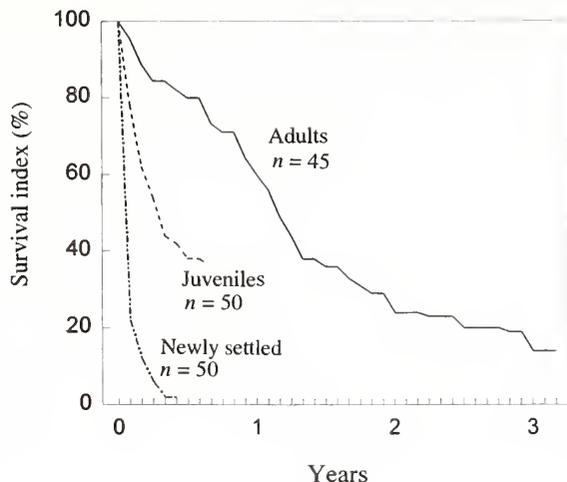


Figure 12

Survival index (percentage of fish returning to their territories) for newly settled, juvenile and adult *A. lineatus* at the Afao site.

Discussion

The life history traits exhibited by *A. lineatus* are common among coral reef fishes (e.g. Sale, 1991): it is a territorial fish that spawns year-round but primarily during the austral summer, its pelagic young settle onto the reef in a dense pulse and suffer high mortality, survivors are sedentary but occasionally relocate to new sites, and the fish grow rapidly, have relatively low mortality rates after their first year and may live for many years. Of particular interest in this study was the opportunity to examine fishing pressure on a coral reef species. In this instance, the possibility of emigration rates of a “highly site-attached species” and the rapid initial growth pattern provide a useful context for examining the fisheries data. Additionally, because

another data set is available for this species, we were able to compare locality-specific demographic traits.

Emigration

Acanthurus lineatus is strongly site-attached (adult fish have a 99.9%/day return rate to the same site: Craig, 1996), but it occasionally switches territories. After 3 years of monitoring, 6 of the 45 marked adults remained on site (Fig. 12), whereas 23 adults would have been present with an annual mortality rate of 20% as determined by catch curve. The difference (17/45) indicates that 38% of the adults that disappeared had probably emigrated to other sites. Craig

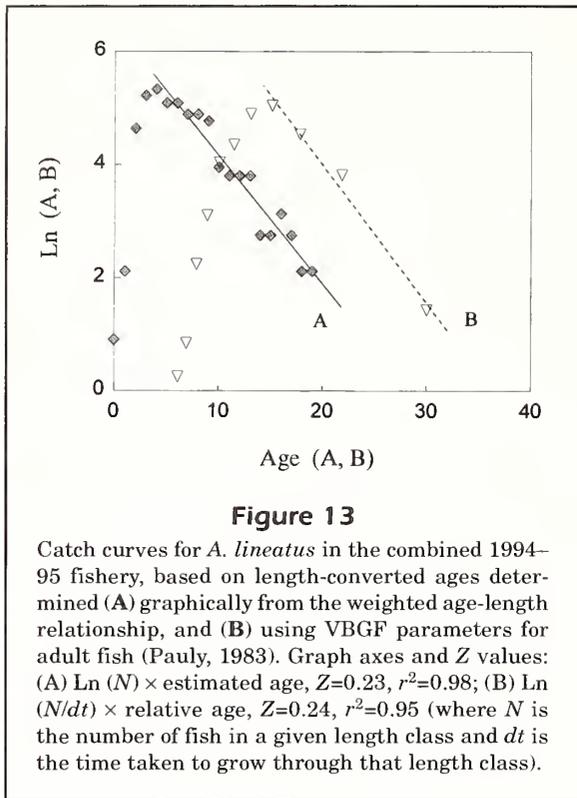
Table 2

Size, age, maturity, and mortality of *A. lineatus* in the artisanal fishery in American Samoa, 1987–95. n = sample size.

	1987	1988	1990	1994	1995
Mean FL (cm)	18.2	17.6	18.9	19.3	18.0
SE	0.04	0.1	1.0	0.5	0.7
Maximum FL (cm)	27.7	28.9	22.4	23.0	23.0
Mean length-converted age	4.6	3.6	5.7	6.2	4.1
Percent immature	46	60	37	29	53
Total mortality (Z_1)	0.22	0.23	0.19	0.23	0.25
(Z_2)	0.25	0.16	0.31	0.23	0.23
n	2,499	1,126	329	720	745

Z_1 = Z derived from a catch curve based on length-converted ages with “adult” VBGF parameters.

Z_2 = Z derived from a catch curve based on graphical conversion of length to age with the age-length relation.

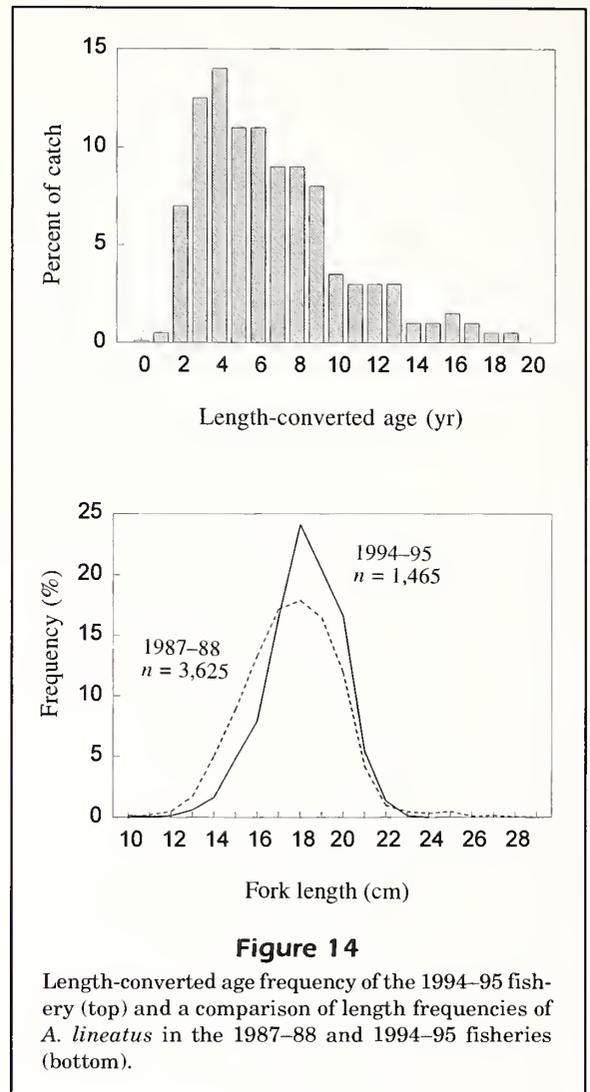


(1996) also monitored the same marked fish described in the present study and reported that an additional 22% of the adults changed territories to nearby locations and were relocated (for the purpose of calculating mortality, these fish were not of course considered deaths). Altogether then, about 60% of the adults changed territories at some point during the 3-year period of observation. This analysis is not thought to be complicated by the loss of fish due to fishing mortality (F), because the 20% mortality rate incorporated F . Further, Afao was a lightly fished area (senior author, unpubl. data).

Emigration probably also accounted for the loss of many juveniles and newly settled recruits shown in Figure 12. Although the annual input of recruits to the reef was high, the observed “survival” rate of these fish during their first year (1%) could not maintain the standing stock of adult fish. To illustrate, the adult density of 40 fish/100m² (Craig, 1996) would lose 8 fish/100m² per year at an annual loss of 20%. To replace those fish with newly settled fish (with an annual input rate of 100 recruits/100m² per year), a survival rate of 8% would be required during their first year.

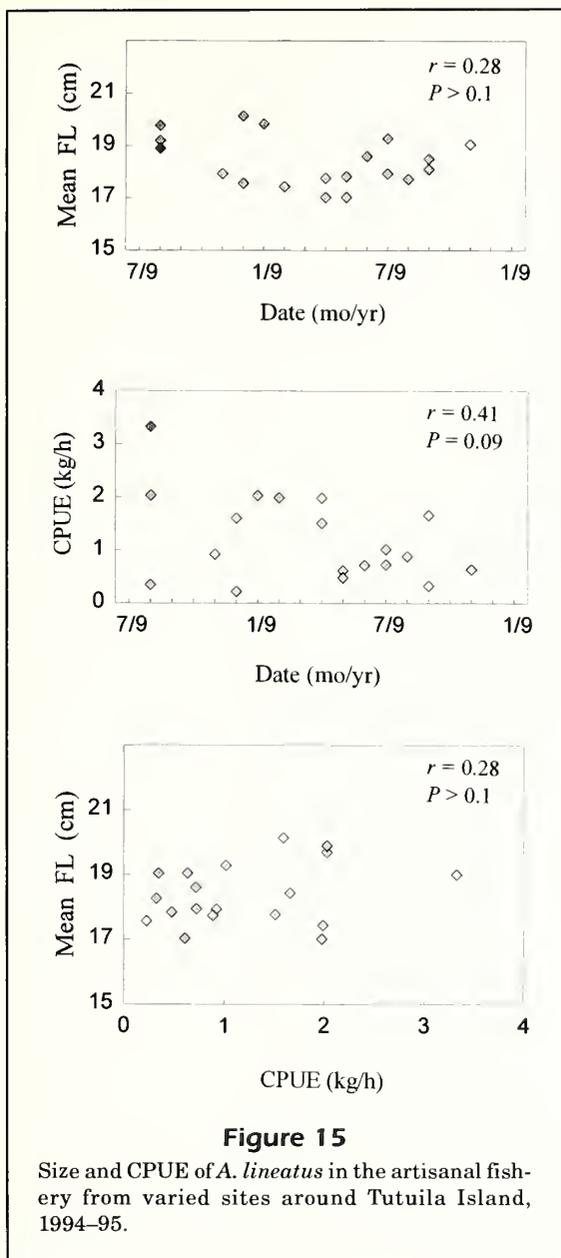
Growth pattern

The rapid growth of young *A. lineatus* was so pronounced that initial VBGF analyses produced age-



dependent estimates of L_{∞} and K . The fish attained most of their adult size during their first year, even though the species was long-lived. There is increasing evidence that this growth pattern is common among coral reef fishes (Choat and Axe, 1996; Hart and Russ, 1996; Newman et al., 1996; Williams et al.⁷). Standard applications of growth models may be inappropriate for populations exhibiting these growth characteristics. Use of a two-phase von Bertalanffy growth curve (e.g. Soriano et al., 1992; Ross et al., 1995) is a possible solution, although care must be taken to establish consistent procedures for separating the two phases of the curve.

⁷ Williams, D., S. Newman, M. Cappo, and P. Doherty. 1995. Recent advances in the ageing of coral reef fishes. Workshop on management of South Pacific Inshore Fisheries, New Caledonia, 26 June–7 July 1995. Joint Forum Fisheries Agency—South Pacific Comm., Biol. Paper 74, 5 p.



Comparison of Samoan and Great Barrier Reef (GBR) populations

There are noteworthy differences between *A. lineatus* populations off Samoa and those on the GBR. Fish grow larger and live up to twice as long on the Great Barrier Reef than those off Samoa (Fig. 16); they are also more sparsely distributed and have lower recruitment rates of newly settled young (Choat and Bellwood, 1985; Choat and Axe, 1996; Craig, 1996; Choat, unpubl. data). Reasons for these differences are speculative and may be complicated by the existence of a fishery in Samoa (see section below).

Perhaps *A. lineatus* in Samoa is comparatively short-lived and maintains its abundance by a high annual input of newly settled young. Why there should be a greater abundance of newly settled fish in Samoa, an oceanic island, than in the extensive reef network of the GBR is unclear.

Fishing pressure

For at least the past 18 years, the catch composition of fish taken by night spear divers has not changed greatly, particularly with respect to the prominent catch of surgeonfishes (Fig. 17). Although Wass⁸ did not identify the species composition of the 1977-80 subsistence catch, local residents report that *A. lineatus* has always been a plentiful and popular food fish.

Indicators of current levels of fishing pressure were ambiguous. Some evidence indicated that overall fishing pressure was low: 1) survival rates of fish age 1 year and older were high (80% per year), 2) estimates of total mortality and the mean size of fish in the fishery changed little over a 9-year period, 3) there was no relation between fish size and CPUE, and 4) an estimate of natural mortality was similar to that of total mortality. However, some of these points are not overly persuasive. First, estimates of natural mortality were derived from empirical equations that embody considerable variability (Gulland, 1984). Second, trends based on fish size are of uncertain value as indicators of fishing pressure due to fish behavior. At night, when *A. lineatus* is harvested, there is an apparent spatial separation of small and large fish. Fish less than about 14 cm are not often encountered in the areas fished (senior author, pers. obs.), perhaps because they remain in shallower areas or hide within smaller crevices during the night. Thus the larger sizes of fish taken by the spear fishermen represent those that were available to them, i.e. there was little opportunity for size selection. Consequently, the mean size of fish harvested could remain relatively stable under increasing levels of fishing pressure until there were no more fish left to catch.

Indications that fishing pressure was affecting the population included 1) decreases in maximum size of fish over a 9-year period, 2) the absence of very old fish in the Samoan population compared with the GBR population, as might be expected in a fished population, and 3) a possible decrease in CPUE. These points, too, are less than compelling. First, the

⁸ Wass, R. 1981. The shoreline fishery of American Samoa, past and present. In J. Munro (ed.), Marine and coastal processes in the Pacific: ecological aspects of coastal zone management: proceedings of the UNESCO seminar at Motupore Island Research Center, 1980, p. 51-63. United Nations Education, Scientific and Cultural Organization, Paris.

decrease in maximum size was counterbalanced by a significant increase in the mean size of the catch during the same period (Fig. 14). Second, the comparison with GBR may not be valid, because natural longevities of the two populations may differ. The two populations are nearly 5,000 km apart and they dwell in different water temperature regimes; thus some geographic variation is likely. Third, the possible CPUE decline was not statistically significant and was also compromised by occasions when fishermen targeted species other than *A. lineatus*. One

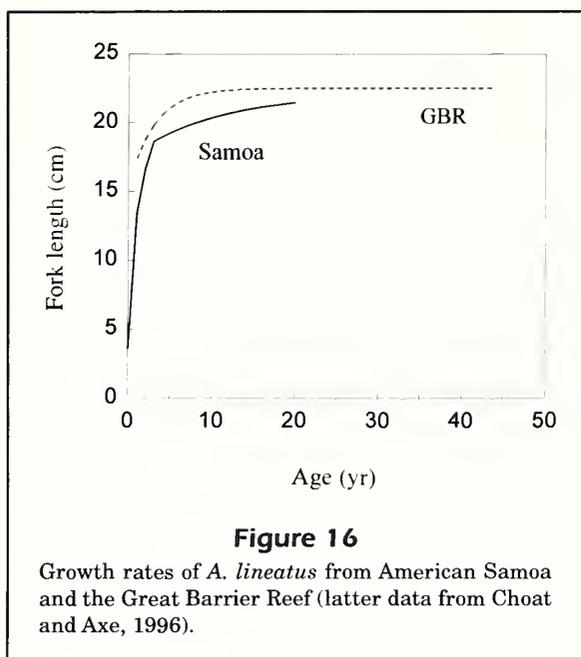


Figure 16

Growth rates of *A. lineatus* from American Samoa and the Great Barrier Reef (latter data from Choat and Axe, 1996).

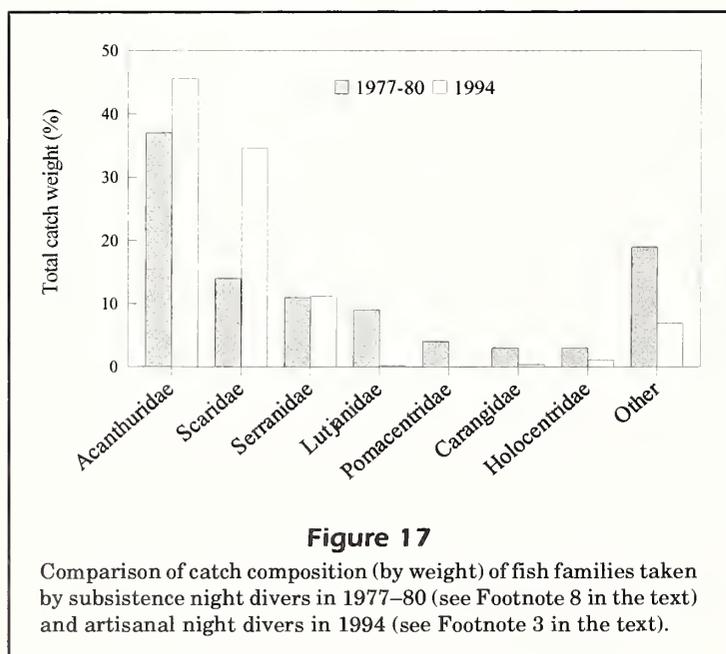


Figure 17

Comparison of catch composition (by weight) of fish families taken by subsistence night divers in 1977-80 (see Footnote 8 in the text) and artisanal night divers in 1994 (see Footnote 3 in the text).

group of fishermen we interviewed had been told before diving that the fish buyer already had enough *A. lineatus*, thus some low CPUE values may indicate a saturated market rather than a depleted stock.

Given the indefinite nature of these indicators, it remains unclear whether fishing pressure is having a significant effect on the demographics of *A. lineatus*, but the composite picture does not indicate substantial overfishing. We acknowledge, however, that localized overfishing is a distinct possibility. Villagers often complained that the night spear fishermen had depleted fish stocks along their village coastline. Although the artisanal fishermen generally rotated areas fished to maximize their CPUE, the villagers living near the area fished might be left with a diminished resource for a period of time.

An additional concern is that an increase in fishing efficiency was in progress in 1995, with a conversion from free diving to scuba diving. Catch-per-unit-of-effort for scuba diving was more than twice that of free diving (3.8 vs. 10.5 kg/h for all species combined). A further concern is that the human population of American Samoa, like that on many other South Pacific islands, is increasing rapidly; thus the demand on nearshore resources seems likely to increase (Craig⁹).

The lack of overt signs of fishing stress for *A. lineatus* in the artisanal fishery is at odds with observed declines in the subsistence fishery on the same coral reefs. Multispecies subsistence catches dropped from 265 and 311 t in 1979 and 1991 (Ponwith²; Wass⁸), to 48 t 1995 (Saucerman³). Catches of *A. lineatus*, a minor component in this fishery, dropped from 8 t in 1991 to 1 t in 1995. Although some of this decline may be attributed to reduced fishing effort, CPUE for most gear types declined as well (Saucerman³).

Causes of reduced subsistence catches are not clear but may include a variety of factors such as fishing for selected species, a reduced reliance on subsistence fishing, and habitat degradation (Craig et al.¹⁰). Coral reefs in American Samoa have been severely damaged in the past 15 years by three hurricanes, an *Acanthaster* starfish invasion, temperature rises that resulted in mass coral bleaching, and sedimentation from land. Whether these en-

⁹ Craig, P. 1995. Are tropical nearshore fisheries manageable in view of projected population increases? Workshop on management of South Pacific Inshore Fish., New Caledonia, 26 June-7 July 1995. Joint Forum Fisheries Agency-South Pacific Comm., Biol. Paper 1, 6 p.

¹⁰ Craig, P., A. Green, and S. Saucerman. 1995. Coral reef troubles in American Samoa. South Pacific Comm., New Caledonia, Fish. Newsletter 72:33-34.

vironmental disturbances have affected fish catches is not known, but it seems possible that these changes may have contributed to the current abundance of *A. lineatus* by creating expansive areas of denuded habitat suitable for the growth of turf algae that *A. lineatus* eats (Craig, 1996). As previously mentioned, live coral covered only 3.5% of the outer reef flat zone inhabited by this species, i.e. over 90% of the habitat seemed ideal for turf algae and *A. lineatus*. As the reefs recover, we speculate that *A. lineatus* may decrease in abundance and become less dominant in artisanal catches.

Acknowledgments

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Abstract.—A total of 12,180 king mackerel, *Scomberomorus cavalla*, collected from 1986 to 1992 from North Carolina to Yucatan, Mexico, and 2,033 collected in 1977 and 1978 from North Carolina to Texas were aged with whole or sectioned sagittal otoliths. Data were analyzed by region—Atlantic Ocean, eastern Gulf of Mexico, and western Gulf—reflecting the currently recognized stocks. Maximum sizes of females aged were 152, 158, and 147 cm FL in the Atlantic, eastern Gulf, and western Gulf, whereas the largest males were 121, 127, and 117 cm FL in those same regions. Maximum ages from the 1986–92 fish were 26, 21, and 24 yr for females and 24, 22, and 23 yr for males in the Atlantic, eastern Gulf, and western Gulf, respectively. Females grew faster and larger than males at every age in each region. A very consistent pattern of greatest growth in the eastern Gulf, intermediate in the western Gulf, and least in the Atlantic was present each year during 1986–92, most noticeably among females. During 1977–78, Atlantic females also had distinctly lower growth than Gulf fish. These consistent regional differences support the current hypothesis that there are three stocks as suggested by previous analyses of other types of data. Within a region and sex, growth was lower in 1977–78 than in 1986–92 in both the Atlantic and eastern Gulf, but higher for western Gulf females.

Spatial and temporal variation in age and growth of king mackerel, *Scomberomorus cavalla*, 1977–1992

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King mackerel, *Scomberomorus cavalla*, are economically valuable and highly sought after by U.S. recreational and commercial fishermen from North Carolina to Texas (Manooch, 1979). They also support a substantial commercial fishery in Mexico (Gulf of Mexico and South Atlantic Fishery Management Councils¹). Some populations have been overfished and since 1983 the species has been managed by a joint fishery management plan of the Gulf of Mexico and South Atlantic Fishery Management Councils.² The species is managed as two stocks, an Atlantic migratory group and a Gulf migratory group, although the Councils recognize that there are actually two groups in the Gulf—an east and a west (Grimes et al., 1987; Johnson et al., 1994; Gulf of Mexico and South Atlantic Fishery Management Councils³). However, the paucity of data from the large Mexican fishery, which has a major impact on the western Gulf stock, precludes managing the two Gulf groups separately. Because tag return data (Sutter et al., 1991) collected during 1975–78 indicated considerable seasonal movement between the Gulf of Mexico and Atlantic Ocean, the boundary between the Gulf and Atlantic stocks was defined as the Volusia-Flagler County line off northeast Florida during November–March and the

Monroe-Collier County line off southwest Florida during April–October. The Gulf stock has been heavily overfished throughout much of its management history, unlike the Atlantic stock, which has never been considered overfished (Mackerel Stock Assessment Panel⁴).

¹ Gulf of Mexico and South Atlantic Fishery Management Councils. 1992. Amendment 6 to the fishery management plan for coastal migratory pelagics in the Gulf of Mexico and South Atlantic. Gulf of Mexico Fishery Management Council, The Commons at Rivergate, 3018 U.S. Highway 301 North, Suite 1000, Tampa, FL 33619-2266; and South Atlantic Fishery Management Council, Southpark Building, Suite 306, 1 Southpark Circle, Charleston, SC 29407-4699, 35 p.

² Gulf of Mexico and South Atlantic Fishery Management Councils. 1982. Fishery management plan, final environmental impact statement, regulatory impact review, final regulations for coastal migratory pelagic resources (mackerels) in the Gulf of Mexico and South Atlantic region. Gulf of Mexico Fishery Management Council, Tampa, FL; and South Atlantic Fishery Management Council, Charleston, SC, var. pagination.

³ Gulf of Mexico and South Atlantic Fishery Management Councils. 1990. Amendment Number 5 to the fishery management plan for the coastal migratory pelagic resources (mackerels), 33 p. Gulf of Mexico Fishery Management Council, Tampa, FL; and South Atlantic Fishery Management Council, Charleston, SC, 33 p.

⁴ Mackerel Stock Assessment Panel. 1994. 1994 report of the mackerel stock assessment panel. Miami Laboratory, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami, FL 33149-1003. Contrib. Rep. MIA-93/94-42.

Several studies have examined spatial, temporal, and gear-related variation in life history and fishery parameters of king mackerel. The parameters have included mean back-calculated sizes, (Beaumariage, 1973; Manooch et al., 1987), von Bertalanffy growth rates (Johnson et al., 1983; Manooch et al., 1987), and size, age, and sex composition of the catch (Beaumariage, 1973; Johnson et al., 1983; Trent et al., 1983; Trent et al., 1987). The usefulness of this information for current stock assessments is limited for several reasons. Much of the previous work was based on data collected 15 to 25 years ago when exploitation was much lower, the species unmanaged, and population size, at least in the eastern Gulf of Mexico, higher. In addition, all age estimates were based on examination of whole otoliths, which results in considerable under-ageing of older, larger fish (Collins et al., 1989). In addition, some studies were geographically limited (Beaumariage, 1973; Trent et al., 1987), and because stock boundaries were unknown when the data were collected, none of the data were partitioned according to stock boundaries.

The primary objective of this study was to examine variation in age and growth in relation to space, time, and sex of king mackerel collected during 1977–78 and 1986–92.

Methods

Most king mackerel used in this study were collected during 1986–92 as part of a continuing cooperative program between the states from North Carolina to Texas and the National Marine Fisheries Service that was designed to provide age and length-frequency data needed to conduct annual stock assessments. Samples from 1977 and 1978 were collected by Johnson et al. (1983) for their age and growth study. All fish were measured to the nearest centimeter fork length (FL) and are reported in our study in those units.

Three regions, which reflect stock boundaries according to current hypotheses (Grimes et al., 1987; Johnson et al., 1994; Gulf of Mexico and South Atlantic Fishery Management Councils³), were sampled during 1986–92. The regions were 1) Atlantic: North Carolina to about Miami, FL; 2) eastern Gulf: Florida Keys through Mississippi, and, during April–October, Louisiana; and 3) western Gulf: Mexico, Texas, and, during November–March, Louisiana. All Louisiana samples were collected during April–October; therefore they were classified as eastern Gulf. We did not adjust the Atlantic–eastern Gulf boundary seasonally, as the current fishery management plan does, because only 378 of the 5,490 Atlantic fish aged

were collected in the area of mixing off eastern Florida during November–March. These 378 fish were used in the analyses.

For the 1986–92 samples, taken from North Carolina to Yucatan, Mexico, we used stratified sampling (Ketchen, 1950), attempting to collect sagittal otoliths from 20 fish from each unique year, region, sex, and 10-cm size-interval combination. That quota was often exceeded for abundant size intervals and not reached for rarer size intervals.

The fish from Johnson et al.'s (1983) study were collected from recreational hook-and-line catches from North Carolina to Texas. Johnson et al. also used stratified sampling, with each sex and 10-cm size-interval combination comprising a stratum. For the analysis, regional classifications were the same as those used for the 1986–92 samples.

In most cases, heads were shipped to our laboratory where otoliths were removed and stored dry. The majority (>90%) of otoliths collected in the United States were taken from recreational hook-and-line catches, and the remainder from various commercial fisheries. All Mexican samples were collected from commercial fisheries.

For the 1986–92 samples, otoliths from males <80 cm and females <90 cm were read whole. The whole otoliths were placed in a black-bottomed dish containing glycerin and examined with a dissecting microscope at 12–25× with reflected light. For larger fish (males ≥80 cm and females ≥90 cm), three transverse sections about 0.7 mm thick were made about the focus with a Beuhler Isomet low-speed saw. Sections were mounted on glass slides with FLO-TEXX, a clear polymer mounting medium. Sections were examined under transmitted, polarized light at 50 or 125× with a compound microscope. Annuli of whole otoliths were identified according to the criteria of Johnson et al. (1983), and sections according to the criteria of Waltz.⁵ The dorsal half of the section was usually read because it was clearer than the ventral. Otoliths collected during 1986–88 were read independently by two readers, and if there was disagreement, a second reading was made. If the second reading disagreed with the first, the otolith was excluded from analysis. After 1988, otoliths were read by the senior author alone.

Ageing methods for the 1977 and 1978 collections were basically the same, except that we sectioned males ≥75 cm and females ≥80 cm FL and used whole ages from Johnson et al. (1983) for fish below these sizes.

⁵ Waltz, W. 1986. Data report on preliminary attempts to assess and monitor size, age, and reproductive status of king mackerel in the south Atlantic Bight. South Carolina Wildl. Mar. Res. Dep. MARMAP rep. for contract 6-35147.

Ages, to the nearest whole year, were assigned solely on the basis of number of visible annuli for fish collected from mid-July through December. Fish collected 1 January through mid-July had one year added to their age if the marginal increment was estimated to be >80% of the previous annual increment. Ages from samples collected by Johnson et al. (1983) were adjusted similarly with their marginal increment data. This adjustment was necessary because an annulus typically forms during the spring (Beaumariage, 1973; Johnson et al., 1983) but is often difficult to distinguish until later in the summer.

Von Bertalanffy growth equations were fitted to quarterly observed lengths-at-age by using Marquardt's nonlinear regression procedure (SAS Institute, Inc., 1988). Annual ages were converted to quarterly ages by adding 0.25 to the age if the fish was collected during April–June, 0.50 if collected during July–September, and 0.75 if collected during October–December. Quarterly ages were used to minimize the variance about the sizes-at-age because observed annual sizes-at-age, especially for young (1–2 yr old) fish that are growing faster than older fish, can vary considerably depending on month of capture.

For the 1986–92 data, we tested for differences in von Bertalanffy equations between sexes within regions and among regions within a sex, i.e. we compared fitted growth curves, using an F -statistic derived from the multivariate Hotelling's T^2 (Bernard, 1981; Vaughan and Helser, 1990). Estimates of the parameters L_∞ , K , and t_0 are often correlated, making univariate statistical tests inappropriate for comparing differences between like parameters from two groups of fish (Bernard, 1981). To analyze the 1977–78 growth data, we simply examined plots of the von Bertalanffy curves and their 95% confidence limits. We did not use Hotelling's T^2 to test the 1986–92 data for interannual differences, the 1977–78 data for any growth differences, or to compare the 1977–78 and 1986–92 data, primarily because size and age distributions of the samples varied considerably among regions (and to some extent between sexes) and secondarily because the sample size was sometimes quite small. Von Bertalanffy parameter estimates, which are used as data for the Hotelling's T^2 test, would certainly be influenced by sample size and age distributions; if the two groups being tested had dissimilar distributions, then a significant difference might not be biologically meaningful.

Bernard (1981) noted that one of the assumptions for Hotelling's T^2 is that the two sets of estimates being compared have a common variance structure. However, citing Ito and Schull (1964), "if the variance-covariance matrices are unequal, the probability of a Type I error and correspondingly the power

of the T^2 deviate from tabulated values with the same degrees of freedom. However, when both N_1 and N_2 are equal, different variance-covariance matrices do not effect the error level or the power of the test." To run each test with equal sample sizes so we could avoid the problems just mentioned, we randomly sampled from the larger group a number of observations equal to the sample size of the smaller group, then used parameter estimates derived from that sample in the test. However, all growth curves shown in the figures in the present study were based on the full number of available observations.

Results

We aged 14,213 king mackerel—12,180 collected during 1986–92, 2,033 from 1977–78. The numbers of females and males aged from 1986–92 were 3,407 and 2,083 from the Atlantic, 2,753 and 1,285 from the eastern Gulf, and 1,662 and 990 from the western Gulf. From the 1977–78 collections, the numbers of females and males aged were 323 and 128 from the Atlantic, 1,011 and 343 from the eastern Gulf, and 188 and 40 from the western Gulf (Table 1). The geographical distribution of the 1986–92 samples varied annually, and although fish were collected off every coastal state from Virginia to Texas and in Veracruz, Campeche, and in Yucatan, Mexico, the greatest proportion were collected in North Carolina in the Atlantic region, northwest Florida in the eastern Gulf, and south Texas in the western Gulf (Table 1). Most fish collected in 1977–78 came from North Carolina, northwest Florida, and Louisiana (Table 1).

Size and age distributions

Size distributions of aged fish were similar among regions during 1986–92, although females tended to predominate at larger sizes (Fig. 1). In contrast, in 1977–78, size distributions differed markedly, among both regions and sexes (Fig. 1). Males do not grow as large as females, and this difference was reflected in their narrower size distributions (Fig. 1; Table 2). Annual size distributions of aged fish, 1986–92, showed similar ranges each year but some variation in modal sizes (Table 2). The maximum sizes of females aged from 1986–92 were 152 (age 18 [yr]), 158 (age 18), and 147 (age 11) cm for the Atlantic, eastern Gulf, and western Gulf; sizes of males ranged to 121 (age 20), 127 (age 16), and 117 (age 13) cm for those same regions. Maximum sizes of 1977–78 samples were slightly smaller than those from 1986–92 in 5 out of 6 region and sex combinations, most likely because the older data had much smaller

Table 1

Geographical distribution of aged king mackerel for 1977–78, 1986–92, and each year from 1986 to 1992. N.E. Florida = Nassau-Flagler County. E. Florida = Volusia-Palm Beach County. S.E. Florida = Broward-Dade County. S. Florida = Monroe County. S.W. Florida = Sarasota-Collier County. W. Florida = Citrus-Manatee County. N.W. Florida = Escambia-Levy County. N. Texas = Jefferson-Calhoun County. S. Texas = Aransas-Cameron County.

Region	State or area	Number aged																	
		Females									Males								
		77–78	86–92	86	87	88	89	90	91	92	77–78	86–92	86	87	88	89	90	91	92
Atlantic Ocean	Virginia		20	—	—	—	16	1	—	3	—	3	—	—	—	1	1	—	1
	N. Carolina	234	1,982	64	134	68	313	454	402	547	71	1,239	59	101	37	255	274	230	
	S. Carolina	88	568	55	99	113	70	55	78	98	56	255	31	25	50	38	38	31	42
	Georgia	—	292	24	5	45	98	63	13	44	—	144	5	9	15	41	35	2	37
	N.E. Florida	—	52	21	31	—	—	—	—	—	—	6	5	1	—	—	—	—	—
	E. Florida	—	459	30	56	22	5	21	171	154	—	379	63	77	74	6	14	12	133
	S.E. Florida	—	34	6	15	10	3	—	—	—	—	57	14	20	23	—	—	—	—
Eastern Gulf	S. Florida	6	215	5	1	2	29	36	75	67	12	132	6	2	3	27	31	24	39
	S.W. Florida	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—
	W. Florida	—	110	2	—	—	—	—	—	108	—	14	2	2	—	—	—	—	10
	N.W. Florida	532	1,209	51	94	96	227	128	321	292	283	643	7	49	22	125	79	215	146
	Alabama	—	303	50	172	54	7	9	3	8	—	122	22	60	29	—	9	1	1
	Mississippi	7	290	31	55	51	6	69	47	31	—	104	7	8	31	4	26	12	16
	Louisiana	466	628	23	61	56	46	39	195	208	48	265	22	14	12	12	2	108	95
Western Gulf	Louisiana	147	1	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—
	N. Texas	41	281	—	45	90	54	14	47	31	38	181	4	27	56	30	14	23	27
	S. Texas	—	1,026	48	158	130	184	134	206	166	—	553	44	103	39	79	74	102	112
	Veracruz	—	225	—	—	6	47	75	50	47	—	183	—	—	9	44	31	53	46
	Campeche	—	21	—	—	—	13	8	—	—	—	16	—	—	—	7	9	—	—
	Yucatan	—	106	—	—	62	—	1	37	6	—	57	—	—	19	—	—	24	14

samples sizes and the sampling was more limited geographically and temporally.

During 1986–92, the overall age distributions of samples were quite similar among regions and between sexes within regions, but during 1977–78 they varied noticeably (Fig. 2). Maximum ages of king mackerel from 1986–92 in the Atlantic, eastern Gulf, and western Gulf were 26 (137 cm), 21 (127–150 cm), and 24 (144 cm) for females and 24 (117 cm), 22 (110 cm), and 23 (101 cm) for males. Maximum ages from 1977–78 samples from the same respective regions were 20, 19, and 18 for females and 18, 19, and 19 for males. Fish older than age 20 were very rare in the 1986–92 samples—only 22 of 7,822 females (0.15%) and 13 of 4,358 males (0.18%).

Growth

Growth was significantly different between sexes ($P < 0.01$ in 1986–92) in each region during 1986–92 and 1977–78, and females grew faster and larger than males at every age (Fig. 3; Table 3). Although we did not test the 1977–78 data with Hotelling's T^2 ,

it is obvious that the confidence limits do not overlap (Fig. 3). During 1986–92, the predicted sizes at age of females were at least 20 cm larger than males by age 13, 9, and 11 in the Atlantic, eastern Gulf, and western Gulf, respectively.

Age-at-size was highly variable in all regions for both sexes, especially after fish reached 70 cm FL (Tables 4 and 5). For example, Atlantic females 100.1 to 110.0 cm FL ranged from age 4 to 20, whereas males from that same region and size ranged from age 6 to 22.

The pooled 1986–92 data showed that growth was highest in the eastern Gulf, intermediate in the western Gulf, and lowest in the Atlantic for both sexes, and the differences, which were greatest among females, were statistically significant ($P < 0.01$) (Fig. 3; Table 3). Asymptotic length (L_{∞}) was the parameter most often (7 of 9 instances) responsible for the significant differences between growth curves (Table 3), although twice it was t_0 . Estimates of L_{∞} were 126.7, 134.1, and 137.8 cm for Atlantic, western Gulf, and eastern Gulf females, and 96.4, 102.8, and 102.6 cm for males (Table 6). Above age 7 years, the predicted size at age of eastern Gulf

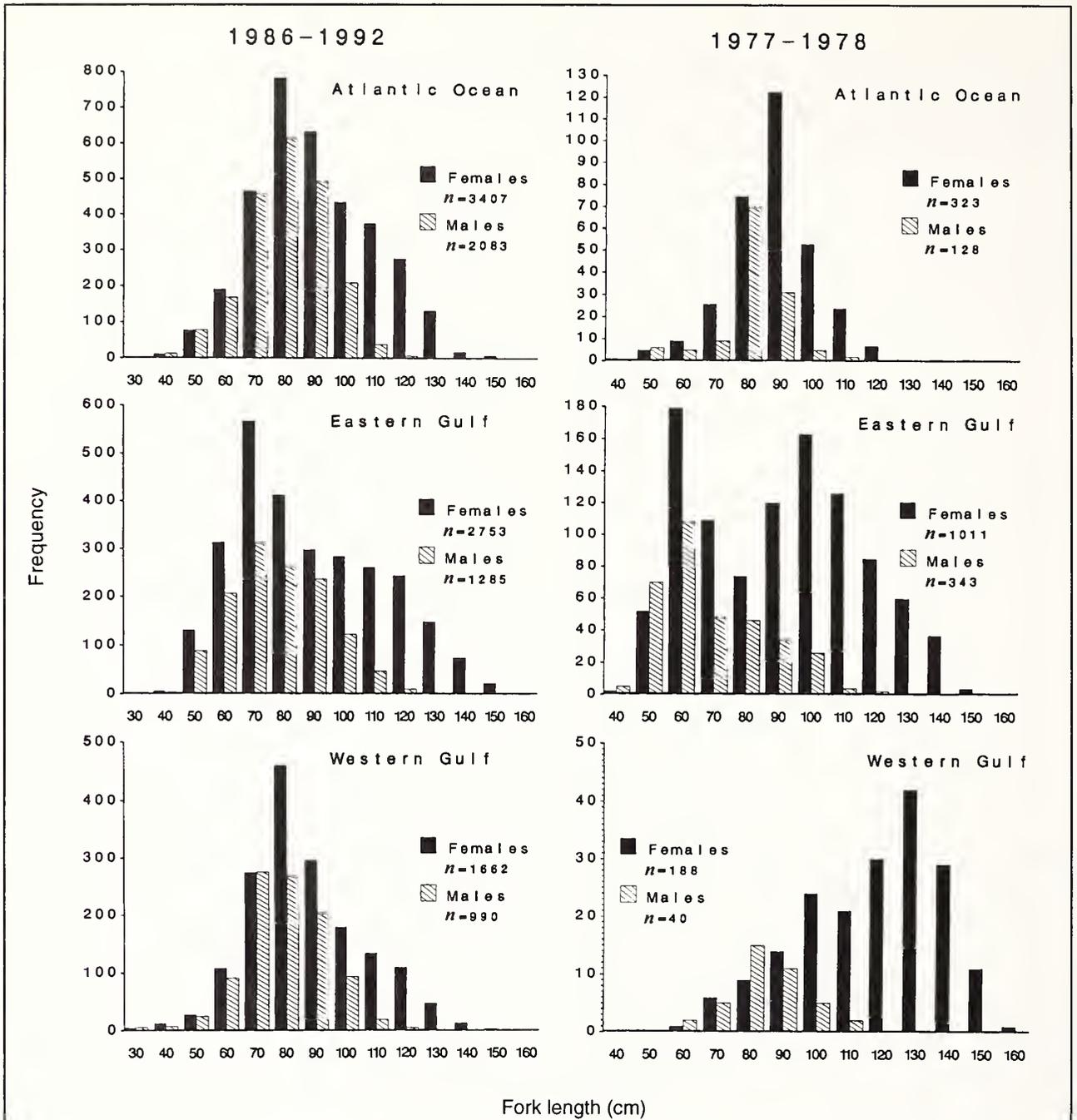


Figure 1

Length-frequency distribution by sex and region of king mackerel included in the analysis and collected during 1977-78 and 1986-92.

females averaged 12.2 cm (SD=0.4) larger than Atlantic females, whereas eastern Gulf males averaged 6.9 cm (SD=0.4) larger than Atlantic males.

The pattern of highest growth in the eastern Gulf, intermediate growth in the western Gulf, and lowest growth in the Atlantic seen in the pooled 1986-92 data was very consistent and present each year during that period. These consistent regional differ-

ences were especially noticeable among females (Fig. 4). Among males, the eastern Gulf growth curve was clearly higher than that for the Atlantic each year, whereas the growth curve for the western Gulf was intermediate in younger fish but converged with the eastern curve at about age 12-14 (Fig. 5).

In 1977 and 1978, as during 1986-92, growth of females was lowest for Atlantic fish; however, unlike

Table 2

Annual length frequency distributions of aged king mackerel, 1986–1992, by region and sex. See Figure 1 for overall 1977–78 and 1986–92 size distributions.

Region	Size interval FL (cm)	Number aged													
		Females						Males							
		86	87	88	89	90	91	92	86	87	88	89	90	91	92
Atlantic Ocean	20–39.9	—	—	—	—	1	—	—	1	—	—	3	—	—	—
	40–59.9	23	72	7	14	14	16	17	36	50	12	5	27	20	13
	60–79.9	94	83	86	129	135	193	248	102	86	91	122	115	117	239
	80–99.9	57	83	91	205	230	289	315	35	88	87	195	186	107	217
	100–119.9	21	58	53	127	150	116	196	3	9	9	16	34	31	26
	120–139.9	5	42	21	30	57	50	67	—	—	—	—	—	—	1
	140–159.9	—	2	—	—	7	—	3	—	—	—	—	—	—	—
Total	200	340	258	505	594	664	846	177	233	199	341	362	275	496	
Eastern Gulf	20–39.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	40–59.9	30	26	9	93	20	58	49	7	14	1	45	22	83	23
	60–79.9	50	135	94	79	99	242	267	20	69	37	58	60	128	170
	80–99.9	34	60	58	65	55	124	206	31	46	53	43	53	129	96
	100–119.9	30	73	55	39	66	153	133	8	11	5	22	11	20	17
	120–139.9	11	72	35	35	33	56	58	—	—	1	—	1	—	1
	140–159.9	7	17	8	4	6	8	1	—	—	—	—	—	—	—
Total	162	383	259	315	279	641	714	66	140	97	168	147	360	307	
Western Gulf	20–39.9	—	—	—	6	—	4	—	—	—	—	7	—	2	—
	40–59.9	—	3	11	12	14	8	29	—	3	8	9	11	6	35
	60–79.9	14	54	76	68	107	171	83	20	47	43	62	58	130	103
	80–99.9	19	88	101	124	70	108	104	27	69	65	64	53	56	57
	100–119.9	9	42	64	51	32	42	33	1	11	7	18	6	8	4
	120–139.9	6	15	36	32	10	7	2	—	—	—	—	—	—	—
	140–159.9	—	1	—	5	1	—	—	—	—	—	—	—	—	—
Total	48	203	288	298	234	340	251	48	130	123	160	128	202	199	

during 1986–92, western Gulf females grew faster and larger than eastern Gulf females according to the growth curves (Fig. 3). Among males, growth also appeared to be lowest in the Atlantic, although the differences were slight (Fig. 3).

There was interannual variation in growth within a region and sex during 1986–92; however, it probably reflected sample differences as much as any actual differences (Tables 1 and 2); therefore we did not test these growth curves statistically.

Plots of the von Bertalanffy curves (Fig. 6) suggested that growth was slightly less in 1977–78 than in 1986–92 in the Atlantic and eastern Gulf for both sexes, whereas western Gulf females grew faster in 1977–78 than in 1986–92. The average differences (and standard errors) in predicted size at age between 1986–92 and 1977–78 for all ages above age 7 were 1) eastern Gulf females: $+2.0 \pm 0.1$ cm; 2) eastern Gulf males: $+2.9 \pm 0.1$ cm; 3) Atlantic females: $+5.8 \pm 0.1$ cm; 4) Atlantic males: $+1.7 \pm 0.1$ cm; and 5) western Gulf females: -9.6 ± 0.6 cm.

Discussion

Our findings were based on data collected as part of a long-term, stratified, nonrandom sampling program (following the suggestions of Ketchen [1950]) designed to provide age-length keys for annual stock assessments. Most fish sampled were caught by hook and line and gill nets, both of which are size-selective gears. Goodyear (1995), using computer simulations, demonstrated that samples equally stratified by length and those from size-selective fisheries often yield biased estimates of mean size-at-age; for this reason he recommended that only simple random sampling be used to generate models of fish growth. He found that most often mean lengths-at-age were overestimated by 5–15% for all but the youngest age classes, which were sometimes underestimated. Goodyear explained that at the youngest ages, the smaller individuals of an age class are often sampled disproportionately to their true abundance, whereas for older ages, the same happens for

the larger (faster growing) fish in a given age class.

Given Goodyear's (1995) findings and our nonrandom sampling design, it may be that our growth models overestimated length-at-age to some degree for all but the youngest age classes, but probably not as much as Goodyear found in his study. Although we had sampling quotas for each year, region, sex, and 10-cm size interval combination, for many different reasons we invariably exceeded those quotas

for all but the rarest size classes, often greatly for the most common length intervals; Table 2 and Figure 1 provide clear evidence of this. Because of this oversampling, our actual design fell somewhere between simple random sampling and length-stratified sampling, and thus should have reduced the bias to some extent. Given this rather small potential bias and the fact that our sample sizes and spatial and temporal coverages greatly exceeded all previous

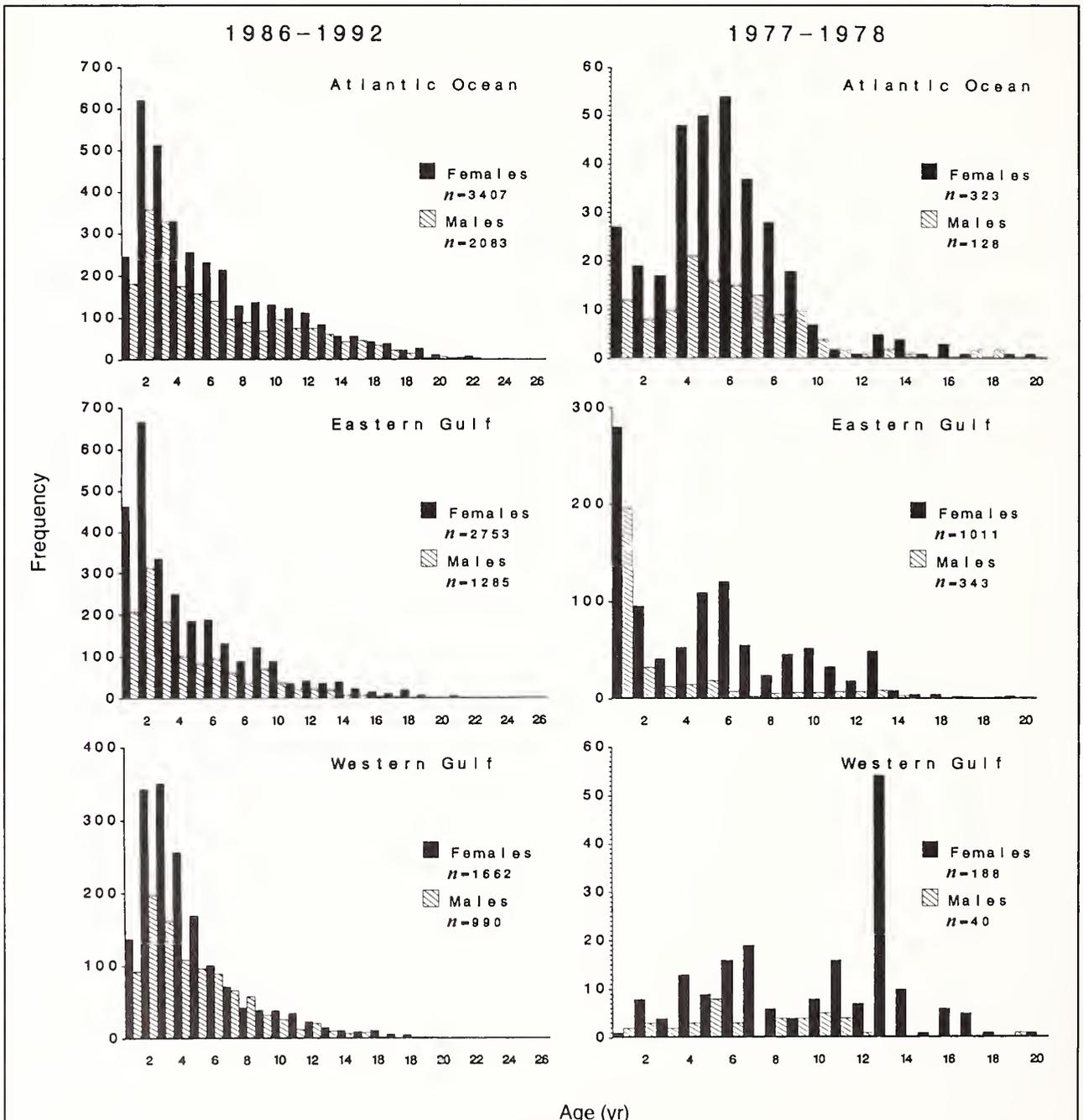


Figure 2

Age distributions by sex and region of king mackerel included in the analysis and collected during 1977-78 and 1986-92.

king mackerel studies (all of which sampled size-selective fisheries and only one (Beaumariage, 1973) of which clearly used simple random sampling), we feel our growth estimates are the best available. Most important, there is no obvious reason to suspect that

the bias would be greatly different among regions or among years; thus our conclusions about the temporal and regional differences in growth should be valid.

Our finding of similar maximum longevity for both sexes differs from all previous studies (except

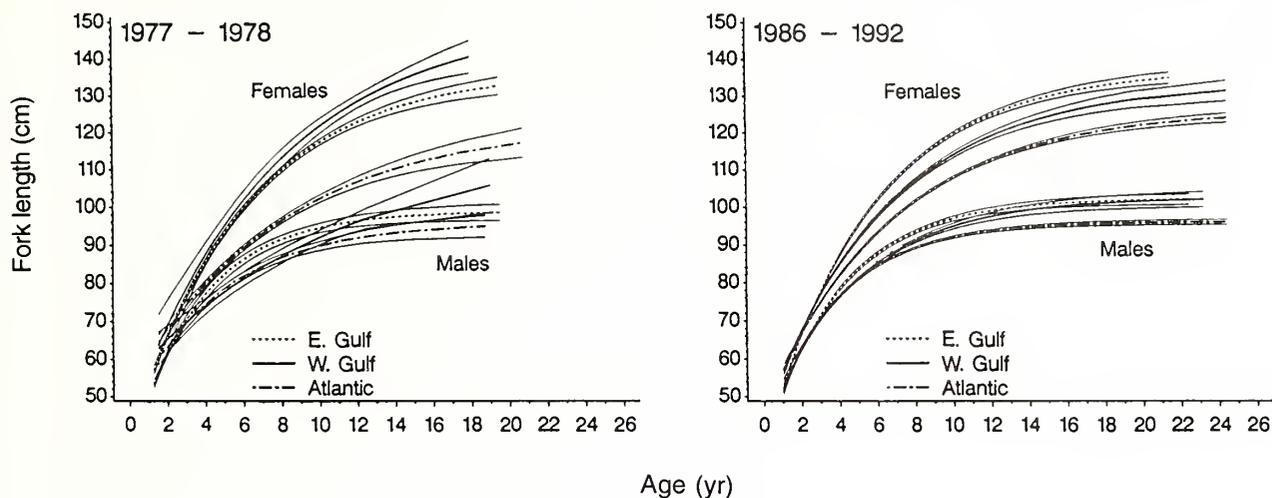


Figure 3

Von Bertalanffy growth curves and 95% confidence limits by region and sex for king mackerel collected during 1977-78 and 1986-92. Growth curves were calculated by using individual quarterly observed sizes-at-age. The upper three curves in each panel represent females; the lower three represent males.

Table 3

Results of Hotelling's T^2 tests comparing 1986-92 von Bertalanffy growth curves for king mackerel. The larger group in each comparison was randomly subsampled so that its sample size equaled that of the smaller group. Underlined F 's in right three columns indicate parameters that did not significantly affect growth differences. Values in bold = parameter which most affected growth differences. NS = not significant. n = sample size for each group in the comparison. AOF = Atlantic Ocean females; EGF = eastern Gulf females; WGF = western Gulf females; AOM = Atlantic Ocean males; EGM = eastern Gulf males; WGM = western Gulf males.

Groups compared	Calculated F^1	n	Denom. df^2	Critical value of F needed for 95% Roy-Bose simultaneous confidence limits to bracket zero		
				L_∞	K	t_0
AOF-EGF	363.8 ²	2,753	5,502	28.4	2.6	17.7
AOF-WGF	51.2	1,662	3,320	3.2	0.1	1.2
EGF-WGF	37.6	1,662	3,320	0.5	2.8	8.2
AOM-EGM	46.3	1,285	2,566	16.5	0.6	0.1
AOM-WGM	10.1	990	1,976	9.8	7.9	5.7
EGM-WGM	10.7	990	1,976	0.0	2.3	4.0
AOF-AOM	369.6	2,083	4,162	211.8	53.2	11.4
EGF-EGM	259.5	1,285	2,566	133.3	13.1	0.1
WGF-WGM	103.1	990	1,976	46.2	5.0	0.0

¹ Critical $F = 3.12$ ($\alpha = 0.05$, 2-tailed test) for all tests.

² Numerator $df = 3$ for all comparisons (3 parameters).

Beaumariage, 1973) that reported that females lived longer than males. The 26-year-old female and 24-year-old male we found are the oldest king mackerel reported. Collins et al. (1989), in the only other study that used sectioned otoliths, found a 21-year-old female as well as 16-year-old males. The oldest fish reported in all other studies that used whole otoliths, was age 14 for females and age 12 for males

(Beaumariage, 1973; Johnson et al., 1983; Manooch et al., 1987; Sturm and Salter; 1990). Our findings support those of Collins et al. (1989), i.e. that sectioned sagittae provide higher age estimates than whole otoliths for king mackerel, especially for fish >85 cm FL. Among females ages 8–12 from the Johnson et al. (1983) study (the 1977–78 collections in our study), our age estimates based on sagittal

Table 4
Total age distributions by 10-cm length class, by region, for all female king mackerel collected during 1986–92.

Size (cm)	Age (yr)																								n
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	24	
Atlantic Ocean																									
35	25.0	50.0	25.0																						4
45	9.8	84.3	5.9																						51
55	65.1	34.9																							126
65	26.6	69.3	3.8	0.3																					290
75	5.0	41.0	40.7	11.2	1.8	0.4																			735
85	0.7	8.7	22.9	27.0	20.8	11.5	5.7	1.4	0.8	0.3	0.1	0.1													722
95		1.6	7.4	8.8	13.7	18.4	18.0	9.0	7.4	6.3	4.7	2.5	1.4	0.6	0.2										511
105				1.6	5.1	11.0	15.0	10.5	11.3	10.5	10.5	8.6	5.1	3.2	2.9	1.6	1.9	0.5	0.5	0.3					373
115					1.2	2.7	5.9	9.2	11.2	12.1	10.9	12.7	8.9	5.6	6.2	5.3	3.0	1.8	1.8	0.9			0.6		338
125						0.9	2.3	1.8	6.0	7.8	10.6	9.6	11.5	9.2	8.3	7.8	8.7	4.1	5.5	3.2	1.4	1.4			218
135							2.9		2.9	2.9		2.9	8.8	8.8	8.8	8.8	11.8	8.8	17.6	2.9			5.9	2.9 ¹	34
145															42.9			14.3	14.3		14.3	14.3			7
155												25.0						50.0				25.0			4
Eastern Gulf																									
35	100.0																								4
45	12.5	87.5																							72
55	91.6	8.4																							249
65	34.1	58.8	6.6	0.4																					454
75	3.1	62.7	25.2	8.4	0.6																				512
85	0.3	16.7	43.4	24.4	7.7	3.9	2.6		0.3	0.3	0.3														311
95		1.8	13.7	31.7	23.2	16.9	4.6	1.8	3.5	1.4	0.7	0.4		0.4											284
105			0.7	11.3	22.5	24.5	13.9	8.9	9.9	5.0	0.3	0.7	1.0		0.3										302
115				1.7	8.4	16.0	22.3	13.0	16.0	11.3	4.6	1.3	1.7	0.8	1.3	1.3	0.4								238
125					2.2	8.6	8.1	11.8	15.1	17.2	6.5	10.8	6.5	5.9	2.7	0.5	0.5	2.2	0.5	0.5	0.5	0.5			186
135						0.9	2.8	13.2	7.5	3.8	14.2	11.3	12.3	9.4	4.7	6.6	9.4	1.9				1.9			106
145							2.3	2.3	9.1	2.3	11.4	22.7	9.1	11.4	4.5	9.1	6.8	2.3	6.8						44
155															25.0		50.0	25.0							4
Western Gulf																									
35	100.0																								10
45	91.7	8.3																							12
55	2.5	70.0	27.5																						80
65	35.1	51.0	9.9	4.0																					151
75	1.6	41.4	41.6	12.9	2.3	0.2																			442
85		15.2	33.0	29.6	15.7	4.7	0.8	0.8	0.3																382
95			0.5	11.2	27.1	28.5	16.8	9.3	2.8	1.4	0.9	0.9	0.5												214
105				0.6	12.2	15.4	21.8	19.2	10.9	7.1	6.4	3.8	0.6		0.6					0.6	0.6				156
115					1.7	10.3	8.5	12.0	10.3	12.8	13.7	11.1	9.4	4.3	0.9	0.9	1.7	0.9	1.7						117
125					2.9	2.9	4.3	4.3	12.9	7.1	12.9	12.9	10.0	8.6	8.6	7.1	2.9	1.4	1.4						70
135							4.2	4.2		16.7	16.7	4.2	12.5	12.5	8.3	16.7	4.2								24
145										16.7	16.7						33.3	16.7						16.7	6

¹ This size class also contained one fish (2.9%) at age 26.

sections exceeded their original estimates based on whole otoliths 67–100% of the time.

The slightly higher maximum ages in the Atlantic than in the eastern or western Gulf during 1986–92 may reflect lower fishing mortality rates for the Atlantic than for the Gulf where age structure was truncated by fishing pressure⁴; alternatively, this finding may be a sampling artifact. A much higher proportion of Atlantic samples were collected at fishing tournaments, which target larger and older fish, and Atlantic sample sizes exceeded eastern and western Gulf sample sizes by 36% and 107%; therefore the chances of obtaining an older fish were greater.

That females grew faster and attained larger maximum sizes than males agrees with previous studies

(Beaumariage, 1973; Johnson et al., 1983; Manooch et al., 1987; Collins et al., 1989; Sturm and Salter 1990). The large variation in ages within size intervals that we found was also noted by Johnson et al. (1983).

Significant differences in growth among the three regions for both sexes during 1986–92 and the persistence of that pattern in each of the seven years support the hypothesis that there are three stocks as suggested by allozyme, mark-recapture, catch and fishing effort, and juvenile birth-date distribution data (Grimes et al., 1987; Johnson et al., 1994; Gulf of Mexico and South Atlantic Fishery Management Councils³). That similar differences between Atlantic and eastern Gulf growth were present in 1977–78 is further evidence that these growth differences

Table 5

Total age distributions by 10-cm length class, by region, for all male king mackerel collected during 1986–92.

Size (cm)	Age (yr)																							n	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22		23
Atlantic Ocean																									
35	100.0																								4
45	100.0																								58
55	61.6	37.6	0.8																						125
65	13.7	71.1	14.8	0.4																					263
75	0.8	19.3	43.0	21.8	10.0	2.7	1.1	0.6		0.3	0.2	0.2													632
85		0.4	3.5	6.3	16.8	20.7	12.4	10.9	7.6	7.6	5.4	5.0	0.9	0.9	1.1	0.2	0.2				0.2	0.2			542
95				0.3	0.9	2.3	5.8	6.4	7.3	13.1	11.3	11.0	13.1	8.1	7.8	5.8	2.9	2.6			0.3	0.6	0.3		344
105						3.1	3.1	4.1	2.0	7.1	5.1	7.1	11.2	10.2	11.2	10.2	9.2	6.1	4.1	3.1	2.0	1.0			98
115										6.2	6.2	12.5			12.5	18.8	12.5				6.2		12.5	6.2 ¹	16
125																					100.0				1
Eastern Gulf																									
35																									
45	8.8	91.2																							57
55	74.8	25.2																							155
65	13.9	73.0	13.1																						267
75	0.7	27.8	43.7	19.0	6.0	1.8	0.7	0.4																	284
85		0.4	8.4	15.1	24.4	26.1	9.2	5.0	8.0	2.1	0.4	0.8													238
95			1.5	4.5	4.0	11.9	14.9	9.5	18.4	12.4	6.0	8.5	5.0	1.5	1.0	0.5	0.5								201
105			1.6	3.1		4.7	7.8	7.8	17.2	9.4	17.2	4.7	10.9	4.7	3.1	1.6	3.1	1.6					1.6		64
115						4.8	9.5	4.8	14.3		4.8	9.5	4.8	9.5	19.0	4.8				9.5	4.8				21
125										33.3						33.3		33.3							3
Western Gulf																									
35	9.1	90.9																							11
45	85.7	14.3																							7
55	70.3	28.4	1.4																						74
65	9.3	56.5	29.0	5.2																					193
75	2.1	22.5	33.9	24.3	11.4	4.6	0.7	0.4																	280
85		1.3	3.9	11.3	22.9	23.4	16.9	10.8	4.8	3.5	0.4	0.9													231
95				2.7	7.5	14.4	15.1	17.1	13.0	10.3	6.2	7.5	2.7	2.1	0.7					0.7					146
105						2.5	7.5	15.0	5.0	5.0	2.5	15.0	12.5	7.5	12.5	5.0			5.0	2.5				2.5	40
115										11.1	11.1	11.1	22.2	11.1	11.1	22.2									9

¹ This size class also contained one fish (6.2%) at age 24.

are consistent features of king mackerel populations. Assuming that these differences persisted from 1977 to 1992, during which time exploitation rates varied considerably (Mackerel Stock Assessment Panel⁴), we suggest that these differences are not just temporary density-dependent responses to varying population sizes or exploitation rates.

Our findings of regional (stock) growth differences are also consistent with those of Gold et al. (in press), who compared mtDNA haplotypes and found weak genetic differences between Atlantic and Gulf king mackerel. Although our results are not indicative of genetic discontinuity, our data demonstrate that the three groups of fish experience sufficiently different environmental and fishery conditions to produce identifiable and consistent differences in growth.

Contrary to our finding of regional differences in growth within sexes, Beaumariage (1973) reported that growth rates did not differ for either sex between the Gulf and Atlantic coasts of Florida. His results may reflect that many of his Atlantic fish were collected off southeast Florida during winter and thus may have been Gulf-group fish. In addition, the use of whole otoliths for ageing undoubtedly introduced error in length-at-age estimates, possibly obscuring regional differences.

Johnson et al. (1983) reported that female king mackerel from Louisiana grew faster than females

from other areas of the Gulf and from the Atlantic. However, their predicted sizes-at-age for Louisiana females ages 4–8, the ages with adequate sample sizes ($n=16-78$) that could be accurately aged with whole otoliths, were no more than 3.1 cm different from our eastern Gulf fish. For fish older than age 8, their estimates were increasingly larger than ours, most likely because the use of whole otoliths resulted in underageing these larger fish.

The growth differences between 1977–78 and 1986–92, i.e. lower growth during the former period seen in both sexes in the Atlantic and eastern Gulf (Fig. 6), could be a density-dependent response. Populations were much larger in the late 1970's and early 1980's than during 1986–92 (Mackerel Stock Assessment Panel⁴). The key point to remember is that within sexes, the growth differences among regions clearly present in 1986–92 apparently existed as far back as 1977–78.

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Table 6

Von Bertalanffy parameters and 95% asymptotic confidence intervals for male and female king mackerel by region for fish collected during 1986–92 and 1977–78, calculated using quarterly observed sizes-at-age.

Collection years		Parameter	Females			Males		
			<i>n</i>	Estimate	Asymptotic 95% confidence interval	<i>n</i>	Estimate	Asymptotic 95% confidence interval
1986–92	Atlantic	L_{∞}	3,407	126.7	125.0 to 128.5	2,083	96.4	95.7 to 97.1
	E. Gulf	L_{∞}	2,796	137.8	135.8 to 139.8	1,330	102.6	101.1 to 104.1
	W. Gulf	L_{∞}	1,662	134.1	130.6 to 137.7	995	102.8	100.5 to 105.2
	Atlantic	K	3,407	0.145	0.137 to 0.154	2,083	0.262	0.248 to 0.276
	E. Gulf	K	2,796	0.172	0.163 to 0.181	1,330	0.247	0.227 to 0.267
	W. Gulf	K	1,662	0.150	0.136 to 0.164	995	0.203	0.180 to 0.226
	Atlantic	t_0	3,407	-3.15	-3.41 to -2.90	2,083	-1.98	-2.19 to -1.78
	E. Gulf	t_0	2,796	-1.83	-1.98 to -1.67	1,330	-1.84	-2.09 to -1.59
	W. Gulf	t_0	1,662	-2.69	-3.02 to -2.37	995	-2.74	-3.16 to -2.32
1977–78	Atlantic	L_{∞}	323	122.7	115.5 to 129.9	128	95.9	92.3 to 99.6
	E. Gulf	L_{∞}	1,011	137.1	133.4 to 140.8	343	99.0	96.6 to 101.3
	W. Gulf	L_{∞}	188	151.5	138.2 to 164.8	40	116.0	93.1 to 138.9
	Atlantic	K	323	0.124	0.096 to 0.151	128	0.211	0.159 to 0.262
	E. Gulf	K	1,011	0.160	0.145 to 0.175	343	0.269	0.229 to 0.309
	W. Gulf	K	188	0.127	0.080 to 0.175	40	0.094	0.026 to 0.163
	Atlantic	t_0	323	-4.54	-5.59 to -3.49	128	-3.14	-4.26 to -2.02
	E. Gulf	t_0	1,011	-2.12	-2.39 to -1.85	343	-1.63	-2.04 to -1.22
	W. Gulf	t_0	188	-2.78	-4.52 to -1.03	40	-6.78	-11.1 to -2.45

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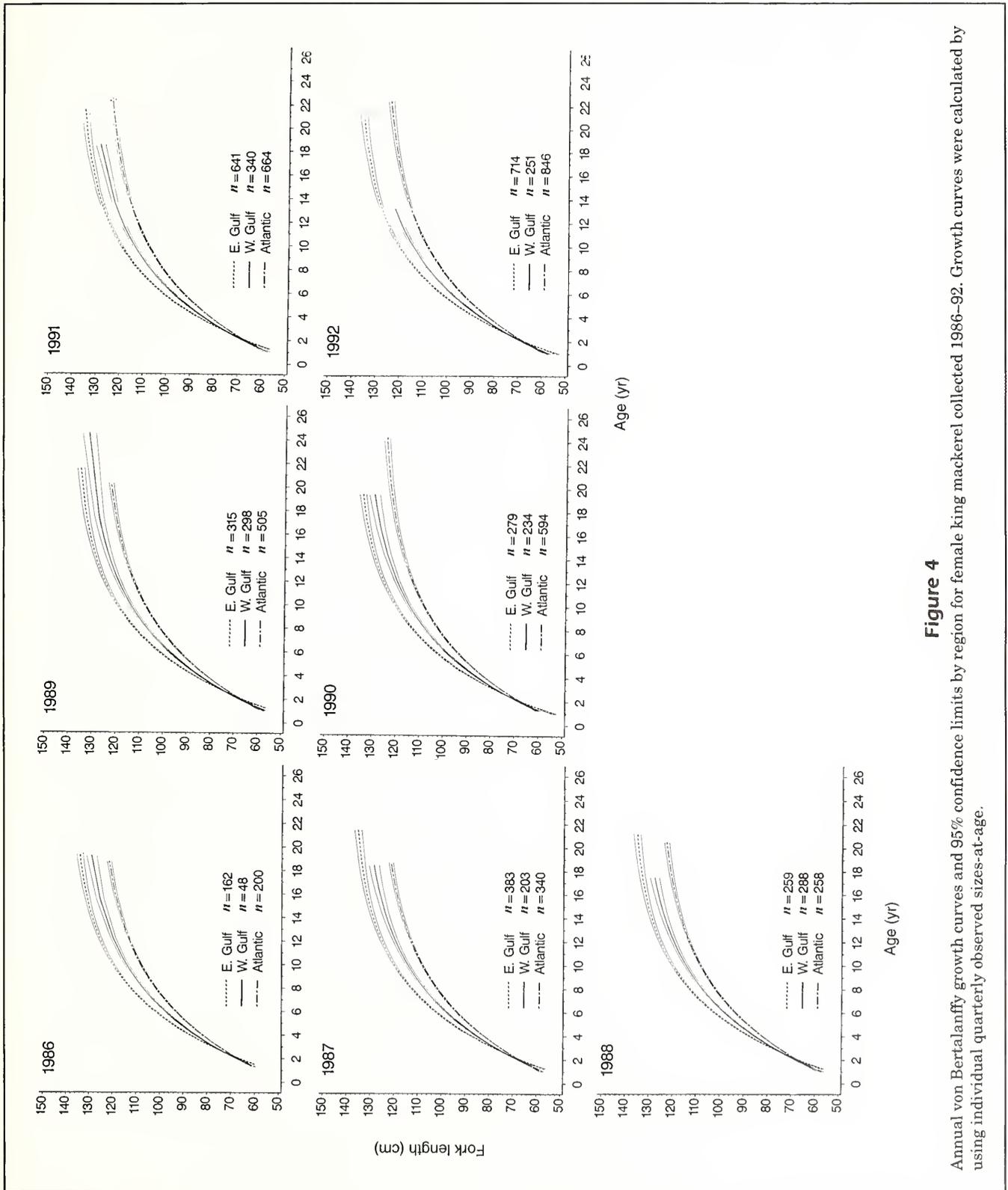


Figure 4 Annual von Bertalanffy growth curves and 95% confidence limits by region for female king mackerel collected 1986-92. Growth curves were calculated by using individual quarterly observed sizes-at-age.

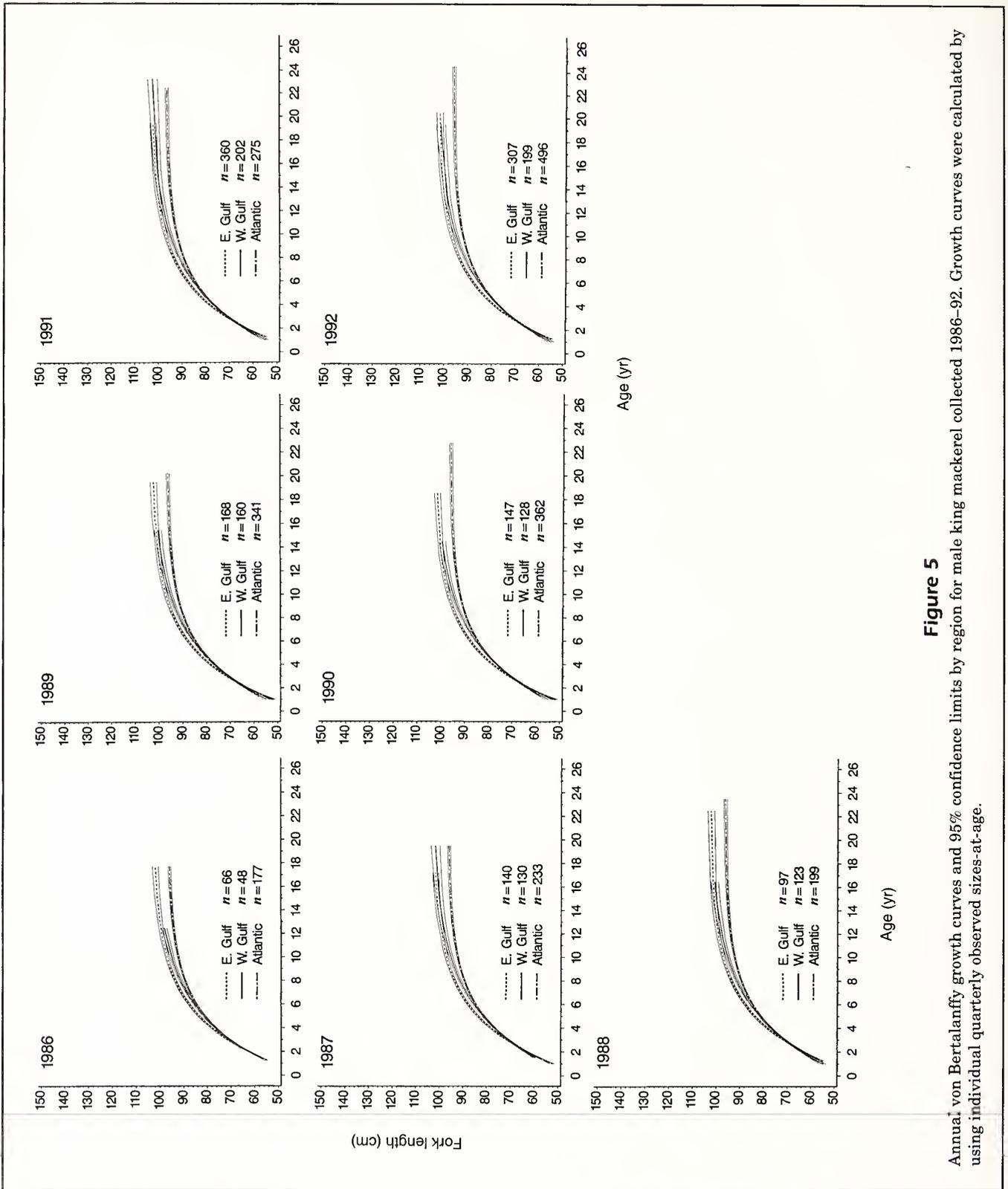
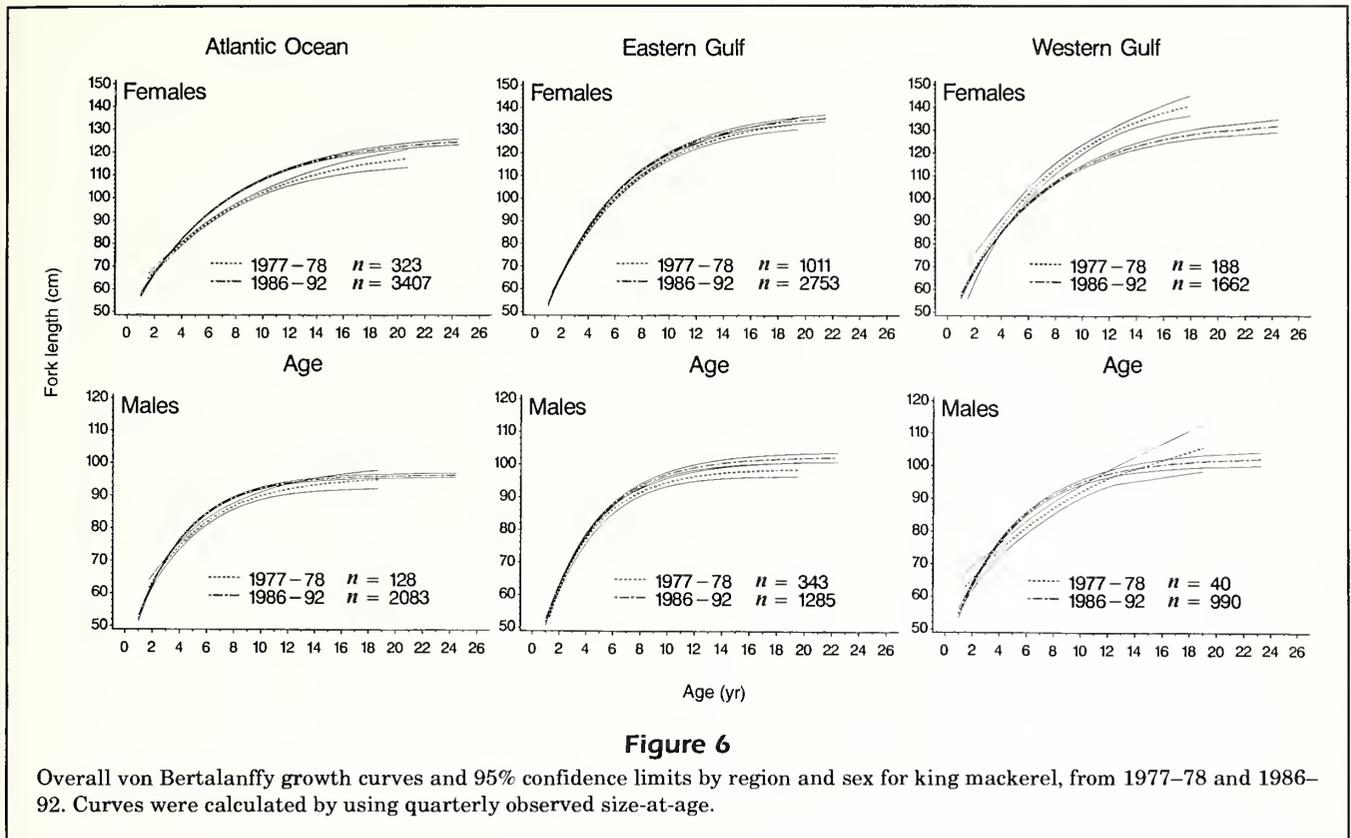


Figure 5

Annual von Bertalanffy growth curves and 95% confidence limits by region for male king mackerel collected 1986-92. Growth curves were calculated by using individual quarterly observed sizes-at-age.

with large numbers of processed otoliths. Doug Vaughan, NMFS, Beaufort Laboratory, provided programs and valuable statistical advice concerning

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Abstract.—White seabass, *Atractoscion nobilis*, is a valuable recreational and commercial species, but much of its early life history is undescribed. The coast and two bays of San Diego County were sampled each month for two years with a depth-stratified sampling design to determine habitat, food habits, age, and growth rate of recently settled fish. Age was estimated from otolith increments and validated with fish of known age, reared in the laboratory. A few recently settled fish were caught in the bays at depths <1 m, but most inhabited shallow water (4–8 m) along the coast from May to October. This depth distribution coincides with that of the mysid *Metamysidopsis elongata*. Fish abundance in this zone was low, however, reaching a maximum of 24/ha in July. The smallest white seabass collected were about 7 mm SL and 26 d old, but previous studies indicate that smaller and presumably younger fish were probably extruded through the trawl. According to combined results, most larvae settled 2–3 weeks after being spawned. Juveniles remained at a depth of 4–8 m for 2–3 months, fed primarily on abundant mysids, and associated with drifting macrophytes ($r=0.52$, $P=0.015$, $n=21$). Growth during this period was 1.3 mm/d, similar to that observed in the laboratory. At about 100 mm SL (~100 d old), juveniles appeared to move out of the area. The shallow waters just beyond the breaking waves may be preferred by young white seabass because abundant food and warm water promote rapid growth and drifting macrophytes provide a refuge from predators.

Age, growth, distribution, and food habits of recently settled white seabass, *Atractoscion nobilis*, off San Diego County, California

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White seabass, *Atractoscion nobilis* (family Sciaenidae), is a highly desired recreational and commercial species found in waters off the coasts of southern and Baja California as well as in the Gulf of California. Adults inhabit the nearshore zone over rocky bottoms and in kelp beds and can attain a weight of 38 kg (Young, 1973). Population size has not been estimated, but since the 1920's, commercial and recreational landings off California have continued to decline and the range of the species has contracted (Collins, 1981; Methot, 1983). Management efforts to stabilize and restore the population have been largely unsuccessful. Reductions in the catch and distribution of white seabass have been attributed largely to overfishing (Thomas, 1968; Vokovich and Reed, 1983; MacCall, 1986), but the importance of other mechanisms, such as increased natural mortality of fish at early life history stages, has not been evaluated.

Despite the historic value of this species, much of its early life history was unknown until recently. Moser et al. (1983) described the development of the early life stages and historic distribution of larvae in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling area off south-

ern and Baja California. In several laboratory studies, growth, survival, energetics, and feeding behavior of larvae have been examined (Kim, 1987; Dutton, 1989; Orhun, 1989), as well as the development of sensory systems and predator-avoidance behavior (Margulies, 1989).

Less is known about the early juvenile stage because few early juveniles have been caught until recently. Early studies suggested that juveniles inhabit either the surf zone or kelp canopy along the open coast, or bays and estuaries (Thomas, 1968; Feder et al., 1974; Maxwell¹). Allen and Franklin (1988, 1992) have since demonstrated that late larvae and early juveniles inhabit shallow water along the open coast of southern California and Channel Islands and semiprotected embayments in the vicinity of Long Beach Harbor. However the nursery area for white seabass has not been clearly defined and the relative importance of the open coast and bays as nurseries has not been

¹ Maxwell, W. D. 1977. Progress report of research on white seabass, *Cynoscion nobilis*. Calif. Dep. Fish Game, Mar. Resour. Admin. Rep. 77-14, 14 p. [Available from Calif. Dep. Fish Game, 330 Golden Shore, Suite 50, Long Beach, CA 90802.]

evaluated. In addition, food habits, age, and growth of these fish in the wild have not been examined.

The specific goals of this study were to determine 1) the depth distribution of early juvenile white seabass along the open coast and in bays of San Diego County, 2) size-specific food habits of white seabass, and 3) age and rate of growth.

Materials and methods

Sampling design

Most white seabass were obtained from a survey originally designed to sample settled California halibut, *Paralichthys californicus* (Kramer, 1990). Two bays (Mission Bay and Agua Hedionda Lagoon) and the open coast of San Diego County were sampled monthly from September 1986 to September 1988 with a depth-stratified sampling design. The coast was sampled at four primary sites with a 1.6 m × 0.35 m beam trawl (Fig. 1). At each site, four benthic tows were made in each of three bottom depth intervals (strata): 4–8, 9–11, and 12–14 m. A few tows

were made in water as shallow as 3 m on days when the sea was calm. Tows were made parallel to shore at about 0.6 m/s for 10 min. The exact depth of tows within each stratum was chosen at random. Sampling depth was maintained along the chosen 1-m depth contour with the aid of a fathometer. An odometer attached to the trawl recorded tow distance, which ranged from 250 to 450 m. An additional four sites were sampled from April to October 1988 by biologists at San Diego State University (SDSU) with identical gear, but only at the 4–8 and 9–11 m depth strata.

A similar sampling design was used to sample the two bays. Mission Bay and Agua Hedionda Lagoon were subdivided into five and three blocks respectively to sample the various habitats adequately within each bay (Fig. 1). Each block was further subdivided into three depth strata: 0–1, 1–2, and 2–4 m. Within each stratum and block, three benthic tows were made at random locations with a 1.0 m × 0.35 m beam trawl equipped with an odometer. In the two deeper strata, the trawl was towed by a 5-m skiff for 5 min, covering a distance of 100–250 m. In the 0–1 m stratum, the trawl was towed by hand for a measured distance of 20–50 m. The 0–1 m depth strata

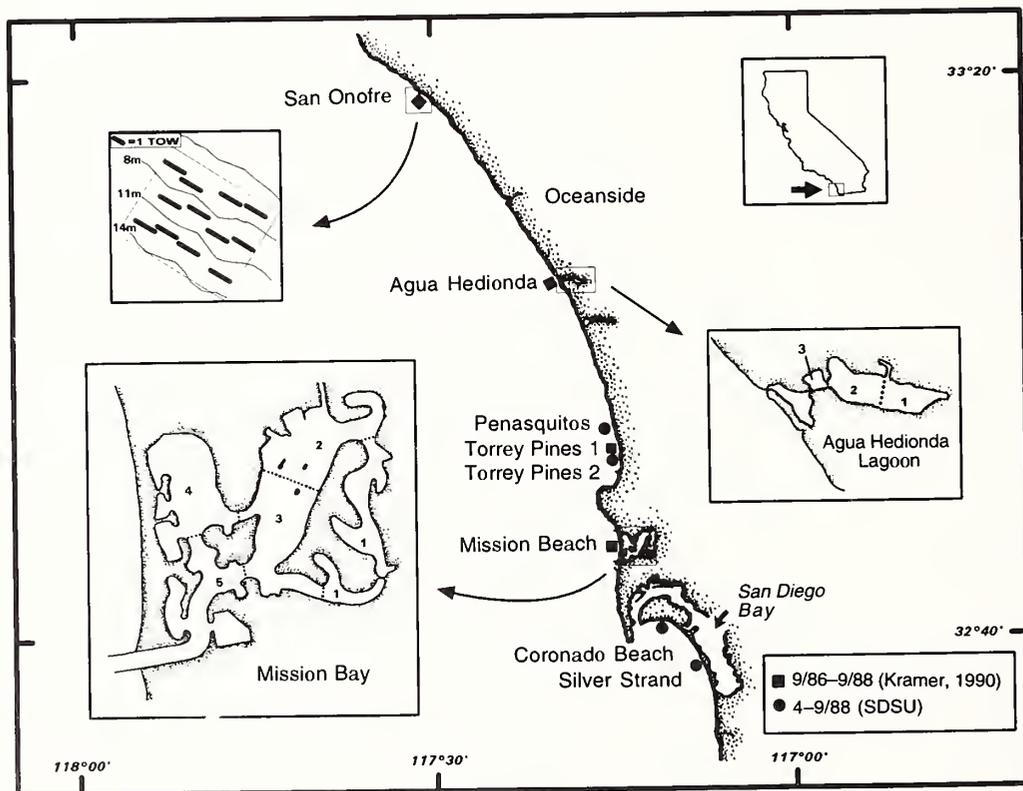


Figure 1

Map of San Diego County showing location of the eight coastal sites and sampling areas (blocks) within Mission Bay and Agua Hedionda Lagoon. Four coastal sites were sampled by Kramer (1990) and four were sampled by San Diego State University (SDSU). The sampling design used along the coast is also shown.

tum was also sampled with a 1 m × 6 m beach seine. Three hauls were made in each block over a measured distance of 15–50 m with the width of the seine fixed at 4 m. In addition, three tows were made each month in blocks 2–5 of the 2–4 m stratum in Mission Bay with the 1.6-m beam trawl (Fig. 1). The mesh size of all three nets was 3 mm. All hauls were made during the day. Monthly sampling in Agua Hedionda Lagoon was not initiated until March 1987.

Tow distance, water temperature, and the presence and type of drift macrophytes in the net were recorded at the end of every tow. Beginning in April 1988, the weight of drift macrophytes in each tow was also recorded at the four coastal sites sampled by SDSU biologists. White seabass were either frozen or preserved in 80% ethanol and later measured to 0.1 mm standard length (SL) in the laboratory. Lengths of alcohol-preserved fish were adjusted by 3.6% to compensate for shrinkage. Average shrinkage was estimated by measuring a subsample of white seabass before and several months after preservation in ethanol. Sagittae and stomach contents were removed and stored in 80% ethanol. Fish were then dried at 60°C for two days and weighed.

White seabass were also obtained opportunistically (i.e. sporadically) from the coastal habitat with a 7.6-m headrope otter trawl and a 15.2-m beach seine (6-mm mesh). These fish were used only in the food habits and growth portions of this study.

Distribution and abundance

Abundance was calculated as the number of fish caught divided by the product of tow distance (from odometers) and net width. Mean abundance of fish along the coast was calculated for each site by depth stratum ($n=4$ tows). Monthly differences in abundance among the three depth strata were compared by using the Kruskal-Wallis test, with $a=3$ depths, and $n=4$ (1987) or $n=8$ (1988) sites (Sokal and Rohlf, 1981). Monthly mean abundance in bays was calculated for each bay by block and depth stratum. Block means were averaged to produce a mean for each bay and the two bays were averaged to yield a grand mean for each depth stratum. Because estimates of monthly mean abundance did not differ among the two gear types (paired t -test; mean difference=0.50 fish/ha, $t=0.27$, $df=8$, $P=0.79$), trawl and seine samples within the 0–1 m depth stratum were pooled to produce an improved estimate of abundance.

The relation between abundance of white seabass and drift macrophytes was estimated by testing for a correlation between abundance of white seabass and drift macrophytes in each tow and for a correlation between mean abundances at each site ($n=4$

tows). Abundance of macrophytes (g/m^2) was log-transformed prior to analysis. Biomass of macrophytes was recorded only from April to October 1988 at the four secondary sites along the coast that were sampled by SDSU biologists.

Food habits

The stomach contents of 142 white seabass collected in bays and along the coast with all gear types were examined. For each fish, prey items were identified, counted, sorted into one of ten major prey categories, dried at 60°C for 1–2 d, and weighed to either 1 μg (for samples <25 mg) or to 0.1 mg (for samples >25 mg). White seabass were grouped into six length classes: 6–10, 10–18, 18–25, 25–35, 35–55, and 55–150 mm SL. Class intervals were chosen so that each interval contained similar numbers of fish. Mean prey weight and frequency of occurrence of each prey category were calculated for the six length classes. Six individuals with empty stomachs were excluded from calculations of frequency of occurrence and mean weight of prey.

Age and growth

The ageing method was validated by using laboratory-reared fish of known age. Eggs obtained from captive broodstock were placed in 7-m³ flow-through tanks and reared at 17–20°C on a diet of marine rotifers, brine shrimp, euphausiids, and chopped mackerel. White seabass were sacrificed at irregular intervals between 13 and 76 d after hatching and stored in 80% ethanol. Sagittae were mounted in Eukitt mounting media and ground in the sagittal plane with 15- μm grit sandpaper and polished with 0.3- μm grit lapping film. Increments were counted on the right sagitta from the central primordium to the mid-ventral margin. Each sagitta was read in one session by one observer, with neither age nor length of the fish known to the reader. The rate of increment deposition and age at first increment formation were estimated by linear regression.

A subsample of 50 wild larval and juvenile white seabass was aged with the technique described above. Individuals were selected at random from several length classes to represent equally the size range of fish collected. The subsample included fish caught in bays, on the coast, and in both years. Growth rates were estimated by fitting a Gompertz function ($L_t = L_0 e^{G(1 - e^{-gt})}$) to length-at-age and weight-at-age data. The ages of the remaining individuals were estimated from the resulting age-length relation. The date each fish was spawned was calculated by subtracting the age of the fish and an additional two days (incubation time at ~16°C; Orhun, 1989) from date of cap-

ture. The error associated with the estimated spawn dates is therefore the same as that associated with the age-length relation.

Growth of wild white seabass was compared with growth of three groups reared in the laboratory. Eggs spawned on 8 May, 24 June, and 25 September 1989 were reared as described above. Mean length-at-age was estimated from random subsamples ($n=16-76$ fish) taken at irregular intervals during rearing. Linear growth models were fitted to the length-at-age data for both reared and wild fish to facilitate statistical comparisons of growth rates with ANCOVA. Although growth of white seabass from hatching to 150 mm SL was nonlinear, growth over a smaller size range of 6–104 mm SL was described equally well by linear models ($r^2 \geq 0.94$).

Results

Distribution and abundance

The overall abundance of white seabass in the bays and along the coast of San Diego County was low.

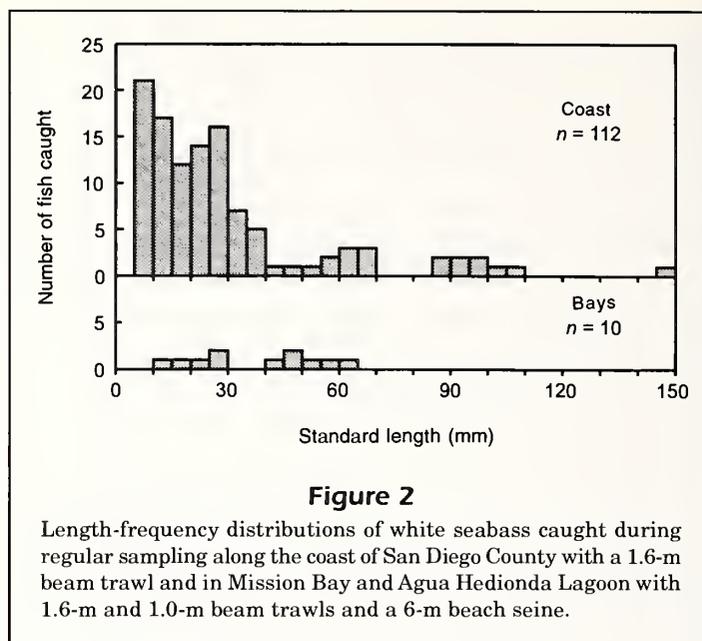


Figure 2

Length-frequency distributions of white seabass caught during regular sampling along the coast of San Diego County with a 1.6-m beam trawl and in Mission Bay and Agua Hedionda Lagoon with 1.6-m and 1.0-m beam trawls and a 6-m beach seine.

During regular sampling, a total of 112 white seabass were caught in 1,250 tows along the coast and 10 white seabass were caught in 2,527 tows in the bays.

Most tows caught no white seabass. Lengths of fish ranged from 6.2 to 149 mm SL ($x = 30.2$ mm SL), but 80% were smaller than 40 mm SL (Fig. 2). About 40 fish (33%) were smaller than 15 mm SL, the approximate length at metamorphosis (Moser et al., 1983).

White seabass were caught primarily in shallow water in both coastal and bay habitats. Along the coast, nearly all white seabass (97%) were collected in the shallowest (4–8 m) depth stratum, with the highest density at 6 m (Fig. 3). Only three fish were taken in deeper water and these were among the largest caught, ranging from 92 to 149 mm SL. In the bays, all ten fish were caught in the shallowest (0–1 m) stratum.

Settled (demersal) white seabass were present in shallow strata only during spring and summer, although one fish, the 149-mm-SL juvenile, was caught in January 1988. Along the coast, white seabass were caught from June to August 1987, and from May to October 1988, when sampling ended (Fig. 4). In both years, abundance was highest in July, with mean densities of 15/ha (1987) and 24/ha (1988). White seabass were found in 54 of 210 tows (26%) made in the 4–8 m

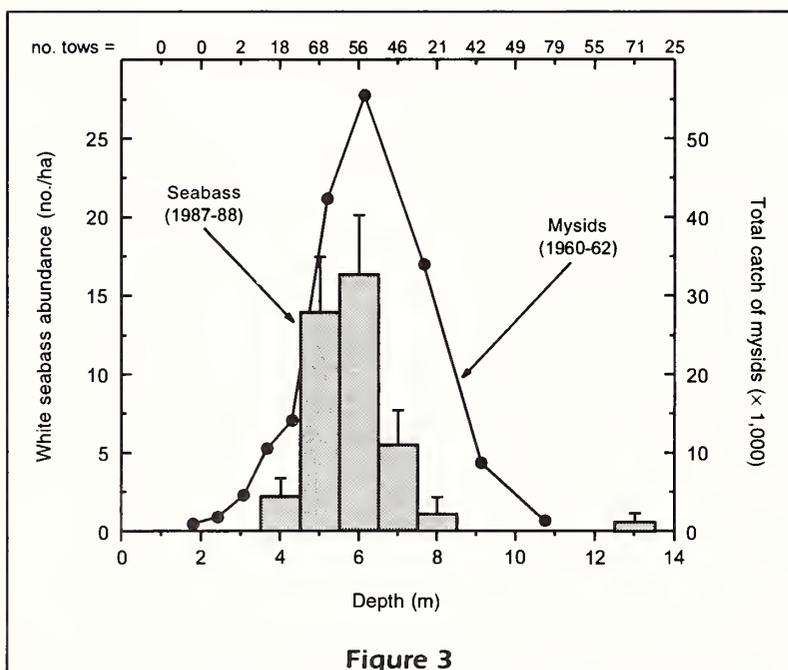


Figure 3

Distribution of white seabass and the mysid *Metamysidopsis elongata* along the coast in relation to depth. White seabass abundance is the mean (± 1 SE) during months fish were captured (Jun–Aug 1987, May–Oct 1988). Number of tows at each depth during this period is indicated at the top of the graph. Mysid data are redrawn from Clutter (1967) and represent total number of *M. elongata* caught from 1960 to 1962 at a site ~3 km south of the Torrey Pines 2 site (Fig. 1). Sampling effort for mysids was similar for all depths.

stratum during these nine months. Because most tows in the 4–8 stratum caught no white seabass, the variance associated with the estimates of abundance within the stratum was high. As a result, abundance in the 4–8 m stratum did not differ statistically from that in the 9–11 and 12–14 m strata (generally zero) except in June 1987 and from June to July 1988 (Kruskal-Wallis test, $P < 0.05$, $n = 4$ or 8). The temperature in the 4–8 m stratum during the summer ranged from 16 to 20°C, an average of 1.2 and 1.8°C warmer than the two deeper strata.

Although the relative abundance of settled white seabass was lower in the bays than along the coast, the two estimates could not be compared statistically because different nets were used to sample the two habitats. In addition, only 10 fish were caught in the two bays, making estimates of abundance sensitive to capture of individual fish. Estimates of mean density in the 0–1 m stratum in the bays from April to August ranged from 0 to 5 per ha in 1987 and from 0 to 10 per ha in 1988 (Fig. 4). The high April 1988 estimate resulted from a single fish caught in a short tow. Mean abundance during these five months (total catch ÷ total area swept) was 1.3/ha in 1987 and 3.1/ha in 1988. Monthly estimates for bays were about 0.8–12 times lower than estimates for the coast during the same period.

Abundance of white seabass within the 4–8 m coastal stratum was related to the abundance of drift macrophytes. Drift macrophytes were common in the 4–8 m stratum and were recorded in 188 of 205 tows (92%) made during the nine months when white seabass were present. Macrophytes were present in 49 of 52 tows (94%) that caught white seabass. The drift material was mainly giant kelp (*Macrocystis pyrifera*) and surf grass (*Phyllospadix torreyi*), but filamentous red and other brown algae were dominant at times. In 1988, weight of macrophytes in each tow was recorded at the four sites sampled by SDSU biologists. At these sites, abundance of white seabass in each tow was weakly correlated with the abundance of drift macrophytes in each tow in the 4–8 m coastal stratum ($n = 77$, $r = 0.29$, $P = 0.01$, Fig. 5A). Because white seabass were not abundant, an average of the four tows made at each site was also calculated. Mean abundance of white seabass at each site ($n = 4$ tows) and mean abundance of drift macrophytes were more strongly correlated ($n = 21$, $r = 0.52$,

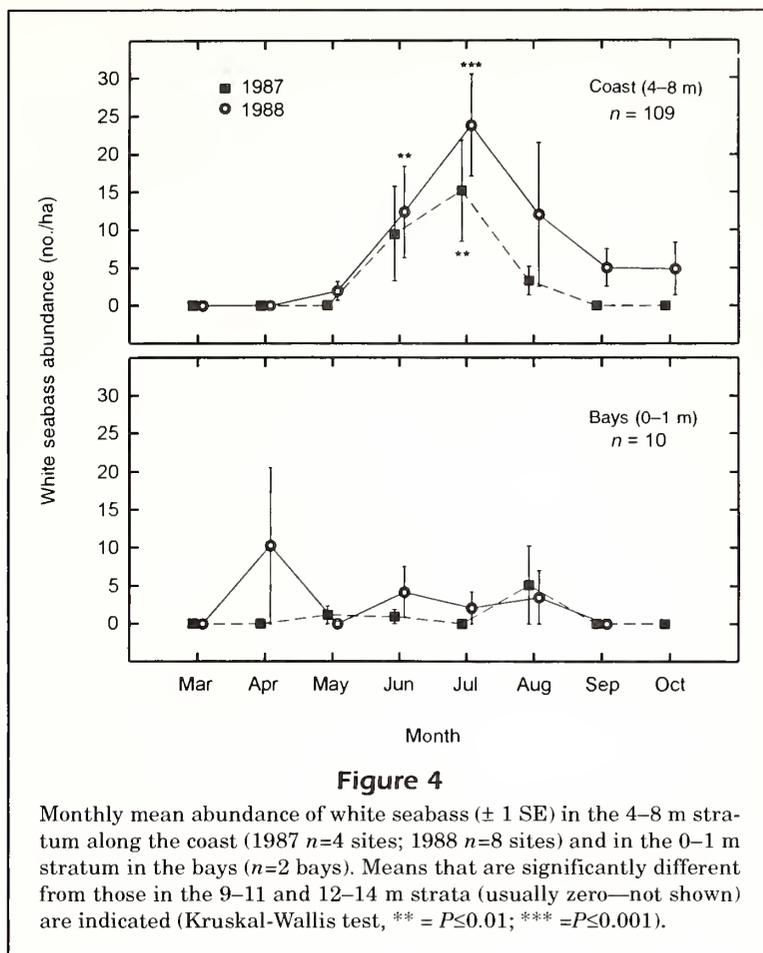


Figure 4
Monthly mean abundance of white seabass (± 1 SE) in the 4–8 m stratum along the coast (1987 $n = 4$ sites; 1988 $n = 8$ sites) and in the 0–1 m stratum in the bays ($n = 2$ bays). Means that are significantly different from those in the 9–11 and 12–14 m strata (usually zero—not shown) are indicated (Kruskal-Wallis test, ** = $P < 0.01$; *** = $P < 0.001$).

$P = 0.015$, Fig. 5B). Drift macrophytes were also present in the two deeper strata, but only three white seabass were caught at those depths.

Food habits

Along the coast, white seabass of all length classes fed almost exclusively on mysid crustaceans. For each length class, mysids composed from 74% to 99% of the diet by weight and were found in 78–100% of stomachs that contained food (Table 1). These mysids were not identified to species but were probably *Metamysidopsis elongata*, the numerically dominant mysid in the nearshore coastal habitat (Clutter, 1967; Roberts et al., 1982). Larger white seabass ate larger mysids, although fish > 0.2 g dry weight (~ 40 mm SL) fed on mysids of similar mean weight (Fig. 6). Mysids also dominated the diet of the 10 fish caught in the bays.

Prey of secondary importance varied with white seabass length class. Larvae (6–10 mm SL) fed on copepods, fish of intermediate length (10–55 mm SL) fed on gammarid amphipods, and larger juveniles

(35–150 mm SL) preyed on shrimp and fishes. Most fish in the stomachs were well digested and difficult to identify, but the sagittae closely resembled those of white croaker, *Genyonemus lineatus*, and queenfish, *Seriphus politus*. One case of cannibalism was observed; a 7-mm larva was eaten by a 35-mm juvenile. Most shrimp were well digested, but at least two individuals were identified as belonging to the genus *Crangon*. Other items found in the stomachs included nematodes, bits of algae and surf grass,

portions of crustaceans, and sand. The stomachs of six white seabass (5%) were empty or contained only nonfood items such as sand.

Age and growth

Otolith increments formed daily in sagittae of laboratory-reared white seabass (Fig. 7). The slope of the regression of observed number of increments on age was 0.96 and did not differ from unity ($r^2=0.96$, $n=25$, $P<0.01$, 95% confidence limits on slope: 0.89 and 1.04 increments/d). The first increment formed 3–4 d after hatching, a period that corresponds to yolk absorption and onset of feeding (Kim, 1987; Orhun, 1989).

Age was estimated for 50 wild white seabass ranging from 6.2 to 104 mm SL. The ten smallest fish that were aged ranged from 6.2 to 9.2 mm SL and were estimated to be 26–32 d old (Fig. 8). The age of a fish that was 15 mm SL, the length at metamorphosis, was estimated to be about 40 d. The largest juvenile aged (104 mm SL) was estimated to be 108 d old. The range of estimated ages suggests that white seabass remain in the nursery for 2–3 months after settlement. It should be noted that the oldest validated age was 76 d. A 149-mm-SL juvenile was not aged because it was probably much older than the oldest validated age.

Growth of these fish was rapid in terms of length and weight. The parameters of the Gompertz model relating age and length were estimated as $L_0=0.202$, $G=6.64$, and $g=0.0273$, where L_0 is length at time t_0 , G is the instantaneous growth rate at time t_0 , and g is the rate of decrease of G (Fig. 8A). This equates to a maximum growth rate of 1.57 mm/d at 70 d. Weight also increased rapidly. The parameters relating weight and age were $W_0=2.72 \times 10^{-7}$, $G=17.58$, and $g=0.0256$, where W_0 is weight at time t_0 (Fig. 8B).

Wild fish between 6 and 104 mm SL grew at rates similar to those of laboratory-reared fish. Wild fish grew at a linear rate of 1.31 mm/d, compared with laboratory rates of 1.15, 1.32, and 1.04 mm/d for groups spawned in May, June, and September 1989 (Fig. 9). Linear growth models were used to facilitate statistical analysis by ANCOVA. Linear models fitted the data well, with coefficients of determination (r^2) of 0.94–0.99 for the four groups. The rate of growth (slopes) did not differ among the four groups (ANCOVA, $F=1.40$, $P=0.25$). However, the June laboratory group was significantly larger at a given age than the wild fish (ANCOVA, $F=5.05$, $P<0.01$; Tukey pairwise comparison), but the remaining groups did not differ in their length-at-age.

The distribution of spawning dates, based on counts of otolith increments, indicated that spawning occurred from March to July in 1987, and from

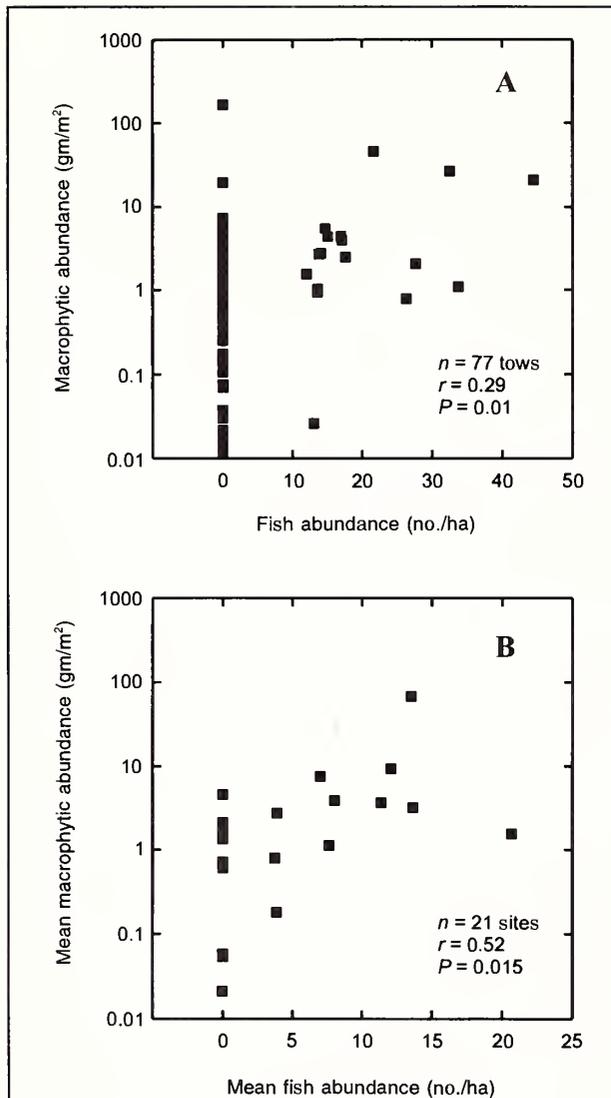


Figure 5

Relations between (A) abundance of drift macrophytes and abundance of white seabass in each tow, and (B) mean abundance of drift macrophytes and mean abundance of white seabass at each site ($n=4$ tows) in the 4–8 m stratum from April to October 1988 at the four coastal sites sampled by SDSU. Sample size, Pearson correlation coefficient (r), and P -values are shown.

Table 1

Mean dry weight in micrograms (μg) and as a percentage of total weight (in parentheses) and frequency of occurrence of prey items in stomachs of white seabass caught along the coast. Six fish with empty stomachs were excluded from the analysis. n = sample size.

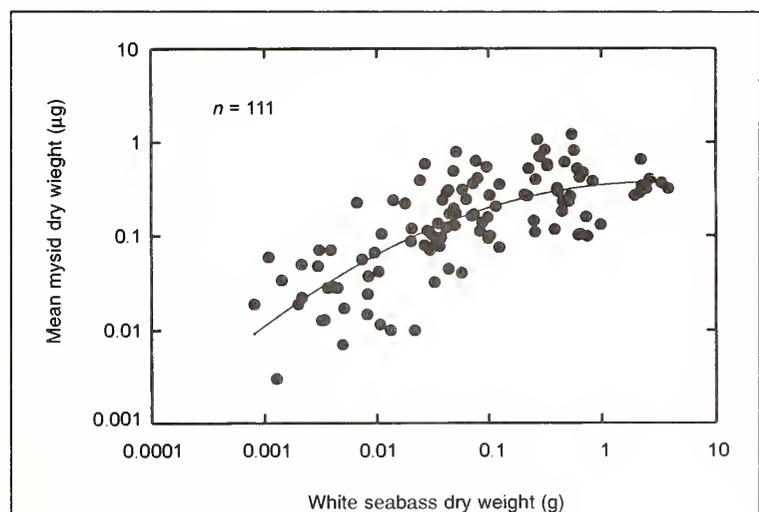
Prey category	Length class and mean length (mm SL)					
	6-10 (7.9)	10-18 (13.7)	18-25 (21.8)	25-35 (29.1)	35-55 (44.8)	55-150 (79.2)
Mean Dry Weight in μg and (%)						
Mysids	46 (75)	154 (91)	467 (99)	1,417 (99)	2,329 (78)	8,270 (74)
Copepods	10 (16)	2 (1)	—	—	—	—
Gammarid amphipods	—	7 (4)	—	5 (<1)	11 (<1)	—
Fish	—	—	4 (1)	—	97 (3)	768 (7)
Shrimp	—	—	—	—	186 (6)	211 (2)
Nematodes	—	—	—	—	6 (<1)	15 (<1)
Macrophytes	—	—	<1	—	55 (2)	647 (6)
Crustacean parts	5 (8)	2 (1)	—	5 (<1)	—	459 (4)
Sand	—	—	—	1 (<1)	185 (6)	—
Unidentified	—	5 (3)	—	—	99 (3)	814 (7)
Total	61	170	471	1,428	2,968	11,184
Frequency of occurrence (%)						
Mysids	78	91	100	96	100	100
Copepods	11	5	—	—	—	—
Gammarid amphipods	—	5	—	11	5	—
Fish	—	—	5	—	25	25
Shrimp	—	—	—	—	5	5
Nematodes	—	—	—	—	5	10
Macrophytes	—	—	5	—	25	50
Crustacean parts	11	5	—	4	5	15
Sand	—	—	—	4	5	—
Unidentified	—	5	—	—	15	10
n	18	22	20	27	20	20

March to the beginning of September in 1988 (Fig. 10). In both years, most of the young white seabass collected were spawned in June. The distribution of spawning dates derived from estimated ages agreed closely with those based upon direct ageing.

Discussion

Spawning season

Larval and juvenile white seabass collected off San Diego County were spawned from March to September, with the greatest number spawned in June in both years (Fig. 10). This seasonal pattern of spawning, inferred from counts of otolith increments, agrees with previous estimates based on larval abundance and adult spawning condition. Moser et al. (1983) observed that eggs and larvae were most abundant in CalCOFI

**Figure 6**

Relation between white seabass dry weight and mean dry weight of mysids (total weight of mysids plus total number of mysids) in the stomachs of 111 white seabass.

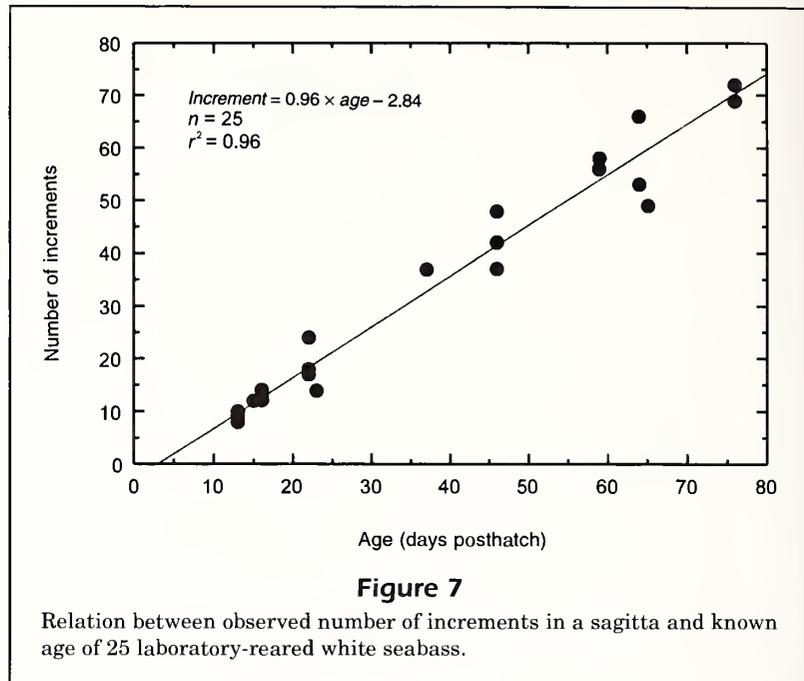
plankton samples in July and that 95% of fish were captured between May and August. Adults begin to mature in early March (Clark, 1930) and spawn off southern California from April to August. Peak spawning activity is in May and June (Skogsberg, 1939).

Size and age at settlement

The smallest larvae caught during the present study were 6–7 mm SL, which would seem to indicate that white seabass begin to settle at about this size. However, white seabass as small as 4.2 mm SL were collected along the open coast north of San Diego County in 1988 and 1989 with a trawl containing 2-mm mesh in the codend (Allen and Franklin, 1992); therefore the smallest settled larvae were probably not retained by our net. More than 20% of the individuals collected in that study were <5 mm SL and 50% were <7 mm SL. This size distribution suggests that many larvae caught off San Diego County had settled at lengths of 4–5 mm SL. Larvae up to 7.2 mm SL have been collected from the water column (Moser et al., 1983), indicating that some individuals settle at >5 mm SL.

Given that many white seabass settled at 4–5 mm SL, the average age at settlement must be less than one month. The 10 smallest fish caught and aged in this study ranged from 6.2 to 9.2 mm SL and were 26–32 d old (Fig. 8). Although smaller (4–5 mm SL) fish were not aged, they were probably much younger. In the laboratory, white seabass reared at 15°C hatch at a length of 2.8 mm SL after 2 d and grow to 4 mm SL in 10 d and to 5 mm SL in 15–19 d (Moser et al., 1983; Orhun, 1989). At this rate of growth, a 4–5 mm SL settled fish would have spent only 12–21 d in the pelagic habitat.

Allen and Franklin (1992) hypothesized that most white seabass larvae that settle along the coast of southern California are spawned off Baja California and advected northward. However, a short pelagic phase of 2–3 weeks suggests that many of these larvae are spawned within the Southern California Bight (SCB). The direction of larval transport is difficult to predict because the behavior and position of white seabass larvae in the water column is unknown. During spring and early summer, poleward-flowing undercurrents over the continental slope and equatorward-flowing surface currents over the continental shelf (Hickey, 1993) could transport larvae along the coast in either direction. However, mean



seasonal current velocities in the SCB region in spring and early summer are generally less than 20 cm/s, although short-term velocities can be higher (Hickey, 1993). At 20 cm/s, larvae could be transported a maximum of 200–360 km in 12–21 d. It therefore seems unlikely that the 4–5 mm SL white seabass caught in the northern and middle SCB by Allen and Franklin (1992) were spawned off Mexico. These larvae, which represented a large proportion of the total catch, were almost certainly spawned off California. Of course older larvae collected in the middle SCB or young larvae caught off San Diego County could have been spawned off either California or Mexico.

Nursery location

The depth distributions of settled white seabass on the coast and within bays suggests that these fish prefer shallow water beyond the surf zone. Along the open coast, nearly all fish were caught at depths of 4–8 m, a region which begins just beyond the breaking waves. In the bays, all 10 fish were caught just beyond the shore break at a depth of 0–1 m. Previous observations in other regions are consistent with this conclusion. Settled white seabass have been collected beyond the breaking waves along semi-protected and exposed shores in and around Long Beach Harbor (Allen and Franklin, 1988). White seabass were not collected along protected shores, but depths <1.5 m were not sampled. On the open coast north of San Diego County, settled white seabass were also more abundant along the 5-m

depth contour than along the 10-m contour (Allen and Franklin, 1992). Although this distribution supports the conclusion that white seabass prefer shallow water, 30–40% of the settled fish were caught at the 10-m contour (Allen and Franklin, 1992). Most of the fish collected at 10 m were taken along one section of coastline between Ventura and Point Dume; thus the preference for shallow water may be modified by local conditions.

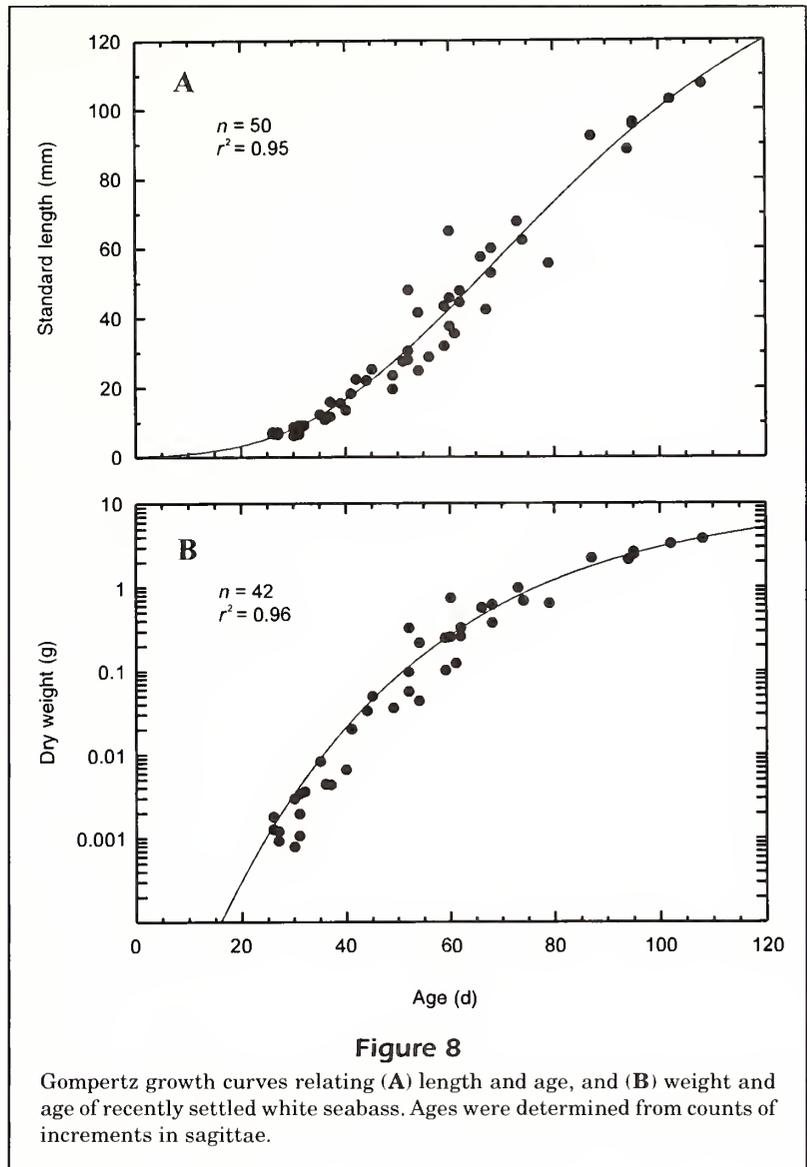
Greater densities of settled fish along the open coast than in the bays suggests that the primary nursery for white seabass is the open coast. However, this difference in densities may reflect lower capture efficiencies of the 1.0-m trawl and beach seine in comparison with the 1.6-m trawl used on the coast. Although net efficiencies could not be estimated for white seabass because of low abundance, Kramer (1990) found no difference in efficiency of these same nets for California halibut <40 mm SL. Net efficiencies probably did not differ greatly for small white seabass either, and thus the low catch of settled fish in the two bays was due to low abundance. In ichthyofaunal surveys of other southern California bays over the last several decades, only a few early juvenile white seabass have been caught (Dixon and Eckmayer, 1975; Klingbeil et al., 1975; Horn and Allen, 1981). Although depths of 0–1 m may not have been sampled intensively, data from these surveys support the view that bays as a whole are not important nurseries for white seabass.

The small size of southern California bays must also limit their importance as nursery areas for white seabass. As an example, Kramer (1990) estimated there were only 92 ha of habitat available between 0 and 1 m in Mission Bay and only 10 ha in Agua Hedionda Lagoon, compared with roughly 2,500 ha of habitat available between 5 and 8 m along the coast of San Diego County. Most of the remaining bays on the southern California coast are also small and many are periodically closed off from the sea by shifting sandbars (Zedler, 1982).

Nursery features

The narrow depth distribution of settled white seabass along the coast suggests that one or more fea-

tures of this zone enhance survival of young fish. Survival in shallow nurseries may be higher because of faster growth resulting from abundant food or warmer water, or lower predation rates (Bergman et al., 1988; Karakiri et al., 1989). Two features of the white seabass nursery that may promote rapid growth of juveniles are the abundant mysids and warmer water. Mysids, the principal prey of all sizes of white seabass collected, appear to be much more abundant within the nursery than at adjacent depths. Clutter (1967) sampled mysids at depths of 2–14 m during 1960–62 at a site 3 km south of the Torrey Pines 2 site (Fig. 1). Although the center of the depth distribution varied among months by 1–2 m, the mysid *Metamysidopsis elongata* was most numerous in the middle of the white seabass nursery



(Fig. 3). Other species of mysids were much less abundant. Density of *M. elongata* within the nursery can be quite high. Clutter's data indicate that the mean density of mysids at 6 m was over 4,000/m³, whereas Roberts et al. (1982) estimated that the mean density of mysids at 6 m near the San Onofre site was over 100/m³. Mysids are also about an order of magnitude more abundant during spring and summer, when white seabass are in the nursery (Clutter, 1967).

Mysids are not only abundant within the nursery; their broad size distribution makes them suitable prey for both recently settled larvae and much larger juveniles. Mature *M. elongata* brood and release relatively large young that remain in shallow water (Clutter, 1967). This reproductive strategy results in a population of mysids in the nursery that ranges over 100-fold in individual weight (Fig. 6). Although larger fish eat larger mysids, juveniles >40 mm SL can apparently feed on the largest mysids available (Fig. 6). At about this size, a transition from mysids to larger prey such as fish and shrimp also begins. The diets of other closely related sciaenids show a similar shift. Small (10–40 mm SL) sand seatrout, *Cynoscion arenarius*, small (15–30 mm SL) spotted seatrout, *C. nebulosus*, and juvenile (50–129 mm SL) weakfish, *C. regalis*, all feed extensively on mysids and at larger sizes shift to eating fish (Stickney et al., 1975; Sheridan, 1979; McMichael and Peters, 1989). Large juvenile, sub-adult, and adult white seabass feed principally on fish (Quast, 1968; Thomas, 1968).

A second feature of the shallow nursery that may enhance growth and survival of settled white seabass is warm water. Temperatures in the 4–8 m stratum during the summer ranged from 16 to 20°C, an average of 1.2 and 1.8°C warmer than the two deeper strata. The effect of a 1–2°C increase on growth has not been calculated for juveniles, but Orhun (1989) observed that a temperature increase from 15 to 17°C resulted in an increase in growth rate (dry weight gain) from 13.8%/d to 16.7%/d in 4–21 d old larvae. Temperature may have less influence on growth of juveniles, but any increase in growth rate will accumulate over the 2–3 months that juveniles are in the shallow nursery. Houde (1987) has demonstrated that a small increase in growth rate acting over a moderate time interval can reduce stage duration and theoretically result in substantial increases in survival and cohort size.

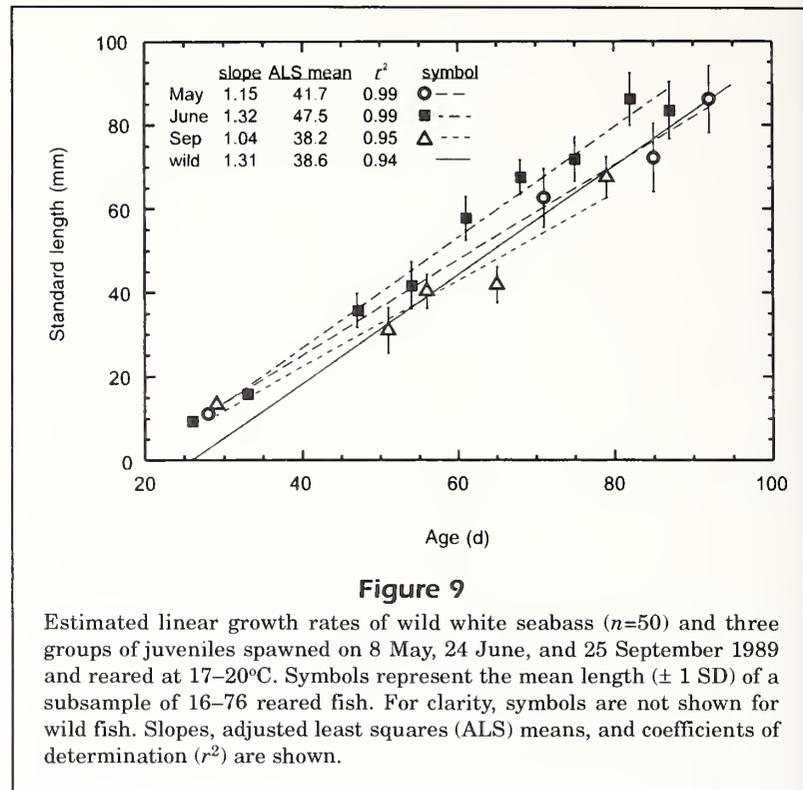


Figure 9

Estimated linear growth rates of wild white seabass ($n=50$) and three groups of juveniles spawned on 8 May, 24 June, and 25 September 1989 and reared at 17–20°C. Symbols represent the mean length (± 1 SD) of a subsample of 16–76 reared fish. For clarity, symbols are not shown for wild fish. Slopes, adjusted least squares (ALS) means, and coefficients of determination (r^2) are shown.

Correlations between abundances of drift macrophytes and white seabass suggest that macrophytes are also an important feature of the nursery. Although the correlation among abundances in single tows was weak ($r=0.29$), the sensitivity of this analysis was poor because the catch of white seabass was low; a maximum of only two white seabass was caught in a single tow at these stations. The correlation among mean abundances in the four tows at each site—the mathematical equivalent of making longer tows—was stronger ($r=0.52$) and does suggest that white seabass are more common near drift macrophytes. Allen and Franklin (1992) also noted that white seabass were rarely caught unless drift algae was present. It is possible that white seabass are simply more vulnerable to the trawl when drift macrophytes are present, but numerous studies with drop nets and purse seines have demonstrated that many juvenile fishes associate with drift macrophytes (Kulczycki et al., 1981; Robertson and Lenanton, 1984; Kingsford and Choat, 1986). Small white seabass may associate with drift macrophytes because they harbor suitable prey or serve as a refuge from predation.

In addition, the nursery area may be preferred by white seabass because the risk of predation could be lower than at adjacent depths. Unfortunately this hypothesis is difficult to evaluate. Surveys of the nearshore areas of southern California show that

predators of small benthic fishes are present both within the white seabass nursery and in deeper water (Love et al., 1986). Some of these predators, such as the California lizardfish (*Synodus lucioceps*), are less abundant within the white seabass nursery than at 12–18 m, whereas other species, such as California halibut (*Paralichthys californicus*), are more abundant within the nursery than in deeper water (Ford, 1965; Love et al., 1986; Allen, 1990). However predation risk will depend not only on the total number of vertebrate and invertebrate predators at a particular depth, but also on the size and ontogenetic distribution of predators as well as species-specific probabilities of encounter, detection, and capture (Bailey and Houde, 1989; Fuiman and Margurran, 1994). A detailed study is required to determine if the risk of predation to settled white seabass is lower in the nursery than in deeper waters.

Conclusion

The shallow water along the open coast just beyond the breaking waves appears to be the primary nursery for white seabass. Survival of young white seabass is probably influenced by the abundance of mysids and drifting macrophytes as well as by water temperature in the nursery during spring and summer. However, it is not known if survival in the nursery is an important determinant of year-class success for white seabass. Year-class success in most marine fishes is generally believed to be set during the larval stage. However, poor correlations between larval abundance and subsequent recruitment for some species indicate that survival of older fish, perhaps early juveniles, may be equally important (Sissenwine, 1984; Bradford, 1992). Further studies are needed to evaluate the importance of survival of early life history stages in determining the distribution and abundance of white seabass populations off southern California.

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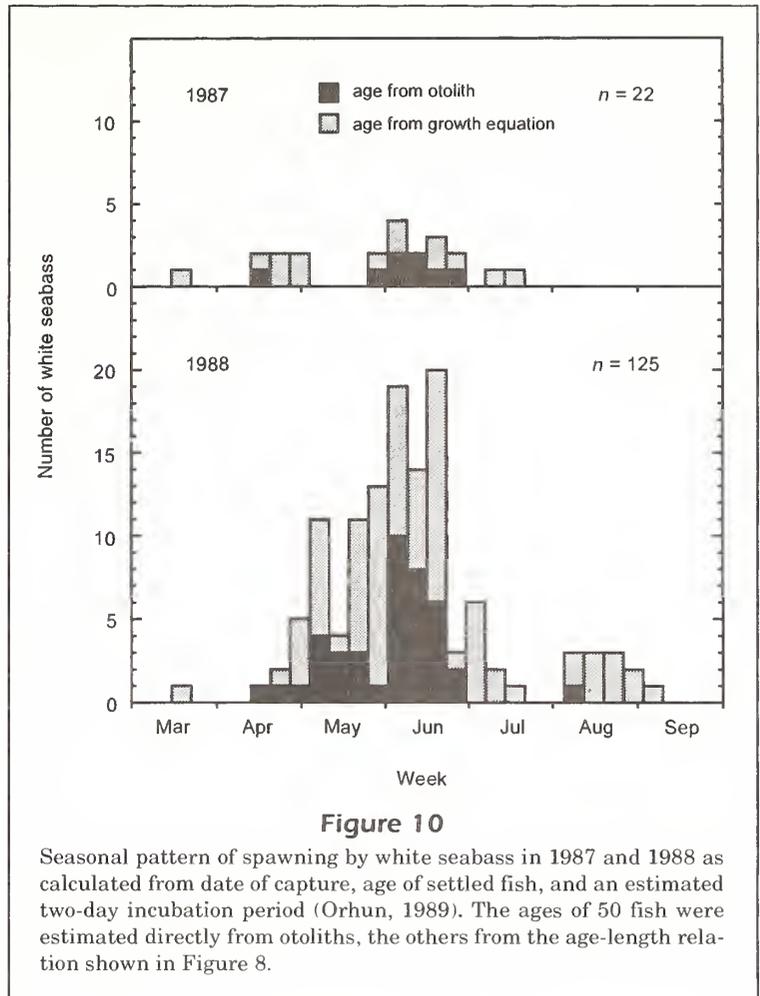


Figure 10

Seasonal pattern of spawning by white seabass in 1987 and 1988 as calculated from date of capture, age of settled fish, and an estimated two-day incubation period (Orhun, 1989). The ages of 50 fish were estimated directly from otoliths, the others from the age-length relation shown in Figure 8.

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Abstract.—Fish larvae and zooplankton were sampled during seven consecutive months from four regions of Wilson Inlet, an estuary in south-western Australia. Mouth size, prey size, and dietary composition of larvae of the gobiids *Afurcagobius suppositus*, *Pseudogobius olorum*, and *Favonigobius lateralis*, the blennioid *Parablennius tasmanianus*, and the syngnathid *Urocampus carinirostris* were determined. Dietary niche overlap (DNO) was calculated for co-occurring species pairs, both with and without incorporating a measure of relative prey (zooplankton) abundance. Significance of DNO was assessed 1) objectively, with bootstrapping of the dietary data and 2) subjectively, by assigning significance to values >0.6 . The diet of *A. suppositus* was dominated by harpacticoids, polychaete larvae, and the calanoid *Gladioferens imparipes*, whereas diets of the other species were dominated by copepod nauplii and postnaupliar stages of the cyclopoid *Oithona simplex*, the proportions of the latter increasing with growth of the larvae. Small numbers of large and small prey items were found in the stomachs of *A. suppositus* (mean=2.5), which had the largest mouth, whereas large numbers (mean=28.7) of small prey and no large items were found in the stomachs of *P. tasmanianus*, which had the second largest mouth. Between these extremes, *P. olorum*, *U. carinirostris*, and *F. lateralis* each ate mostly small and intermediate-size prey, supplemented by a few large prey. The data did not support the hypothesis that an increase in the difference in gape size between species would decrease the prevalence of significant DNO. The lack of a consistent relation between mouth size and DNO among the five species is evidence that interspecific dietary differences reflect differences in feeding behavior. With bootstrapping, the prevalence of significant ($P < 0.05$) DNO between species pairs was 32.6% when prey data were included in the analyses and 46.5% when prey data were not included. By subjectively assigning significance to DNO values >0.6 , we obtained substantially less conservative estimates that indicated the prevalence of significant DNO was $>53\%$.

Analysis of diet and feeding strategies within an assemblage of estuarine larval fish and an objective assessment of dietary niche overlap

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Starvation has been considered a major cause of mortality in larval fish (e.g. Hunter, 1984), although evidence from the field has been difficult to obtain (Heath, 1992). If starvation occurs within an assemblage of larval fish, competition for food is expected to contribute to that starvation. However, indications of any such competition may go undetected if the diet of only a single species is examined or if the influence of other planktivores (Fortier and Harris, 1989) is not considered. In the case of larval fish, relatively few studies have examined in detail the diets of several co-occurring species (e.g. Last, 1980; Laroche, 1982; Govoni et al., 1983; Watson and Davis, 1989). Furthermore, no study has objectively assessed the significance of dietary niche overlap (DNO), where DNO refers to the amount of sharing of food resources among larval fish. Assessments of whether dietary overlap within or between species (including larval fish) is significant have been based on indices that range from 0 for no overlap to 1 for complete overlap, with values greater than 0.5, 0.6, or 0.7 considered to be significant (e.g. Harmelin-Vivien et al., 1989; Cervel-

lini et al., 1993; Vega-Cendejas et al., 1994; Hartman and Brandt, 1995). However, because these cutoff points are arbitrary, they are not necessarily biologically significant, as in the case with fish larvae where individuals of co-occurring species may be confronted with large concentrations of the same prey type and thus any similarities in diet may be due to chance encounters.

Although dietary compositions of larval fish have been considered in the context of the abundance of the zooplankton prey of those larvae (e.g. Dagg et al., 1984; Jenkins, 1987; Hirst and DeVries, 1994; Welker et al., 1994), no study of dietary overlap between larval fish has incorporated data on their zooplankton prey. This analysis is necessary in order to assess whether there is a likelihood of competition for food.

Differences in mouth structure of fish may lead to differences in feeding success on particular prey types (Lavin and McPhail, 1986). Co-occurring larvae of different species with similar-size mouths may therefore exhibit a higher rate of significant DNO than those with mouths of different size. Because fish larvae usually swallow prey

whole, mouth size limits prey size; thus prey width is typically the limiting dimension for ingestion (e.g. Hunter, 1984, Heath, 1992). It is therefore important to examine mouth size and prey width when exploring the trophic relations of larval fish.

The first aim of this study was to examine the relation between mouth width, prey width, and dietary composition of the larvae of five teleosts in an estuary. The dietary data were then used to examine the extent of DNO between these species with a technique that takes into account relative prey concentrations. With this procedure we were able to test the hypothesis that divergence in gape size between species should be accompanied by a decrease in the prevalence of significant DNO between these species. Bootstrapping was used to assess whether species-pair DNO values were significant. The results of using this robust approach were compared with those obtained when relative prey concentrations were not included in the calculation of DNO and when a subjective level of >0.6 was considered to be significant for the DNO values.

Materials and methods

Sampling methods

This study was carried out in Wilson Inlet (35°00'S, 117°24'E), an estuary in southwestern Australia that comprises a 48 km² basin with two main tributaries, the Denmark and Hay rivers. Although samples were collected monthly between July 1988 and June 1989, the data used in this paper are restricted to those obtained between October 1988 and April 1989 when fish larvae were most abundant. Ichthyoplankton and zooplankton were sampled from open waters of the upper, middle, and lower basin, and the central channel of the lower saline reaches of the Denmark River, located 10.7, 8.3, 2.0, and 7.3 km, respectively, from the estuary mouth. The water depth in each region was between 2 and 3 m.

Sampling was initiated soon after sunset to reduce the likelihood of larvae avoiding the plankton nets. Fish larvae were collected with a pair of 500- μ m-mesh conical nets, each with a mouth diameter of 0.6 m and a length of 2 m. The nets were attached to either side of a powerboat and towed for 10 min just below the surface of the water at a speed of 1.5 m/s. During each ichthyoplankton tow, three to five zooplankton samples were taken from the surface with a conical, 53- μ m-mesh net with a mouth diameter of 0.35 m. The volumes of water filtered during each ichthyoplankton and zooplankton tow were measured with flowmeters. The zooplankton tows were 7–10 s

in duration. The flowmeter in the zooplankton net was closely observed during each tow. A tow was immediately terminated if the propeller speed suddenly decreased—a sign that the net was clogging. Samples were fixed in a 5% solution of formalin, which was replaced with 70% ethanol on the following day. The detailed results of the zooplankton sampling are given in Gaughan and Potter (1995).

Laboratory procedures and data analyses

Zooplankton were identified and counted under a dissecting microscope from subsamples of the replicate samples. Counts were standardized to numbers/m³; thus mean concentrations of taxa at each region within each month were able to be calculated. Relative proportions of those zooplankton taxa that contributed to larval diets at any time during the study were calculated for each sample. These represented relative resource availability (R_i).

The gobiids *Pseudogobius olorum*, *Afurcagobius suppositus*, and *Favonigobius lateralis*, the blenniid *Parablennius tasmanianus*, and the syngnathid *Urocampus carinirostris* were chosen for the present study because their larvae are abundant in Wilson Inlet from late spring to early autumn (Neira and Potter, 1992), collectively contributing 70.8% of the total open-water assemblage of larval fish in this estuary between September 1987 and April 1989.

All larvae of each species in a sample were removed and counted. Body length (BL) of each larva (i.e. the distance from the snout to tip of notochord in preflexion and flexion larvae and from the snout to the posterior end of the hypural plate in postflexion larvae [Leis and Trnski, 1989]) was measured to the nearest 0.1 mm. Since a focus of this study was the comparison of mouth width with prey width, the diets of individual size classes of larvae were determined. However, because the analyses of DNO were undertaken for co-occurring species within individual samples, the dietary data for all size classes of each species were pooled (see below).

The smaller larvae of *P. olorum*, *P. tasmanianus*, *F. lateralis*, and *A. suppositus* were each grouped into 1.0-mm length classes. Because *P. olorum* and *P. tasmanianus* >5 mm BL and *F. lateralis* and *A. suppositus* >6 mm BL were rarely caught, larvae of these four species longer than these respective lengths were each grouped into single length classes. Because the length range of *U. carinirostris* was relatively wide, the larvae of this species were grouped into length classes with intervals of 3 or 4 mm, depending on the numbers caught.

Items in the gut were identified and counted. Maximum widths of intact dietary items, which typically

represent the limiting dimension for ingestion, were measured to 0.01 mm with an ocular micrometer in a compound microscope. Mouth width of larvae at the widest point of the upper jaw was similarly measured on a subsample of at least 50 larvae of each species. Widths of prey and mouth widths of larvae of each species were then plotted against body length of larvae.

Proportional utilization (p_i) of each prey type was calculated for length classes within each species with data pooled across regions and months. Proportional utilization was also calculated across length classes for the larvae of each species within a sample. Guts that were empty or contained only unidentifiable material were not included in these calculations.

Relative feeding prevalence of all larvae within samples were correlated against the corresponding estimates of zooplankton abundance to determine if there was any evidence that zooplankton abundance was limiting feeding success. The average DNO exhibited between all species within samples was likewise compared with zooplankton abundance.

Calculation of dietary niche overlap

Interspecific DNO was calculated for species-pairs within individual samples, i.e. for each site within a given month. Because this part of our study focused on examining niche relations between species, pooled diets for each species within a sample were considered to represent the average diet of each species. Furthermore, comparisons were limited to those samples in which ≥ 10 larvae of each of two or more species contained food. By pooling data across size classes we were able to compare more DNO data. Although the use of average diets would reduce the robustness of a parametric test of significance, we used nonparametric techniques for assessing the significance of DNO.

Sufficient numbers of larvae were obtained for analysis in 13 of the 28 ichthyoplankton samples (7 months \times 4 regions) to allow 43 pairwise comparisons to be made between the diets of co-occurring species.

Besides the DNO values that were calculated and that incorporated prey abundance data, the results of this technique were also evaluated against calculations of DNO that did not incorporate such data. Because prey abundance data are incorporated into prey utilization data prior to calculating DNO (see below), the same formula was used to calculate DNO both with and without consideration of prey concentrations. DNO was measured with the symmetric niche overlap coefficient (Pianka, 1973)

$$\Phi_{ij} = \left(\sum p_{ij} p_{ik} \right) / \sqrt{\left(\sum p_{ij}^2 \sum p_{ik}^2 \right)},$$

where p_{ij} and p_{ik} = the proportional utilization of prey type i by species j and k , respectively.

Using the p_i data directly, we were able to provide a basis for calculating DNO without prey abundance data. To incorporate prey abundance data, the geometric mean (g_i) of p_i and electivity (e_i) was used (Winemiller and Pianka, 1990), instead of p_i as in the original formula. The geometric mean gives a better indication of ecological similarity by reducing those biases within both p_i and e_i that can result from the presence of very abundant or very rare prey types (Winemiller and Pianka, 1990). Electivity is the p_i value that has been weighted by resource availability (R_i) as $e_i = p_i/R_i$. These values were calculated within the DNO algorithm and are not presented. Note that g_i can be used with other overlap indices because it is calculated prior to the calculation of the overlap value.

Bootstrapping of the resource matrix of a pair of species was used to obtain a null distribution of 1,000 pseudo-DNO values against which the significance of observed DNO could be assessed (Winemiller and Pianka, 1990). These calculations were performed for species pairs at sites within months. In each one of the 1,000 runs, the algorithm randomly reassigned the g_i values for each prey type (e.g. resource states $i \dots p$) within each larval species j and k , but among the resource types used by both j and k (e.g. amongst $g_{ij} \dots g_{nj}$ and $g_{ik} \dots g_{pk}$). A g_i value for one of the species pair may thus be reassigned to a resource state which was used only by the other species.

The null hypothesis (H_0) for each test was that the dietary compositions of the larvae of the two species were not the same. The null hypothesis was rejected if more than 95% of the 1,000 pseudo-DNO values were less than the observed DNO. Such cases indicated that the observed value was larger than would be randomly expected at $P < 0.05$.

The prevalence of significant DNO calculated with g_i and bootstrapping was then compared with that obtained with p_i , i.e. when R_i was not taken into account. These results were also compared with those obtained when the significance of DNO was arbitrarily set at values > 0.6 .

Results

Zooplankton

Zooplankton were very abundant in Wilson Inlet between October 1988 and April 1989; there was a total mean monthly concentration of 342,746 organisms/m³ (range = 48,641–2,951,209/m³). Concentrations exceeded 100,000/m³ in 26 of the 28 zooplank-

ton samples. Mean monthly concentrations of zooplankton in Wilson Inlet were similar from October 1988 to April 1989; only January had a significantly ($P < 0.05$) higher concentration (Gaughan and Potter, 1995).

All copepods, irrespective of stage, contributed 74.7% of the total mean concentration of zooplankton (Table 1). The cyclopoid *Oithona simplex*, the calanoids *Gladioferens imparipes* and *Acartia simplex*, and several species of harpacticoids were the only copepods that were common in Wilson Inlet (Gaughan and Potter, 1995). Considering just the copepods, adults of *A. simplex* and *G. imparipes*, which represented the largest prey types consumed by fish larvae in Wilson Inlet, contributed only 2.9% of the total mean concentration of this taxonomic group. The smaller species and developmental stages of copepods were thus approximately 33 times more abundant than the adults of *A. simplex* and *G. imparipes* collectively. The mean concentrations and relative contributions of other zooplankton taxa that were eaten by larval fish during this study are shown in Table 1.

Numbers of prey items consumed and dietary composition of fish larvae

The total number of larvae of each species examined during this study are shown in Table 2, and the numbers of larvae in size classes of each species which contained food are shown in Figure 1.

The mean number of prey items found in each larva was less than five for *A. suppositus* and *F. lateralis*,

between five and ten for *P. olorum* and *U. carinirostris* and 28.7 for *P. tasmanianus* (Table 2). Likewise, the maximum numbers of prey consumed were much lower for the first four species than for *P. tasmanianus* (Table 2). The number of prey ingested by larvae increased with body size only in the case of *U. carinirostris*.

Various developmental stages of copepods dominated the diets of larval fish in Wilson Inlet; the rotifer *Synchaeta cf. baltica* and the larvae of bivalves and polychaetes were also occasionally important (Fig. 1). Only the postnaupliar stages of copepods in the diets were identified to species. Each of the common types of copepod contributed to the diets of fish larvae.

During the growth of *P. olorum*, *F. lateralis*, *U. carinirostris*, and *P. tasmanianus*, the contribution of copepod nauplii declined while that of postnaupliar stages increased (Fig. 1). *Oithona simplex* was particularly important to *P. olorum* and *U. carinirostris*, representing over 30% of the diet of the three largest size classes of the former species and over 40% of the diet of all size classes of the latter species. By contrast, despite the increased contribution by *O. simplex* to larger size classes of *P. tasmanianus*, copepod nauplii dominated the diet of all size classes, contributing > 40% to each (Fig. 1). The diet of *F. lateralis* < 4.0 mm BL consisted mainly of copepod nauplii and to a lesser extent of bivalve larvae and *O. simplex*. The main prey types of *F. lateralis* from 6.0–7.9 mm BL were harpacticoids (40.9%), calanoid copepodites (20.6%), and phytoplankton (15.6%).

Polychaete larvae, copepod nauplii, and harpacticoids each contributed over 25.0% of the diets of the smallest size class of *A. suppositus*, whereas harpacticoids alone contributed 60.0% to larvae > 6.0 mm BL (Fig. 1). Harpacticoids also contributed 15.3 and 27.0% of the diet in the 4.0–4.9 and 5.0–5.9 mm length classes, respectively. *Gladioferens imparipes*

Table 1

Mean monthly concentrations and relative contributions of zooplankton in Wilson Inlet between October 1988 and April 1989.

Taxa	Mean concentration (no. organisms/m ³)	Relative contribution (%)
Copepod nauplii	164,827	48.1
Calanoid copepodites	33,755	9.8
<i>Oithona simplex</i>	44,629	13.0
<i>Acartia simplex</i>	6,771	2.0
<i>Gladioferens imparipes</i>	719	0.2
Harpacticoids	5,523	1.6
Polychaete larvae	34,997	10.2
Bivalve larvae	18,435	5.4
<i>Synchaeta cf. baltica</i>	9,787	2.9
Other taxa	23,303	6.8
Total	342,746	

Table 2

Mean and maximum numbers of prey per larva for five teleost species in Wilson inlet. n = the total number of larvae of each species examined.

Species	n	Mean prey/larva	Maximum prey/larva
<i>Pseudogobius olorum</i>	1,946	7.7	30
<i>Favonigobius lateralis</i>	451	4.0	15
<i>Afurcagobius suppositus</i>	485	2.5	19
<i>Parablennius tasmanianus</i>	469	28.7	103
<i>Urocampus carinirostris</i>	434	9.7	23

was abundant only in the diet of the 4.0–4.9 and 5.0–5.9 mm length classes (Fig. 1).

Prey width and larval mouth width

Urocampus carinirostris had the smallest mouth, *P. tasmanianus* and *A. suppositus* the widest mouths (Fig. 2, A, D, E). The shapes of the mouths were most

similar in the case of *P. olorum* and *F. lateralis* (Fig. 2, B and C). Although mouth width of *U. carinirostris* increased linearly with body length (Fig. 2A), such an increase in the other four species was best described by a polynomial function (Fig. 2, B–E: Table 3). Mouth width of *U. carinirostris* increased slowly from 0.19 mm at 8 mm BL to 0.28 mm at 19 mm BL (Fig. 2A). The rate at which mouth width increased with body length was greater for the other four species (Fig. 2, B–E). In *A. suppositus*, mouth width increased from 0.33 mm at 3.5 mm BL to 0.68 mm at 6.0 mm BL (Fig. 2E). The smallest larvae of *P. olorum*, *F. lateralis*, and *P. tasmanianus* had narrower mouths (<0.15 mm) than both *A. suppositus* and *U. carinirostris*, owing to their smaller size upon arrival in the plankton (Fig. 2, A–E). However, mouth widths of the first three of these species exceeded the maximum recorded for *U. carinirostris* (0.28 mm) by the time each had attained 5 mm BL and approached 0.60 mm in larger larvae.

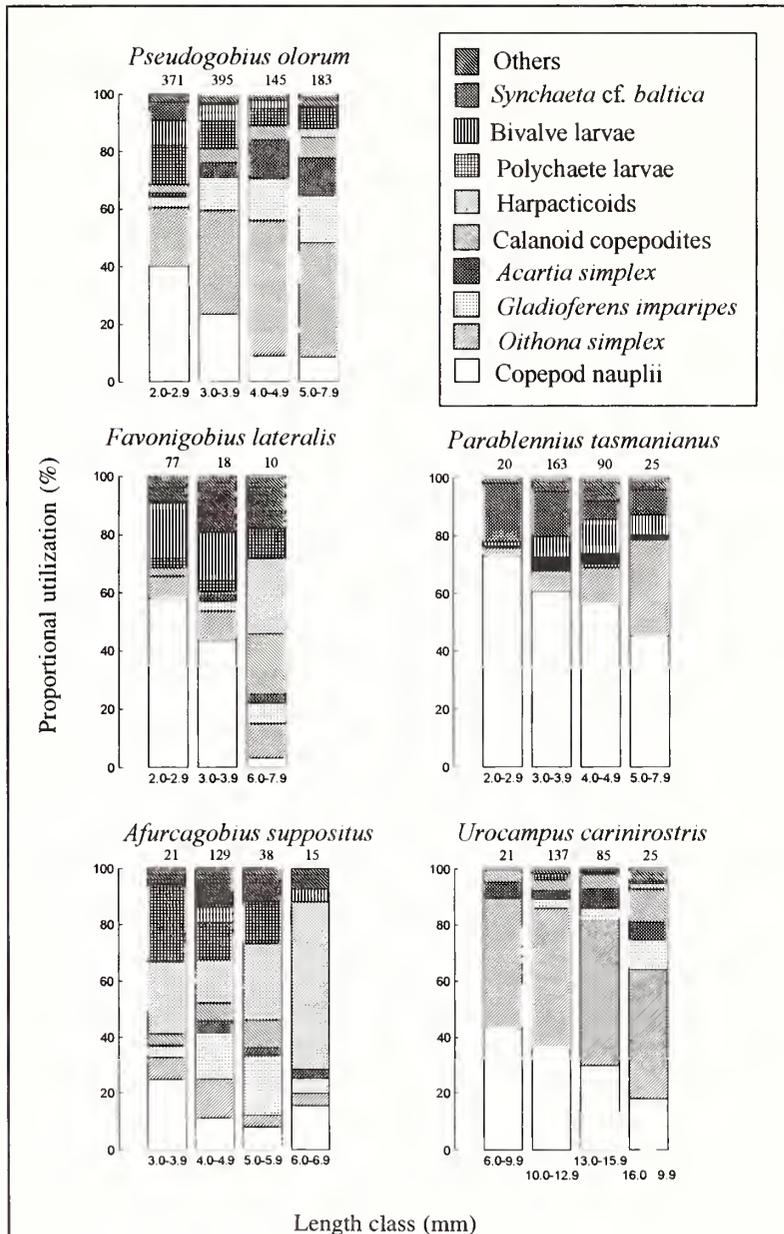


Figure 1

Proportional utilization (p_i , %) for length classes of larvae of five species of fish caught at four sites in Wilson Inlet between October 1988 and April 1989. The numbers of larvae that contained food in each size class are shown above the bars.

The slope describing the relation between prey width and larval length for each species was less than 0.03. The extent to which prey width increased with length was thus very small for each species. Minimum prey width for each species was about 0.04 mm (Fig. 2, A–E). The large numbers of prey of each species with widths of 0.04–0.08 mm were predominantly attributable to copepod nauplii. Prey widths of between 0.04 and 0.18 mm predominated in *U. carinirostris*, *P. olorum*, and *F. lateralis* (Fig. 2, A–C).

Parablennius tasmanianus ate mainly prey 0.04–0.13 mm wide, but with a maximum width of only 0.18 mm (Fig. 2D). *Afurcagobius suppositus* consumed the largest prey items, i.e. postnaupliar stages of *G. imparipes* and *A. simplex*, with widths of 0.12–0.30 mm and 0.10–0.16 mm respectively. As with the other species, *A. suppositus* also ate smaller items (0.04–0.10 mm) (Fig. 2E).

As *U. carinirostris*, *P. olorum*, *F. lateralis*, and *P. tasmanianus* grew, they continued to eat many prey <0.10 mm wide, even though the smaller larvae of each were capable of eating prey >0.10 mm (Fig. 2, A–D). Prey width was about 0.10 mm narrower than mouth width for most of the length range of *U. carinirostris* (Fig. 2A). The widths of the larger

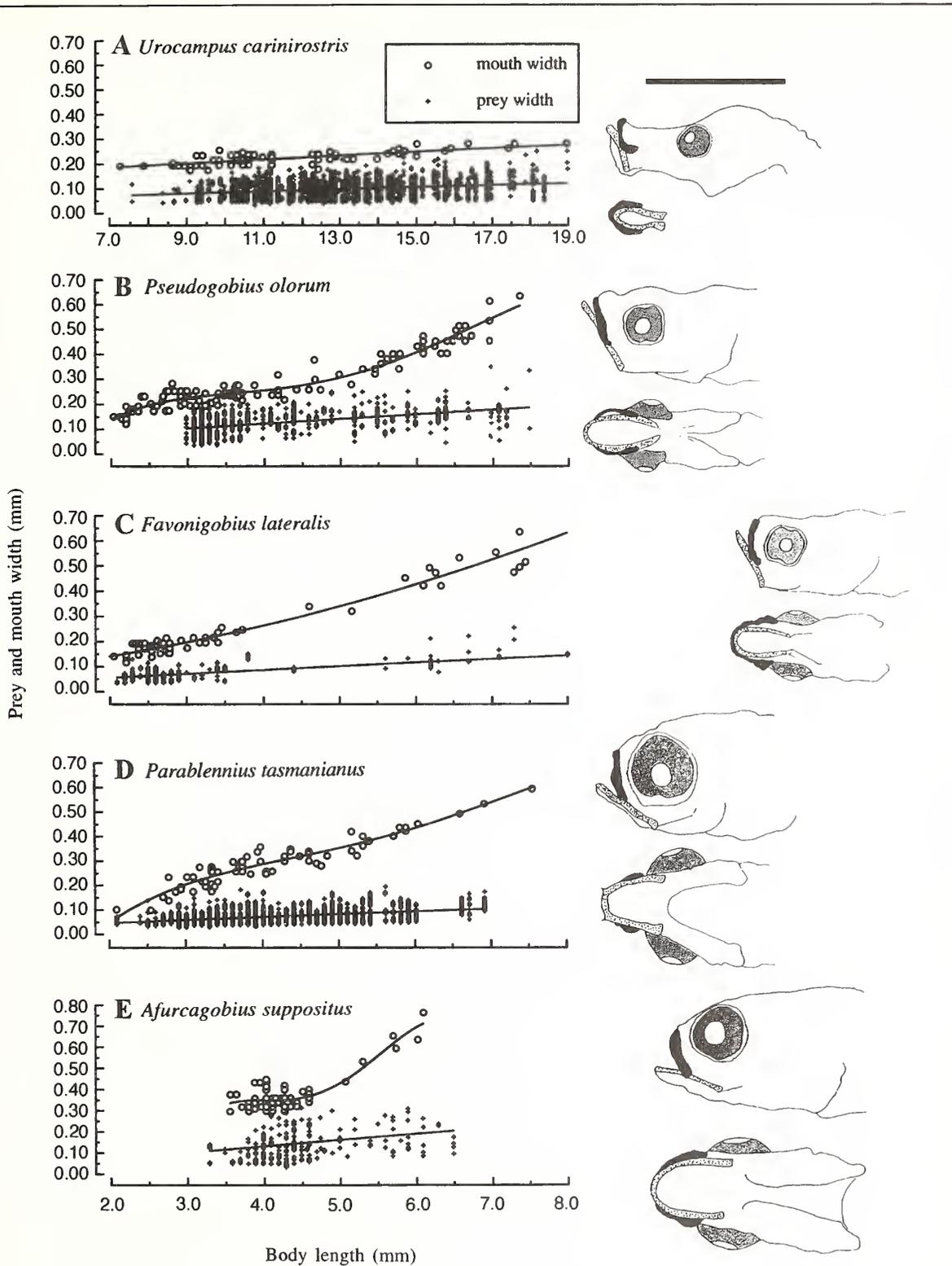


Figure 2

Prey width and larval mouth width for larvae of five species of fish caught in Wilson Inlet between October 1988 and April 1989. Lateral and ventral views of the head of a representative larva of each species are also given; the upper jaw is indicated in black, the lower jaw is indicated with stippling (scale bar equals 1.0 mm). The examples were each taken from a 5.0-mm-BL larva, except the example of *Urocampus carinirostris*, which was taken from a 10.5-mm-BL larva.

Table 3

The relations between mouth width (MW) and body length (BL) for the larvae of five teleost species in Wilson Inlet.

Species	n	Regression function	r ²
<i>Urocampus carinirostris</i>	69	$MW = 0.139 + 0.006(BL)$	0.453
<i>Afurcagobius suppositus</i>	50	$MW = -15.666 + 14.256(BL) - 4.687(BL^2) + 0.671(BL^3) - 0.035(BL^4)$	0.849
<i>Pseudogobius olorum</i>	98	$MW = -0.729 + 0.839(BL) - 0.273(BL^2) + 0.038(BL^3) - 0.002(BL^4)$	0.921
<i>Favonigobius lateralis</i>	50	$MW = 0.061 + 0.029(BL) + 0.005(BL^2)$	0.963
<i>Parablennius tasmanianus</i>	66	$MW = -0.517 + 0.411(BL) - 0.073(BL^2) + 0.005(BL^3)$	0.889

Table 4

The number of cases of significant dietary niche overlap (DNO) for larvae of five teleost species in Wilson Inlet between October 1988 and April 1989. Co-occurring species were compared only when ≥ 10 individuals of each contained food in their guts. The number of cases for which pairwise comparisons could be made is shown as *n*. The number of significant cases are presented for DNO calculations I) that used zooplankton concentrations and II) that did not use zooplankton concentrations. Within these categories, the number of significant cases were determined a) at $P < 0.05$ from a null distribution derived from bootstrapping and b) with an arbitrary cutoff level for significance at an overlap value > 0.6 . DNO was measured with a modification of Pianka's (1973) symmetric niche overlap coefficient.

	<i>Pseudogobius olorum</i> n (I) (II) (a, b) (a, b)	<i>Afurcagobius suppositus</i> n (I) (II) (a, b) (a, b)	<i>Favonigobius lateralis</i> n (I) (II) (a, b) (a, b)	<i>Parablennius tasmanianus</i> n (I) (II) (a, b) (a, b)
<i>Afurcagobius suppositus</i>	5 (0, 2) (0, 0)	—		
<i>Favonigobius lateralis</i>	4 (1, 2) (1, 2)	1 (0, 0) (0, 0)	—	
<i>Parablennius tasmanianus</i>	8 (1, 4) (3, 6)	1 (0, 0) (0, 0)	4 (2, 4) (3, 4)	—
<i>Urocampus carinirostris</i>	8 (7, 7) (8, 8)	2 (1, 1) (0, 1)	4 (1, 2) (2, 3)	6 (1, 4) (2, 4)
Totals	n (I) (II) (a, b) (a, b) 43 (14, 23) (20, 28)			
Percent of total	(32.6, 53.5) (46.5, 65.1)			

prey items consumed by *P. olorum* < 4.0 mm BL were similar to mouth width, as was also the case with *F. lateralis* of 2.0–2.5 mm BL and *A. suppositus* of 4.0–4.5 mm BL. For each of these three gobiid species, the maximum prey width of larvae > 5 mm BL was far less than mouth width. This difference exceeded 0.20 mm in the larger gobiid larvae. Likewise, maximum prey widths for larval *P. tasmanianus* approached mouth width in smaller larvae but were much less for larger larvae (Fig. 2D).

Dietary niche overlap

Dietary niche overlap between *P. olorum* and *U. carinirostris* ranged from 0.543 to 0.983 and was significant on seven of the eight occasions in which these species co-occurred (Table 4). Although DNO ranged from 0.764 to 0.980 on the four occasions that *P.*

tasmanianus and *F. lateralis* co-occurred, overlap was significant only twice (Table 4). There were a few other cases of significant DNO amongst the larval fish assemblage; DNO was particularly low between *A. suppositus* and the other species, being significant only with *U. carinirostris* on one occasion.

Of the 43 pairwise comparisons that could be made between the diets of co-occurring larvae of the five species, there were 14 cases (32.6%) of significant DNO (Table 4). This increased to 20 (46.5%) if zooplankton data were not included in the calculations of DNO's. If DNO > 0.6 had been considered significant, the number of significant cases increased from 32.6% to 53.5% for calculations which included zooplankton data and from 46.5% to 65.1% for those which did not include these data.

The magnitudes of the differences for the prevalence of significant DNO found by using bootstrap-

ping (18.6% and 20.9%) were greater than those obtained by accounting for zooplankton abundance data (11.6% and 13.9%, Table 4).

Relation between zooplankton abundance and both feeding prevalence and mean DNO

Zooplankton abundance at sites within months was not significantly related to either feeding prevalence ($P > 0.05$, $r = 0.346$, $n = 26$) or mean DNO ($P > 0.1$, $r = 0.146$, $n = 15$) of fish larvae within the corresponding samples.

Discussion

Numbers of prey consumed and prey size

Afurcagobius suppositus, because it ingested larger prey types, e.g. *G. imparipes*, consumed the least number of prey. The other species ate larger numbers of small and intermediate-size prey, e.g. copepod nauplii and *O. simplex*. The significant increase in numbers of prey with length for *U. carinirostris* only was probably attributable to the fact that the magnitude of the range of length of individuals examined for this species was 12 mm, whereas that of the other species was less than 6 mm.

Despite marked increases in mouth width during the growth of each species except *U. carinirostris*, average prey width of the five species increased only slightly with growth. Although smaller larvae consumed prey almost as wide as their mouths, larger larvae typically ate prey far smaller than their mouth size. Furthermore, the smaller larvae of each species consumed some prey items almost as wide as those eaten by larvae in the larger size classes. These data indicate that mouth width was not limiting the ingestion of larger prey types among larvae in the larger size classes.

The dominance of relatively small prey in the diets of larval fish in Wilson Inlet reflects the dominance of these types of zooplankton in the environment. During the study period, copepod nauplii, *O. simplex*, calanoid copepodites and harpacticoids were 33 times more abundant than the adults of *G. imparipes* and *A. simplex* collectively, the only common large prey. Thus, as has previously been found for other larval fish (e.g. Ware and Lambert, 1985; Kellermann, 1990), prey availability strongly influenced the sizes of prey consumed.

From an early age and size, *Afurcagobius suppositus* ate larger prey than the other four species. Since this species hatches at a more advanced stage and with better developed fins than the other four

species (Neira et al., in press), they were probably superior swimmers and thus more efficient at capturing larger prey. Greater mobility may have also resulted in *A. suppositus* searching a larger volume of water (Hunter, 1984), which would increase the rate at which the larger and less abundant zooplankton were encountered. The possession of a larger mouth apparently allows *A. suppositus* to take advantage of larger prey in presumably more frequent encounters.

Mouth size and DNO

Although *A. suppositus* had the largest mouth and consumed the largest and most diverse prey, the relative differences in mouth size of the other four species were not accompanied by corresponding differences in the size and composition of prey. A lack of a predictive relation between mouth size and diet has previously been recorded for fish larvae from another estuary (Laroche, 1982) and more recently for larvae of freshwater fish in an experimental situation (Bremigan and Stein, 1994). In Wilson Inlet, this situation was further highlighted by the lack of a relation between the prevalence of significant DNO and the mouth structure of the five species. Thus, the prevalence of significant DNO was not particularly high between *P. olorum* and *F. lateralis* (Table 4), the species with the most similar mouth structure, whereas *P. olorum* and *U. carinirostris* had very similar diets, as indicated by the high prevalence of significant DNO (Table 4), but had different-size mouths. Conversely, the diet of *A. suppositus* overlapped significantly only with that of *U. carinirostris*, the species with the smallest mouth. *Parablennius tasmanianus* and *F. lateralis*, the only other species-pair to exhibit more than one case of significant DNO, also had dissimilar mouths. Finally, *A. suppositus* and *P. tasmanianus* had the largest mouths but the most divergent diets.

Along with the general lack of a relation between mouth size and diet, the relatively frequent occurrence (32.6%) of significant DNO amongst the larval fish in Wilson Inlet, when prey abundance was taken into account, was also attributable to the high concentrations of relatively limited choices of acceptable prey types. The lack of a relation between concentrations of zooplankton and both feeding prevalence and mean DNO within samples was also probably a result of consistently high concentrations of zooplankton. Consequently, significant DNO among larval fish in Wilson Inlet provided no evidence of competition for food. Furthermore, Gaughan and Potter (1995) found that abundances of zooplankton and larval fish were significantly correlated at only two of the four sampling regions in Wilson Inlet. The lack of a rela-

tion at the other two regions was due to large fluctuations in the abundance of zooplankton between months. These fluctuations did not appear to influence monthly trends in the abundance of fish larvae, probably because concentrations of zooplankton typically remained high ($>100,000/m^3$).

Because in this study we were limited to examining the diets of larval fish, a complete assessment of dietary relations and the potential for competition within the plankton community could not be undertaken. However, other zooplankton taxa (e.g. *Sagitta minima*) sufficiently large to have used the same food resources as larval fish were rare in Wilson Inlet, contributing less than 0.2% of the total numbers of zooplankton (Gaughan and Potter, 1995).

Feeding strategies

The diets of the fish larvae from Wilson Inlet may be viewed as representing a spectrum of feeding strategies. The diet of *A. suppositus* is distinguished from those of the other four species by its broader composition, the larger size of its prey items, and the smaller numbers of prey consumed. At the opposing end of the spectrum, *P. tasmanianus* larvae consumed large numbers of small prey items. The feeding strategies of the larvae of *P. olorum*, *F. lateralis*, and *U. carinirostris* lay between these extremes; these species consumed many small and intermediate-size prey which were occasionally supplemented with larger prey items.

Because the trophic character of a species may be influenced by both size and structure as well as behavior (Lavin and McPhail, 1986), the small influence of mouth width on the size of prey consumed by larval fish in Wilson Inlet indicates that the different feeding patterns among larval species probably resulted from behavioral differences (Bremigan and Stein, 1994). These patterns, which occurred despite the high concentrations of zooplankton, may enhance survival, and hence recruitment, if marginally low concentrations of zooplankton were present at temporal or spatial scales beyond those sampled.

Evaluation of methods

In this study, we examined a technique for assessing DNO that consists of two parts (accounting for zooplankton abundance in the calculation of DNO and objectively assessing significance of DNO with bootstrapping). This technique was substantially more conservative than that which did not consider zooplankton abundance and which did subjectively assess significance. Prevalence of significant DNO thus doubled (32.6% to 65.1%) when zooplankton

data were not included in the calculations and an arbitrary cutoff point of 0.6 was used to test for significance. The less conservative techniques of measuring DNO and assessing its significance would have therefore overestimated the degree of DNO among fish larvae in Wilson Inlet.

A large overestimation of DNO would likely have led to a different interpretation of the data. For example, the higher rate of significant overlap may have led to the conclusion that competition for food was sufficiently high to influence markedly the survival rate of fish larvae in Wilson Inlet. In contrast, the lower prevalence of overlap is more consistent with our previous hypothesis that food is unlikely to be limiting for the open-water assemblage of larval fish in Wilson Inlet (Gaughan and Potter, 1995).

Although concentrations of potential zooplankton prey are not necessarily directly related to their availability, we suggest that inferences regarding competition for food among larval fish may be misleading if data on the abundance of the zooplankton are not considered when measuring DNO. In studies of other taxa, or even of adult fish, where the abundances of prey in the environment may be very difficult or impossible to estimate without bias, resource availability can be estimated in a circular manner with proportional-utilization data (see Winemiller and Pianka, 1990). However, because the majority of fish larvae and their potential prey are planktonic, small, and relatively immobile (thus highly susceptible to capture with plankton nets), estimates of prey concentrations in the environment should be used to calculate DNO for larval fish. Likewise, because a subjective assessment of the significance of DNO is inadequate, bootstrapping techniques may prove to be useful in making an objective examination of dietary relations, which are typically awkward to analyze statistically (Winemiller and Pianka, 1990; Baltanás and Rincón, 1992).

Finally, although the two parts of the technique used in this study, i.e. objectively assessing significance and accounting for zooplankton abundance, each contributed to the overall result, individually the former had a greater influence (18.6% and 20.9%) on the estimated prevalence of significant DNO than the latter (11.6% and 13.9%). Even though the direction and magnitude of the differences between the two parts of this technique may apply only to the current study, this finding further suggests that both the incorporation of prey abundance data and an objective assessment of significance need to be considered in an analysis of dietary overlap because either may have more influence on the apparent prevalence of significant DNO.

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Abstract.—Aspects of the life history of red porgy from the South Atlantic Bight (SAB) were examined for four periods (1972–74, 1979–81, 1988–90, and 1991–94), and annual changes in the age and growth of red porgy were described for data collected during 1988–94. The life history of red porgy during 1972–74 was assumed to represent that of an unfished population, although this population had been subject to light fishing pressure. From 1972–74 to 1979–81, the back-calculated size-at-age increased slightly for ages 2–8. By 1988–90 and 1991–94, however, the back-calculated size-at-age for the same age classes was significantly smaller than that in 1979–81. In addition, size-at-maturity and size-at-sexual-transition occurred at progressively smaller sizes for 1988–90 and 1991–94. The mean size-at-age (observed and back-calculated) declined for most ages between 1988 and 1994. Von Bertalanffy growth curves fitted to the mean back-calculated size-at-age for each year showed similar decreasing trends. Changes in life history may be a response to sustained 20-year overexploitation that has selectively removed individuals predisposed towards rapid growth and larger size.

Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972–1994*

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The red porgy, *Pagrus pagrus*, is a protogynous sparid distributed throughout the Atlantic Ocean and Mediterranean Sea at depths of 18 to 280 m (Manooch and Hassler, 1978; Vassilopoulou and Papaconstantinou, 1992). In the South Atlantic Bight (SAB) off the southeastern coast of the United States, red porgy are commonly associated with sponge or coral habitat (or both) with rocky outcrops and rocky ledges (Grimes et al., 1982), frequently referred to as “live bottom.” Areas of live bottom are distributed patchily throughout the SAB, and patch size can range from square meters to square kilometers (Powles and Barans, 1980). Nevertheless, red porgy in the SAB are thought to constitute a single stock (Manooch and Huntsman, 1977).

Red porgy are an important segment of the commercial fisheries of the SAB, averaging 6% of the snapper-grouper landings since 1978 (SAFMC¹). Similarly, red porgy make up a considerable portion of the recreational harvest of reef fishes in the SAB (Huntsman et al.²). The fishery for red porgy in the SAB has, however, experienced a serious decline in landings since 1982 (Vaughan et al., 1992; Huntsman et al.²), as well as a decline in fishery-independent catch per unit of effort (CPUE) (Fig. 1). Estimates of stock size derived from virtual

population analysis (VPA) showed a peak population size in 1975 and a steady decline through 1992 (Vaughan et al., 1992; Huntsman et al.²). Although estimates of stock size derived from fishery-independent CPUE for 1993–1995 suggest a slight population recovery (Harris, personal obs.), the spawning stock ratio, estimated at 18% in 1993, is still considerably below the 30% level used by the South Atlantic Fishery Management Council to define when a species is overfished (Huntsman et al.²).

Apart from a size limit instituted in 1992, management of the fishery has remained essentially unchanged, in spite of an apparent continual decline of the resource. The ability of fishermen to locate good fishing areas (i.e. patches of live bottom) precisely using LORAN-C and Global Positioning Systems technology and

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¹ SAFMC. 1991. Amendment 4, regulatory impact review and final environmental impact statement for the snapper grouper fishery of the South Atlantic Region. South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC, 225 p.

² Huntsman, G. R., D. S. Vaughan, and J. C. Potts. 1993. Trends in population status of the red porgy *Pagrus pagrus* in the Atlantic Ocean of North Carolina and South Carolina, USA, 1971–1992. South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC 29422.

an increase in the number of vessels participating in the snapper-grouper fishery in the SAB resulted in a steadily increasing fishing mortality from 1972 through 1993 (Huntsman et al.²). For new management regulations to be considered, current life history data need to be made available. The most recent published discussion of SAB red porgy life history was based on data collected between 1972 and 1974 (Manooch, 1976; Manooch and Huntsman, 1977).

It has been shown that age structure, size-at-age, and reproductive strategies of a population will change in a predictable fashion that responds to declining abundance (Lack, 1968; Rothschild, 1986). There is, however, concern over the extent and permanence of these changes (Edley and Law, 1988; Bohnsack, 1990). The effect of sustained heavy exploitation, combined with current management strategies in regard to particular size restrictions and quotas or bag limits on the life history of a fished stock, is poorly documented. Staff of the Marine Resources Monitoring, Assessment, and Prediction Program (MARMAP), a federally funded program based at the South Carolina Department of Natural Resources in Charleston, SC, have collected life history data on red porgy since 1979. When combined with data collected from 1972 through 1974 (Manooch, 1976; Manooch and Huntsman, 1977), data spanning 24 years were available to determine if the life history of the red porgy population in the SAB had changed.

Long-term life history data and the increase in fishing pressure provide a mechanism to test the impact of sustained exploitation on the life history of a reef fish species in the SAB. Therefore, the objectives of this paper were to describe temporal changes in the age, growth, and reproduction of red porgy for four periods during 1972–94 and to identify annual changes in age and growth that occurred during 1988–94.

Methods

Red porgy were collected from 1979 to 1994 during standard MARMAP sampling with chevron traps, hook-and-line gear, Florida traps, and blackfish traps (Collins, 1990; Collins and Sedberry, 1991) in the SAB from Cape Fear, North Carolina, to Cape Canaveral, Florida. Specimens were collected during daylight

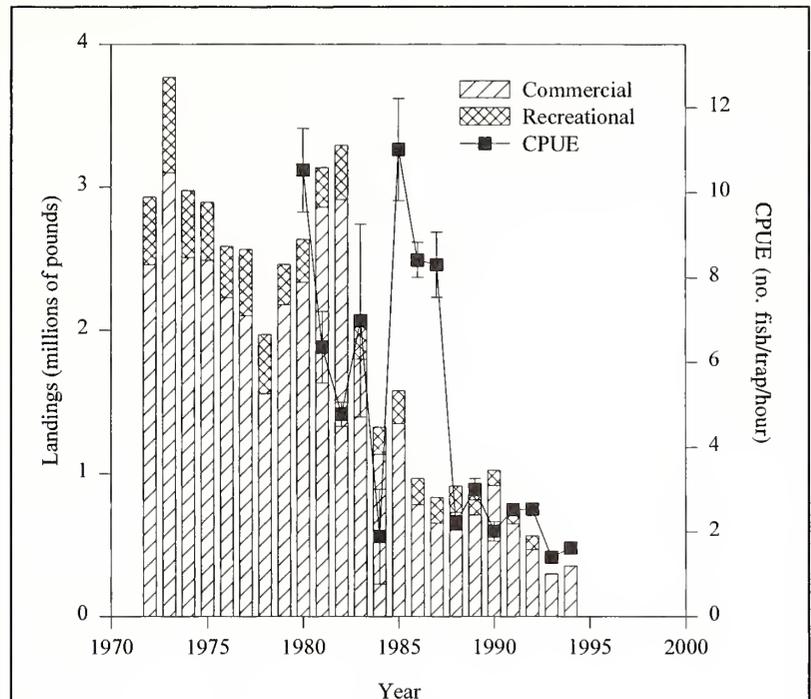


Figure 1

Commercial and recreational landings of red porgy since 1972. Recreational landings are from headboat surveys conducted by the Beaufort Laboratory of the National Marine Fisheries Service (70%), and the Marine Recreational Fisheries Statistics Survey (30%). CPUE = MARMAP trap catch per unit of effort.

hours primarily between May and August of each year.

MARMAP sampling strategies changed slightly between 1979 and 1994. From 1979 to 1987, samples were collected randomly from four large areas of live bottom (identified by using underwater television) with hook-and-line gear, blackfish traps, and Florida traps to follow trends in the abundance of the various species. Additional sites outside these areas were sampled as time and weather conditions allowed (see Collins and Sedberry, 1991). Traps were baited with cut clupeids, buoyed off the research vessel, and soaked for one to four hours. Hook-and-line gear consisted of bandit reels (commercial bottom-fishing hook-and-line gear) or rod and reel with 6/0 Penn Senator high-speed reels and Electramate electric motors. Terminal gear always consisted of three hooks fished vertically and baited with cut squid or cigar minnow (*Decapterus* sp.). All fishes caught were measured (mm fork length [FL]), and the total weight for each species, from each collection, was recorded (g). All red porgy collected during these years were kept for life history studies.

In 1988 and 1989, a chevron trap was added to the gear used to sample reef fishes. During these years, the research vessel was anchored over a known live

bottom area that was verified with underwater television. Each of the three trap types (blackfish, Florida, and chevron) was deployed either from the bow, stern, or midships of the research vessel (see Collins, 1990). Hook-and-line collections were taken with rod and reel and with the three-hook terminal rig. Fishes were processed as described for 1979–87. All red porgy collected in 1988 and 1989 were kept for life history studies.

Based on the data collected during 1988 and 1989, a decision was made to discontinue the use of blackfish and Florida traps in 1990 because chevron traps sampled a greater species diversity (Collins, 1990). During the late 1980's, all live bottom locations identified during underwater television surveys and from sampling in previous years were plotted with LORAN-C coordinates to the nearest 0.1 μ s and included in a sample site database. Currently, there are over 2,500 live bottom sites in the MARMAP database, from which 300–600 randomly chosen sites have been sampled each year since 1989. In addition, since 1989, the SAB has been stratified on the basis of latitude. Zone 1 includes all sites sampled south of 32°N, zone 2 all sites between 32°N and 33°N, and zone 3 all sites north of 33°N. Buoyed chevron traps were deployed from the research vessel and soaked for approximately 90 minutes. Hook-and-line (rod-and-reel) collections were made for 30 minutes at dawn or dusk. All fishes sampled were processed as in previous years. Because of concerns about potential gear selectivity, the length frequency of all red porgy caught by all four gear types during 1988 and 1989 was compared.

Since 1989, fork lengths (cm) and total weight (10 g) were recorded for all red porgy sampled in each zone for each year with a Limnoterra FMB-IV electronic fish measuring board and a Toledo electronic scale interfaced with a XT-type personal computer. In 1990 and 1994, all red porgy collected during sampling were used for life history studies. In 1991–93, up to 15 fish from each 1-cm size class and all fish larger than 350 mm FL were kept from each zone for life history studies. Red porgy used for life history studies were measured to the nearest mm (total length [TL], FL, and standard length [SL]) with a Limnoterra FMB-IV electronic fish measuring board interfaced with a XT-type personal computer. Individual weights were measured to the nearest gram with a triple beam balance.

Age and growth

Sagittae were removed at sea and stored dry. In the laboratory, the whole right otolith was immersed in cedar wood oil and examined for annuli (one translucent and one opaque zone) (Manooch and Hunts-

man, 1977) with a dissecting microscope with incandescent reflecting light and an ocular micrometer (1979–87) or with a dissecting microscope and reflected light from a fiber-optic light source (1988–94). The latter microscope had an attached Hitachi KP-C550 video camera connected to a personal computer equipped with a MATROX frame grabber and OPTIMAS image analysis software. The digitized image was viewed on a television monitor, and annuli were measured with OPTIMAS software. For both systems, measurements were taken from the core of each otolith to the outer edge of each opaque zone and to the edge of the otolith on a straight line midway between the posterodorsal dome and the most posterior point on the otolith (Frizzel and Dante, 1965). Annuli on this plane were consistently clearer and easier to enumerate, especially for older fish. For years where large numbers of red porgy were collected, a minimum of 350 randomly chosen fish were aged per year. All fish larger than 350 mm (FL) were aged for all years. The first reader collected measurements from all otoliths, whereas the second reader counted increments from a randomly chosen 35% of otoliths for each year. If agreement between the two counts was less than 90% for any year, the second reader read all otoliths for that year. When counts differed, otoliths were reread by both readers and discarded from further analyses if a difference in readings persisted.

Back-calculated lengths-at-age were computed by using the scale proportional hypothesis (Francis, 1990):

$$L_i = - (a/b) + (L_c + a/b) (O_i / O_c),$$

where L_i = length at the formation of the i th increment;

O_i = otolith radius at the formation of the i th increment;

O_c = otolith radius at the time of capture;

L_c = fish length at the time of capture;

a = intercept of otolith radius on fish length regression;

b = slope of the otolith radius on fish length regression.

Lengths were backcalculated to the most recently formed increment for comparisons of annual growth (1988–94) and to all increments for comparisons between periods (1979–81, 1988–90, and 1991–94). The SigmaPlot curve-fitting module with the Marquardt-Levenburg algorithm was used to fit von Bertalanffy growth curves to the mean back-calculated length-at-age for each year or period (SigmaPlot, 1994).

Because red porgy are protogynous sparids, and undergo a size- and behavior-related transition from

females to males, no comparison of size-at-age or growth rates were undertaken for the sexes separately. Life history data collected during four periods (1972–74, 1979–81, 1988–90, and 1991–94) were compared. The first study (1972–74) used red porgy sampled from headboats operating from North and South Carolina (see Manooch, 1976; Manooch and Huntsman, 1977). Specimens were collected throughout the year and gonads from 736 fish were examined macroscopically to assess sex and stage of maturity (Manooch, 1976). Scales from 3,278 individuals were examined to determine ages, and 222 fish were aged from whole otoliths (Manooch and Huntsman, 1977).

Red porgy collected during 1979–81, 1988–91, and 1991–94 were grouped by period. Otolith radius to fork length least-squares regressions were fitted separately for each period (except that of 1972–74) owing to concerns about temporal changes in somatic growth. Von Bertalanffy growth curves (von Bertalanffy, 1938) were fitted to the mean back-calculated size-at-age for each of the four study periods. Size-at-age was backcalculated for all increments measured. Mean observed and back-calculated sizes-at-age were compared between periods for each age with a single-factor ANOVA. Size and age distributions and size-at-age were compared between the three latitudinal zones sampled with single factor and two-way ANOVA's. It appeared from observations during sampling that larger fish may be associated with the shelf break; therefore size and age distributions, and size-at-age were also compared for different depths. Because the shelf break is located at about 48 m, two depth zones—0 to 45 m and 46 to 90 m—were compared. The same tests were performed in comparing annual data collected between 1988–94.

Reproduction

The posterior portion of the gonads of red porgy from 1979 to 1994 was removed from the fish and fixed in 10% seawater formalin for 1–2 weeks, then transferred to 50% isopropanol for 1–2 weeks. Gonad samples were processed with an Auto-Technicon 2A Tissue Processor, vacuum infiltrated, and blocked in paraffin. Three transverse sections (6–8 μm thick) were cut from each sample with a rotary microtome, mounted on glass slides, stained with double-strength Gill haematoxylin, and counter-stained with eosin y. Sex and reproductive state were assessed by one reader according to histological criteria (Table 1). Specimens with developing, ripe, spent, or resting gonads were considered sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the

yolk vesicle stage and specimens with beta, gamma, or delta stages of atresia. Sex ratios, size-at-first-maturity, and the percent of mature females by 20-cm size class were calculated for all functional males and females, 1989–94. Sex ratio, size-at-first-maturity, and the percent of mature females were determined by size class for 1979–81, 1988–90, and 1991–94, and chi-square (χ^2) analysis was used to determine if there were significant differences in the proportion of males to all fish collected during the three periods and if there were differences in size-at-maturity between periods.

Results

1979–1994

A total of 20,756 (13,120 during 1972–74) red porgy were sampled during the four periods, of which 4,503 were aged and 4,293 sexed and staged (Table 2). The mean FL of fish collected from 1979 to 1994 showed a declining trend; however, there was no trend in mean age (Table 2). Increment formation was assumed to be annual (Collins et al., 1996; Manooch and Huntsman, 1977).

Age and growth

The mean observed size-at-age declined markedly from 1972–94 through 1991–94. Except for fishes aged 2–8 yr collected during 1979–81, the mean sizes-at-age for all ages for the three periods between 1979 and 1994 were smaller than those during 1972–94 (Fig. 2). The observed sizes-at-age in 1988–90 and 1991–94 were significantly smaller than those during 1979–81 ($P < 0.01$) for ages 2 through 8. Red porgy aged 3 through 5 collected during 1991–94 were also significantly smaller than fish of the same age collected during 1988–90 ($P < 0.01$). We were unable to include data collected by Manooch and Huntsman (1977) in our statistical analyses. The mean back-calculated size-at-age showed trends similar to the mean observed size-at-age (Fig. 3). Fish aged 2–8 were significantly smaller during 1988–90 and 1991–94 than during 1979–81, and fish aged 2–5 significantly smaller in 1991–94 than in 1979–81 and 1988–90.

The von Bertalanffy growth curves derived from mean back-calculated lengths for each period (Fig. 4) showed similar trends. The theoretical mean maximum fork length (L_{∞}) declined by 100 mm from 1972–74 to 1991–94 (Table 3). The theoretical growth rate (k) was higher between 1991 and 1994 than between 1972 and 1974. This difference is a reflection of the large decline in L_{∞} , rather than an increase in growth

Table 1

Histological criteria developed by MARMAP (Charleston, SC) to determine reproductive stage in red porgy, *Pagrus pagrus* (see D'Ancona, 1949, 1950; Wallace and Selman, 1981; Alekseev, 1982, 1983; Hunter et al., 1986; Sadovy and Shapiro, 1987; Matsuyama et al., 1988; West, 1990; Roumillat and Waltz¹).

Reproductive state	Male	Female
Immature (virgin)	No primary males found. Juveniles were either females or, infrequently, simultaneous or transitional (see below).	Previtellogenic oocytes only; no evidence of atresia. In comparison with resting female, most previtellogenic oocytes <80 μm , area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles and are not as elongate, germinal epithelium along margin of lamellae is thicker, ovarian wall is thinner.
Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and dorsomedial sinuses.	Oocytes undergoing cortical granule (alveoli) formation through nucleus migration and partial coalescence of yolk globules.
Running and ripe	Predominance of spermatozoa in lobules and dorsomedial sinuses; little or no occurrence of spermatogenesis.	Completion of yolk coalescence and hydration in most advanced oocytes. Zona radiata becomes thin. Postovulatory follicles sometimes present.
Developing, recent spawn	Not assessed.	Developing stage as described above as well as presence of postovulatory follicles.
Spent	No spermatogenesis; some residual spermatozoa in lobules and sinuses.	More than 50% of vitellogenic oocytes with alpha- or beta-stage atresia.
Resting	Little or no spermatocyte development; empty lobules and sinuses.	Previtellogenic oocytes only; traces of atresia. In comparison with immature female, most previtellogenic oocytes >80 μm , area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongate and convoluted, germinal epithelium along margin of lamellae is thinner, ovarian wall is thicker.
Mature specimen, stage unknown	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive stage.	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive stage.
Simultaneous (bisexual)	Presence of distinct ovarian and testicular regions in approximately equal amounts and of the same reproductive state. This gonad structure was infrequently observed in both juvenile and adult fish.	
Transitional	Ventrolateral proliferation of active testicular tissue (spermatogonia through spermatozoa) along the outer surface of the ovarian wall in spent or resting ovary (functional protogyny) or immature ovary (juvenile protogyny). As testicular tissue envelops regressing ovary, ovary collapses laterally and sperm sinuses form within former ovarian wall.	

¹ Roumillat, W. A., and C. W. Waltz. 1993. Biology of the red porgy, *Pagrus pagrus*, from the southeastern United States. MARMAP Final Data Report, South Carolina Department of Natural Resources, Charleston, SC, 38 p.

rate (i.e. the negative relation between L_{∞} and k). However, k was highest for the 1979–81 period, when L_{∞} was also still relatively high.

Reproduction

Our examination of 4,293 gonads ($n=1,397$, 1979–81; $n=727$, 1988–90; $n=2,169$, 1991–94) revealed that

sexual transition was occurring at smaller sizes in the later periods. There was a significant increase ($P<0.001$) in the number of males with time (Table 4). However, in 1988–90 and in 1991–94, the proportion of males to the total number of fish sexed was significantly greater at smaller sizes than during 1979–81 (Table 4). At 301–350 mm TL, male red porgy made up 24% of the fish that were sexed dur-

Table 2

Sampling data for the four study periods 1972–74, 1979–81, 1988–90, and 1991–94.

Year	Fish sampled	No. aged	Mean fork length (mm)	Mean age (years)	No. sexed
1972–74	13,120	222	—	—	—
1979–81	1,933	1,177	293	3.07	1,397
1988–90	1,853	1,261	254	2.44	727
1991–94	3,850	1,843	257	3.062	2,169
Total	20,756	4,503	268	2.86	4,293

ing 1991–94, in contrast with 7% at the same size interval during 1979–81 ($P < 0.001$; Table 4). In 1979–81, male red porgy constituted 12% of the fish examined at 351–400 mm TL compared with 32% in 1988–90 ($P < 0.01$) and 49% in 1991–94 ($P < 0.001$; Table 4).

Size-at-maturity of female red porgy has also changed. Female red porgy became sexually mature at smaller sizes in 1991–94 than in 1979–81. During 1991–94, female red porgy first became sexually mature at 176–200 mm TL (mean age=0.9). In 1979–81, the first mature female was at 201–225 mm TL (mean age=0.9) (Table 5). There were significantly more mature females (54%; $P < 0.001$) at 251–275 mm TL (mean age=1.9) in 1991–94 than during 1979–81 (27%; mean age=1.7).

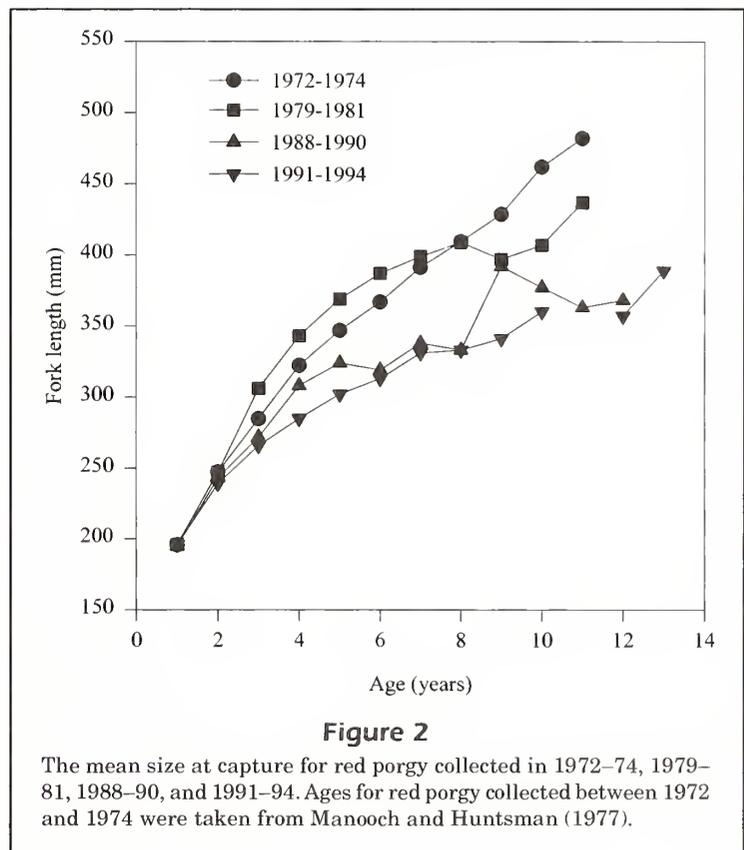
1988–1994

A total of 2,629 live bottom stations and 5,265 red porgy were sampled May through August 1988–94, of which 4,349 specimens were kept for life history studies (Table 6). The majority of the samples were collected with chevron traps. During 1988 and 1989, there was no difference between the size range of red porgy collected in chevron traps and the size range of red porgy collected in blackfish traps, Florida traps, hook-and-line gear, or all three of these gear types combined (Fig. 5). Similarly, there was no difference in the size range of red porgy sampled by hook-and-line gear and chevron traps between 1990 and 1994 (Fig. 5). Between 1988 and 1991, however, the mean size of red porgy captured with hook and line was significantly larger each year than the mean size of porgy taken with the remaining gear types ($P < 0.05$), although there was no significant difference between mean size of fish captured with the gear types used in 1993 and mean size of fish captured with the gear types used in 1994. The size of red porgy sampled during 1988–94 ranged from 90 to 501 mm

Table 3

Von Bertalanffy growth equation parameters derived from the mean back-calculated fork length for each time period.

Parameter	1972–74	1979–81	1988–90	1991–94
k	0.226	0.343	0.273	0.281
L_{∞}	459.3	391.4	382.7	356.4



FL. The mean size was 256 mm FL, with the highest frequency occurring at 240 mm FL. The length frequency of aged red porgy was very similar to the length frequency of all red porgy sampled.

Age and growth

Ages were obtained for 2,935 (67%) of the red porgy otoliths collected (Table 6). Agreement between the first and second reader averaged 93%, and was never less than 90% for any year. The mean observed size-at-age declined for most ages between 1988 and 1994 (Table 7), although there was a significant increase in the mean age of red porgy over the study period (Fig. 6; $P < 0.01$; $r^2 = 0.94$). The mean observed size-at-age for red porgy 2 years and older sampled during 1988 and 1989 was significantly larger than all other years, with the mean observed size-at-age in 1992 and 1993 consistently the smallest (Table 7; Fig. 7). Above age 6, growth rates appeared to taper off sharply for all years (Fig. 7). Age-6 red porgy collected during 1988 had the third highest mean length recorded for all age classes in any year. Similar to the mean observed size at age, mean back-calculated size at the most recent annulus was significantly larger for 1988 and 1989 compared with other years for ages 2 and greater and also appeared to reach asymptotic size at age 6 for each year (Table 8; Fig. 8).

The von Bertalanffy growth curves fitted to the mean back-calculated size at most recent age (ages 1–10) for each year demonstrated some differences between years (Fig. 9), with growth curves from 1988 and 1989 showing larger fish at age, and higher L_{∞} and k . Both k and L_{∞} tended to decrease dur-

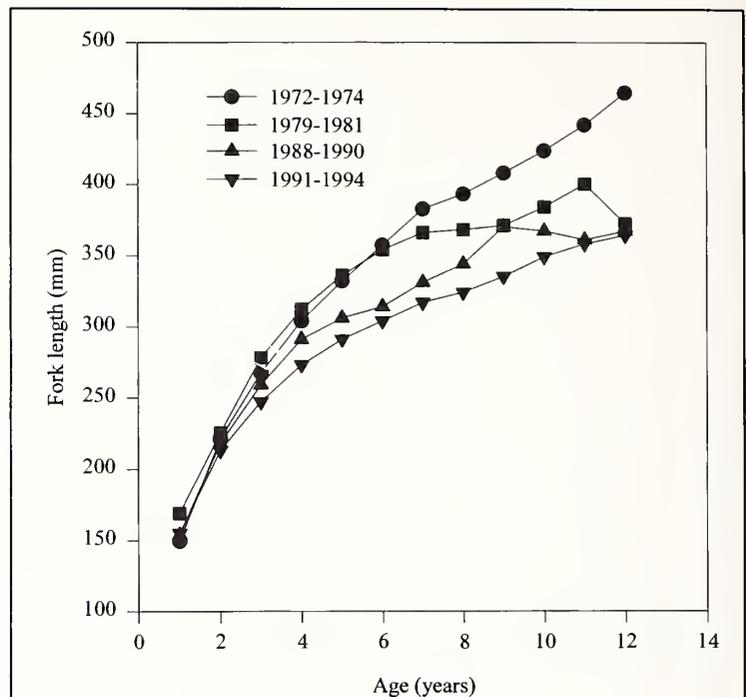


Figure 3

The mean back-calculated size at age for red porgy collected in 1972–74, 1979–81, 1988–90, and 1991–94. Back-calculated lengths for red porgy collected between 1972 and 1974 were derived from scale ages.

ing the study period, although neither of these trends were significant (linear regression; $P > 0.05$; Fig. 10).

No significant differences were apparent in size distribution, age distribution, or size-at-age between

Table 4

Percentage of male red porgy relative to the total number of individuals sexed during 1979–81, 1988–90, and 1991–94. A significant difference (χ^2 ; $P < 0.01$) in the proportion of males for a particular size class collected during 1979–81 is denoted by "A". A significant difference (χ^2 ; $P < 0.01$) in the proportion of males that were collected during 1988–90 is denoted by "B".

Size (mm TL)	1979–81			1988–90			1991–94		
	Total	Males	%Males	Total	Males	%Males	Total	Males	%Males
<200	19	—	—	16	—	—	57	—	—
200–250	216	—	—	140	2	1.43	372	4	1.08
251–300	271	10	3.69	163	5	3.07	491	33	6.72 ^B
301–350	313	21	6.71	226	25	11.06	814	194	23.83 ^{AB}
351–400	239	29	12.13	136	44	32.35 ^A	371	183	49.33 ^{AB}
401–450	160	38	23.75	38	17	44.74 ^A	57	25	43.86 ^A
451–500	158	108	68.35	8	4	50.00	6	4	66.67
501–550	18	12	66.67	—	—	—	1	—	—
551–600	2	1	50.00	—	—	—	—	—	—
Total	1,397	220		727	97		2,169	443	

the three latitudinal zones. However, significant differences were apparent in the size and age distribution between the two depth zones ($P < 0.05$), with larger and older fish occurring in the deeper zone. There were no significant differences in the size-at-age between these two zones ($P > 0.05$).

Discussion

Samples were collected from throughout the SAB during 1988–94. However, 69% of the collections and 73% of the aged red porgy were taken from zone 2 (32°N–33°N). Zone 2 was sampled most frequently because it was most accessible from Charleston, South Carolina, the base of operations (latitude 32° 45'N). Once settled, red porgy do not appear to move very much (Parker, 1990) and could experience differential growth rates because of differing environments. Therefore the concentration of sampling in zone 2 could have resulted in biased estimates of size-at-age. However, the comparison of size-at-age of red porgy showed no significant differences between latitudinal or depth zones; therefore, although there may be localized differences in growth rates, perhaps associated with different patches of live bottom, the mean growth rate appears to be similar throughout the region. The mean depth and temperature of areas sampled in the MARMAP surveys have not changed significantly since 1987; thus these environmental variables, at least, have not caused the life history changes in red porgy (Fig. 11).

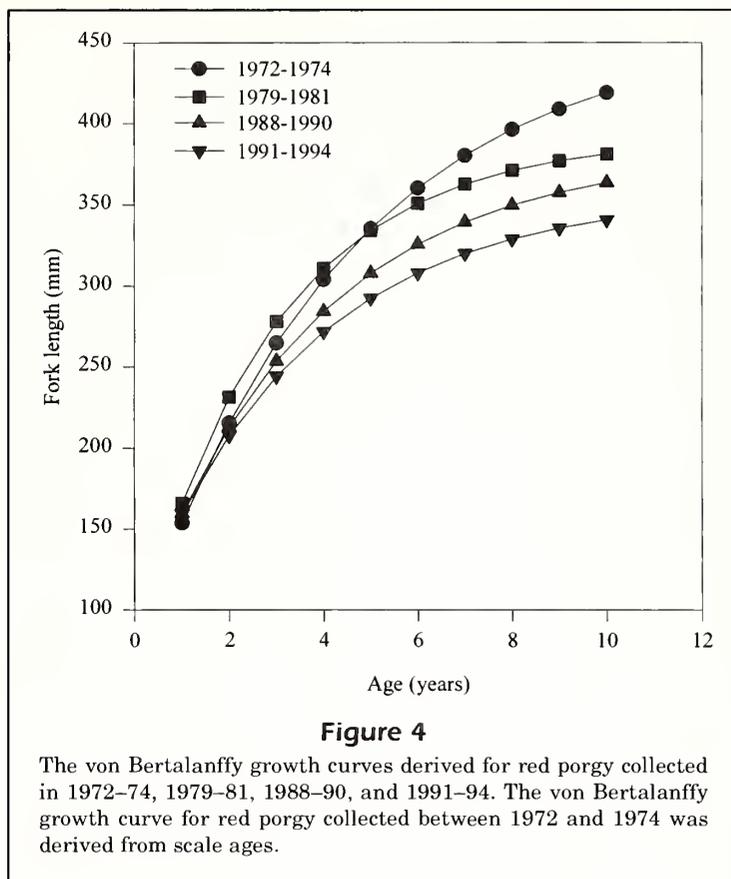


Figure 4

The von Bertalanffy growth curves derived for red porgy collected in 1972–74, 1979–81, 1988–90, and 1991–94. The von Bertalanffy growth curve for red porgy collected between 1972 and 1974 was derived from scale ages.

There were significant differences in size and age by depth, with larger and older fish occurring in deeper water. This difference may be due to fishermen operating in deeper water with larger hooks and baits to target groupers, thus reducing the availability of this gear to red porgy, particularly to smaller

Table 5

Percentage of red porgy females that were sexually mature relative to all females collected during 1979–81 and 1991–94. A significant difference (χ^2 ; $P < 0.01$) in the proportion of mature females is denoted by "A".

Size (mm TL)	1979–81			1991–94		
	Total females	Number mature females	Percent mature females	Total females	Number mature females	Percent mature females
<200	16	—	—	55	2	3.64
200–225	91	1	1.10	182	4	2.20
226–250	85	11	12.94	156	26	16.67
251–275	103	28	27.18	157	85	54.14 ^A
276–300	78	77	98.72	211	189	89.57
>300	512	512	100.00	615	606	98.54
Total	885	62	1,376	912		

individuals. Therefore, red porgy in deeper water may experience reduced fishing mortality in comparison with those in shallower waters. In shallower water,

fishermen reduce hook and bait size to catch smaller fishes, and more red porgy of all sizes are landed. Alternatively, the increase in size and age with depth

Table 6

Sampling data for 1988–94, collected from the RV *Oregon* (1988–89) and the RV *Palmetto* (1990–94).

Year	Trap collections	No. porgy	Hook-and-line collections	No. porgy	No. processed	No. aged
1988	84	294	261	170	427	371
1989	65	248	198	174	388	345
1990	348	957	111	44	997	545
1991	306	830	33	25	519	426
1992	324	1,107	25	1	494	419
1993	414	722	52	45	538	385
1994	370	1,107	38	11	986	444
Total	1,911	5,265	718	470	4,349	2,935

Table 7

Mean observed fork length (mm) at age for red porgy (standard error in parenthesis).

Age (yr)	1988	1989	1990	1991	1992	1993	1994
1	191 (2) <i>n</i> =124	203 (3) <i>n</i> =70	197 (3) <i>n</i> =78	200 (2) <i>n</i> =126	190 (2) <i>n</i> =78	206 (3) <i>n</i> =70	186 (1) <i>n</i> =53
2	256 (2) <i>n</i> =107	248 (2) <i>n</i> =149	234 (2) <i>n</i> =218	237 (2) <i>n</i> =110	228 (2) <i>n</i> =119	245 (3) <i>n</i> =78	253 (2) <i>n</i> =101
3	284 (3) <i>n</i> =95	284 (4) <i>n</i> =54	264 (2) <i>n</i> =180	274 (3) <i>n</i> =71	261 (3) <i>n</i> =72	267 (3) <i>n</i> =104	264 (3) <i>n</i> =50
4	328 (7) <i>n</i> =26	305 (5) <i>n</i> =39	295 (5) <i>n</i> =26	282 (4) <i>n</i> =70	287 (3) <i>n</i> =64	290 (4) <i>n</i> =59	283 (3) <i>n</i> =106
5	386 (34) <i>n</i> =2	328 (6) <i>n</i> =18	314 (10) <i>n</i> =16	303 (8) <i>n</i> =17	305 (4) <i>n</i> =43	308 (5) <i>n</i> =35	297 (3) <i>n</i> =86
6	334 (7) <i>n</i> =4	305 (34) <i>n</i> =3	317 (13) <i>n</i> =5	335 (7) <i>n</i> =13	310 (7) <i>n</i> =14	305 (5) <i>n</i> =25	313 (5) <i>n</i> =32
7	374 (10) <i>n</i> =5	340 (35) <i>n</i> =3	308 (7) <i>n</i> =6	339 (20) <i>n</i> =5	321 (7) <i>n</i> =8	359 <i>n</i> =1	334 (5) <i>n</i> =9
8	352 (3) <i>n</i> =4	335 <i>n</i> =1	307 (9) <i>n</i> =3	322 (5) <i>n</i> =4	328 (5) <i>n</i> =2	348 (25) <i>n</i> =6	324 (6) <i>n</i> =4
9	389 <i>n</i> =1	394 (42) <i>n</i> =2	384 (17) <i>n</i> =2	362 <i>n</i> =1	344 (8) <i>n</i> =6	322 (18) <i>n</i> =2	
10		372 (28) <i>n</i> =2		361 (16) <i>n</i> =4		344 (7) <i>n</i> =2	390 <i>n</i> =1
11		363 <i>n</i> =1					
12		368 <i>n</i> =1			360 <i>n</i> =1	354 <i>n</i> =1	
13					390 (9) <i>n</i> =2		

could reflect a gradual movement of red porgy towards deeper water as they age. Grimes et al. (1982) suggested that red porgy associated with shallow reefs may temporarily move to deep water in response to unusually cold water temperatures. However, tagging studies have shown that settled red porgy undertake very little long-term movement (Grimes et al., 1982; Parker, 1990). Another reef species, black sea bass (*Centropristis striata*), has shown limited movement of larger fish to deeper water (Ulrich and Low³; Harris and McGovern, personal obs.).

Fishing mortality (F) of red porgy has increased since 1972, although between 1972 and 1975 it showed a slight decline (Vaughan et al., 1992). The

F for fully recruited ages (5–9) increased from 0.2 in 1976 to 1.3 in 1991 (Huntsman et al.², Murphy VPA, $M=0.28$). The F for ages 1–4 showed similar trends, although the magnitude of the increase was less (Huntsman et al.², Murphy VPA, $M=0.28$). Owing to the changes in the life history of red porgy since 1972, these estimates of fishing mortality are probably high; yet, the increasing trend in fishing pressure is evident. Except for an increase during 1981–83, landings of red porgy have been declining since 1973 (Fig. 1). Similarly, the number of recruits to age 1 have declined steadily since 1974 (Huntsman et al.², Murphy VPA, $M=0.28$). An estimate of SSR in 1993 was only 18% (Huntsman et al.², Murphy VPA, $M=0.28$). Again, the changes in the life history of red porgy since 1972 indicate that Huntsman et al.² may have underestimated the decline in the abundance of age-1 fish.

Concurrent with the fishery becoming increasingly overexploited, there has been corresponding change

³ Ulrich, G. F., and R. A. Low. 1992. Movement and utilization of black sea bass, *Centropristis striata*, in South Carolina. Final Unpubl. Rep. NOAA Award No. NA90AA-D-FM656, 11 p.

Table 8

Mean back-calculated fork length (mm) at age for red porgy (most recent annulus; standard error in parenthesis).

Age (yr)	1988	1989	1990	1991	1992	1993	1994
1	163 (2) <i>n</i> =124	180 (3) <i>n</i> =70	173 (4) <i>n</i> =78	166 (2) <i>n</i> =126	159 (2) <i>n</i> =78	171 (2) <i>n</i> =70	161 (2) <i>n</i> =53
2	230 (2) <i>n</i> =107	233 (2) <i>n</i> =148	218 (2) <i>n</i> =218	219 (2) <i>n</i> =110	210 (2) <i>n</i> =119	227 (3) <i>n</i> =78	237 (2) <i>n</i> =101
3	266 (3) <i>n</i> =95	273 (3) <i>n</i> =54	252 (2) <i>n</i> =180	259 (3) <i>n</i> =71	246 (3) <i>n</i> =72	257 (3) <i>n</i> =104	253 (3) <i>n</i> =50
4	316 (6) <i>n</i> =26	300 (6) <i>n</i> =38	286 (5) <i>n</i> =26	271 (3) <i>n</i> =70	274 (3) <i>n</i> =64	281 (4) <i>n</i> =59	275 (3) <i>n</i> =106
5	382 (31) <i>n</i> =2	325 (7) <i>n</i> =18	304 (11) <i>n</i> =16	292 (8) <i>n</i> =17	298 (4) <i>n</i> =43	301 (5) <i>n</i> =35	291 (3) <i>n</i> =86
6	328 (7) <i>n</i> =4	301 (32) <i>n</i> =3	311 (13) <i>n</i> =5	326 (6) <i>n</i> =13	299 (7) <i>n</i> =14	298 (6) <i>n</i> =25	307 (5) <i>n</i> =32
7	369 (10) <i>n</i> =5	339 (34) <i>n</i> =3	294 (7) <i>n</i> =6	331 (18) <i>n</i> =5	313 (6) <i>n</i> =8	354 <i>n</i> =1	329 (5) <i>n</i> =9
8	347 (3) <i>n</i> =4	335 <i>n</i> =1	300 (10) <i>n</i> =3	314 (5) <i>n</i> =4	320 (4) <i>n</i> =2	351 (20) <i>n</i> =7	320 (6) <i>n</i> =4
9	389 <i>n</i> =1	392 (40) <i>n</i> =2		354 <i>n</i> =1	335 (8) <i>n</i> =6	292 <i>n</i> =1	
10		371 (27) <i>n</i> =2	378 (17) <i>n</i> =2	350 (16) <i>n</i> =4		336 (4) <i>n</i> =2	382 <i>n</i> =1
11		362 <i>n</i> =1					
12		367 <i>n</i> =1			356 <i>n</i> =1	349 <i>n</i> =1	
13					382 (8) <i>n</i> =2		

in the life history of red porgy during a 22-year period (1972 to 1994). The first study of age and growth on red porgy (1972–74) (Manooch and Huntsman, 1977) was assumed to describe a stock with the same life history as the virgin population, even though it

was subject to light fishing pressure. By the late 1970's and early 1980's, the growth pattern of the stock had changed. The mean observed and back-calculated lengths-at-age as well as the von Bertalanffy growth curve for the 1979–81 period showed a larger size at age for ages 2–6 but a lower theoretical maximum size. The increase in growth rate, and resultant increase in size-at-age observed during this period, is considered a typical density-dependent response to an increase in mortality as the depressed population responds to an increased availability of resources (Pitcher and Hart, 1982; Rothschild, 1986). The decrease in theoretical maximum size between 1979 and 1981 may have resulted from the selective removal of larger individuals from the population by fishermen and not from a biological change in the theoretical maximum size that the fish could attain.

During the mid 1980's through the early 1990's, increasing fishing pressure apparently continued the selective removal of larger, faster growing individuals from the population, further exacerbating the changes in the life history of red porgy. By 1988–90, mean back-calculated sizes-at-age were significantly smaller for all ages except age 1 in comparison with 1979–81. In 1988–90, the values of k and L_{∞} were smaller than during 1979–81 and 1972–74, indicating a reduced growth rate and a lower theoretical maximum attainable size. Mean back-calculated size-at-age for specimens collected between 1991 and 1994 were significantly smaller than those collected in 1988–90, except for ages 1, 7, and 10. These temporal reductions in the size-at-age and growth rates suggest that many individuals genetically predisposed towards rapid growth and larger size may have been selectively removed from the population, leaving behind individuals that tend to be slower growing and smaller.

Red porgy also responded to the continued removal of larger individuals from the population over many generations by females becoming sexually mature at smaller sizes during 1991–94 than during 1979–81. Manooch (1976) reported that female red porgy became mature at much larger sizes than those

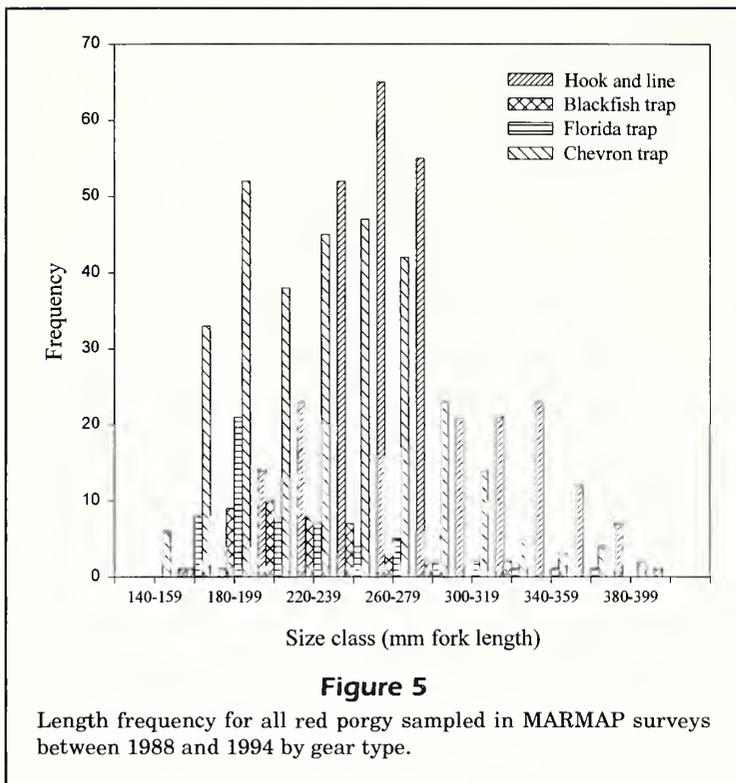


Figure 5

Length frequency for all red porgy sampled in MARMAP surveys between 1988 and 1994 by gear type.

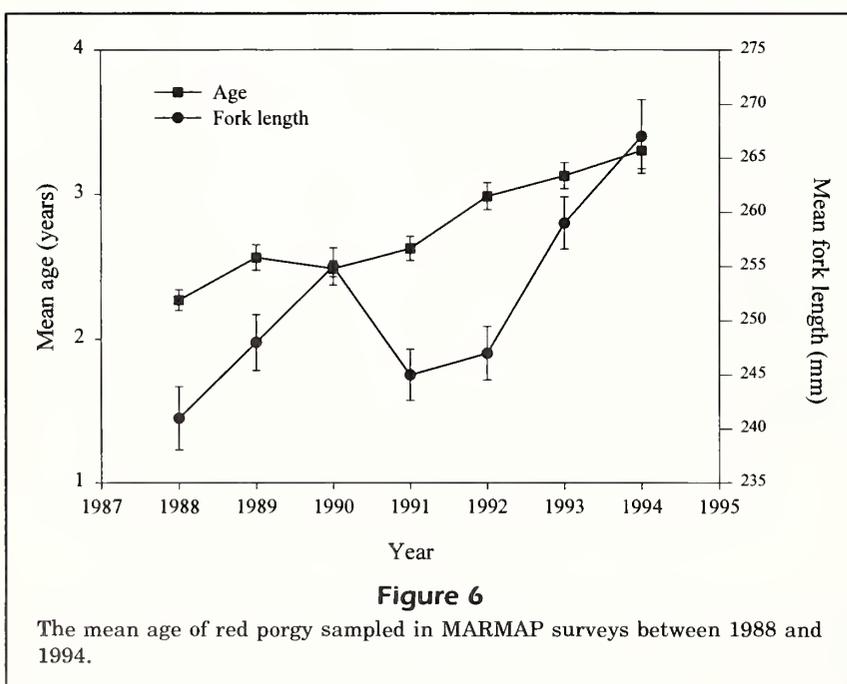


Figure 6

The mean age of red porgy sampled in MARMAP surveys between 1988 and 1994.

found in the present study. Furthermore, the red porgy population has responded to increased fishing pressure by undergoing sexual transition and by producing significantly more males at smaller sizes in recent years than during 1979–81. Koenig et al. (1996) reported that gag, *Mycteroperca microlepis*, a protogynous grouper, was undergoing sexual transition at much smaller sizes during 1991–93 in the Gulf of Mexico than were reported by Hood and Schlieder (1992) for the same region, during 1977–80. Changes in life history aspects of gag from the Gulf of Mexico were attributed to steadily increasing fishing pressure.

The decrease in mean size-at-age, growth rates, and size-at-maturity during 1988–1994 is probably a continuation of the changing life history pattern of the population that has resulted from sustained fishing pressure and indicates the degree of change that can occur over relatively short periods of time. These relatively rapid changes in size-at-age may reflect the inability of an overfished or depressed population to absorb or respond to further decreases in population size. Apart from the decreases in size-at-age apparent from recent years, the mean age and fork length of the population has increased since 1988. These increases may be due to a decline in the number of younger fish recruiting to the population. The net effect of fewer young fish in the population (and therefore samples) would be an increase in the mean age and size of the sampled fish. Length-frequency data collected in MARMAP surveys since 1988 indicates no strong recruiting year class (age-1) since 1990. Huntsman et al.² found that the estimated number of 1-year-old red porgy had declined steadily since 1973 (Murphy VPA, $M=0.28$); their results also indicate that the population may be experiencing a decline in recruitment.

A decline in recruitment may be attributed to several factors that are the result of sustained overfishing. First, as the number of fish in the population declines, fewer and fewer females are available to spawn, resulting in a decline of total potential egg production (Vaughan et al., 1992; Huntsman et al.²). Second, decreases in size-at-maturity and size-at-age result

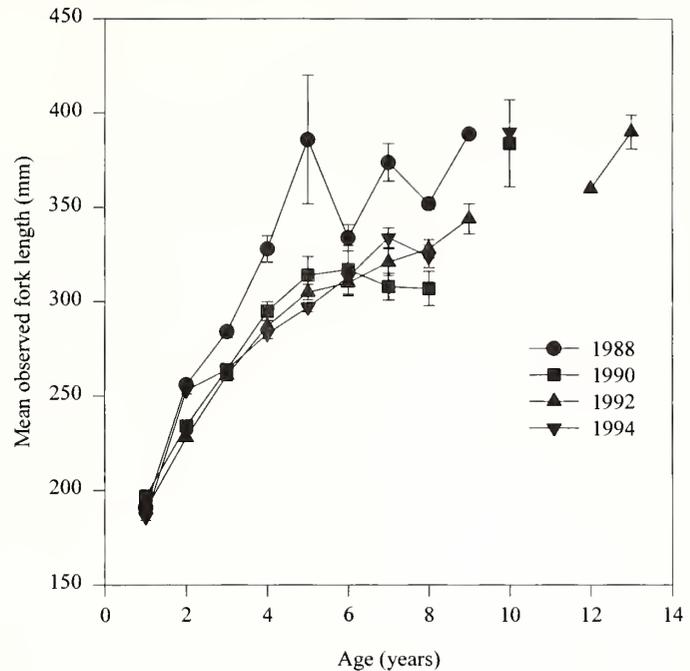


Figure 7

The mean observed size-at-age of red porgy for every second year between 1988 and 1994.

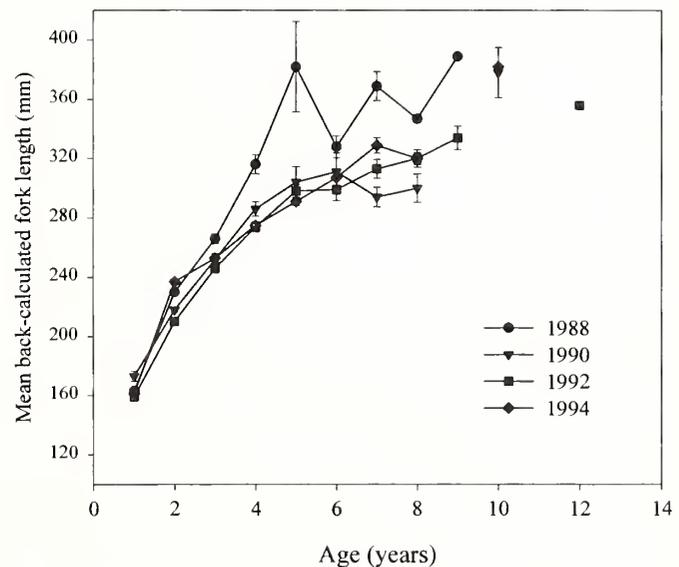


Figure 8

The mean back-calculated size-at-age for every second year between 1988 and 1994.

in fish that are less fecund than larger fish (Manooch, 1976). Finally, smaller females may produce eggs that are poorer in quality than those produced by larger

females because smaller individuals put more energy into somatic growth rather than into reproductive tissue (Rothschild, 1986). Zhao and McGovern⁴ found that an apparent population size threshold at 30% of the virgin spawning biomass existed for vermilion snapper (*Rhomboplites aurorubens*) in the SAB, below which recruitment failure was almost inevitable. A similar situation may exist for red porgy in the SAB, with recruitment failure exacerbated by the reduction in size of mature females.

Reproductive (i.e. recruitment) failure may also be affected by the change in size of male red porgy, as well as the changes in sex ratio that have occurred since 1972–74. Currently, some red porgy undergo transition at 200–250 mm FL. The sex ratio in 1991–94 at 352–400 mm FL was 1.3 males for each female. In 1972–74, the sex ratio for this size class was 0.06 males per female (Manooch, 1976, macroscopic sexing). Males began to outnumber females only above 451 mm FL. Koenig et al. (1996) have hypothesized that sperm limitation may be a factor in the decline of gag, *Mycteroperca microlepis*, in the northern Gulf of Mexico as the number of males in the population has declined. The size and number of male red porgy

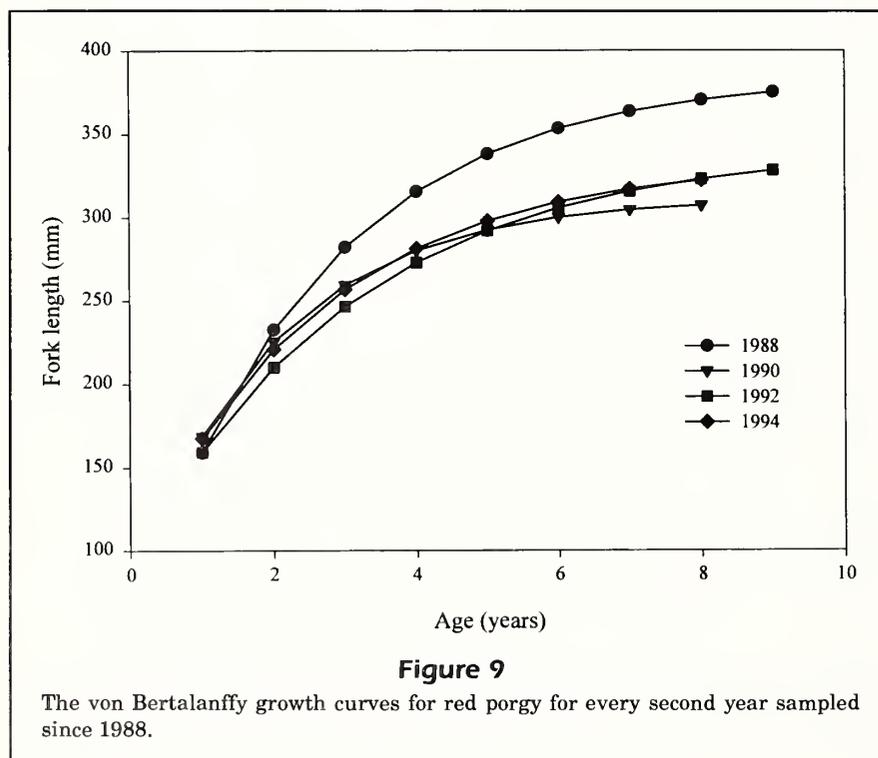
in the population have similarly been greatly reduced. The reduction in size and number of males may also be a significant factor in the decline in the number of 1-year-old red porgy recruiting to the SAB population.

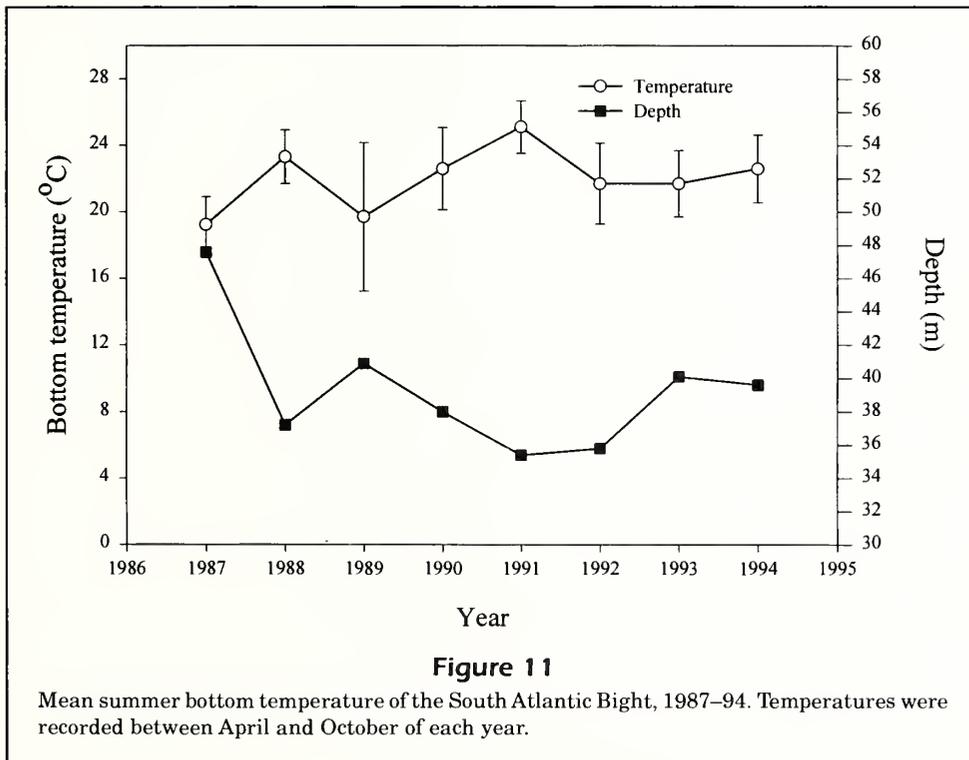
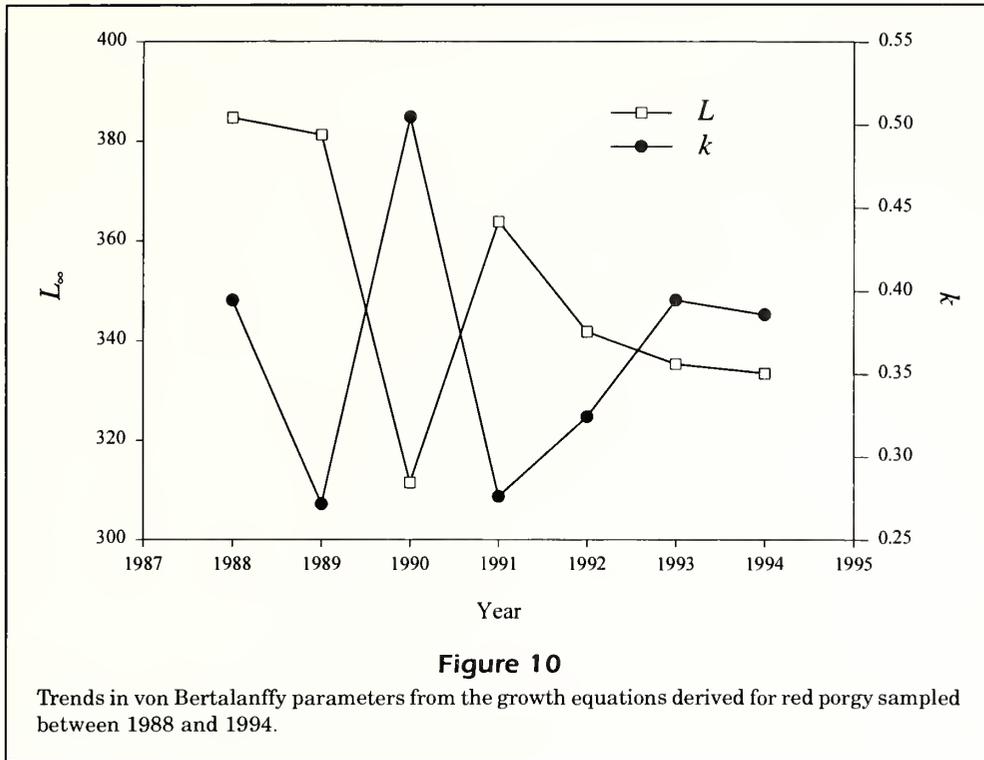
Huntsman et al.² concluded that the red porgy population of the SAB was overfished and that the population was severely depressed. These conclusions were based on the results of Murphy and separable VPA's that used only two age length keys—one from 1972–74 and one from 1986—and that used von Bertalanffy parameters and a length-weight relation from 1972–74. The life history of red porgy has changed markedly since 1986. In fact, as this study shows, significant decreases in size-at-age have occurred within a matter of years in this heavily fished population. The dramatic changes in the life history of red porgy and the resultant changes in parameters used for stock assessment suggest the status of the population in the SAB needs to be reassessed.

Protogynous fishes may be particularly vulnerable to sustained heavy fishing pressure and size selective mortality (Huntsman and Schaaf, 1994), particularly if sex reversal occurs primarily in response to exogenous controls (sociodemographic factors) (Koenig et al., 1996). The decline in size at sex transition since 1979 suggests that the timing of transition in red porgy is not determined by size, but rather by some social or behavioral stimulus.

Red porgy probably do not aggregate to spawn; instead they appear to be permanently schooled on the available areas of live bottom in the SAB. Koenig et al. (1996) suggested that if a population of protogynous fish remained aggregated throughout the year, transition could occur year-round and thus the normal male to female ratio could be maintained. If the numerical sex ratio is maintained, the impact of overfishing on a protogynous species is reduced (Huntsman and Schaaf, 1994). The increase in the sex ratio seen from 1979–81 to 1988–90 may represent overcompensation for the depletion of males from the population. The males of many reef-associated protogynous sparids show strong territoriality (van der Elst, 1988). If these males are more aggressive and are more likely to be caught by fishermen (Koenig et al.,

⁴ Zhao, B., and J. C. McGovern. 1995. Population characteristics of the vermilion snapper, *Rhomboplites aurorubens*, from the southeastern United States. Report to the South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC 29422, 35 p.





1996; Gilmore and Jones, 1992), then another fish, presumably the largest (=dominant) female would take over that territory and begin to undergo transition (Shapiro, 1981). As modern technology allows

fishermen to locate good fishing sites precisely, all large fish could be removed from an area. The increase in the number of males seen during 1988-90 may also be a function of fish size. As large males

were removed from the population, smaller fish could occupy the now vacant territory and undergo transition. As new males became increasingly smaller, the size of the territory they could successfully hold might also become smaller, freeing territory for additional males. However, as the size of the fish declined even further, it is possible that the males would be unable to compete against other species, thereby further reducing the available habitat for red porgy males and reducing the sex ratio to the same level as that found in 1979–81.

It has been hypothesized that the selective removal of individuals predisposed to rapid growth and greater size may cause a genetic shift resulting in a population of slower growing, smaller individuals than those found in the unfished population (Bohnsack, 1990; Sutherland, 1990). Edley and Law (1988) found that individuals of a population of *Daphnia magna* subjected to size-selective mortality of its large individuals for 10 generations did not return to the size and growth rates of a control population, even after the size selective pressure was removed. Changes in the life history of red porgy over the last two decades strongly confirm the hypothesis of Bohnsack (1990) and Sutherland (1990). Although exploitation may not last long enough to result in a permanent genetic shift to slower growing, smaller individuals, phenotypic changes have already occurred. Failure to consider the potential evolutionary changes that could be induced in a population through fishing mortality could result in a reduction of the maximum potential yield of that stock (Law and Grey, 1989). In addition, a reduced population of smaller red porgy could have implications in reef fish community structure, i.e. the role of smaller red porgy in a reef habitat may be different, or smaller red porgy may be less able to compete for more desirable habitat.

Current management strategies only enhance the impact of the size selective mortality associated with fisheries. In 1992, Amendment 4 of the SAFMC snapper-grouper management plan was enacted, requiring a minimum size of 12 inches (305 mm TL) for red porgy in catches (SAFMC¹). Fishermen tend to target larger fish because these bring the largest return (economic for commercial fishermen, aesthetic for recreational fishermen). Size-at-maturity for red porgy females was 270 mm TL in 1972–74; 200–225 mm TL in 1979–81; and 175–200 mm TL in 1991–94. However, 100% maturity occurred at 350 mm TL during 1972–74 and >300 mm TL in 1991–94. Thus, many faster growing individuals may reach legal size before they are sexually mature or when they have only had the opportunity to spawn once or twice. Slower growing individuals would take longer to reach the size limit and have a greater chance to spawn be-

fore becoming available to the fishery, thus further exacerbating the effect of size-selective mortality.

The SAB population of red porgy has undergone significant changes in life history, presumably in response to sustained, long-term size-selective overexploitation. Individuals in the population are smaller, have reduced growth rates, a reduced theoretical maximum size, and undergo sexual maturity and transition at smaller sizes now than 20 years ago. The selective pressure of fishing mortality may be causing a genetic shift towards a slower growing, smaller population. Unless appropriate management measures are taken, sustained overfishing could result in a permanent genetic shift in the fish or a total collapse of the stock (or both).

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Abstract.—The *Exxon Valdez* oil spill occurred just prior to the spring migration of Pacific herring, *Clupea pallasii*, from offshore feeding grounds to nearshore spawning areas in Prince William Sound (PWS), Alaska. Most or all of the life stages of herring in PWS may have been exposed to oil after the March 1989 spill. Delayed impacts from the spill were suspected as one possible cause in the unprecedented crash of the adult herring population in 1993 and stimulated studies to assess reproductive success. In spring 1995, mature herring were collected from four sites in PWS and from three uncontaminated sites in southeast Alaska (SE) to determine if reproductive impairment was evident in PWS herring six years after the spill. Herring were artificially spawned and their eggs were reared in a laboratory until hatching. Observed response parameters included fertilization success, hatching times, hatching success, as well as larval viability, swimming ability, and spinal abnormalities. Responses of all year classes combined or those restricted to the same year class did not differ significantly between regions ($P > 0.50$); the best and worst responses generally occurred in the SE. Within each site, response of the 1989 year class (most likely impacted by the oil spill in PWS) generally did not differ significantly from any other year class. To verify macroscopic observations, a subset of larvae from the 1989 year class was also inspected microscopically for yolk and pericardial abnormalities, and yolk volume was measured—but no significant regional differences were observed for any of these morphological categories. Based on the parameters examined in this study, evidence of reproductive impairment of Pacific herring in PWS by the spill was not detected in 1995, and the chances of detecting any oil-related effects against natural background variation appeared to be negligible.

Reproductive success of Pacific herring, *Clupea pallasii*, in Prince William Sound, Alaska, six years after the *Exxon Valdez* oil spill

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The *Exxon Valdez* oil spill (EVOS) in Prince William Sound (PWS), Alaska, occurred just a few weeks prior to the Pacific herring, *Clupea pallasii*, spawning season. Most or all of the life stages of herring in PWS may have been exposed to oil after the March 1989 spill. Biologically available hydrocarbons were present in the upper water column of PWS for several weeks following the spill (Short and Harris, 1996a), and residual oil may have persisted in some areas into 1990 (Short and Harris, 1996b). An estimated 40–50% of the egg biomass in PWS was deposited within the oil trajectory (Brown et al., 1996a). The failure of the 1989 year class to recruit to the fishery and the subsequent crash of the 1993 population (Meyers et al., 1994) suggested that the early life stages of herring were impacted either from exposure of prespawning adults or from direct exposure of eggs and larvae. Thus, as fish exposed to oil were recruiting into the fishery (20% by age 3, 80% by age 4, 100% by age 5; Funk¹), the herring population crashed, and recovery was minimal through the 1996

season (Wilcock²). Genetic damage, physical deformities, and small size were reported for newly hatched larvae following the spill (Brown et al., 1996a; Hose et al., 1996; Norcross et al., 1996; Marty et al., in press), but long-term effects remain unknown. In a preliminary study in 1992, Kocan et al. (1996b) observed decreased reproductive success in herring from an oil-contaminated area in PWS compared with an uncontaminated area; results were inconclusive, however, because only two sites were compared. Delayed effects from the spill were suspected as one possible cause of the population decline and stimulated the

¹ Funk, F. In prep. Age-structured assessment of Pacific herring in Prince William Sound, Alaska and forecast of abundance for 1994. Regional Information Report, Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, PO Box 25526, Juneau, AK 99802-5526.

² Wilcock, J. 1996. Alaska Department of Fish and Game. Commercial Fisheries Management and Development Division, PO Box 669, Cordova, AK 99574. Personal commun.

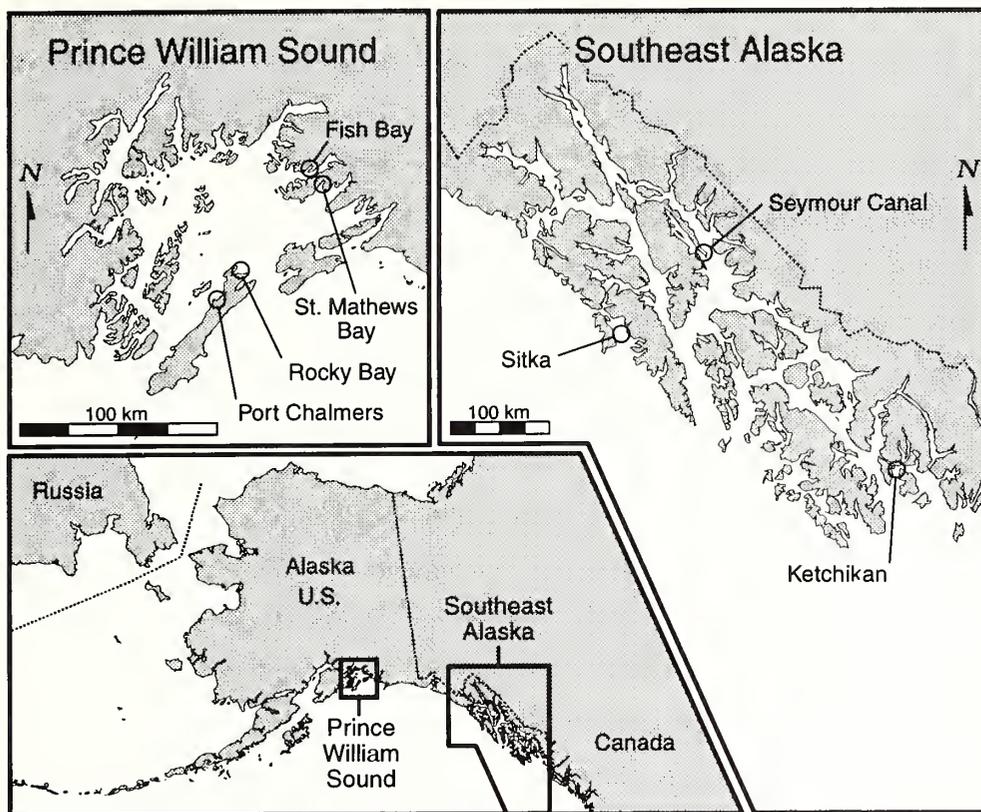


Figure 1

Collection sites of mature Pacific herring in Prince William Sound and southeast Alaska in spring 1995.

need for more definitive studies to assess the reproductive success of herring.

The purpose of this study was to determine if reproductive impairment, a possible result of the spill, was evident in PWS herring six years after the spill. There were two major focuses in the study: 1) a comparison of reproductive success between regions (PWS and southeast Alaska [SE]) and 2) a comparison of reproductive success between year classes within sites, particularly the 1989 year class (most likely impacted by the oil spill) with other year classes in PWS.

Sites sampled within PWS included all areas where spawning occurred in 1995; spawning was absent in areas that were heavily contaminated with oil in 1989. For example, Naked Island, which was in the middle of the spill trajectory, had 22 km of spawned eggs in 1989 (Brown et al., 1996a) but none in 1995. Although some have speculated that herring home to the same general spawning area each year (Zijlstra, 1963; Hourston, 1982), site fidelity is poorly understood. Thus, the herring we sampled in PWS in 1995 may or may not have been exposed to oil at some earlier time in their life history (as adults, eggs, or larvae).

Methods

Herring were collected at four sites in PWS and at three sites in SE (Fig. 1); all sites had been used for spawning in previous years. Two of the sites in PWS (St. Mathews Bay and Fish Bay) were not directly contaminated by the oil spill, whereas the other two sites (Port Chalmers and Rocky Bay) were at least lightly contaminated. Shortly after the spill, elevated hydrocarbon levels were detected in mussels at Rocky Bay (Brown et al., 1996b) and in seawater at Port Chalmers (Carls³). Additionally at Port Chalmers, concentrations of oil metabolites in bile of adult herring sampled in spring 1990 were similar to metabolite concentrations observed in 1989. This finding suggested continued contamination (Brown et al., 1996b). Herring were collected in St. Mathews Bay on 7 April, in Fish Bay on 14 April, at Port Chalmers on 30 April, and in Rocky Bay on 1 May 1995. In SE, herring were collected in waters off Sitka on 29–30 March, in waters near Ketchikan on 11 April, and in Seymour Canal on 13 May 1995.

³ Carls, M. G. 1996. Prince William Sound oil database. Auke Bay Laboratory, National Marine Fisheries Service, NOAA, 11305 Glacier Hwy., Juneau, AK 99801.

Mature herring were captured during or just prior to spawning at all sites, sorted by size, and artificially spawned. Capture gear included gill net, cast net, and purse seine. Fish were chilled immediately after capture and transported within two hours to a field laboratory, except Seymour Canal fish, which were transported directly to Auke Bay Laboratory (ABL). To approximate the different age classes present, fish were sorted by sex and size (usually in 10-mm increments; e.g. 220–230 mm fork length). Six or more size classes were usually identified at each site. From each size class, 25 females were artificially spawned with males of the same size; generally 3 males contributed sperm for all 25 crosses. Size classes of fish were processed at random. Each fish was assigned an identification number, measured to the nearest mm (fork length), and weighed to the nearest 0.1 g (wet weight). To determine age, three scales were removed from the left side of each spawned fish near the posterior margin of the dorsal fin, placed on a glass slide, and covered with a second slide.

For spawning, testes were removed, sealed in a plastic bag and maintained in chilled seawater until use; ovarian membranes were cut longitudinally, and eggs were removed with a hydrocarbon-free stainless steel spatula similar to that used by Brown.⁴ From each female, approximately 150 eggs were deposited with a gentle swirling motion onto a 25 × 75 mm glass slide placed on the bottom of a shallow plastic dish filled with seawater. Each slide was then placed in a staining rack and suspended in its own 1-L beaker of seawater. Milt was prepared from collected testes by cutting sections from each into small segments; segments plus a small amount of seawater were mixed with a spatula. A few milliliters of the milt mixture were added to each beaker containing eggs. Eggs and milt remained in contact for 5 min; the milt was then poured off, and the eggs were gently rinsed in seawater. Slides were kept in staining racks and maintained in ambient seawater with constant aeration until they were transported to ABL by air. To transport the eggs, staining racks were placed in plastic seawater-filled containers, which were then placed in coolers with blue ice.

Slides with eggs from each site were randomly distributed among twelve 600-L tanks with flow-through seawater. Slides were suspended from monofilament line attached to a pivoting overhead framework designed to cause slow egg movement (1 rpm) through the water. During the first 16–18 days of incubation,

all slides were maintained in the seawater bath. A few days before hatching, each slide was isolated in a 1-L glass jar that contained seawater and that was surrounded by flowing seawater. Lighting was natural, supplemented by overhead fluorescent light during daylight hours. Seawater flow was approximately 1 L/min at 3.9°C, warming to 7.1°C with normal seasonal change. Salinity was 32 ± 1 ppt.

Reproductive success of female herring was defined as the production of physically and functionally normal larvae. Key reproductive parameters included hatching success and larval viability, swimming ability, and spinal abnormalities. These four parameters were sensitive to oil in laboratory studies (Carls et al.⁵). Other parameters examined included fertility and hatching times. Fertility was not considered a key parameter because it may have been negatively influenced by unavoidable handling conditions at the different sites and by variable periods in the storing of gametes prior to spawning. Hatching times were not considered a key parameter because they were strongly influenced by seasonal increases in water temperature.

Fertilization success and stage of development were determined 1 to 10 days after spawning. Excess eggs were removed from all slides by scraping—i.e. those along slide margins susceptible to mechanical damage and clumps of eggs not directly exposed to water. This process was accomplished in water with minimal exposure to air.

Isolated eggs were inspected every two days to determine onset of hatching. Once hatching began, larvae were counted and assessed daily for swimming ability and gross physical deformities. Without exposing eggs to air, we changed the seawater in each jar every two days prior to hatching and daily after hatching began. All hatched larvae were collected, anesthetized with tricaine methanesulfonate, and preserved in 10% phosphate buffered formalin. Approximately the first and last 10% of larvae hatched from each female were preserved in separate bottles. Live larvae were preserved separately from dead larvae. After hatching was completed, remaining eggs were inspected; infertile eggs and dead embryos were counted.

A subset of preserved larvae was scored for yolk-sac edema, pericardial edema, and yolk volume. Ten females from the 1989 year class were randomly selected from each site, and 10 larvae per female were randomly selected from the central portion of hatched eggs for analysis. At Fish Bay, only five females from

⁴ Brown, E. D. 1995. Alaska Department of Fish and Game. Commercial Fisheries Management and Development Division, PO Box 669, Cordova, AK 99574. Personal commun.

⁵ Carls, M. G., D. M. Fremgen, J. E. Hose, S. W. Johnson, and S. D. Rice. In prep. Effects of incubating herring (*Clupea pallasi*) eggs in water contaminated with weathered crude oil. Auke Bay Laboratory, National Marine Fisheries Service, NOAA, 11305 Glacier Hwy., Juneau, AK 99801.

the 1989 year class were present; therefore the number of larvae analyzed per female was doubled. Sitka and St. Mathews Bay were excluded because of an insufficient number of females from the 1989 year class. Lateral views of larvae were displayed digitally, and specimens were rotated to align eyes in order to minimize variance. Yolk shapes were generally elliptical; major and minor axes were measured perpendicular to the body axis. Yolk volume was estimated from these linear measures according to the method of Hourston et al. (1984). Yolk-sac edema was indicated if the anterior margin of the yolk membrane was bounded by an area of clear fluid. Pericardial edema was scored if the pericardium was unusually large or convex ventrally.

Data processing and statistics

To assess the general health of parent fish, condition factor (K) was calculated for each female according to the method of Bagenal and Tesch (1978):

$$K = \frac{100(W)}{FL^b},$$

where W = somatic wet weight in g;

FL = fork length in cm; and

b = the value determined by site from length-weight regressions.

Gonad weight was subtracted from body weight to avoid variation in spawning condition.

Times of hatching among sites, which were temperature dependent, were compared by using peak hatching times as the estimator. Peak hatching day was defined as the day the most larvae hatched from eggs of a given female; if two hatch peaks of equal magnitude occurred, the first peak was reported. Mean incubation temperature for eggs from each female was calculated by weighting mean water-bath temperatures by the number of eggs hatched daily. This method avoided possible under or over estimates of mean incubation temperature caused by early or late hatching of eggs as seasonal temperature increased.

Most observations were expressed as percentages. The denominator used to calculate percentages varied by response parameter (Table 1). Percentages of eggs fertile and initially dead were based on the total number of eggs counted near the beginning of the experiment. Percentages of eggs that hatched were based on the total number of hatched larvae plus the number of dead eggs determined at the endpoint. The number of hatched larvae was subdivided into number live, moribund, and dead. Hearts of moribund larvae were beating, but these larvae were incapable

Table 1

Description of key response parameters used to evaluate reproductive impairment in Pacific herring collected from Prince William Sound and southeast Alaska. Herring were collected in 1995, artificially spawned, and reared in a laboratory until hatching. Moribund larvae were alive (heart beating) but incapable of swimming.

Parameter (%)	Description
Hatch	$100 \cdot (\text{total number of eggs that hatched}) / (\text{total number of eggs that hatched} + \text{total number of dead eggs})$
Live (viable)	$100 \cdot (\text{total number of live larvae excluding moribund larvae}) / (\text{total number of eggs that hatched})$
Effective swimmers	$100 \cdot (\text{total number of effective swimmers}) / (\text{total number of live larvae excluding moribund larvae})$
Spinal abnormalities	$100 \cdot (\text{number of live} + \text{moribund larvae with spinal defects}) / (\text{total number of live} + \text{moribund larvae})$

of movement. Accordingly, percent live was the number of living larvae (excluding moribund larvae) divided by the total number hatched. Swimming of live larvae was categorized as effective, ineffective, or incapable. Effective swimmers were active, frequented the water column, and avoided capture. Ineffective swimmers were generally more lethargic than effective swimmers and were more likely to be found on jar bottoms. Incapable swimmers were unable to swim in a straight line and were often capable only of spasmodic twitching. Swimming of moribund and dead larvae was, by definition, nonexistent; thus the number of live larvae was used as the denominator for swimming categories. Because larvae quickly became distorted after death, spinal aberrations were assessed only in live and moribund larvae. Percentage of spinal abnormalities, therefore, was the number of larvae with spinal aberrations divided by the sum of live and moribund larvae.

One-way analysis of variance (ANOVA) was used to examine differences among sites, among age classes, and between regions. Each reproductive parameter was tested separately by individual age class and for all age classes combined; percentage data were arc-sine transformed and corrected for small n as necessary (Snedecor and Cochran, 1980). To account for variance among sites, the F -test comparison between regions was:

$$F = \frac{MS_{\text{between regions}}}{MS_{\text{among sites}}}$$

where MS = mean square.

Somatic weight, FL, and K were analyzed similarly. Age-class responses within site were compared because in PWS different age classes were potentially exposed to varying levels of oil (Table 2). When the overall ANOVA was significant ($P \leq 0.05$), a priori multiple comparisons were used to identify which ages differed:

$$F = \frac{MS_{\text{between age classes}}}{MS_{\text{error}}}$$

Maternal age was used as the standard in all age comparisons because ages frequently differed in the male and female crosses. Age-3 and age-4 herring were not exposed to oil at any life stage in PWS; therefore they were combined as site-specific controls. Few older age fish were captured; thus, ages \geq age 9 were combined and reported as 9+.

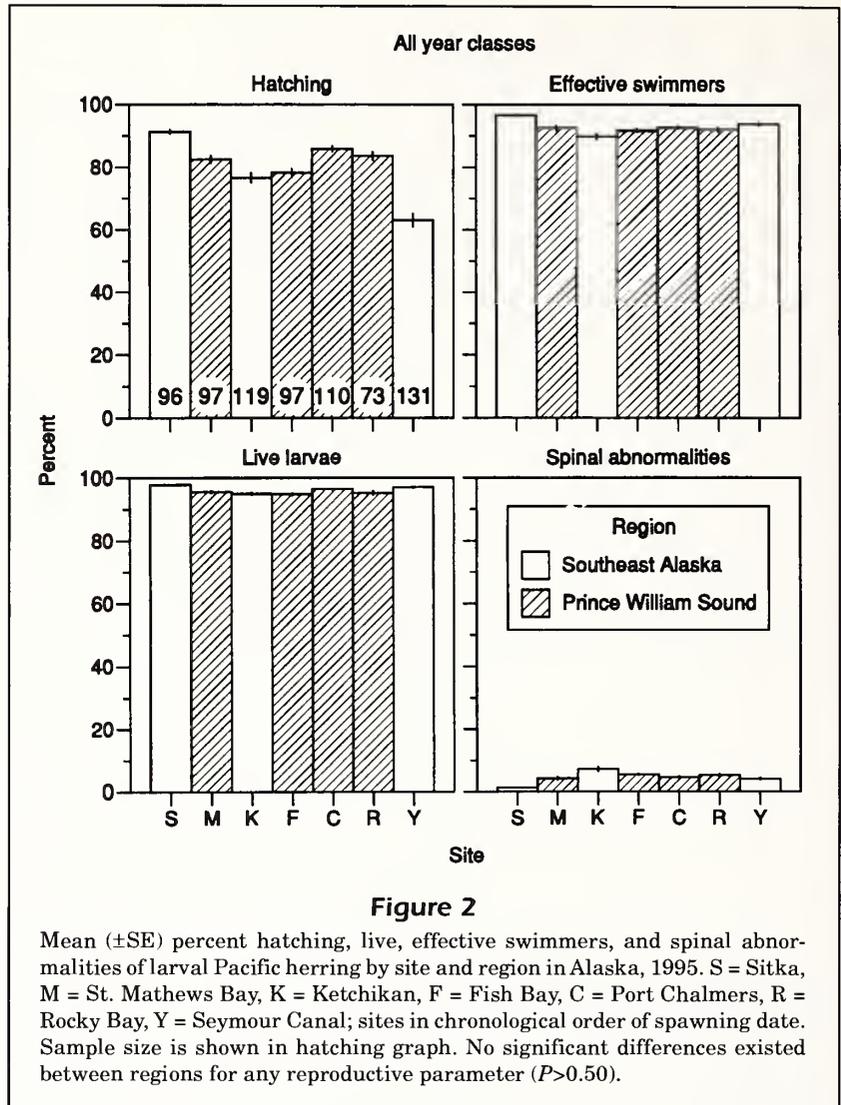
Because cold storage of adult fish (mean time of fish capture to mean spawning time) varied among sites (0.7–12.9 h), we also examined the possible effect of storage time on all reproductive parameters with storage time as a covariate in the ANOVA. Storage times up to 7 h did not significantly affect any of the key reproductive parameters ($P \geq 0.376$, except $P = 0.084$ for % live larvae). We repeated the ANOVA for regional differences with storage times in the model as a covariate and restricted the analysis to include only those fish sampled within the same time period (≤ 7 h).

Scored yolk-sac edema was analyzed with the Kruskal-Wallis nonparametric test (SAS Institute Inc., 1989). Yolk-sac edema was also re-expressed as a percentage by female, arcsin-transformed, and analyzed by ANOVA. Yolk volume was analyzed by ANOVA.

Results

Regional comparison

Herring sampled from all sites appeared healthy and showed no obvious external signs of disease. For fish of the same age, there were no significant differences



in FL ($P \geq 0.09$), weight ($P \geq 0.09$), or condition factor ($P \geq 0.41$) between regions. For herring in PWS, mean FL ranged from 196 to 260 mm and mean weight from 60.7 to 151.7 g, whereas in SE, mean FL ranged from 198 to 253 mm and mean weight from 65.1 to 140.4 g (Table 3).

For all age classes combined, reproductive success of herring did not differ significantly between regions ($P > 0.50$); the best and worst responses generally occurred in SE, whereas PWS sites were intermediate (Fig. 2). Statistical power of these tests was high (≥ 0.99) and remained high for most analyses. Restricting the analysis to fish stored for ≤ 7 h did not alter the overall results; no significant ($P > 0.39$) regional differences existed for any reproductive parameter. In SE, mean responses ranged from 63 to 91% for hatching success, 95 to 98% for live larvae, 90 to 96% for effective swimmers, and 1 to 7% for

Table 2

Age, year class, and possible oil exposure for Pacific herring collected in Prince William Sound, Alaska, in 1995. The *Exxon Valdez* oil spill occurred in March 1989.

Age	Year class	Possible oil exposure	Age	Year class	Possible oil exposure
3	1992	no direct oil exposure of any life stage	6	1989	all life stages likely exposed to oil
4	1991	no direct oil exposure of any life stage	7	1988	juveniles at time of spill
5	1990	all life stages possibly exposed to residual oil	8	1987	juveniles or immature at time of spill
			9+	1986	mature—reproductive at time of spill

Table 3

Fork length (mm) and somatic weight (g) of mature female Pacific herring captured in southeast (SE) and Prince William Sound (PWS), Alaska, in spring 1995. Values are mean (\bar{x}) and \pm standard error; sample size = n .

		Age (yr)									
		3	4	5	6	7	8	9	10	11	
Fork length	SE	\bar{x}	198	211	217	221	236	234	241	236	253
		\pm	1.9	2.9	2.0	1.2	1.3	3.5	8.4	3.5	7.7
		n	86	21	49	94	95	15	3	2	3
PWS		\bar{x}	196	219	225	236	242	260	259	259	260
		\pm	1.1	2.3	1.1	1.7	1.0	3.2	1.3	2.2	2.9
		n	81	18	65	25	149	10	16	7	13
Weight	SE	\bar{x}	65.1	79.1	87.2	91.7	112.9	112.7	117.5	108.3	140.4
		\pm	1.8	3.2	2.1	1.7	1.9	5.1	4.6	6.4	14.7
		n	81	21	49	93	94	15	3	2	3
PWS		\bar{x}	60.7	90.3	95.0	107.4	121.0	149.0	147.8	148.9	151.7
		\pm	1.2	2.2	1.3	2.7	1.5	8.3	3.3	6.8	5.1
		n	80	18	65	25	149	10	16	7	13

spinal abnormalities. In PWS, mean responses ranged from 78 to 86% for hatching success, 95 to 96% for live larvae, 92 to 93% for effective swimmers, and 4 to 6% for spinal abnormalities. Among all sites, reproductive success was consistently best at Sitka (e.g. highest hatching success=91% and fewest spinal abnormalities=1%) and worst at Seymour Canal or Ketchikan (e.g. lowest hatching success=63% and most spinal abnormalities=7%) (Fig. 2). Of the sites in PWS, reproductive success was usually best at St. Mathews Bay or Port Chalmers (e.g. highest hatching success=86% and fewest spinal abnormalities=4%) and worst at Fish Bay (e.g. lowest hatching success=78% and most spinal abnormalities=6%) (Fig. 2). Similarly, when reproductive success was estimated for each age class individually, regional differences were not significant ($P>0.50$). This finding was true for all age comparisons—ages 3 to 9+.

For example, age-6 (1989 year class) herring in PWS did not differ significantly from those in SE (Fig. 3). Among all sites where more than four age-6 fish were collected (excluding St. Mathews Bay and Sitka), hatching success ranged from 66% (Seymour Canal) to 91% (Port Chalmers), live larvae from 95% (Fish Bay) to 98% (Port Chalmers), effective swimmers from 93% (Rocky Bay) to 96% (Port Chalmers), and spinal abnormalities from 2% (Port Chalmers) to 6% (Fish Bay).

No significant regional differences were observed in progeny of the 1989 year class scored for physical condition. Only one larva of 500 had pericardial edema. Analyzed with the Kruskal-Wallis test, the site with the most yolk-sac edema (Port Chalmers) was significantly different from that with the least (Ketchikan), but there was no regional trend. Percentages of larvae with yolk-sac edema were low

($\leq 16\%$), and differences among sites and between regions were not significant ($P \geq 0.348$) (Fig. 4).

Yolk volume in larvae from the 1989 year class did not differ significantly ($P = 0.486$) between regions but may have been related to incubation temperature. The largest and smallest mean yolk volumes were observed in PWS but closely overlapped those in SE (Fig. 4). Although scatter was high ($r^2 = 0.13$), yolk volumes declined significantly ($P < 0.001$) as temperature increased. It is possible, however, that site differences and incubation temperature were confounding factors.

Comparison among age classes within sites

Reproductive success differed significantly among some age classes at Sitka, Ketchikan, Port Chalmers, and Rocky Bay but not among age classes at St. Mathews Bay, Fish Bay, and Seymour Canal (Figs. 5–8). The few significant differences we observed were highly variable, inconsistent among sites, and no pattern existed for the 1989 year class. For example, at Rocky Bay, age-3 and age-4 fish had a significantly lower percentage of live larvae than age-5, age-6, and age-7 fish (Fig. 6), whereas at Sitka, age-3 and age-4 fish had a significantly higher percentage of effective swimmers and a significantly lower percentage of spinal abnormalities than age-7 fish (Figs. 7 and 8).

Other parameters

Hatching times decreased steadily with increasing incubation temperature (Fig. 9). For Sitka, the first site sampled, peak hatching occurred about 33 d after start of incubation at a mean temperature of about 4.5°C , whereas at Seymour Canal, the last site sampled, peak hatching occurred about 26 d after start of incubation at a mean temperature of about 6.0°C .

Fertility did not differ significantly ($P > 0.50$) between regions for all ages combined or when the comparison was restricted to fish of the same age. For all ages combined, fertility in SE ranged from 80%

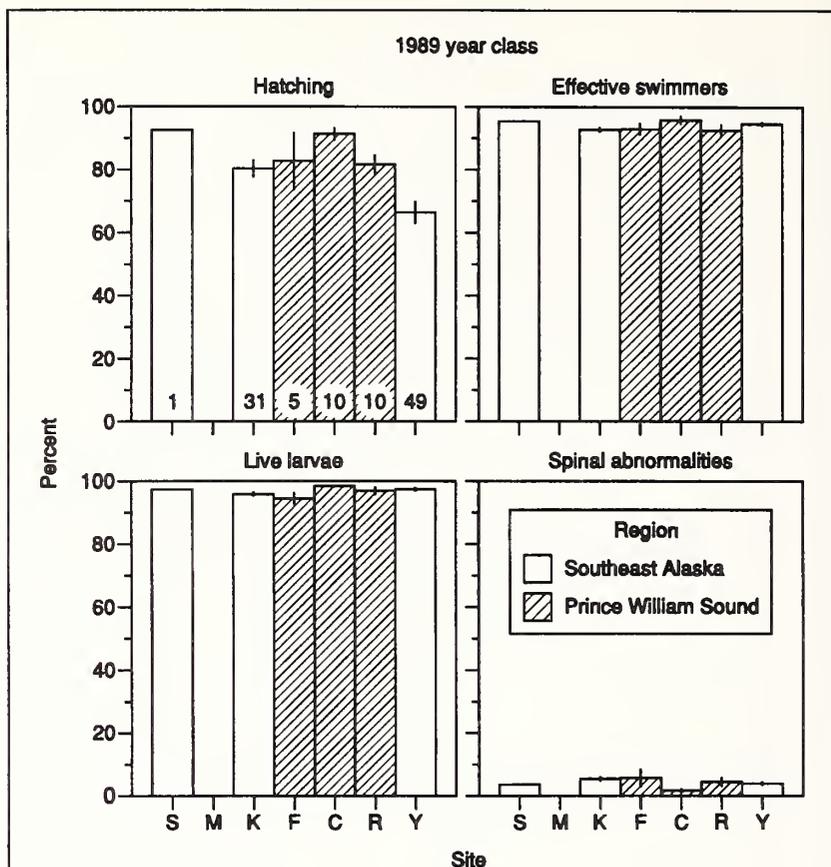


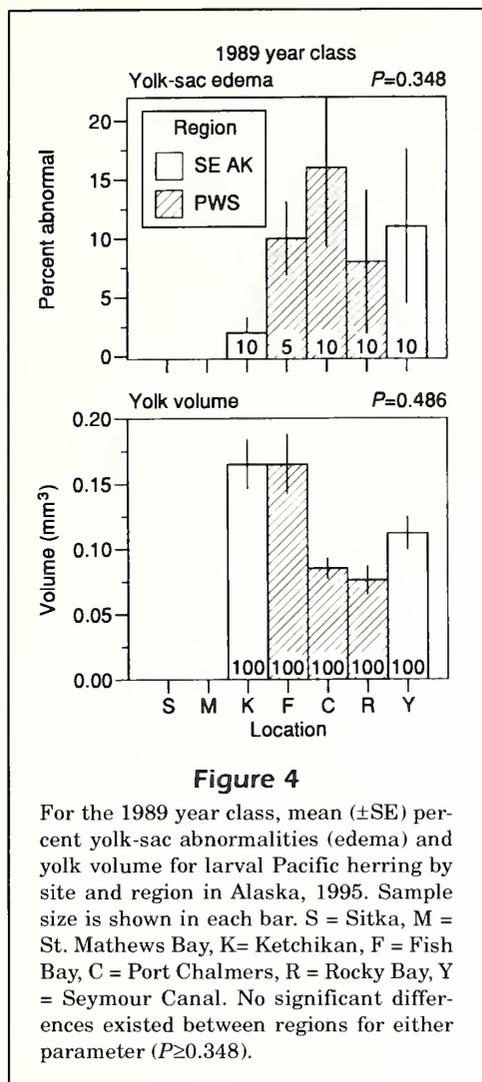
Figure 3

For the 1989 year class, mean (\pm SE) percent hatching, live, effective swimmers, and spinal abnormalities of larval Pacific herring by site and region in Alaska, 1995. The 1989 year class, sampled in Prince William Sound in 1995, was more likely exposed to oil as eggs or larvae than were other year classes. S = Sitka, M = St. Mathews Bay, K = Ketchikan, F = Fish Bay, C = Port Chalmers, R = Rocky Bay, Y = Seymour Canal. Sample size is shown in hatching graph. Progeny of the 1989 year class did not differ significantly between regions for any reproductive parameter ($P > 0.50$).

at Seymour Canal to 96% at Sitka; in PWS, fertility ranged from 88% at Fish Bay to 94% at St. Mathews Bay.

Discussion

Six years after the spill, reproductive impairment was not detected in PWS herring. This conclusion was reached by comparing reproductive success of fish collected in PWS and SE and among age classes within specific sites. Specifically, hatching success, larval viability, and fertility did not differ significantly between PWS and SE, including response of the 1989 year class. In fact, discrimination of responses between regions was not possible because the best and worst responses were usually found in



one region (SE). Therefore, the chances of detecting any oil-related effects against the natural background variation were negligible when herring were compared between regions. Although responses among some age classes within Port Chalmers and Rocky Bay were occasionally significant, these differences were highly variable, did not indicate reproductive impairment of the 1989 year class, and were inconsistent between sites.

Of the four key reproductive parameters we examined, spinal defects were particularly important because exposure of herring eggs to oil frequently causes spinal defects (Linden, 1978; Kocan et al., 1987; Rice et al., 1987; Pearson et al.⁶), that could

result in reduced swimming ability and long-term survival. Spinal defects, however, can also occur naturally as a result of other environmental factors. In our study, herring from an uncontaminated site, Ketchikan, had the highest percentage of spinal defects (7%). Ketchikan samples were collected at least 40 km from any urban area, and it is unlikely that these fish were exposed to industrial or other urban pollutants. Whether the incidence of spinal defects at Ketchikan was just random noise or a response to some underlying environmental factor is impossible to determine, but it is evidence that similar results could occur in PWS without implicating oil as a cause. In fact, a 10% incidence of gross abnormalities was observed in PWS herring 23 years prior to the spill (Smith and Cameron, 1979).

Reproductive success of herring in PWS was consistently better in 1995 than that reported in earlier studies. For example, we observed a mean hatching success of 78–86% compared with 53% in 1976 (Smith and Cameron, 1979), 62%⁷ in 1989 (McGurk et al.⁸), 85% in 1990 (McGurk et al.⁹), 59–79% in 1991 (Kocan et al., 1996a), and 19–56% in 1992 (Kocan et al., 1996b). The viable hatching¹⁰ that we observed in PWS (79%) also exceeded previously reported percentages; 53%¹¹ in 1989 (McGurk et al.⁸), 57% in 1990 (McGurk et al.⁹), 35–37%¹² in 1991 (Kocan et al., 1996a), and 13–33%¹² in 1992 (Kocan et al., 1996b). Incidence of spinal abnormalities in PWS was about 5% in our study compared with 7% in 1989 (McGurk

⁷ To avoid desiccation effects, and because egg survival was significantly less in the +1.5-m collections in the McGurk et al.⁸ data set, these data were not included in this comparison. Estimated egg survival was 59% when the +1.5-m data were included.

⁸ McGurk, M., D. Warburton, T. Parker, and M. Litke. 1990. Early life history of Pacific herring: 1989 Prince William Sound herring egg incubation experiment. Final report, contract number 50ABNC-7-00141, Triton Environmental Consultants LTD., No. 120-13511 Commerce Parkway, Richmond, British Columbia, Canada V6V 2L1.

⁹ McGurk, M., T. Watson, D. Tesch, B. Mattock, and S. Northrup. 1991. Viable hatch of Pacific herring eggs from Prince William Sound and Sitka Sound, Alaska, in 1990. Report number 2060/WP 4269, Triton Environmental Consultants LTD., No. 120-13511 Commerce Parkway, Richmond, British Columbia, Canada V6V 2L1.

¹⁰ To conform with McGurk et al.^{8,9}, % viable hatch was defined as 100 [(no. live larvae - no. abnormal larvae)/(no. hatched eggs)] \times (no. eggs hatched/no. eggs total). The value defined by Kocan et al. (1996, a and b) as % viable larvae is nearly synonymous with % viable hatch. Our % live larvae (Table 1) included abnormal larvae, but McGurk et al.^{8,9} excluded abnormal larvae in their definition of % viable larvae (% viable = 100 (no. live larvae - no. abnormal larvae)/no. hatched).

¹¹ As previously, +1.5-m data were not included; estimated % viable hatch was 50% when these data were included.

¹² Percent viable larvae values reported by Kocan et al. (1996, a and b) should be increased by 2% to approximate percent viable hatch.

⁶ Pearson, W. H., D. L. Woodruff, S. L. Kiesser, G. W. Fellingham, and R. A. Elston. 1985. Oil effects on spawning behavior and reproduction in Pacific herring (*Clupea harengus pallasii*). Final Report OF-1742 to American Petroleum Inst., Battelle Marine Res. Lab., Sequim, WA, 108 p. [API publication 4412.]

et al.⁸). Although procedural differences between earlier studies and ours may partially account for differences in assessment of reproductive success, the responses we observed in 1995 were consistently the best.

To interpret the effects of the spill on herring in PWS, it is necessary to understand the life stage exposed and the magnitude and duration of exposure.

Which life stages were impacted, and to what extent, however, is largely a matter of conjecture. Adult fish may have encountered oil before, during, or after spawning, but determining what percentage of the population was significantly impacted is impossible. Metabolites of aromatic hydrocarbons were detected in adult herring (Haynes et al.¹³), but sample sizes

were very low. Nematode prevalence in adult body cavities differed significantly between contaminated and uncontaminated areas (Moles et al., 1993), also indicating adult exposure. The duration and magnitude of oil exposure of herring eggs and larvae is also unknown. After hatching, herring larvae from both contaminated and uncontaminated sites may have been exposed to oil as they passively traversed the spill trajectory. For example, some of the largest concentrations of larvae in June were found in the southwest portion of PWS, well within the oil trajectory (Norcross et al., 1996). By inference, juvenile herring occupying the same nearshore habitat used by juvenile salmonids may have also been exposed to oil: such exposure was documented in juvenile pink and chum salmon (Carls et al., 1996).

Response of wild herring to an oil spill can be partially inferred from laboratory studies. For example, exposure of mature herring to hydrocarbons in the laboratory did not cause discernible damage in progeny, including fertility, viability, and larval swimming, physical, and genetic abnormalities (Rice et al., 1987; Carls et al.¹⁴). In contrast, the early life

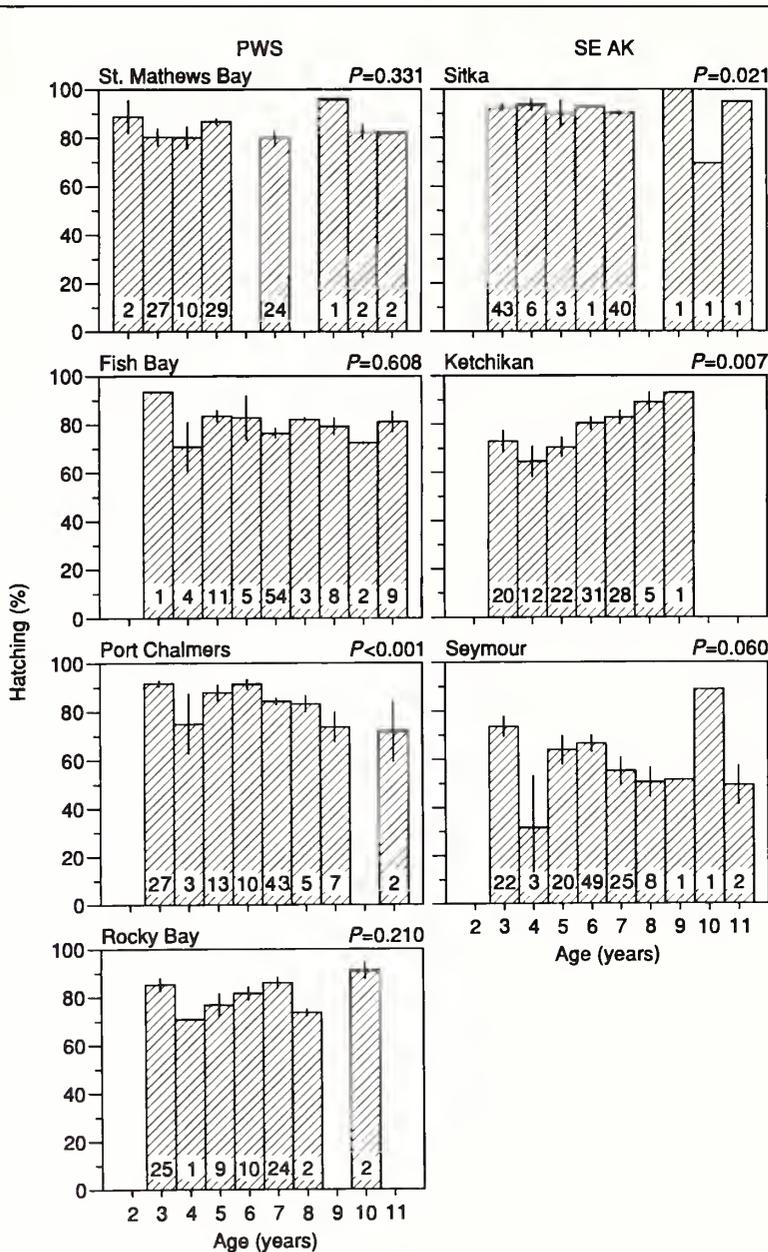


Figure 5

Mean (\pm SE) percent hatching of larval Pacific herring by female parent age, site, and region in Alaska, 1995. Sample size is shown in each bar. Overall P -value from ANOVA is listed above each graph. Significant differences were Ketchikan, ages 3 and 4 < age 6, 7, and 8 ($P \leq 0.015$); Port Chalmers, ages 3 and 4 > age 9+ ($P = 0.050$).

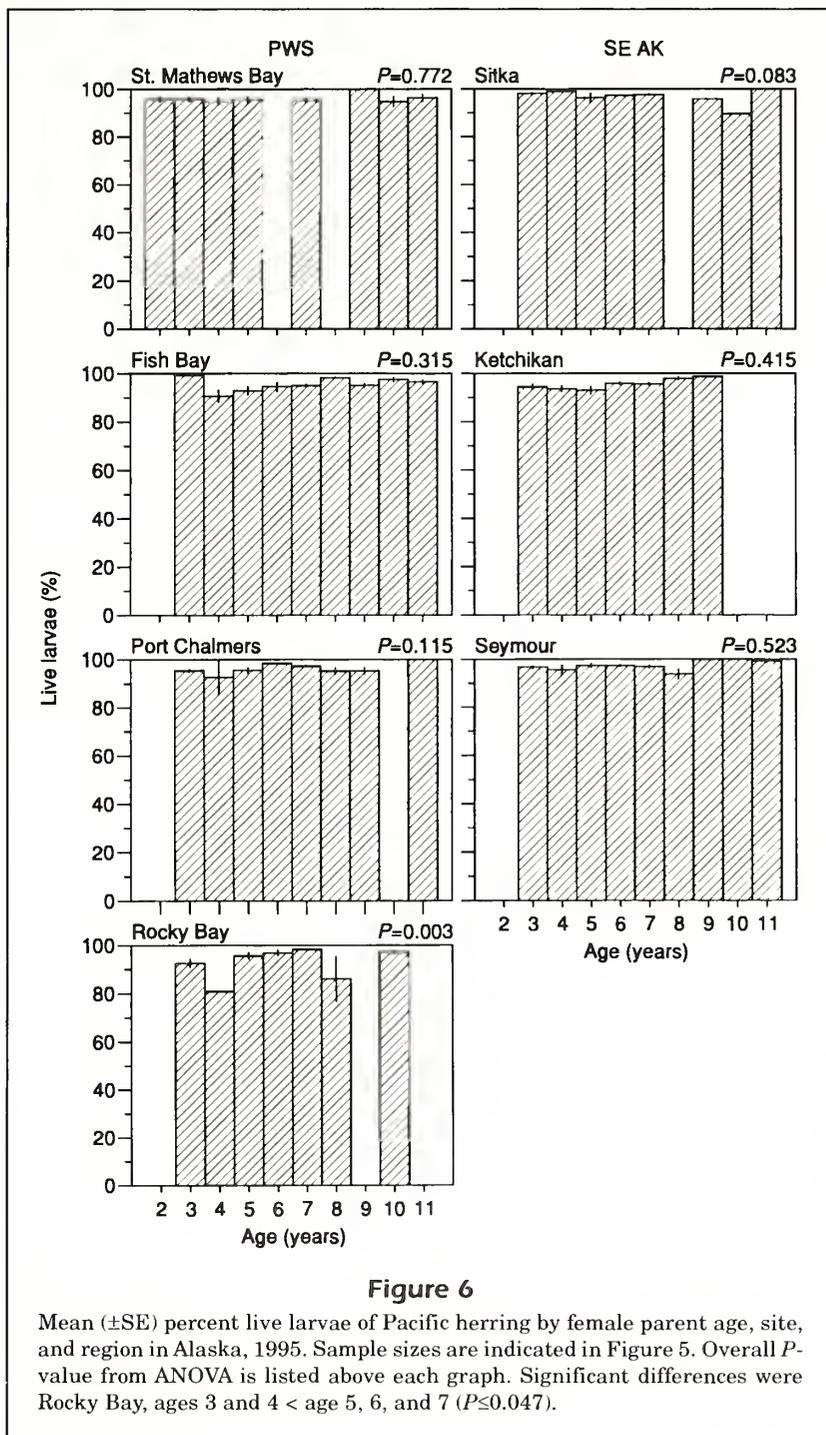
¹³ Haynes, E., T. Rutecki, M. Murphy, and D. Urban. 1995. Impacts of the Exxon Valdez oil spill on bottomfish and shellfish in Prince William Sound, Exxon Valdez oil spill state/federal natural resource damage assessment final report (fin/shellfish study no. 18). Auke Bay Laboratory, National Marine Fisheries Service, 11305 Glacier Hwy., Juneau, AK 99801.

¹⁴ Carls, M. G., D. M. Fremgen, J. E. Hose, D. Love, and R. E. Thomas. 1995. The impact of exposure of adult pre-spawn herring (*Clupea harengus pallasi*) on subsequent progeny. Chapter 2 in Carls et al., Exxon Valdez oil spill report, restoration project 94166, annual report; the impact of exposure of adult pre-spawn herring (*Clupea harengus pallasi*) on subsequent progeny, p. 29-49. Auke Bay Laboratory, NMFS, NOAA, 11305 Glacier Hwy., Juneau, AK 99801.

stages of herring are more susceptible to the effects of oil according to laboratory (Linden, 1978; Pearson et al., 1985; Carls, 1987; Kocan et al., 1987; Rice et al., 1987) and field studies (Brown et al., 1996a; Norcross et al., 1996). Abnormal larvae have poor survival potential (Kocan et al., 1996a), and thus the exposure of eggs and larvae to oil in PWS may have resulted in increased mortality. Furthermore, the same oil concentrations that caused significant genetic damage also caused significant physical damage in developing embryos (Carls et al.⁵); thus early death would likely preclude recruitment of genetically damaged individuals to spawning populations.

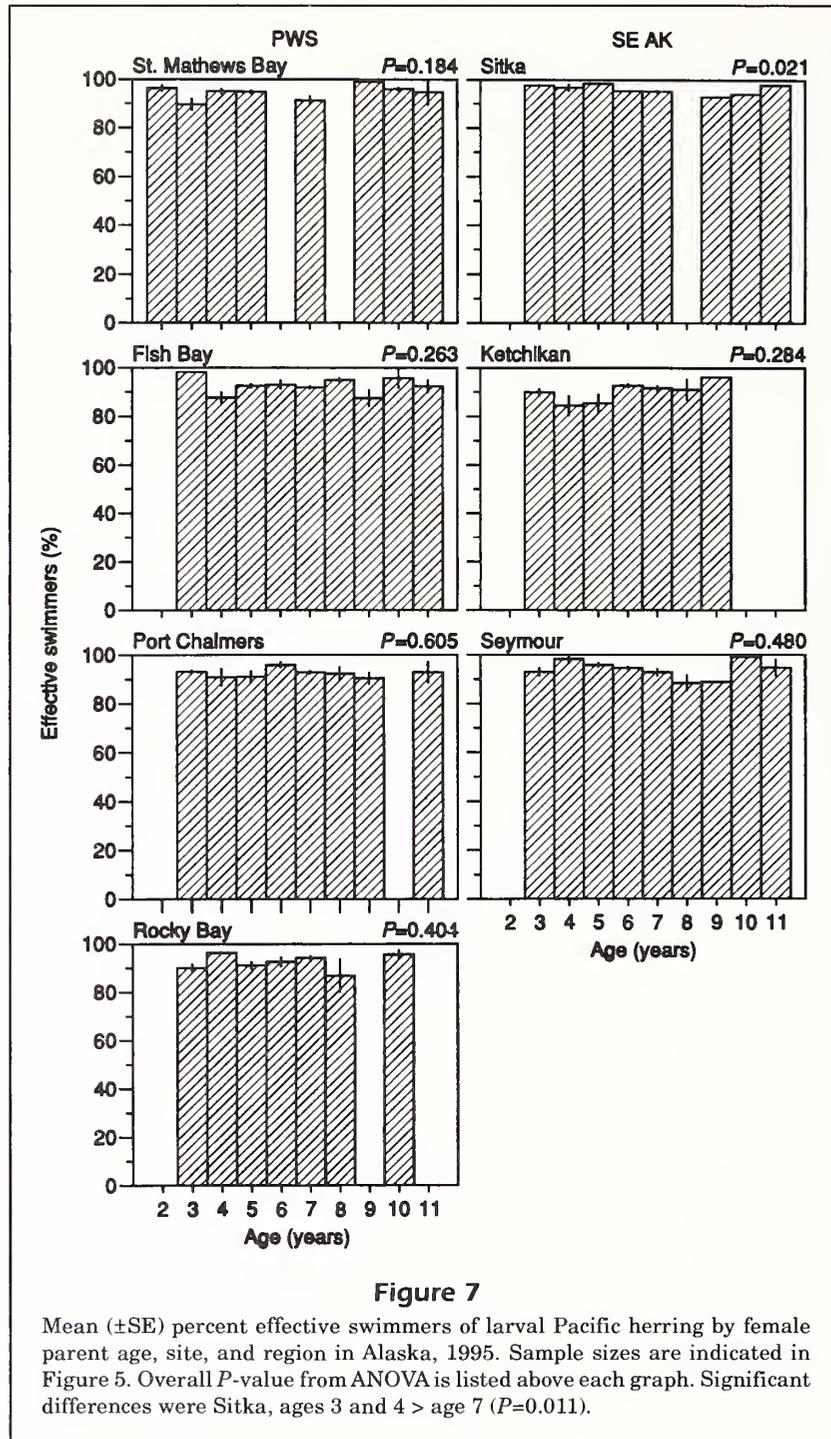
Although genetic damage was detected in larvae collected in the oil-contaminated areas of PWS in 1989 (Hose et al., 1996; Brown et al., 1996a), we did not inspect larvae for genetic damage. Concomitant laboratory measurements of larvae that had been artificially contaminated indicated that genetic response was not a more sensitive measure of oil exposure than the parameters we examined (Carls et al.⁵). In addition, artificial exposure of prespawning adults to relatively high oil concentrations (58 ppb, initial PAH) did not cause genetic defects in artificially spawned progeny (Carls et al.¹⁴). Other defects observed in larvae from PWS in 1989 included physical damage, assessed by scored indices (Hose et al., 1996). Carls et al.⁵ observed that two of these indices, pericardial edema and finfold condition, were more sensitive to oil damage than was the genetic response. Because we did not detect significant pericardial abnormalities in larvae from PWS six years after the spill, it is likely that the genetic condition of these larvae has not been adversely affected.

The failure of the 1989 year class of herring in PWS to recruit to the spawning population may have been partly attributable to the spill, but it is impossible to separate oil effects from other natural factors. At the sites we sampled in PWS, the 1989 year class usually represented <4.0% of the spawning popula-



tion (ADF&G¹⁵). Larval survival in PWS was reduced an estimated 52% in 1989 as a result of the spill (Brown et al., 1996a); such loss supports inferences of poor survival that are based on laboratory obser-

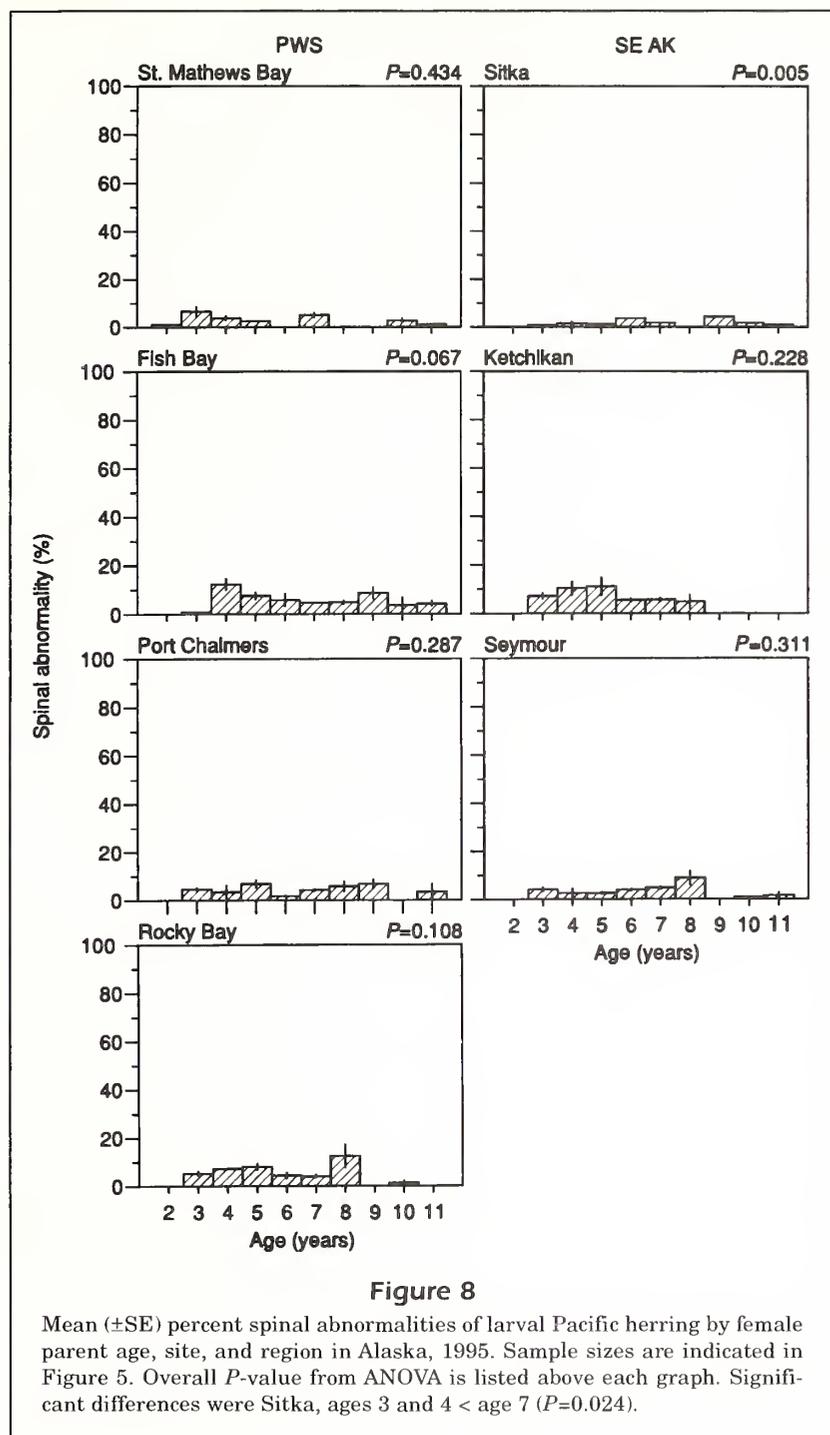
¹⁵ ADF&G (Alaska Department of Fish and Game). 1995. Herring test fishery data. Commercial Fisheries Management and Development Division, PO Box 669, Cordova, AK 99574.



vation. Natural environmental conditions, however, can also cause a high degree of variability in herring recruitment (Stevenson, 1962; Anthony and Fogarty, 1985). For example, the 1989 year class at Sitka also represented a small proportion of the spawning population in 1995 (<2%; ADF&G¹⁶); therefore factors other than oil are important determinants of cohort size.

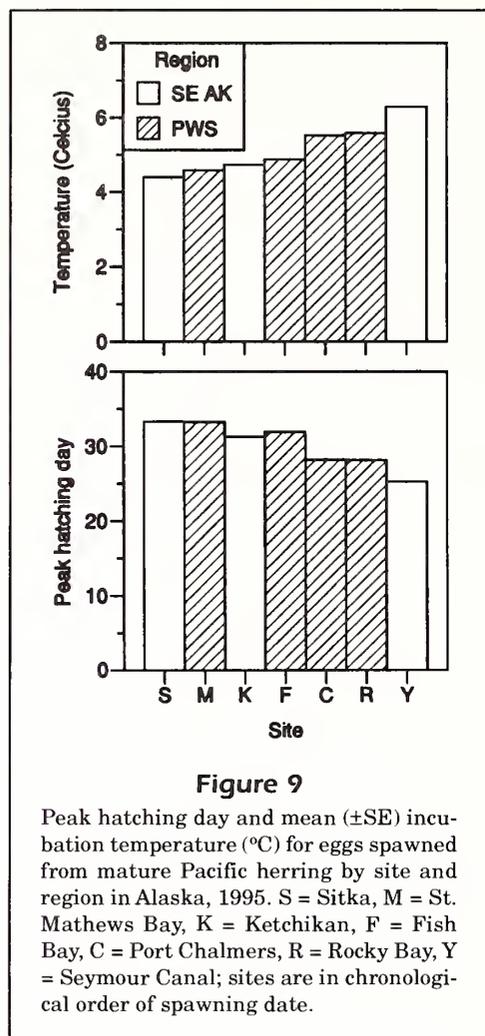
Whether or not herring in PWS were ever reproductively impaired by the EVOS is unknown, but the time lapse between the spill and our study probably precluded any detection of reproductive impairment.

¹⁶ ADF&G (Alaska Department of Fish and Game). 1995. Herring test fishery data. Commercial Fisheries Management and Development Division, 304 Lake St., Room 103, Sitka, AK 99835.



Measurable effects likely declined most rapidly during the first year as the most adversely affected individuals died. Although oil-related abnormalities were observed in larvae immediately following the spill, both developmental and genetic damage progressively decreased with time (Brown et al., 1996a) and were undetectable in 1990 and 1991 (Hose et al., 1996). The extent of spawning-site fidelity in

herring is poorly understood, but unaffected individuals from other geographic areas have probably joined remaining, less affected spawners, diluting possible residual effects. The disease epidemic observed in PWS in 1993 (Meyers et al., 1994) may have removed additional marginal spill survivors. Thus, it is not particularly surprising that reproductive impairment was not detected in 1995.



Understanding the long-term implications of exposure of Pacific herring to oil in PWS was the principal objective of this research. Regardless of the life stage of herring and the likelihood of possible oil exposure, herring we sampled in PWS in 1995 appeared to be reproductively fit and similar to herring in SE. Although herring stocks are still depressed in PWS, factors other than reproductive impairment are probably limiting recovery.

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Abstract.—We examine the population to population variability of intrinsic rate of natural increase, r_m , of Atlantic cod, *Gadus morhua*. The intrinsic rate of increase is positively related to temperature, contrary to the expectation that r_m might increase as the high and low temperature limits of habitability for cod are approached. For the parameter regime considered, r_m has a simple dependence on age-at-maturity and the number of replacements each spawner can produce at low population densities ($\bar{\alpha}$). It is shown that $\bar{\alpha}$ has no significant temperature dependence, and thus the covariation of r_m and temperature arises from the influence of temperature on age-at-maturity. We demonstrate that our estimates of r_m are robust and thus may be of use in estimating the recovery time of depleted populations.

Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*

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Perhaps the most fundamental of all ecological parameters is the intrinsic rate of natural increase, r_m (Cole, 1954; Pimm, 1991). High r_m will be selected for in populations that experience frequent excursions to low density (Charlesworth, 1994). Populations subjected to strong environmental variability should evolve toward high r_m (MacArthur and Wilson, 1967), which will impart resilience to the population. However, allometric (cross species) comparisons (Fenchel, 1974; Henemann, 1983; Charnov, 1993) suggest that r_m chiefly depends on metabolic rate or somatic growth rate. Perhaps, the influence of environmental variability on r_m can be more readily discerned in cross population comparisons for a single species. In this paper we examine 20 populations of Atlantic cod, *Gadus morhua*, to determine their maximum growth rates. We also discuss how these estimates help predict the recovery times of severely overfished populations.

Atlantic cod lends itself to a study of this nature because there is a wealth of good quality biological data collected for stock management purposes. Moreover, these cod populations occupy a broad span of latitudes, including regions that are thought to represent the northern and southern limits of habitability for cod, and there is evidence that population variability increases as these extremes are approached (Myers, 1991). The increase in population variability at the limits of the range of cod could impose constraints on r_m that would mask the simple dependence of r_m on metabolic rate or somatic growth rate apparent in cross species comparisons. In fact, we will show, in what we believe is an unanticipated result, that even for a within-species comparison, there is strong coupling between r_m and metabolic rate or somatic growth rate (as represented by age at maturity or temperature). Our results have implications for the recovery rates of a number of

recently collapsed Atlantic cod populations (Hutchings and Myers, 1994).

Methods

Model

For fish populations, reproduction is generally expressed as recruitment, the number of juvenile fish reaching, in a given year, the age of vulnerability to fishing gear. Thus, the reproduction curve (Royama, 1993) for fish is displayed as a spawner-recruitment curve (Ricker, 1954), and r_m must be derived from the slope of this curve near the origin (low population). This derivation will be presented immediately following a brief discussion of the standard population-recruitment curves.

Juvenile fish become vulnerable to fishing gear, that is, they recruit at an age designated as j' . We consider the Ricker spawner-recruitment model which describes the number of recruits at age j' in year $t+j'$, $N_{t+j',j'}$, resulting from a spawning stock biomass (SSB) of S_t . We follow the usual convention in fisheries science of assuming that the number of eggs produced is proportional to the biomass of spawners.

The Ricker model has the form

$$E(N_{t+j',j'}) = \alpha S_t e^{-\beta S_t}, \quad (1)$$

where α = the slope at the origin (measured perhaps in recruits per kilogram of spawners). Density-dependent mortality is assumed to be the product of β multiplied by the spawning biomass (S_t).

For the forthcoming calculations the slope at origin, α , must be standardized. First consider

$$\hat{\alpha} = \alpha \cdot \text{SPR}_{F=0},$$

where $\text{SPR}_{F=0}$ is the spawning biomass resulting from each recruit (perhaps in units of kg of spawning fish per recruit) in the limit of no fishing mortality ($F=0$). This quantity, $\hat{\alpha}$, represents, on a lifetime basis, the number of recruits per recruit at very low spawner abundance or, equivalently, the number of spawners produced per spawner (assuming that there is constant survival from recruit to spawner).

The quantity, $\tilde{\alpha}$, required for our calculations is the number of spawners produced by each spawner per year (after a lag of a years, where a is age-at-maturity).

If adult survival is p_s then $\hat{\alpha} = \sum_j p_s^j \tilde{\alpha}$, or summing the geometric series

$$\tilde{\alpha} = \hat{\alpha}(1 - p_s) = \alpha \cdot \text{SPR}_{F=0}(1 - p_s). \quad (2)$$

If the annual survival fraction for spawners was zero, the population of spawners, N_t , would obey the following equation:

$$N_{t+a} = \tilde{\alpha} N_t. \quad (3)$$

Equation 3 has the solution $N_{t=na} = \tilde{\alpha}^n N_0$, where N_0 is the number of spawners at $t = 0$. It follows that the natural growth rate, per annum, of the population is

$$r_m = (1/a) \log \tilde{\alpha}, \quad (4)$$

for the limit of small p_s . The analogous result for the case of overlapping generations is derived below.

When adult survival is not zero ($p_s \neq 0$), one has an age-structured spawning population, and r_m cannot be derived in the simple manner presented above. Rather, one must solve the Euler-Lotka equation (Charlesworth, 1994) to obtain r_m in this situation.

The Euler-Lotka equation is

$$\sum_j l_j m_j e^{-r_m j} = 1, \quad (5)$$

where l_j = the fraction of animals surviving to age j ; and

m_j = the number of offspring per animal produced at age j .

We now assume that $m_j = m_0$ for fish of age a and older, and also, for $j \geq a$, $l_j = l_a p_s^{j-a}$, where l_a is the fraction of juveniles that survive from age zero to age a , and, again, p_s is the annual survival fraction of spawners. It follows from Equation 5 that

$$l_a m_0 \sum_{j=a}^{\infty} p_s^{j-a} e^{-r_m j} = 1. \quad (6)$$

A little manipulation, and the summing of a geometric series, allows Equation 6 to be written as

$$\frac{l_a m_0 e^{-r_m a}}{1 - p_s e^{-r_m}} = 1. \quad (7)$$

Since m_0 is the number of age-zero fish produced by each spawner, and since l_a is the fraction of age-zero fish surviving through the juvenile stage to maturity, it follows that $m_0 l_a = \tilde{\alpha}$, and thus Equation 7 can be expressed as

$$(e^{r_m})^a - p_s (e^{r_m})^{a-1} - \tilde{\alpha} = 0. \quad (8)$$

We have bracketed the e^{r_m} term to emphasize that Equation 8 is a simple algebraic equation for $\chi = e^{r_m}$. Note that in the limit $p_s = 0$, we recover Equation 4 from Equation 8. Equation 8 is very similar to Equation 1 of Goodman (1984), amounting to a translation into parameters available for fish populations. Equation 8 may also be obtained as the low density limit of the simplified age-structured model of Clark (1976), as modified by Mertz and Myers (1996).

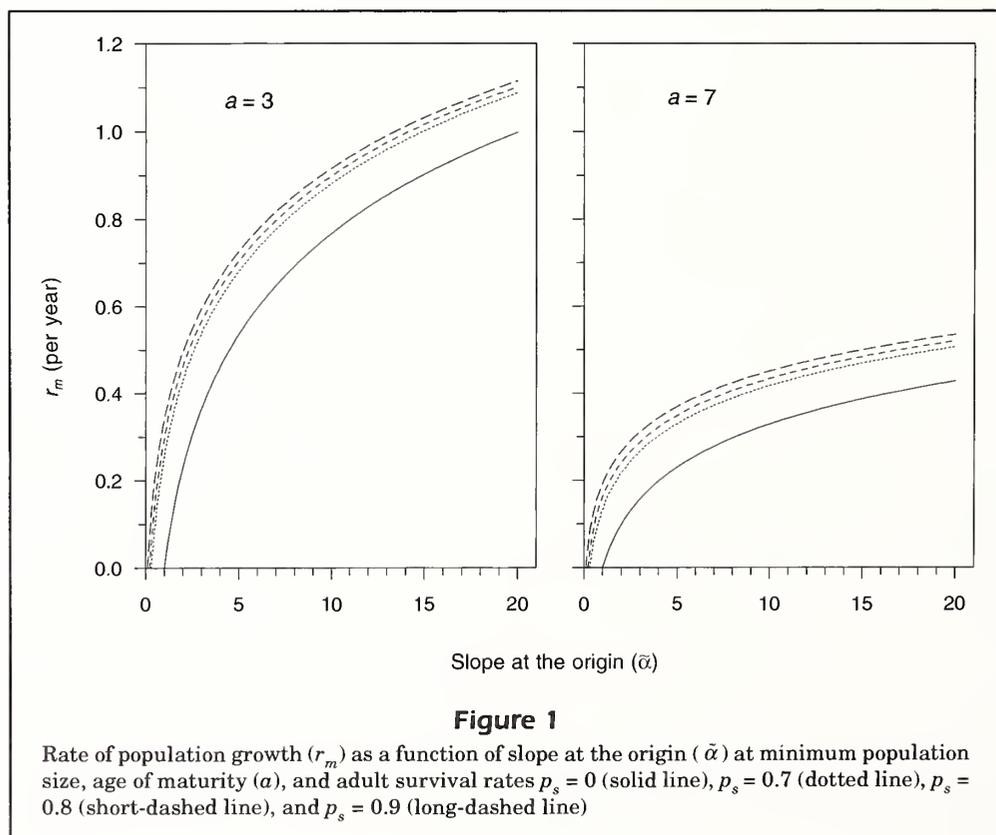
It is clear for a moderately large slope at the origin ($\tilde{\alpha}$) that age of maturity (a) is the most important factor in determining r_m (Fig. 1). The solid line in Figure 1 shows, for reference, the case $p_s = 0$, for which r_m may be calculated from Equation 4. The three broken lines in Figure 1 represent $p_s = 0.7$, 0.8, 0.9, a range that should encompass all North Atlantic cod stocks (see next section). For this range, survival after reproduction (p_s) has only a minor effect on r_m .

Data sources and treatment

The data we used are estimates obtained from assessments compiled by Myers et al. (1995b). Population numbers and fishing mortality were estimated by using sequential population analysis (SPA) of commercial catch-at-age data for most marine popula-

tions. Sequential population analysis techniques include virtual population analysis (VPA), cohort analysis, and related methods that reconstruct population size from catch-at-age data (see Hilborn and Walters, 1992) chapters 10 and 11, for description of the methods used to reconstruct the population history). Briefly, the commercial catch-at-age is combined with estimates from research surveys and commercial catch rates to estimate numbers-at-age in the final year and to reconstruct previous numbers-at-age under the assumption that commercial catch-at-age is known without error and that natural mortality-at-age is known and constant.

The population boundaries in the North Atlantic generally follow those of the Northwest Atlantic Fisheries Organization (NAFO) or the International Council for the Exploration of the Sea (ICES) (Fig. 2). Many populations cover more than one NAFO or ICES unit area, e.g. the cod population off Labrador and Northeast Newfoundland, known as "northern" cod, inhabits three NAFO divisions (2J, 3K, and 3L) and is designated as 2J3KL cod. There are three minor populations that are not included in the comparative analysis: Flemish Cap, Gulf of Maine, and the English Channel. There are no reliable catch data for the Flemish Cap population (NAFO 3M) or the English Channel population (ICES VIIId), and the



mated parameters (Myers et al., 1995b). Difficulties in estimating density-dependent model parameters are well known for insect and bird populations (Holyoak, 1993; Wolda and Dennis, 1993) and have been extensively studied for exploited fish populations (Hilborn and Walters, 1992). The most important source of statistical bias for exploited fish populations is the nonindependence of spawners and recruitment, i.e. large recruitment usually leads to large spawner abundance (Walters, 1985). Bias in the parameter estimates of the spawner recruit function has been extensively studied with simulations for cod populations by Myers and Barrowman (1995) who found minimal bias in the estimates of the α parameter.

The slope at the origin can be well estimated for cod populations, in spite of the large variability in recruitment, because each population has been reduced to very low levels by overexploitation (Myers et al., 1994). Furthermore, there is no evidence that mortality increases at low population size, i.e. depensation or the Allee effect, that would invalidate the assumption of our spawner recruitment model (Myers et al., 1995).

The disadvantage of using the Ricker model, or any other parametric spawner recruitment model, is that the slope at the origin is influenced by observations far from the origin. We investigated an alternative approach: we regressed recruitment versus spawner biomass with only six observations with the lowest spawner biomass, forcing the regression line through the origin. This simple procedure should be reasonable because all the populations have been reduced to very low levels.

Results

The Ricker model estimates of the slope at the origin and of the population growth rate were estimated for the 20 spawner recruit data sets (Table 1; Fig. 3). The slope at the origin, $\tilde{\alpha}$, did not vary enormously

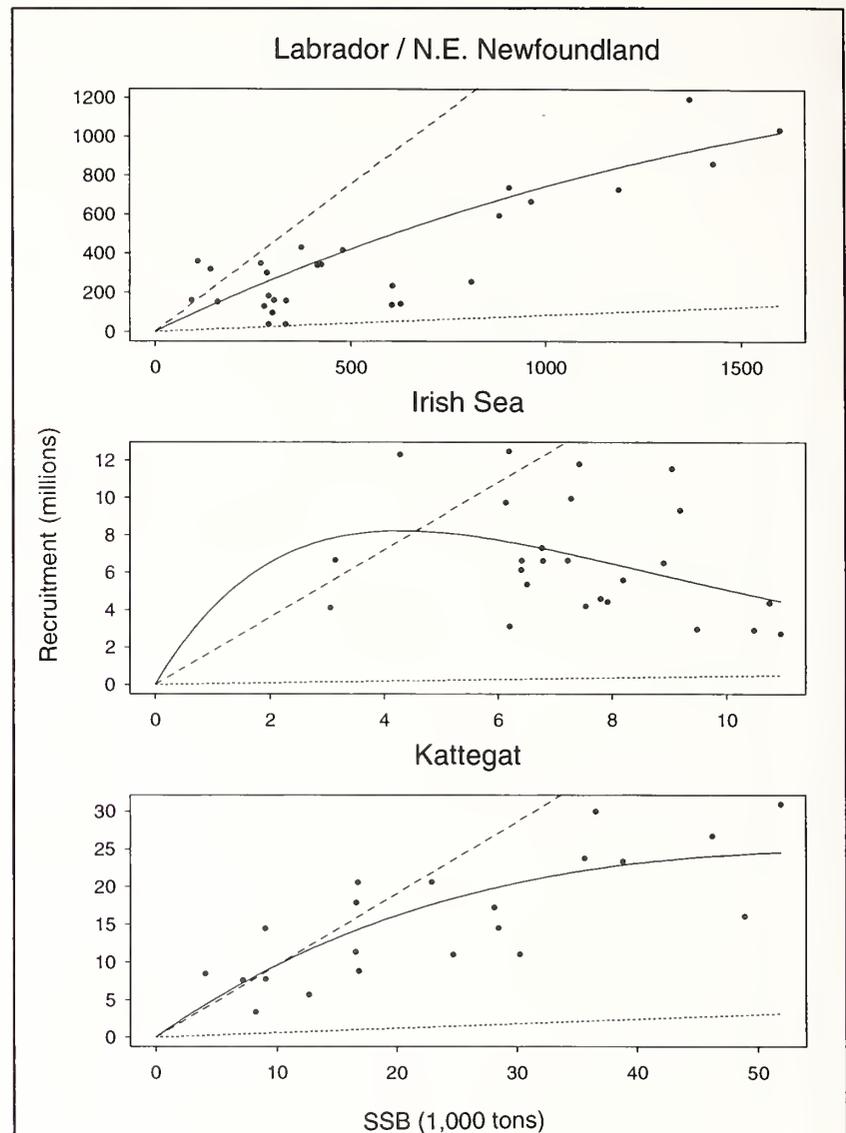


Figure 3

Recruitment versus spawning stock biomass (SSB) for the three representative cod populations. The solid line is the maximum likelihood estimate of the mean for Ricker spawner-recruitment functions under the assumption that the probability distribution for any SSB is given by a lognormal distribution. The dashed line is the median slope at the origin estimated from the six points with the lowest SSB. The straight dotted line is the replacement line with no fishing mortality.

among populations (Fig. 4). There is one population, Irish Sea, for which the $\tilde{\alpha}$ is much larger; we believe that this large $\tilde{\alpha}$ is an overestimate (this will be discussed later).

It is evident that r_m strongly covaries with temperature (Fig. 5; Table 2). It is also clear that this behavior does not arise from any dependence of $\tilde{\alpha}$ on temperature, because $\tilde{\alpha}$ is not correlated with temperature (Fig. 5; Table 2). There is a strong de-

Table 1

Estimates of rate of population growth (r_m), slope at the origin ($\tilde{\alpha}$) estimated from the Ricker model, age of maturity (a), bottom temperature, and NAFO/ICES management units for 20 cod populations in the North Atlantic.

ID no.	Stock location	NAFO/ICES management unit	r_m	$\tilde{\alpha}$	a	Temperature
1	West Greenland	1	0.23	2.4	6	1.75
2	Labrador/N.E. Newfoundland	2J3KL	0.17	2.3	7	0.00
3	S. Grand Bank	3NO	0.27	3.5	6	1.75
4	N. Gulf of St. Lawrence	3Pn4RS	0.20	3.0	7	1.00
5	St. Pierre Bank	3Ps	0.31	4.6	6	2.50
6	S. Gulf of St. Lawrence	4TVn	0.15	1.9	7	1.75
7	E. Scotian Shelf	4VsW	0.36	9.8	6	3.75
8	S.W. Scotian Shelf	4X	0.36	2.5	3.5	6.75
9	Georges Bank	5Z	0.60	2.2	2	8.00
10	S.E. Baltic	22-24	0.74	8.4	3	7.00
11	Central Baltic	25-32	0.53	3.1	3	5.00
12	Celtic Sea	VIIg,f	0.62	5.3	3	11.00
13	Faroe Plateau	Vb	0.44	4.2	4	7.40
14	Iceland	Va	0.24	4.3	7	5.80
15	Irish Sea	VIIa	1.03	23.1	3	10.00
16	Kattegat	South IIIa	0.53	3.8	3	6.50
17	Barents Sea	I	0.26	6.6	7.5	4.00
18	North Sea	IV	0.56	9.0	4	8.60
19	Skagerrak	North IIIa	0.82	11.2	3	6.50
20	West of Scotland	VIa	0.80	6.4	2.5	10.00

pendence of r_m on age-at-maturity, but there is no corresponding significant relation between $\tilde{\alpha}$ and age-at-maturity (Fig. 6). Consistency demands that there be a relation between age-at-maturity and temperature, and, indeed, Table 2 and Figure 7 show that there is a significant correlation between these two variables.

We repeated the above analysis with $\tilde{\alpha}$ calculated at the median slope of the six observations with the lowest spawner abundance. The estimates calculated with this robust procedure were generally comparable with those estimated from the Ricker model, although the Ricker values were generally higher (Fig. 8). The larger discrepancies in the two methods occurred for the populations in which there were low estimates of recruitment at the largest population sizes, e.g. Irish Sea cod (Fig. 3). These points, although they are farthest from the origin, resulted in a higher estimate of the slope at the origin because the Ricker model assumes a linear relation between egg-to-recruit mortality and SSB.

We repeated the regression analysis of rate of population growth and slope at the origin ($\tilde{\alpha}$) at minimum population size versus bottom temperature with the robust estimate of the slope, and found simi-

Table 2

For each of the three variables r_m (population growth rate), $\tilde{\alpha}$ (standardized slope of the spawner-recruit curve at the origin), and a (age-at-maturity), the estimated slope parameter of the regression on temperature (T) (e.g. $r_m = a + bT$) is presented, labeled \hat{b} . For r_m and $\tilde{\alpha}$, there are two b values based respectively on the Ricker fit to each spawner-recruit data set and the median of the first six points of each spawner-recruit data set. Also shown are the significance levels of the regressions on temperature and the corresponding r^2 . The results are presented for the Northwest, Northeast, and entire Atlantic.

Variable	Ricker \hat{b}	Ricker $P(b=0)$	Ricker r^2	Median \hat{b}	Median $P(b+0)$	Median r^2
r_m						
West	0.04	0.001	0.63	0.02	0.03	0.51
East	0.09	0.003	0.64	0.04	0.06	0.35
All	0.06	0.00008	0.59	0.04	0.00003	0.62
$\tilde{\alpha}$						
West	0.32	0.5	0.06	-0.16	0.3	0.15
East	0.83	0.2	0.16	0.09	0.7	0.02
All	0.67	0.04	0.21	0.13	0.2	0.08
a						
West	-0.62	0.00005	0.92	—	—	—
East	-0.45	0.06	0.34	—	—	—
All	-0.47	0.00002	0.65	—	—	—

lar results to those using the Ricker model (Table 2; Fig. 9). We conclude that our results are robust in relation to the method used to estimate $\tilde{\alpha}$.

Discussion

Perhaps remarkably, our study has revealed that the allometric (cross species) approximate inverse proportionality between r_m and age-at-maturity holds within the species Atlantic cod. Despite the much narrower range of r_m used in our single-species comparison (in contrast to the wide variation in r_m found in cross-species studies), the relation between r_m and age-at-maturity prevails over other influences. The expectation that cod populations at the northern and

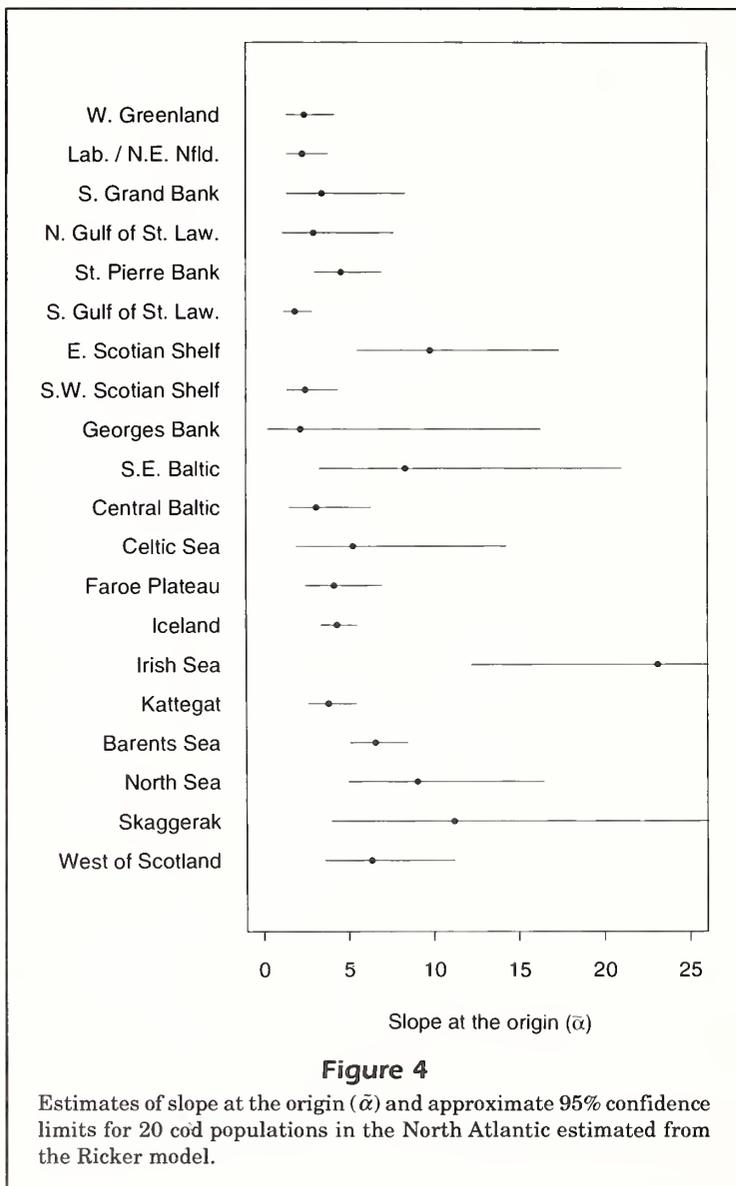
southern extremes of their range should show higher resilience (r_m), because of greater susceptibility to environmental change (Myers, 1991), is not realized.

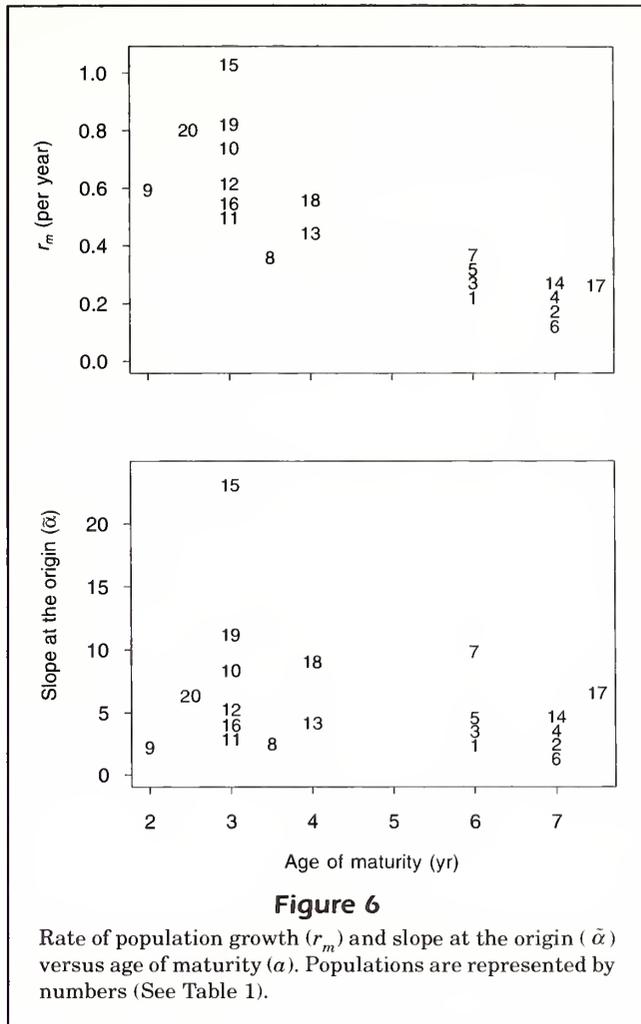
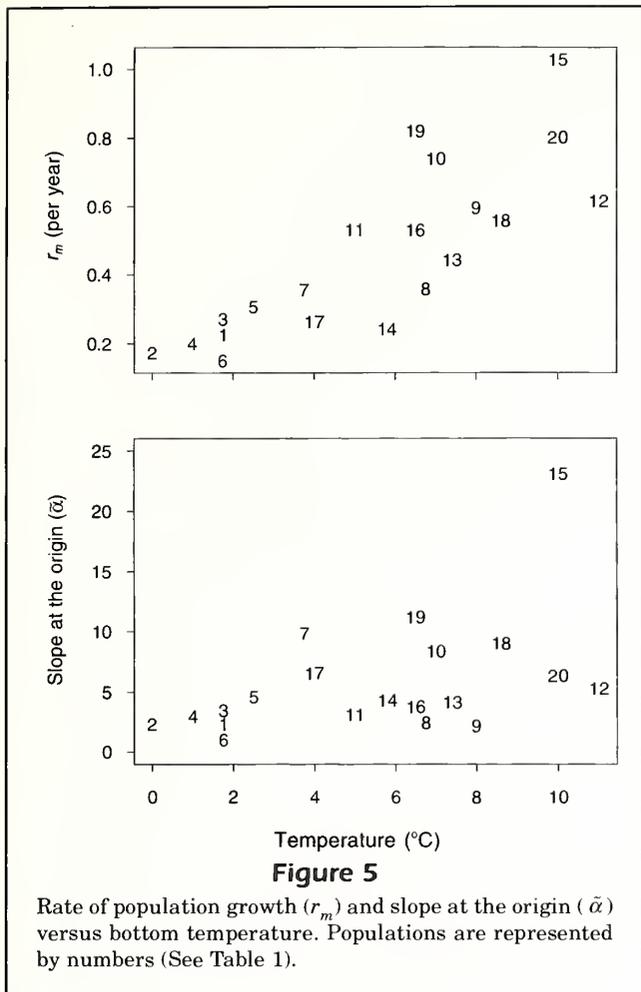
In a similar vein, Roff (1984) suggested that early maturity in fish species may arise through r -selection (in response to extreme environmental variability); our findings show that age-at-maturity appears to be chiefly explained by ambient temperature.

Although we have found a clear relation between r_m and temperature, this was not necessarily expected a priori because mortality is positively related to temperature in comparative studies (Pauly, 1980). That temperature dependent (egg to adult) mortality can offset the effect of temperature-dependent growth is emphasized by the temperature independence of $\tilde{\alpha}$. More specifically, $\tilde{\alpha}$ depends on both fecundity and mortality. Fecundity, being growth dependent (Roff, 1984) increases with temperature; however, mortality also increases with temperature and counteracts the influence of temperature-dependent growth, leaving $\tilde{\alpha}$ temperature independent. (Note that many empirical studies of life histories of fish have found that somatic growth rate and survival covary [Beverton and Holt, 1959; Pauly, 1980; Myers and Doyle, 1983; Hutchings, 1993]).

The relation between r_m and temperature is presumably a metabolic effect, in that fish growth is strongly influenced by temperature (Taylor, 1958; Pauly, 1980), and implies that a fish in a warm environment will reach the required size for maturity at an early age, which tends to increase r_m . Although Birch (1948) has noted, for insect populations, that higher r_m values do not necessarily correspond to higher temperatures, investigators such as Hennemann (1983) and McNab (1980) have suggested that r_m should be closely related to metabolic rate, which is closely linked to temperature. Certainly our presentation corroborates this proposed parallel between metabolism and r_m .

The importance of the determination of r_m has long been known (Lewontin, 1965); however, it is certainly not always the case that age-at-maturity is the dominant factor. For species for which the production of replacement adults at low population density, $\tilde{\alpha}$, is relatively low (e.g. for many mammals and birds), then changes in $\tilde{\alpha}$ or adult survival will have large effects on r_m (Fig. 1). However, for cod, and perhaps many fish, $\tilde{\alpha}$ is relatively large (e.g. around 4). In this case, the effects of reasonable changes in adult





survival (between 0.7 to 0.9) or $\tilde{\alpha}$ have a relatively small effect compared with age-at-maturity (Fig. 1).

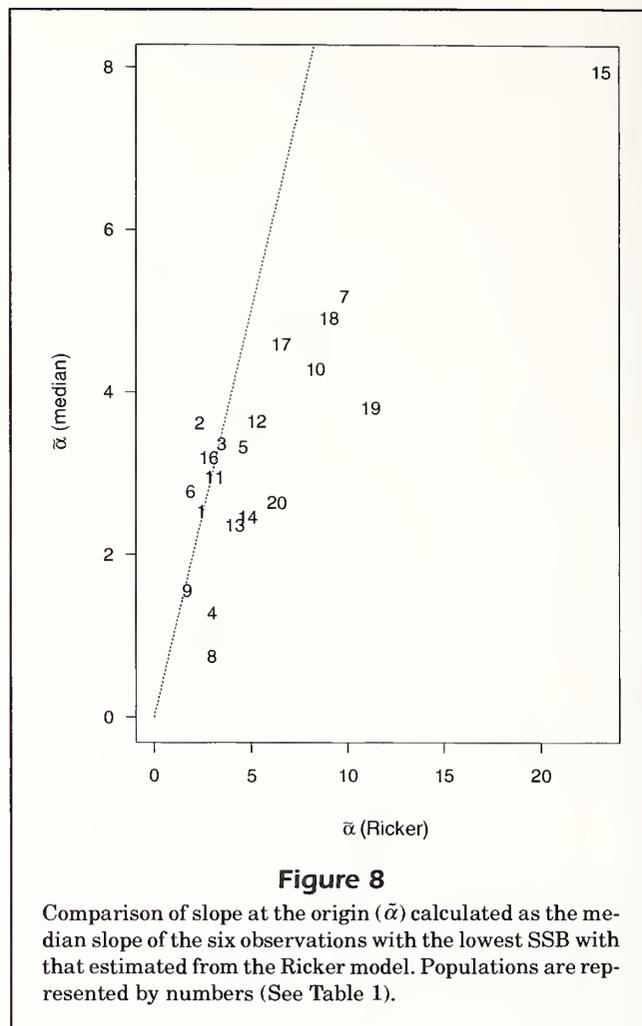
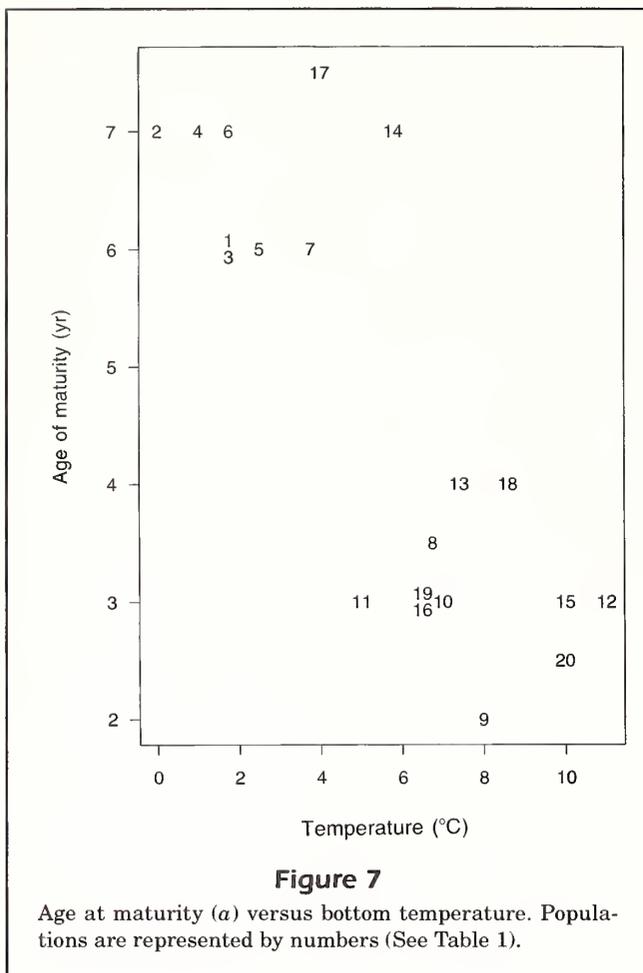
Our study has presented robust estimates (see Fig. 8) of r_m for a variety of Atlantic cod populations, thus establishing recovery times for overfished populations relieved from fishing pressure. At colder temperatures, r_m is around 18% a year for all populations, independent of how we calculate r_m .

A major source of uncertainty in the SPA estimates of recruitment and SSB used in our analysis is that catches are assumed to be known without error. This assumption is particularly important when estimates of discarding and misreporting are not included in the catch-at-age data used in the SPA. These errors are clearly important for some periods of time for some of the cod stocks (Myers et al., 1997), and these errors will affect our estimates of the number of replacements each spawner can produce at low population densities ($\tilde{\alpha}$). However, we have shown that the estimates of r_m are not very sensitive to reasonable changes in this parameter.

We have carried our estimation of the model parameters separately for each stock. An alternative approach is to analyze simultaneously all stocks in models that include separate estimation error for each stock and a parameter describing the variation among stocks. Myers et al.¹ carried out such an analysis using variance components models for the data analyzed in this study and found that the optimal estimates of the variation in $\tilde{\alpha}$ was much less than that estimated, e.g. the very high estimate for Irish Sea cod was found to be overestimated.

The parameters estimated in this study have management implications that go beyond the estimation of population growth rate. In particular, the number of replacements each spawner can produce at low population densities ($\tilde{\alpha}$), is critical for determining

¹ Myers, R., G. Mertz, and N. Barrowman. 1996. Invariants of spawner-recruitment relationships for marine, anadromous, and freshwater species. ICES Council Meeting 1996/D:11, 17 p.



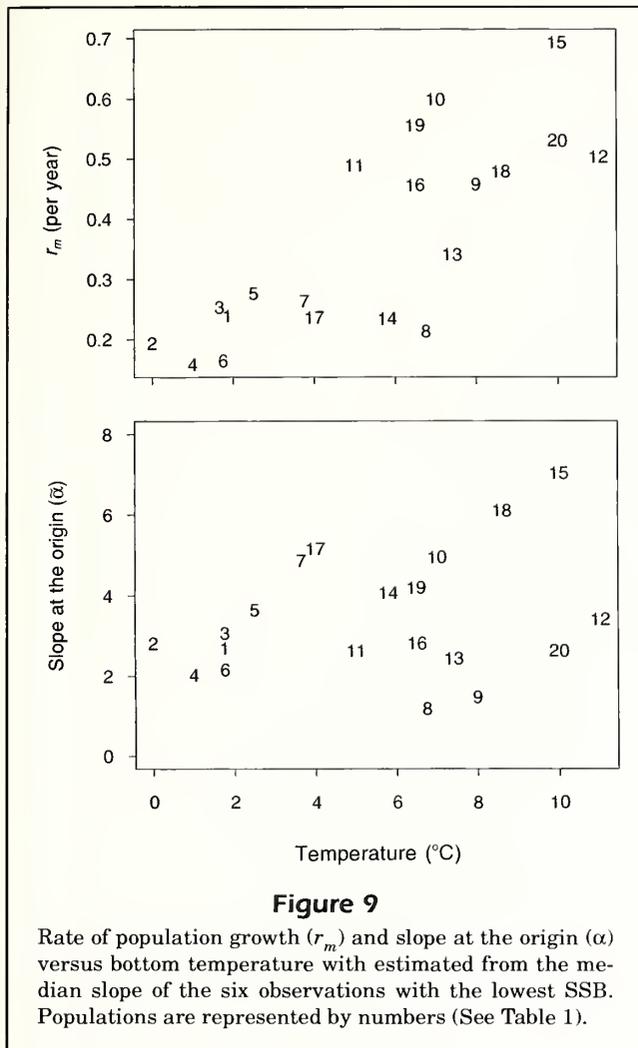
the limits of exploitation (Cook et al., 1997; Myers and Mertz, in press). A comparative approach, such as the one used here, should help refine our understanding of the rational exploitation of fisheries.

We have used as simple a model as possible to estimate r_m . This has the very great advantage that we can compare the crucial demographic parameters (i.e. the replacements each spawner can produce at low population densities ($\tilde{\alpha}$), age-at-maturity (a), and adult survival (p_s) among populations) and can easily study the sensitivity of r_m to errors in each of these parameters (Fig. 1). Furthermore, Hutchings and Myers (1994) found similar estimates of r_m when they used a fully age-structured model for "northern" cod, i.e. cod in NAFO Division 2J3KL.

Previous estimates of the recovery time for depleted cod stocks that have not included a detailed analysis of population growth rate have yielded widely different results. For example, it was initially projected that northern cod would recover close to historic levels of spawning biomass after a two-year fishing moratorium (Lear and Parsons, 1993). This projection has since been shown to be incorrect

(Myers et al., 1996; Hutchings et al., 1997). Roughgarden and Smith (1996) estimated r_m for northern cod to be ≈ 1 by simply taking the greatest difference between adjacent estimates of total population abundance from annual research vessel surveys. That is, they assumed that any change in the estimates represented an increase in population abundance.

However, this change in estimated abundance was almost entirely estimation error (Myers and Cadigan 1995, a and b) and had nothing to do with an increase in abundance. At present (March 1997) there are six Canadian cod populations (2 to 7 in Table 1) that are currently protected by a fishing moratorium because the populations have been greatly reduced by overfishing (Myers et al., 1997). Unfortunately, our results indicate that recovery could require a long period. Under average environmental conditions, our results suggest a doubling time of about 4 years. Given the severe depletion of these populations (some are less than 5% of their maximum observed levels (Myers et al., 1996) recovery to



desired levels of spawning biomass should not be expected for at least a decade of minimal mortality caused by fishing.

Acknowledgments

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Abstract.—Sagittal otoliths were used to determine age and growth of 605 larval and juvenile Atlantic croaker, *Micropogonias undulatus*, collected in the Middle Atlantic Bight and estuarine waters of Virginia. This study is the first to use age-based analysis for young Atlantic croaker collected in this region. A Laird-Gompertz model ($r^2=0.95$) was used to describe the growth of Atlantic croaker up to 65 mm standard length (SL) and 142 days (t): $SL_{(t)} = 2.657 \exp [4.656 [1 - \exp(-0.0081t)]]$; where $SL_{(t)}$ = standard length at day t . Spatial and temporal patterns in the size and age of Atlantic croaker showed a pattern of inshore immigration from offshore spawning grounds, and faster early-season growth compared with late-season growth. Back-calculated hatching dates of Atlantic croaker collected in Virginia estuaries indicated a protracted spawning period over 8 months, from early July 1987 to early February 1988, with at least 82% of spawning occurring from August to October. Regression analysis indicated that early-spawned larvae (July through August) grew more than 39% faster than late-spawned larvae (September through February). Lapillar and sagittal otoliths were compared with light microscopy; ages were underestimated with lapillar otoliths, which were particularly inadequate in determining the age of older juveniles. The relation between SL and sagittal otolith maximum diameter was best described by a fourth order polynomial ($r^2=0.99$) and faster-growing Atlantic croaker had larger otoliths (12%) than the same size slower-growing fish.

Age and growth of larval and juvenile Atlantic croaker, *Micropogonias undulatus*, from the Middle Atlantic Bight and estuarine waters of Virginia

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Atlantic croaker, *Micropogonias undulatus*, range from New York to Florida and along the western and northern Gulf of Mexico (Ross, 1988; Atlantic States Marine Fisheries Commission, 1993). Historically, Atlantic croaker have ranked as one of the top five species in the commercial catch of finfishes in the middle Atlantic region (McHugh and Conover, 1986), although recruitment is highly variable in the species. In Virginia, annual commercial landings have varied by as much as threefold and have apparently declined overall since 1937 (Chesapeake Bay Program, 1988). Similarly, recreational landings have varied by as much as twofold over two years (U.S. Department of Commerce, 1991).

In species with substantial annual recruitment variability, change in the survival rate of prerecruits (larvae and juveniles) is a key factor in determining adult abundance (Houde, 1987). Determination of survival rates of prerecruits relies, in part, on daily age and growth information (Jones, 1992), and although otolith daily increment analysis has become common practice (Jones, 1992), there are few

published age and growth studies on the early life history of Atlantic croaker. Furthermore, there are no age-based estimates of growth for larval and juvenile Atlantic croaker from the Middle Atlantic Bight (MAB: shelf waters from Long Island, NY, to Cape Hatteras, NC) and estuarine waters of Virginia. Comparable age-based studies on the early life history of Atlantic croaker have concentrated on larvae collected in coastal waters south of Cape Hatteras, North Carolina (Warlen, 1982), or the northern Gulf of Mexico (Cowan, 1988).

North Carolina larvae (Warlen, 1982), collected south of Cape Hatteras at Beaufort Inlet, show a twofold decline in length-at-age between early- and late-season collections. Likewise, Cowan (1988) shows a similar slow growth rate for late-season larvae collected in the northern Gulf of Mexico. Warlen's (1982) back-calculated hatching dates indicate a broad spawning season from September to February, with peak spawning in October and November. On the basis of the pattern of progressive increase in mean size and age from the shelf to the estuary and on the basis of seasonal

variability in age of larvae entering the estuary, Warlen (1982) postulates two offshore spawning locations for Atlantic croaker entering Beaufort. Warlen's conclusions imply potential differences in spawning source between larvae entering Chesapeake Bay and some of those entering Beaufort Inlet.

The purpose of the present study was to examine age and growth of larval and juvenile Atlantic croaker from the MAB and estuarine waters of Chesapeake Bay by using daily growth rings on otoliths. Specifically, we investigated the variability of size, size and age of entry into Chesapeake Bay, calculated hatching-date distributions to estimate spawning periodicity, and estimated temporal and spatial differences in growth rates. In addition, we determined if there were significant differences in age counts between lapillar and sagittal otoliths and in size and age counts between left and right sagittal otoliths. Finally, we compared the relation between otolith growth and somatic growth for field-captured Atlantic croaker with results presented in the literature.

Materials and methods

Sampling regime

Larval Atlantic croaker were collected in the MAB (from Cape Henlopen, Delaware, to Cape Hatteras, North Carolina; Fig. 1) from 3 November to 14 November 1987 from the shore to the 91-m (50-fm) contour with a stratified grid system illustrated in the MARMAP Plankton Survey Manual (Jossi and Marak, 1983). Seven additional stations at 2-km intervals were sampled along a transect across the mouth of the Chesapeake Bay. Larvae were sampled in oblique tows with a 60-cm bongo sampler containing 505- μ m mesh. Larval and juvenile Atlantic croaker sampled by Norcross and Hata (1990) were collected monthly from 29 September 1987 to 10 March 1988 at three inshore stations at Virginia's Eastern Shore (Wachapreague, Sand Shoal, and Occohannock Channel) and at two stations at the mouth of the York River (Guinea and Tue Marshes;

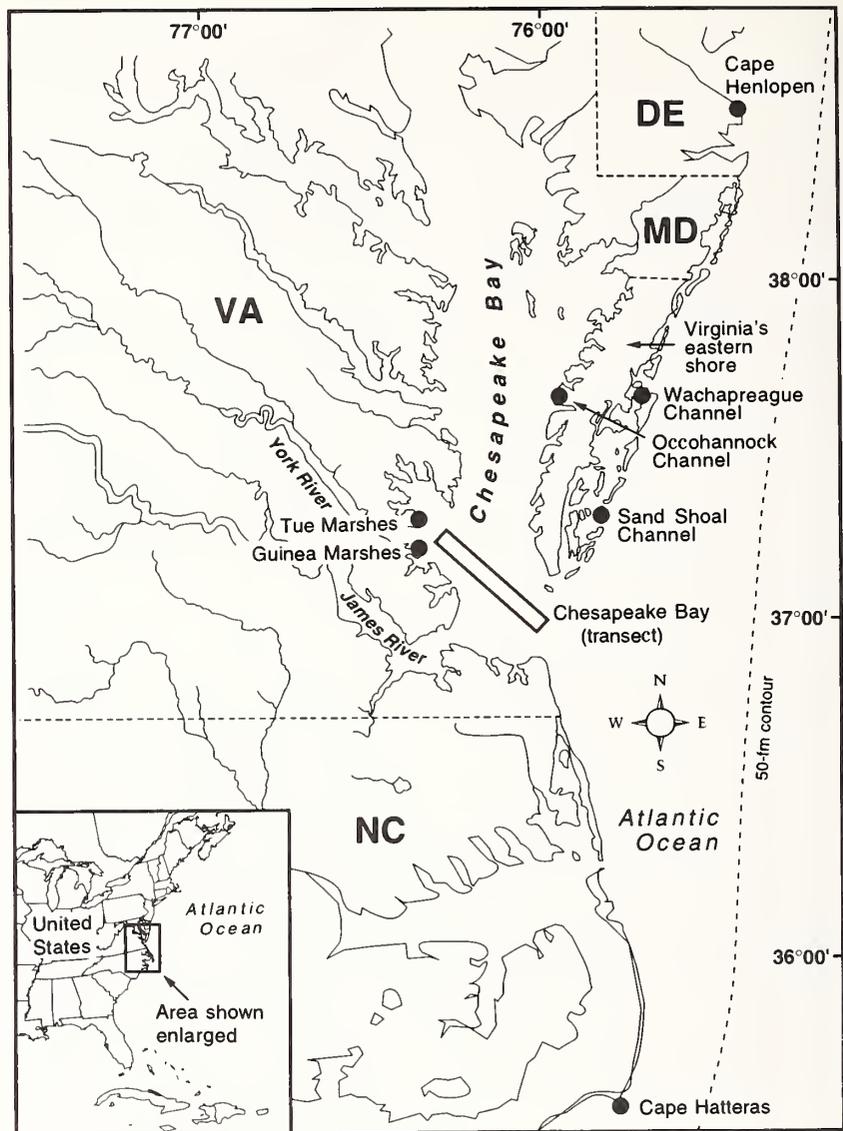


Figure 1

Station locations in estuarine waters of Virginia for collection of larval and juvenile Atlantic croaker from 21 September 1987 to 30 March 1988.

Fig. 1) with two 4.9-m otter trawls (one lined, one unlined) towed simultaneously. The lined net had a 6.4-mm mesh and a 3.2-mm mesh liner, and the unlined net a 15.9-mm mesh. Additional larval and juvenile Atlantic croaker were collected monthly from 21 September 1987 to 1 February 1988 at 8.1-km intervals along a 40.2-km transect running from the mouth of the York River to the mouth of the Chesapeake Bay (Fig. 1) with an otter trawl with a 9.1-m lined net containing 15.9-mm mesh and a 6.4-mm mesh liner. Finally, juvenile Atlantic croaker sampled by Dameron et al.¹ were collected monthly from 25 January to 30 March 1988 in the channels of the York and James Rivers at 8.1-km intervals from the mouth of the two rivers to 56.3 km upstream (Fig. 1) with

an otter trawl with a 9.1-m lined net containing 15.9-mm mesh and a 6.4-mm mesh liner. Otter trawls were towed at 1.0 to 1.5 m/s over the bottom for five minutes. Specimens were preserved in 70% ethanol immediately upon collection. The ethanol was changed within 24 hours and again after two days.

Otolith processing and data analysis

Standard length (SL) measurements were made on fish to the nearest 0.1 mm with an image analysis system for individuals <20 mm SL or with vernier calipers for individuals ≥ 20 mm SL. Sagittal and lapillar otoliths were extracted from at least 30 fish chosen at random from each station and sampling date ($n=605$, 40 from the MAB and 565 from estuarine waters). Otoliths were extracted from all individuals when samples contained less than 30 fish. Only 40 of the 126 larvae collected in the MAB were available for age analysis owing to inadequate preservation. Otolith maximum diameter (OMD) was measured on sagittae from rostrum to postrostrum to the nearest 0.1 mm with an image analysis system—39 otoliths from larvae collected in the MAB and 143 otoliths from randomly selected estuarine larvae and juveniles were measured.

The right sagittal otolith was used in age and growth analyses except when lost or damaged; then the left otolith was used. Procedures for the preparation of otoliths that required sectioning and polishing followed Epperly et al. (1991)—in short, otoliths were sectioned longitudinally, ground, and then polished to the primordia on both sides. Generally, otoliths from fish <15 mm SL did not require grinding or polishing to distinguish daily increments; they were placed directly on glass slides and embedded in Euparal. Otoliths were read at 1,000 \times , under cross-polarized, transmitted light on a monitor with an image analysis system. All specimens were aged without knowledge of fish size or collection date. Three independent age counts were averaged to determine final ages. Age counts were estimated by adding 5 days to the number of daily increments in the otoliths by assuming that increment deposition begins at 5 days posthatching as in spot (*Leiostomus xanthurus*; Peters et al.²).

Paired t -tests were used to determine if there were significant differences in age estimates between lapillar and sagittal otoliths ($n=32$) and in size and age counts between left and right otoliths ($n=30$). Also, the precision of sagittal age counts by the primary reader and a secondary reader were compared ($n=50$) with the indices of average percent error (Beamish and Fournier, 1981), coefficients of variation, and index of precision (Chang, 1982). A paired t -test also was used to determine if there was a significant difference in mean age counts between readers.

To generalize comparisons of mean growth rates and size-at-age of Atlantic croaker across capture sites, stations were grouped geographically into regions. These regions were designated as MAB, Chesapeake Bay, seaside Eastern Shore (includes the Wachapreague and Sand Shoal Channel stations), bayside Eastern Shore (includes the Occohannock Channel station), marshes (includes the Tue and Guinea marsh stations), and rivers (includes the James and York river transects). The length and age of fish were compared among regions sampled with similar gears with independent, two-sample t -tests.

Linear regression comparisons (Rawlings, 1988) were used to compare growth rates (slopes) and size at day 0 (y -intercepts) between early- (September through October) and late-captured (November through March) larvae ≤ 15 mm SL and ≤ 80 d. The analysis was restricted by size because larger, older juveniles were not available during early-season collections. Linear regression comparisons (Rawlings, 1988) were also used 1) to compare growth between early- (July through August) and late-season (September through February) spawned larvae (≤ 19 mm SL) and 2) to compare growth between early- and late-season spawned juveniles (19.1–65 mm SL). Early- and late-spawned larvae and juveniles were analyzed separately so that linear growth patterns could be described for the two life stages. We also used ANCOVA to compare mean size between early- and late-spawned juveniles.

A Laird-Gompertz growth model (Laird et al., 1965) was used to describe the growth of Atlantic croaker larvae and juveniles ≤ 50 mm SL and ≤ 142 d:

$$SL_{(t)} = SL_{(0)} / \exp\{[A_{(0)}/\alpha][1 - \exp(-\alpha t)]\};$$

$SL_{(t)}$ = standard length at day t ;
 $SL_{(0)}$ = assumed standard length at hatching ($t=0$);
 $A_{(0)}$ = specific growth rate at hatching ($t=0$); and
 α = rate of exponential decay of the specific growth rate.

The model was fitted by an iterative, nonlinear least-squares procedure. Age-specific growth rates were subsequently calculated as

¹ Dameron, J. C., P. J. Geer, C. F. Bonzek, and H. M. Austin. 1994. Juvenile finfish and blue crab stock assessment program, bottom trawl survey. Annual data summary report series vol. 1987. Special Scientific Report 124, Virginia Institute of Marine Science, College of William and Mary, Gloucester Pt., VA.

² Peters, D. S., J. C. Devane Jr., M. T. Boyd, L. C. Clements, and A. B. Powell. 1978. Preliminary observations of feeding, growth, and energy budget of larval spot (*Leiostomus xanthurus*). In Annu. Rep. NMFS, Beaufort, NC, p. 377–397.

$$A_{(t)} = A_{(0)} \exp(-\alpha t).$$

Finally, ANCOVA was used to compare mean otolith size between early-captured, fast-growing Atlantic croaker with late-captured, slower-growing Atlantic croaker between 11 and 37 mm SL.

Results

Otolith analysis

Age counts in sagittal and lapillar otoliths were significantly different (*t*-test, $P=0.002$). For older age fish, lapillar counts underestimated sagittal counts, and the disparity increased with increasing age (Fig. 2). Also, no differences were found among size (*t*-test, $P=0.49$) and age counts (*t*-test, $P=0.85$) between left and right sagittal otoliths ($n=30$).

Sagittal age counts by the primary reader showed good precision—the average percent error (APE) of counts was 4.8%, with a coefficient of variation (CV) and index of precision (D) of 6.4% and 3.8%, respectively. For the second reader's age counts these indices were 8.4% (APE), 11.5% (CV), and 6.7% (D). Although the second reader's age counts had relatively low precision, there was no significant difference in mean age counts between readers (*t*-test, $P=0.27$).

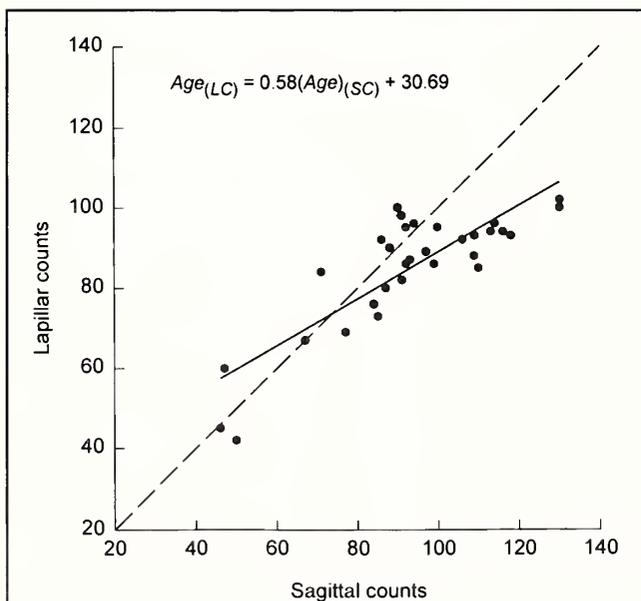


Figure 2

Comparison of sagittal and lapillar otolith age counts ($r^2=0.73$, $n=32$) illustrating reproducibility of sagittal counts (Age_{SC}) with lapillar counts (Age_{LC}). Dashed line represents a one-to-one relation, and the solid line the regression describing the relation between sagittal and lapillar age counts.

Size and age distributions

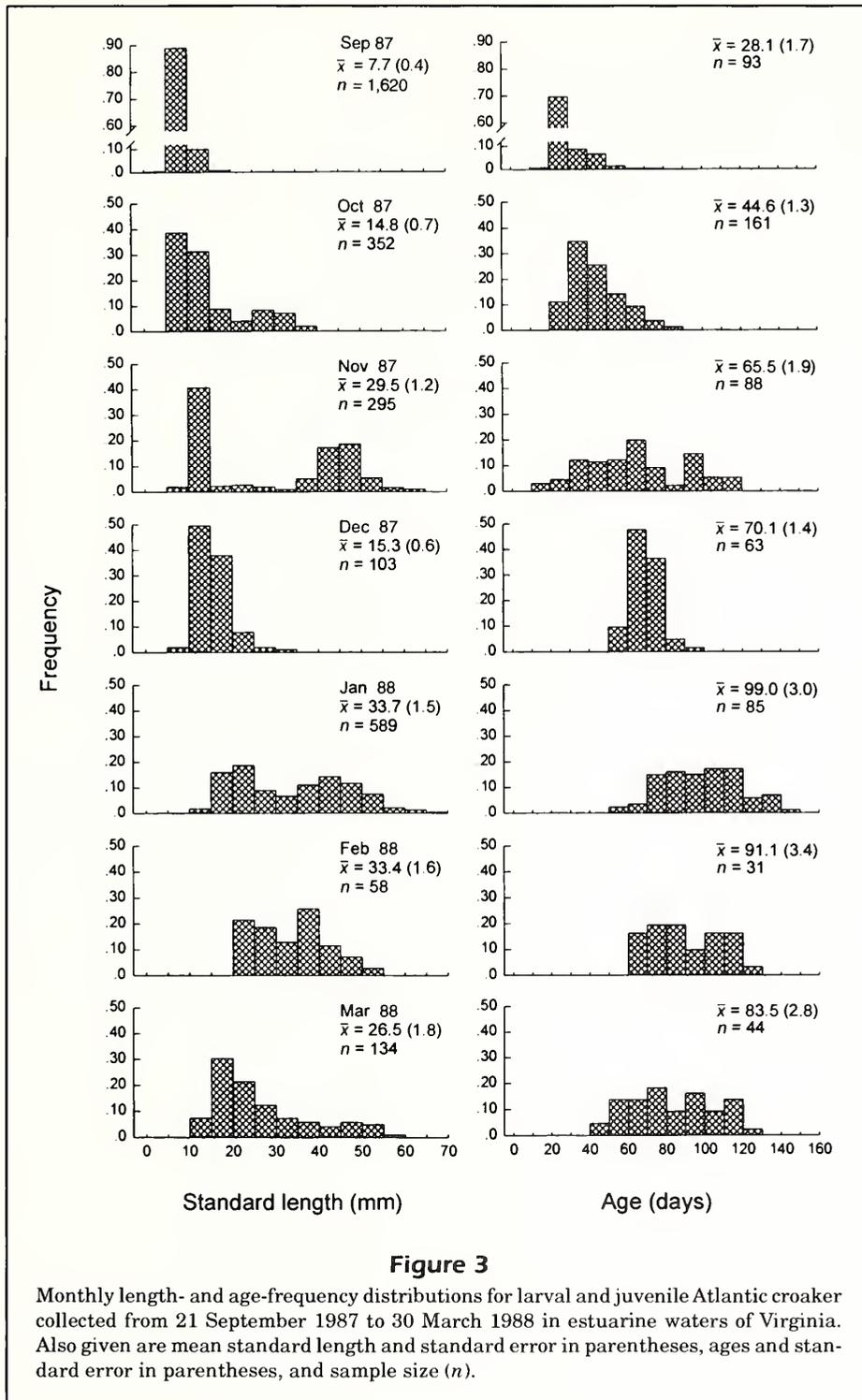
Monthly length- and age-frequency distributions showed that size and age of fish generally increased from September to January (Fig. 3). Size and age appeared to decline in February (although sample sizes were small) and mostly represented fish collected in the rivers after January. Also, length distributions were highly variable in comparison with respective age distributions (Fig. 3). For example, fish collected in November had two distinct length modes, whereas their age frequencies clearly had only one mode. This pattern was also evident for fish collected in October and January; thus size does not appear to be a good predictor of age in these fish.

Generally, smaller and younger fish were found in the seaside Eastern Shore region compared with the bay-side Eastern Shore or marsh regions (*t*-tests, $P<0.001$) over the entire sampling season. This pattern was evident regardless of gear type. Significantly smaller ($P=0.02$) and younger ($P<0.001$) fish were found in the mainstem Chesapeake Bay compared with the rivers inland of the Bay. However, the rivers were sampled only during the later half of the sampling period.

The age of larval Atlantic croaker entering Virginia nursery grounds was examined from specimens collected at the mouth of the Chesapeake Bay (the most seaward station along the Chesapeake Bay transect) and at Wachapreague and Sand Shoal Channels. The youngest larvae (24 d) entered the mouth of the Chesapeake Bay on 21 September 1987 and measured 6.1 to 7.6 mm SL ($n=3$). Fish collected at Wachapreague and Sand Shoal Channels were probably better representatives of the age of larvae that enter Virginia nursery grounds because smaller mesh nets (with 3.2-mm mesh liner which sampled smaller larvae more effectively) were used at these stations. The youngest larvae observed at Wachapreague Channel were collected on 29 September 1987 with a mean size and age of 7.3 mm SL and 26 d, respectively, with the youngest individuals (20 d) measuring 5.4 and 6.1 mm SL ($n=2$). The youngest larvae observed at Sand Shoal Channel were collected on 30 September 1987 with a mean size and age of 8.3 mm SL and 29 d, respectively, with the youngest individuals (23 d) measuring 6.1 and 7.3 mm SL ($n=2$). In conclusion, it appeared that the youngest larvae entered Virginian estuaries at an approximate age of 20 to 26 d, measuring 5.4 to 7.6 mm SL.

Hatching-date distributions

Hatching-date distributions indicated a protracted spawning period of 8 months from 5 July 1987 to 10 February 1988 and with 82% of spawning limited to



August through October. Fish spawned earlier in the season are underrepresented in samples because they have experienced greater cumulative mortality than later spawned fish (Campana and Jones, 1992). Estimates of size- and age-specific mortality are needed to predict hatching-date distributions more accu-

rately, and these were not available. However, the result of greater accumulated mortality on early-spawned fish is to minimize the height of the estimated spawning peak. Hence, our results establish a lower bound of 82% of surviving juveniles spawned from August to October.

Growth

Mean growth rates (mean SL divided by mean age) varied from 0.18 mm/d in the MAB to 0.41 mm/d in Chesapeake Bay (Table 1). Furthermore, early-spawned fish experienced considerably faster growth than late-spawned fish (Table 1).

Early-captured larvae grew 37% faster than late-captured larvae for individuals ≤ 15 mm SL and ≤ 80 d (Fig. 4A). Early-captured individuals were larger at age than late-captured individuals because of different growth rates and not because of larger size at

hatching, as indicated by tests of regression coefficients that showed highly significant differences between slopes ($P < 0.001$) but not between intercepts ($P = 0.16$).

Early-spawned larvae grew 39% faster than late-spawned larvae (Fig. 4B), and once these size differences were established, they persisted through the juvenile stage (Fig. 4C). There was a significant difference between slopes ($P < 0.001$) for early- and late-spawned larvae, whereas, early- and late-spawned juveniles experienced similar growth according to tests of regression coefficients ($P = 0.75$). Furthermore,

Table 1

Mean standard length (mm) and standard error (SE), age (d) (SE), and growth rate (mean SL/mean age) for larval and juvenile Atlantic croaker collected in the Middle Atlantic Bight and estuarine waters of Virginia from 21 September 1987 to 10 March 1988 by hatching month, region, and gear type.

Hatching month	Sample size	Mean standard length \pm SE	Mean age \pm SE	Mean growth
Middle Atlantic Bight (MAB) ¹				
Sep	19	7.9 \pm 0.2	43.7 \pm 0.9	0.18
Oct	21	5.8 \pm 0.4	29.7 \pm 1.5	0.20
Seaside Eastern Shore (SES: Wachapreague and Sand Shoal Channel) ²				
Aug	17	13.2 \pm 1.5	41.0 \pm 3.8	0.32
Sep	115	11.0 \pm 0.5	42.7 \pm 1.8	0.26
Oct	6	13.6 \pm 0.8	56.5 \pm 1.1	0.24
Bayside Eastern Shore (BES: Occohannock Channel) ²				
Aug	1	28.3 \pm 0.0	94.0 \pm 0.0	0.30
Sep	32	14.4 \pm 0.7	67.1 \pm 1.2	0.21
Oct	15	11.0 \pm 0.2	57.5 \pm 0.7	0.19
Chesapeake Bay ³				
Jul	7	25.8 \pm 6.5	77.3 \pm 11.2	0.33
Aug	74	28.9 \pm 2.0	70.5 \pm 3.8	0.41
Sep	21	27.8 \pm 3.4	78.4 \pm 8.0	0.36
Oct	21	35.4 \pm 1.7	94.2 \pm 2.7	0.38
Nov	7	20.4 \pm 1.3	71.6 \pm 1.0	0.29
Marshes (Guinea and Tue Marshes) ²				
Jul	10	24.0 \pm 2.4	71.2 \pm 3.0	0.38
Aug	39	16.5 \pm 1.2	48.6 \pm 2.2	0.34
Sep	75	9.8 \pm 0.3	47.0 \pm 2.2	0.21
Oct	4	10.6 \pm 0.6	60.0 \pm 1.0	0.18
Jan	7	12.7 \pm 0.4	54.7 \pm 2.0	0.23
Rivers (York and James River) ³				
Sep	13	48.5 \pm 2.2	124.3 \pm 1.7	0.39
Oct	25	32.1 \pm 2.1	105.3 \pm 2.2	0.30
Nov	28	27.6 \pm 2.0	91.5 \pm 2.8	0.30
Dec	32	31.8 \pm 2.2	89.5 \pm 2.9	0.36
Jan	15	24.4 \pm 1.7	74.4 \pm 1.4	0.33
Feb	1	10.6 \pm 0.0	49.0 \pm 0.0	0.22

¹ Gear type used was oblique 60-cm bongo nets with 505- μ m mesh.

² Gear type used was a 4.9-m lined trawl net with a 6.4-mm mesh and 3.2-mm mesh liner and a 4.9-m unlined net with a 15.9-mm mesh. The lined and unlined nets were towed simultaneously.

³ Gear type used was a 9.1-m lined trawl net with a 15.9-mm mesh and 6.4-mm mesh liner.

early-spawned juveniles were significantly larger (18%) than late-spawned juveniles when mean size was adjusted by age (ANCOVA, $P < 0.001$, Table 2B).

A Laird-Gompertz growth model fitted the entire range of Virginia data well ($r^2 = 0.95$), although variance in size increased with age (Fig. 5). Standard length at hatching ($SL_{(0)}$) estimated from the Laird-Gompertz growth model (Fig. 5) was 2.7 ± 0.3 mm SL and was similar to size-at-hatching estimates for laboratory-spawned Atlantic croaker from the Chesapeake Bay (2.0 mm SL; Middaugh and Yoakum, 1974) and North Carolina (2.4 mm SL; Jones³), but considerably higher than Warlen's (1982) estimate of 0.9 mm SL for wild-captured Atlantic croaker larvae from North Carolina. The rate of exponential decay of the specific growth rate (α) was estimated at 0.0081 ± 0.0012 (Fig. 6). Changes in age-specific growth (A_t , a function of the rate of exponential decay of specific growth in time) indicated that larvae experienced a decline of daily growth rate from 3.2% at day 20 to 2.3% by day 60 (Fig. 6).

Standard length and otolith maximum diameter (OMD) relation

The relation between sagittal OMD and SL was best described by a fourth order polynomial (Fig. 7). A simple linear model also described the OMD and SL relation fairly well ($SL = 13.5$ (OMD) + 4.2, $r^2 = 0.98$); however, there were strong patterns in the residuals. Otolith growth was similar between early-captured (fast growers captured from September to October) and late-captured (slow growers captured from November to March) groups when compared by slope ($P = 0.50$). However, a significant difference was observed between the two groups when otolith size was adjusted for fish size (ANCOVA, $P < 0.001$, Table 3A). Size-adjusted means indicated that otoliths from the early-captured group were almost 13% larger than otoliths from the late-captured group (Table 3B). Plots of individual otoliths showed very little overlap between groups (Fig. 8).

Discussion

Otolith analysis

We were unable to obtain known-age Atlantic croaker to validate the assumption that incre-

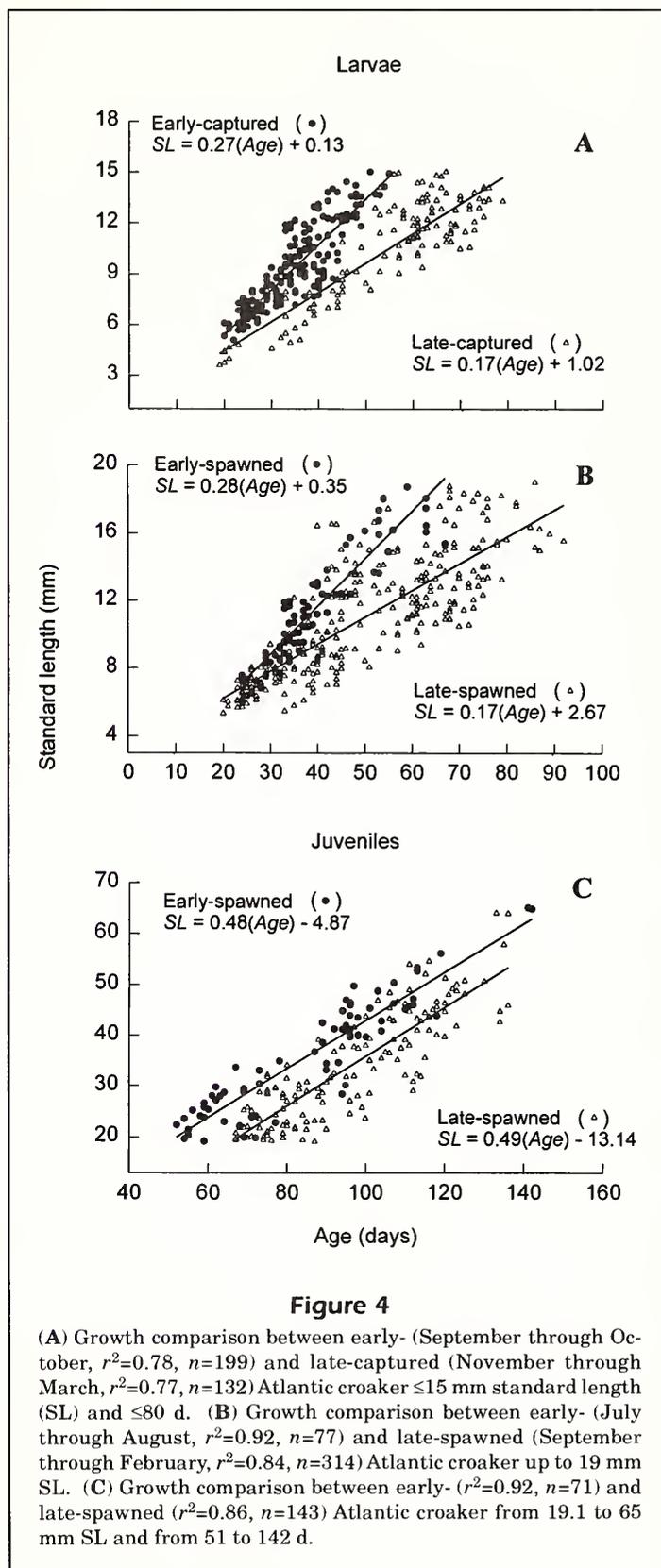


Figure 4

(A) Growth comparison between early- (September through October, $r^2 = 0.78$, $n = 199$) and late-captured (November through March, $r^2 = 0.77$, $n = 132$) Atlantic croaker ≤ 15 mm standard length (SL) and ≤ 80 d. (B) Growth comparison between early- (July through August, $r^2 = 0.92$, $n = 77$) and late-spawned (September through February, $r^2 = 0.84$, $n = 314$) Atlantic croaker up to 19 mm SL. (C) Growth comparison between early- ($r^2 = 0.92$, $n = 71$) and late-spawned ($r^2 = 0.86$, $n = 143$) Atlantic croaker from 19.1 to 65 mm SL and from 51 to 142 d.

³ Jones, C. J. 1995. Applied Marine Research Laboratory, Old Dominion University, Norfolk, VA 23529. Unpubl. data.

ments form daily in larvae. However, daily growth increments have been validated in the otoliths of larval spot, *Leiostomus xanthurus*, a sciaenid relative of Atlantic croaker (Peters et al.²), and we assumed,

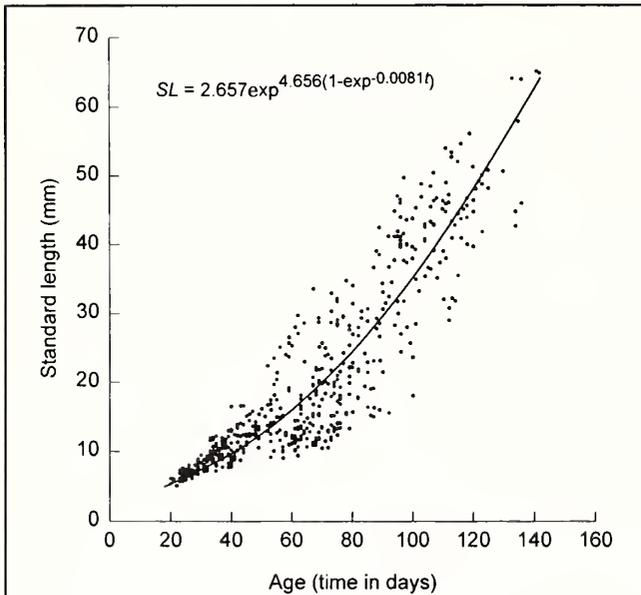


Figure 5

Laird-Gompertz growth model describing growth of Virginia larval and juvenile Atlantic croaker ≤ 65 mm standard length (SL) and ≤ 142 d ($r^2=0.95$, $n=605$).

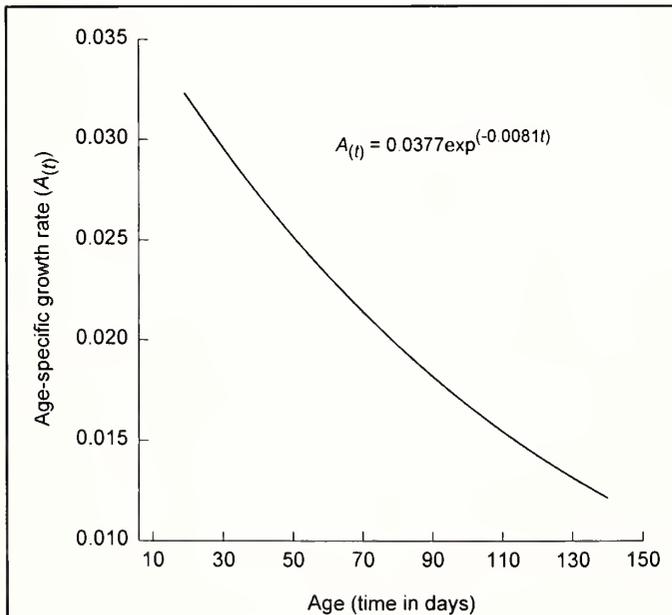


Figure 6

Age-specific growth rate relation determined from the equation $A_{(t)} = A_{(0)} \exp(-\alpha t)$ with $A_{(0)}$ and α from the Laird-Gompertz growth equation (Fig. 2).

therefore, that increment deposition is daily in Atlantic croaker. Peters et al.² also demonstrated that the first daily increment forms in the sagittae of spot at the time of first feeding, which occurs in spot about 5 d after hatching at 18 and 20°C (Powell and Chester, 1985); thus, we added 5 days to our increment counts.

Sagittal otoliths of Atlantic croaker begin to increase growth along their anterior and posterior axes during the late-larval stage, whereas lapilli maintain concentric growth through the juvenile stage, potentially making lapilli preferable when using otoliths to backcalculate growth. In examining the potential for using lapillar counts as a surrogate to sagittal counts, we found under light microscopy that lapillar counts increasingly underestimated sagittal counts as fish increased in age. The microstructure in sagittal otoliths also had better defined increments, leading us to assume that sagittal counts were more accurate predictors of age than lapillar counts. No differences in the size and age counts between left and right sagittal otoliths warranted the replacement of lost or damaged right otoliths with left otoliths.

Size and distribution

Offshore spawning and subsequent estuarine migration of Atlantic croaker have been thoroughly documented by studies with egg and larval size distributions (Hildebrand and Cable, 1930; Wallace, 1940; Haven, 1957; Colton et al., 1979; Morse, 1980; Lewis

Table 2

Growth comparison between early- (July through August) and late-spawned (September through February) Atlantic croaker from 19.1 to 65 mm SL and from 51 to 142 d with an analysis of covariance (ANCOVA) of standard length (SL) of fish (mm), with age (d) as the covariate. Size adjusted means equals the mean SL of fish, adjusted for the effects of age.

A	ANCOVA		
	df	F-value	P-value
Covariate age	1	743.6	$P < 0.001$
Main effect			
Early-spawned vs. late-spawned	1	89.9	$P < 0.001$
Residual sums of squares (d)	5,489.2 (211)		
r^2	0.78		

B		Size adjusted means (mm) (SE)	
Early-spawned:	39.5 (0.6)	Late-spawned:	32.3 (0.4)

Table 3

Otolith comparison between faster-growing early-captured (September through October) Atlantic croaker and slower-growing late-captured (November through March) Atlantic croaker between 11 and 37 mm standard length (SL) with an analysis of covariance (ANCOVA) of the otolith maximum diameter (OMD) of sagittae (mm), with SL of fish (mm) as the covariate. Size-adjusted means equals the mean OMD of sagittae, adjusted for the effects of SL of fish.

ANCOVA			
A	df	F-value	P-value
Covariate standard length	1	1,126.9	$P < 0.001$
Main effect			
Early-captured vs. late-captured	1	36.2	$P < 0.001$
Residual sums of squares (d)			
	1.16 (66)		
r^2	0.95		
B Size adjusted means (mm) (SE)			
Early-captured:	1.54 (0.02)	Late-captured:	1.25 (0.02)

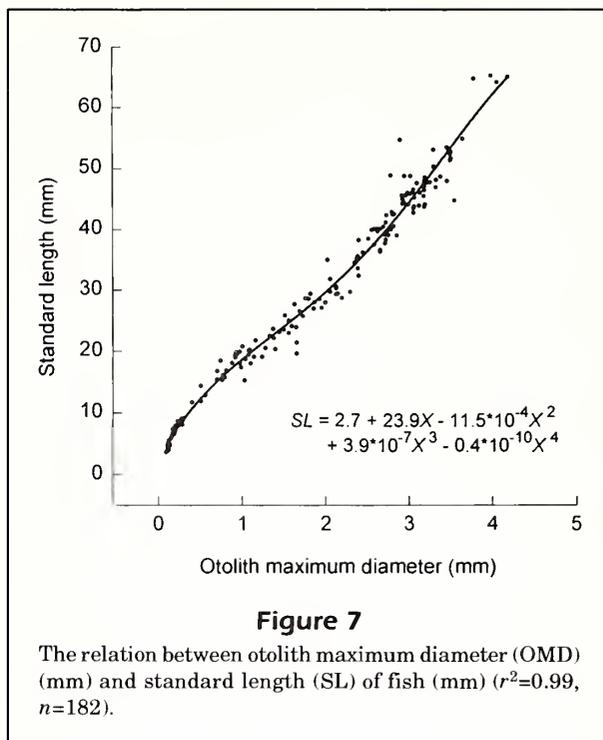


Figure 7

The relation between otolith maximum diameter (OMD) (mm) and standard length (SL) of fish (mm) ($r^2=0.99$, $n=182$).

and Judy, 1983; Warlen and Burke, 1990). However, only two studies (Warlen, 1982; this study) used daily age information from otoliths to support such findings. Daily age information is critical because size-at-age is highly variable in this species, and age-based data provide reliable confirmation of cross-shelf transport of larvae. Warlen (1982) found a general increase in the age of fish entering the Beaufort estuary as the season progressed, and suggested this increase in age was an effect of variable transport distance or rates to the estuary (or both). Seasonal trends observed in this study may be attributed to similar processes.

Mean ages generally increased over time, lagging about 10 d between monthly sampling dates, suggesting constant recruitment over the entire sampling season. However, mean ages in the rivers declined after December. Our samples collected in January along river transects show a gradient of smaller, younger individuals upstream and of larger, older individuals downstream. Bottom waters in the York River experience a winter temperature gradient, with the lowest temperatures occurring in upper reaches of the river (Chao and Musick, 1977; Dameron et al.¹; Land et al.⁴) and the higher temperatures in the Bay mainstem. This bottom water temperature gradient coupled with the increase in size of Atlantic croaker

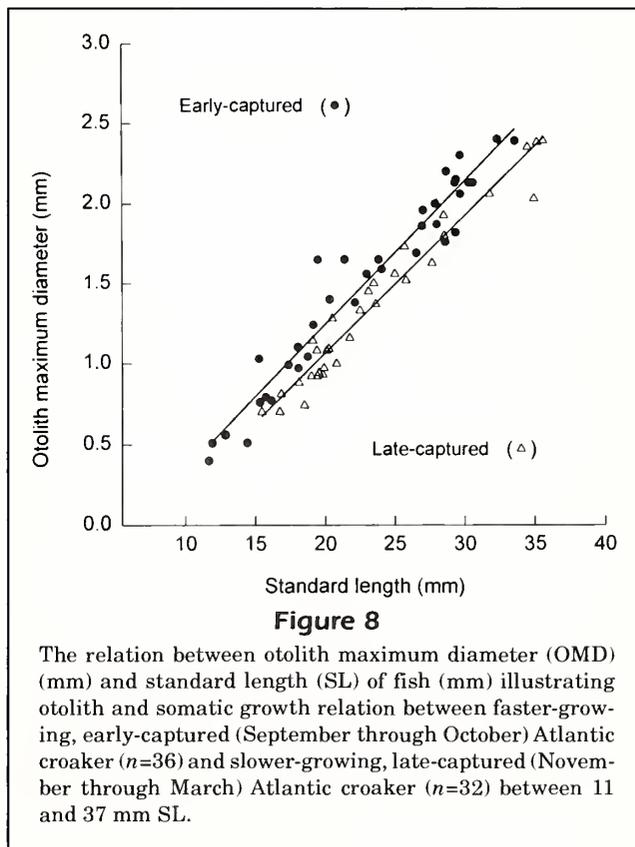


Figure 8

The relation between otolith maximum diameter (OMD) (mm) and standard length (SL) of fish (mm) illustrating otolith and somatic growth relation between faster-growing, early-captured (September through October) Atlantic croaker ($n=36$) and slower-growing, late-captured (November through March) Atlantic croaker ($n=32$) between 11 and 37 mm SL.

⁴ Land, M. F., P. J. Geer, C. F. Bonzek, and H. M. Austin. 1994. Juvenile finfish and blue crab stock assessment program. Bot-

tom trawl survey. Annual data summary report series. Volume 1988. Spec. Sci. Rep. Va. Inst. Mar. Sci., College of William and Mary, Gloucester Point, VA, 171 p.

downstream may indicate movement of larger, older individuals into deeper, warmer waters of the mainstem Chesapeake Bay. Atlantic croaker's sensitivity to low temperatures (Massmann and Pacheco, 1960; Joseph, 1972) may further explain the movement of older and larger fish from the rivers into warmer Bay waters.

Hatching-date distributions

Our estimate of a protracted spawning season from early July 1987 to February 1998, with peak spawning in September, is similar to earlier reports in studies that used the presence of eggs or early larvae to estimate spawning. These studies suggest a protracted spawning period from August through December with peak spawning from August to October (Wallace, 1940; White and Chittenden, 1977; Johnson, 1978; Colton et al., 1979; Morse, 1980; Chittenden et al.⁵). Although our observation that spawning may begin as early as July has not been reported elsewhere, ovaries containing postovulatory follicles recently have been observed in Atlantic croaker from the Chesapeake Bay as early as July (Barbieri et al., 1994). Furthermore, because sexually mature adults do not begin to migrate out of the Chesapeake Bay until early July, and mainly in August and September (Wallace, 1940), limited spawning of Atlantic croaker may occur in proximal coastal waters as suggested by Haven (1957).

Growth

When comparing temporal patterns in growth, it is best to analyze differences between groups by spawning date, rather than by capture date; otherwise older fish are under represented because of their greater accumulated mortality (Campana and Jones, 1992). Temporal growth variability was observed when the data were analyzed both by capture date and spawning date, although a 6% greater difference was observed when the data were analyzed by spawning date.

Seasonal variability in the growth of larval and juvenile Atlantic croaker may result from higher water temperatures or increased food in July and August (or both) (Alden et al.⁶) or from improved

survival of larger, faster-growing fish (Miller et al., 1988; Isley and Grimes, 1996). Hatching dates of faster-growing, early-spawned fish coincided with peak mean surface water temperatures in July and August (26.3° and 26.7°C, respectively; U.S. Department of Commerce⁷) and with peak plankton abundances in the Chesapeake Bay which typically occur in July (Alden et al.⁶). Furthermore, hatching dates of slower-growing fish coincided with increased patchiness and falling plankton abundances which typically begin in September and October (Alden et al.⁶). Warlen (1982) reported similar seasonal growth patterns for North Carolina Atlantic croaker larvae and speculated that slow growth observed in late-captured fish (mid-January to mid-April) might be attributed to colder ocean temperatures and low food availability in mid- to late-winter, or less likely, to smaller egg size of late-spawned larvae.

Recently immigrated larvae collected in Virginia estuaries in this study were larger at age than North Carolina larvae. Monthly mean growth rates (mean SL/mean age) of estuarine collected larvae (26–65 d) in this study ranged from 0.26 to 0.40 mm/d and were considerably higher than weekly mean growth rates (0.16–0.27) for similar age (32–64 d) North Carolina larvae collected in estuarine waters (see Warlen 1982, Table 1). Because this study and Warlen's (1982) were conducted in different years, we cannot eliminate the real possibility that these differences may be temporal, year-to-year changes. Further inter-year studies within Virginia and North Carolina, showing consistent patterns of growth variability, are needed to conclude that there are regional growth differences. However, whether spatial or temporal, or a combination of both, within-season patterns among the two studies are similar, whereas growth rates themselves differ.

Apparently, Atlantic croaker larvae immigrating into estuaries of Virginia and North Carolina can be categorized as early-spawned, fast growers or as late-spawned, slow growers. These seasonal growth differences, coupled with a spatially and temporally extended spawning season suggest that Atlantic croaker encounter variable environmental factors that may affect their survival. Identifying factors that may enhance survival or affect mortality rates of these spatially and temporal explicit groups are of major interest and are worthy of further study.

⁵ Chittenden, M. E., C. M. Jones, L. R. Barbieri, S. J. Bobko, and D. E. Kline. 1990. Initial information on the Atlantic croaker, a final report on development of age determination methods, life history-population dynamics information, and evaluation of growth overfishing potential for important recreational fishes. Final Rep. to Virginia Mar. Res. Comm. VMRC I, Va. Inst. Mar. Sci., College of William and Mary, Gloucester Point, VA, 88 p.

⁶ Alden, R. W., III, R. S. Birdsong, D. M. Dauer, H. G. Marshall, and R. M. Ewing. 1992. Virginia Chesapeake Bay water quality and living resources monitoring programs: executive report, 1985–89. Applied Marine Research Laboratory, Old Dominion University, Norfolk, VA 23529, Report 849, 33 p.

⁷ U.S. Department of Commerce, National Ocean Service, NOAA, Ocean and Lake Level Division Database, Rockville, MD 20874, June 1992.

Standard length and otolith maximum diameter (OMD) relation

We found that in wild-caught larval Atlantic croaker, faster-growing individuals have larger otoliths than similar-size slower-growing individuals. Our results differ from results found for laboratory-reared guppies (*Poecilia reticulata*) (Reznick et al., 1989), pond-reared striped bass (*Morone saxatilis*) (Secor and Dean, 1989), red seabream (*Pagrus major*), and spot (*Leiostomus xanthurus*) (Secor et al., 1989). In these studies, where food ration was controlled, slower-growing individuals had larger otoliths than similar-size faster-growing individuals. However, in Arctic char (*Salvelinus alpinus*), otolith growth rate has been found to continue increasing while somatic growth remains constant when exposed to temperatures above 13°C (Mosegaard et al., 1988). In our study, the early-captured, faster-growing Atlantic croaker, may have experienced otolith growth that exceeded their maximum somatic growth rate.

Unfortunately, there are no quantitative data that can be tested to determine what factors influenced the growth of Atlantic croaker in our samples and what were the subsequent effects on the otolith growth-somatic growth relation. The underlying issue, however, is to examine how the fish and otolith-size relation is affected by temperature responses of somatic growth rate at particular food levels (Mosegaard et al., 1988) and to determine its significance when backcalculating growth from increment widths (Campana and Jones, 1992).

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the senior author in partial fulfillment of the requirement for the M.S. degree, Department of Biology, Old Dominion University, Norfolk, VA 23519.

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Abstract.—Three species of the stromateoid genus *Peprilus* have been found to occur in the northwest Atlantic: *P. triacanthus* (butterfish), *P. burti* (gulf butterfish), and *P. alepidotus* (harvestfish). *Peprilus triacanthus* and *P. alepidotus* reportedly spawn from May through August and June through July, respectively. *Peprilus burti* spawns twice yearly: February through May and September through November. Collections of larvae and juveniles of *Peprilus* spp. from the northern South Atlantic (SAB) and Mid-Atlantic (MAB) Bights during both the spring and summer of 1988 and 1989 suggest that either a combination of species was spawning or that reported spawning dates were suspect. Species identification of *Peprilus* in these collections was determined with morphometric, meristic, and pigment character analyses. Specimens sampled had counts for caudal vertebrae (18–19) and ventral midline melanophores (11–16) consistent with those found for *P. triacanthus* in previous studies. By analyzing otoliths, we estimated larval and juvenile growth rates to be approximately 0.23 mm/day. Backcalculation of hatch dates suggests either two spawning events for *P. triacanthus*, February through mid-April and mid-May through late July, or one extended spawning period beginning in late February and ending in late July. This study reveals that *P. triacanthus* spawns for a much longer period than previously thought. It is possible that *P. triacanthus* spawns during the spring in the SAB and summer in the MAB as a strategy to extend the duration of its spawning period. This strategy is one used by other north-south migrating species and warrants further study.

Temporal and spatial spawning patterns of the Atlantic butterfish, *Peprilus triacanthus*, in the South and Middle Atlantic Bights*

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Three species of the stromateoid genus *Peprilus* (order: Perciformes) are reported to occur in the western North Atlantic: butterfish, *P. triacanthus* (Peck), gulf butterfish, *P. burti* (Fowler), and harvestfish, *P. alepidotus* (Linnaeus). Although the ranges of all three species extend along the eastern coast of North America and the West Indies, there is some question as to which species of *Peprilus* are regular residents in the South Atlantic Bight (SAB) and Mid-Atlantic Bight (MAB) regions (Caldwell, 1961; Haedrich, 1967; Horn, 1970; Perschbacher et al., 1979). This question is extended by the suggestion of possible hybridization between *P. triacanthus* and *P. burti* in the northern portion of the SAB (Horn, 1970; Perschbacher et al., 1979).

Reproduction in *P. triacanthus* and *P. burti* is seasonal and apparently associated with annual migration patterns (Horn, 1970). In the summer and fall, *P. triacanthus* migrates northward and inshore, where it reportedly spawns from late May through August, with a peak in June (Horn, 1970). During winter, *P. triacanthus* migrates offshore and becomes horizontally restricted (Horn, 1970). Movement by *P. burti* is somewhat opposite to that of *P. triacanthus*. *Peprilus burti* migrates offshore during late spring through early fall, then onshore towards shallow bays and inlets dur-

ing the winter and early spring (Horn, 1970). Spawning by *P. burti* is reported to occur during two distinct periods, February through May and September through November (Murphy, 1981). Unlike these other two species, *P. alepidotus* does not exhibit seasonal migration patterns, remaining in shallow waters throughout the year where it spawns during June and July (Horn, 1970).

During the spring and summer seasons of 1988 and 1989, we consistently collected larval and juvenile *Peprilus* from the South Atlantic and Mid-Atlantic Bights. The combination of their location and dates of capture raised the question as to which species were present in our samples. Although most abundant within the MAB region, *P. triacanthus* is reported to spawn during the summer only (Horn, 1970). According to time of capture, the spring-collected larvae in our SAB samples should have been *P. burti* because they were collected before *P. triacanthus* and *P. alepidotus* supposedly begin to spawn (Horn, 1970; Murphy, 1981). However, their occurrence within the South Atlantic and Mid-Atlantic Bights suggests that they were either *P. alepidotus* or *P. triacanthus*. Thus, the overall aim of this study was to identify the species in our samples and to back-

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calculate hatching dates by using validated otolith-increment analysis.

Materials and methods

Collections

Peprilus larvae and juveniles were collected during April and May of 1988 and April of 1989 in the northern SAB, offshore of Cape Hatteras, North Carolina, and June–August of 1988 and 1989 in the MAB, from Long Island, New York, to Cape May, New Jersey (Fig. 1; Table 1).

Fish were collected with a 1-m² Tucker trawl and a 5-m² Frame trawl. The Tucker trawl had three opening-closing 505- μ m mesh nets. Five-minute tows were taken at three primary depth intervals: 0–5 m, 5–10 m, and 10–15 m. For the purpose of this study, all depths were combined. The Frame trawl was fitted with a 2-mm mesh net and towed at the surface for 10 minutes. A flowmeter was attached to each net to estimate the volume of water sampled.

Tucker trawl samples were split in half with a Folsom plankton splitter. One half of each sample was preserved in 5% buffered formaldehyde and used for identification and length and body depth measurements. The other half was preserved in 95% ethanol and used for otolith analysis. Frame samples were preserved in 95% ethanol. Samples were sorted in the laboratory with a dissecting microscope for eggs, larvae, and juveniles.

Morphometrics

Determination of a seasonal difference in body size was accomplished by analyzing body depth (BD) and standard length (SL) for all specimens collected. Measurements were made to the nearest 0.1 mm with either a video-enhanced digitizing system (Optical Pattern Recognition System, BIOSONICS, Inc.) or an ocular micrometer. Standard length was measured from tip of the snout to the tip of notochord. Body depth was measured perpendicular to the longitudinal body axis at the anterior margin of the pectoral base (Ditty, 1981).

To examine differences in body depth between spring and summer seasons, linear regressions of body depth on standard length were calculated for Tucker and Frame cruises, 1988 and 1989. Slopes of regression lines were tested for homogeneity. Allometric effects of growth on body depth were examined

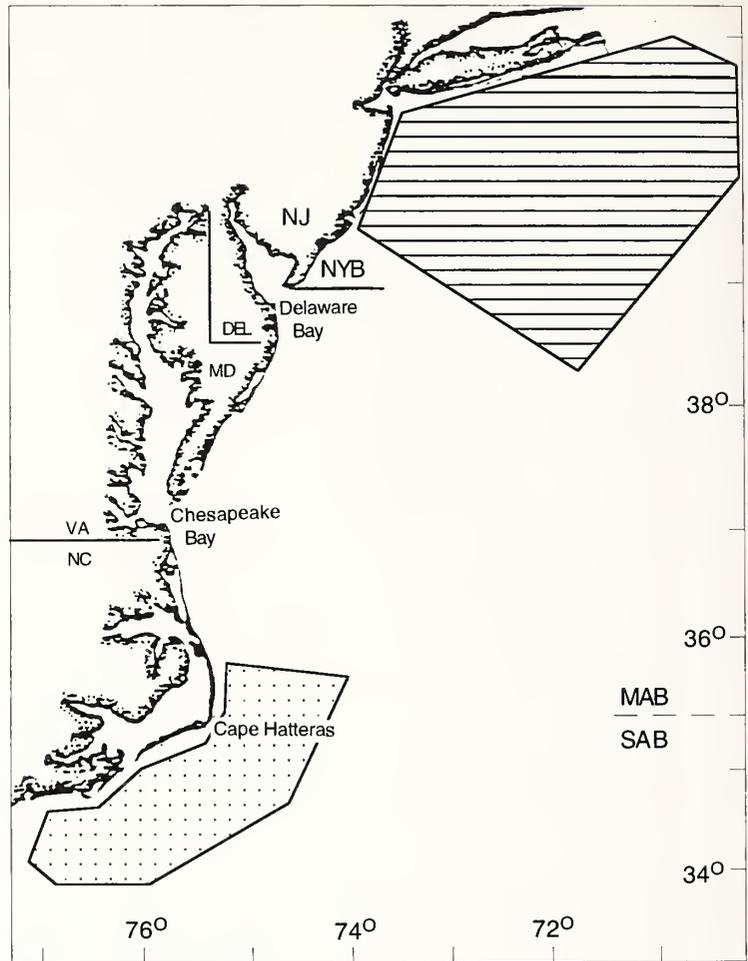


Figure 1

Study area from Cape Hatteras, North Carolina, to Long Island, New York. Dotted and barred areas represent spring and summer sampling areas, respectively.

by calculating regressions of body depth on standard length as a function of standard length.

Meristics

To determine the species composition of the spring- and summer-collected *Peprilus* larvae, two meristic characters were examined: number of caudal vertebrae and number of ventral midline melanophores. Character counts were compared with published data for each of the three possible species (caudal vertebrae: Ditty, 1981; ventral midline melanophores: Ditty and Truesdale, 1983). Subsamples of specimens were either cleared and stained (Taylor, 1967; Wassersug, 1976; Dingerkus and Uhler, 1977; Potthoff, 1984) or x-rayed (Gosline, 1948; Miller and Tucker, 1979; Tucker and LaRoche 1984; Kosenko et al., 1987). Photomicrographs of cleared and stained specimens were taken and slides developed for further

Table 1

List of 1988 and 1989 cruises, sampling dates, number of fish collected, and locations. SAB = South Atlantic Bight; MAB = Mid-Atlantic Bight.

Net	Cruise	Date	No. of fish captured	Location	
1988	Frame	DEL88-5-2	24 April–1 May	71	SAB
		ATLANTIC TWIN	21 May–23 May	29	SAB
		DEL88-7-1	1 June–3 June	3	MAB
		DEL88-7-2	11 June–16 June	22	MAB
		DEL88-7-3	6 July–9 July	4	MAB
		DEL88-7-4	16 July–22 July	99	MAB
		DEL88-7-5	29 July–2 August	50	MAB
		DEL88-7-6	8 August–12 August	110	MAB
	Tucker	DEL88-7-3	6 July–9 July	188	MAB
		DEL88-7-4	16 July–22 July	1,191	MAB
		DEL88-7-5	29 July–2 August	514	MAB
		DEL88-7-6	8 August–12 August	1,063	MAB
	1989	Frame	FE1-89	25 April–29 April	158
ONR1-89			30 May–2 June	8	MAB
ONR2-89			6 June–7 June	4	MAB
FE2-89			7 July–10 July	2	MAB
ONR4-89			18 July–2 August	22	MAB
ONR5-89			14 August–18 August	170	MAB
Tucker		FE1-89	25 April–29 April	201	SAB
		FE2-89	7 July–10 July	445	MAB
		ONR4-89	18 July–2 August	89	MAB
		ONR5-89	14 August–18 August	146	MAB

inspection. Fish were x-rayed with a Kodak Faxitron at settings of 40 kilovolts, 20 milli-amperes and 30 seconds, which gave the best results with Kodak Industry X negatives. These negatives were placed in a Kodak GBX developer and replenisher solution for 2 to 3 minutes, rinsed in water, placed in a Kodak GBX fixer solution for 5 minutes, rinsed for 15 minutes in water, and dried overnight. Caudal vertebrae were counted with the aid of a dissecting scope and included those vertebrae attached to the first fully formed hemal spine and extending to the urostyle (Gosline, 1960).

Caudal vertebrae counts were made for larvae selected to cover the range of sizes (all were larger than 7 mm, the size at which Ditty (1981) found most fish to have adult characters), body depth-standard length ratios (shallow and deep-bodied), and dates of capture (spring and summer) encountered. Caudal vertebrae were counted for a subsample of 34 cleared-and-stained fish and 64 x-rayed fish from the 1988 Frame trawls and 76 x-rayed fish from the 1989 Frame trawls.

Ventral midline melanophores were counted for a subsample of 50 fish (25 from the spring and 25 from the summer) smaller than 4 mm SL (the size at which Ditty based his observations). These fish were randomly chosen from 1989 formalin-preserved collections. Ventral midline melanophores were considered to be those located between the hindgut and notochord tip (Ditty, 1981).

Otolith marking experiment

Otoliths of 22 fish were marked with oxytetracycline hydrochloride (OTC) in August of 1991 to determine if *Peprilus* larvae and juveniles deposit daily rings. Sizes of fish ranged from 10 to 31 mm SL. Fish were acclimated for two days in a five-gallon bucket with built-in screening that allowed water to flow-through the bucket when it was placed in an aerated seawater bath. Fish were fed twice daily with either live *Artemia* nauplii or live field-captured zooplankton during both acclimation and experimental periods. Experimental conditions were maintained as follows: temperature fluctuated between 12°C and 24°C, salinity ranged from 28 to 30‰, pH varied from 7.6 to 8.0 (however, during marking the pH dropped to 6.5 and 6.6), and the photoperiod remained constant at a 14-h light and 10-h dark cycle.

The marking procedure followed those for mass-marking larvae and juveniles (Hettler, 1984; Tsukamoto, 1985; Muth et al., 1988). Briefly, fish were immersed in a 450 mg/L concentration of OTC for a six-hour period. Fish were covered during the marking period to decrease the amount of light because light may interfere with the effectiveness of tetracycline (Secor et al.¹). While immersed in the marking solution, four fish died. The remaining 18 fish were transferred from the marking solution and placed inside

two five-gallon screened buckets. Two additional fish died during the transfer process. Fifteen of the remaining 16 fish survived until the end of the experiment. At four days after marking, four fish were sacrificed. An additional four fish were sacrificed five days after marking. Three fish were sacrificed eight days after marking.

To add a second mark, the remaining four fish were immersed a second time (12 days after the initial marking) and were fed amphipods and brine shrimp that had been immersed in a 450mg/L OTC seawater solution for five hours. These fish were held and fed in a fresh 450 mg/L concentration of OTC for 16 hours. Ten days after the second immersion the remaining four fish were sacrificed.

All specimens were placed in 95% ethanol for preservation. Otoliths were dissected from fish and placed in immersion oil on glass slides. Otoliths were ground with a size-600 carborundem grit and mineral oil slurry. The tetracycline mark was viewed under a Zeiss ultraviolet microscope with a Zeiss FITC acridine-orange excitation filter set. Increments were counted blindly by one reader, a minimum of three times. If the number of increments between counts differed by more than one, the otolith was not used. The number of increments present after the mark was regressed against the number of days since marking; the regression coefficient was compared with unity by using a *t*-test.

Otolith ageing

Otolith ageing was performed to determine a length-age relationship for our combined *Peprilus* spp. samples. The presence of daily increments in temperate and tropical water fishes has been noted by Pannella (1971, 1974). Fish fixed and preserved in 95% ethanol and ranging in size from 6 to 28 mm SL were aged from 1988 spring ($n=30$) and summer ($n=33$) samples to determine seasonal growth rates. Sagittae and lapilli were removed from each fish following the techniques of Brothers (1984). Otoliths were placed in type-B immersion oil and left to clear for one month. Sagittae were analyzed with a video-enhanced digitizing system (Optical Pattern Recognition System) viewed at 250 \times with an oil immersion lens.

Increments were counted blindly by one reader a minimum of two times. If counts differed between

readings by more than three increments, they were not used. Counts were made along the longest radial axis whenever possible (Brothers, 1980). When otoliths were too thick to see increments clearly, they were ground with size-600 carborundem grit and immersion oil to create thinner sections (Brothers, 1980).

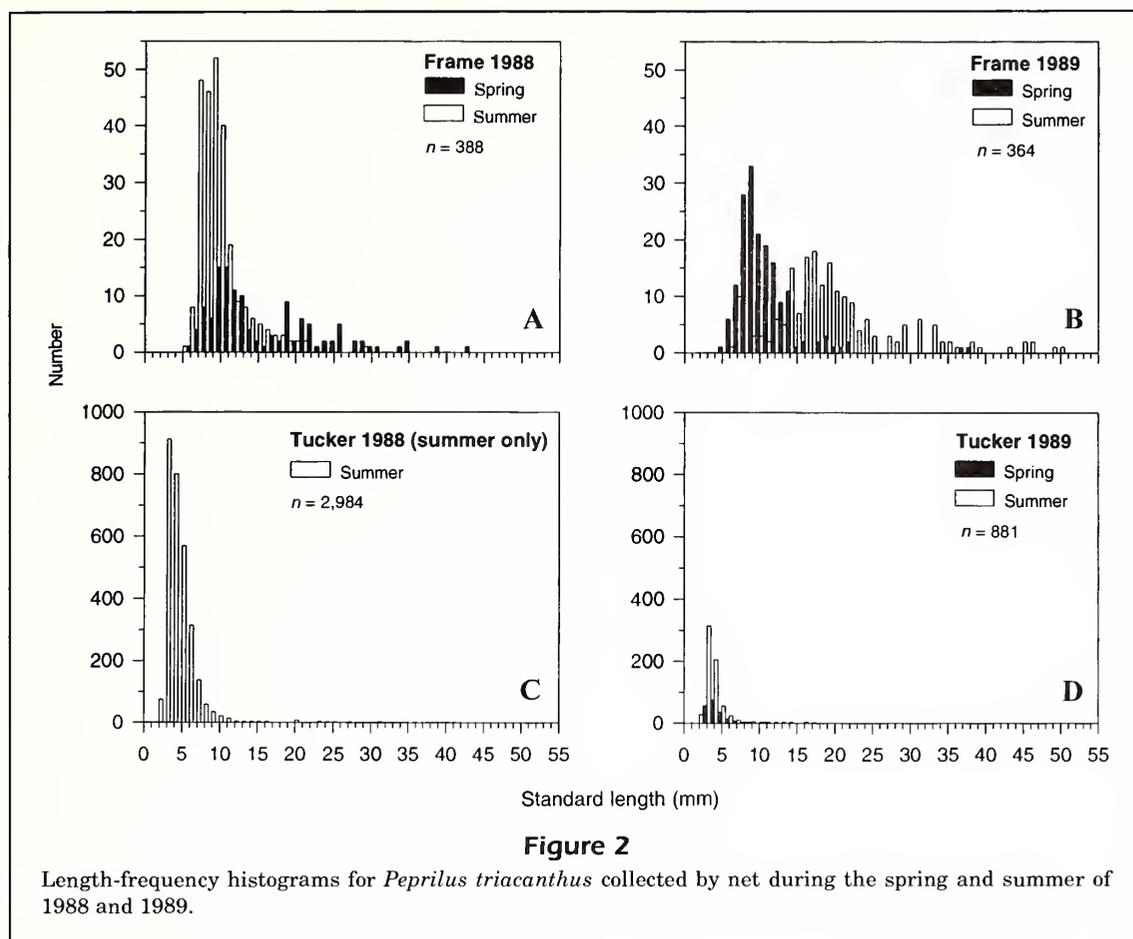
A length-at-age relationship was determined by regressing standard length on age. Because most fish deposit increments on their otoliths either at hatching or yolk-sac absorption (Brothers et al., 1976), a y-intercept of hatch size (1.72 mm; Colton and Honey, 1963) was assigned to the regression. The slope of the spring regression, i.e. growth rate, was compared with the slope of the summer regression by means of a homogeneity of slopes test. To determine date of hatching, an age-on-length relation was first determined. The y-intercept for this equation was determined by the best fit of the data. This regression equation was solved for age by using standard lengths of all 1988 and 1989 Tucker- and Frame-caught fish (size range of 6.0–28.0 mm SL). Hatching dates were backcalculated by subtracting age at capture from the capture date. Hatching date distributions were then plotted to determine spawning date distributions for all 1988 and 1989 Frame-trawl-caught and Tucker-trawl-caught butterfish.

Results

Collection

During 1988, 3,980 *Peprilus* were collected in the Tucker trawl (4 cruises; 196 hauls), and 388 in the Frame trawl (8 cruises; 404 hauls). In 1989, 880 Tucker-trawl-caught (4 cruises; 128 hauls) and 364 Frame-trawl-caught (6 cruises; 158 hauls) *Peprilus* were collected. In 1988, the greatest number of larvae and juveniles were caught in Tucker trawls in the MAB, July ($n=1,191$; 24.3 per haul) through mid-August ($n=1063$; 21.7 per haul). There were no Tucker trawl collections during the spring of 1988 in the SAB. The highest numbers of *Peprilus* were collected in 1989 cruises from mid-July through early August in the MAB ($n=445$; 17.8 per haul). In general, the number of fish collected in the Frame trawl was less than in the Tucker trawl. In the 1988 Frame trawls, *Peprilus* were most numerous during late May ($n=29$; 1.8 per haul) in the SAB and from mid-July ($n=99$; 2.0 per haul) through mid-August ($n=110$; 2.2 per haul) in the MAB. Frame trawls for 1989 had the greatest abundances of larvae during late April ($n=158$; 4.3 per haul) in the SAB and from mid-July through early August in the MAB ($n=170$; 4.4 per haul).

¹ Secor, D. H., E. D. Houde, and D. M. Monteleone. 1995. Development of otolith-marking methods to estimate survival and growth of early life stages of natural and hatchery-produced striped bass in the Patuxent River in 1991. Maryland Department of Natural Resources, Chesapeake Bay Research and Monitoring Division, CBRM-GRF-94-1, 145 p.



Morphometrics

A wide range of sizes of *Peprilus* were collected during both seasons of 1988 and 1989. Because size-frequency distributions had the same mode on all cruises within a season, length frequencies were combined for all fish sampled with a particular gear during each season each year. Spring-collected 1988 fish ranged in size from 6 to 43 mm SL (Frame; Fig. 2A). Similar size distributions of fish were found for the 1989 spring cruises: 4.7 to 37.5 mm SL (Frame; Fig. 2B) and 2 to 6 mm SL (Tucker; Fig. 2D). The 1988 summer trawls collected fish between 5 and 29 mm SL (Frame; Fig. 2A) and 1.3 to 36.0 mm SL (Tucker; Fig. 2C). Summer 1989 fish ranged in size from 6.0 to 50.0 mm SL (Frame; Fig. 2B) and 1.7 to 49.0 mm SL (Tucker; Fig. 2D).

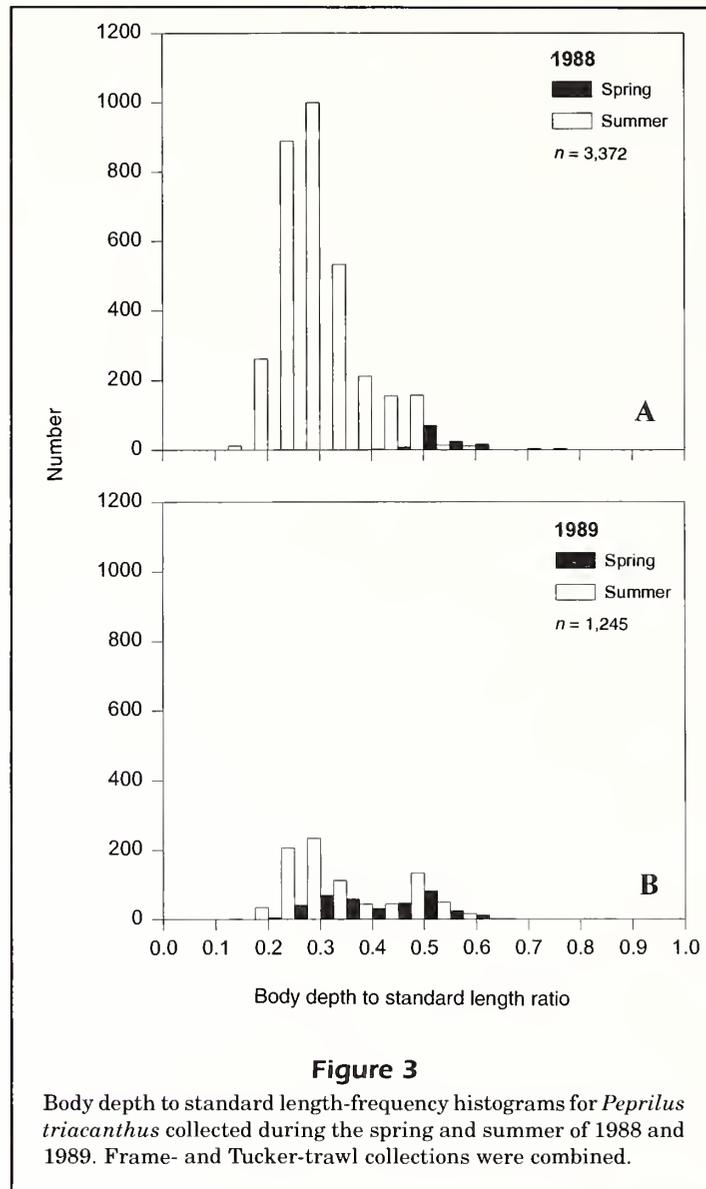
Deep- and shallow-bodied fish were identified from both the spring and summer samples in both years. Fish had BD:SL ratios ranging from 0.119 to 0.750 (Fig. 3, A and B). There was an indication of two modes during both spring and summer of 1989. These BD:SL ranges overlap with ranges reported by Horn (1970) and Ditty (1981) for all species (Table 2). Further analysis of body depth: standard length demon-

strated that body depth increases allometrically with respect to standard length up to a size of 10 to 15 mm SL (Fig. 4). Body depth subsequently remained about 50% of length for each year.

Meristics

Ninety-nine percent of the fish collected with the Frame net in 1988 and 1989 had either 18 or 19 caudal vertebrae (of those, approximately 90% had 19 caudal vertebrae; Table 3). Counts of either 18 or 19 caudal vertebrae are consistent with those reported for *P. triacanthus* (Table 3). The number of caudal vertebrae was not related to body depth. According to Ditty and Truesdale (1983), juvenile *P. burti* and *P. alepidotus* have mean body depth-standard length ratios of greater than 0.557 and caudal vertebrae counts of 17–18. However, our findings indicate that fish with high body depth-standard length ratios also had 19 caudal vertebrae.

The fish we sampled had between 8 and 16 ventral midline melanophores. Ditty (1981) reported ranges of 4 to 8 ventral midline melanophores for *P. burti* and 11 to 17 for *P. triacanthus*. Seventy-six percent of our speci-



mens sampled had 11 to 17 ventral midline melanophores, and 94% had 10 to 16 melanophores. These data suggest the presence of *P. triacanthus* in our samples. On further analysis of pigment patterns, we found no difference among specimens (Rotunno, 1992). These data corroborate our caudal vertebral counts.

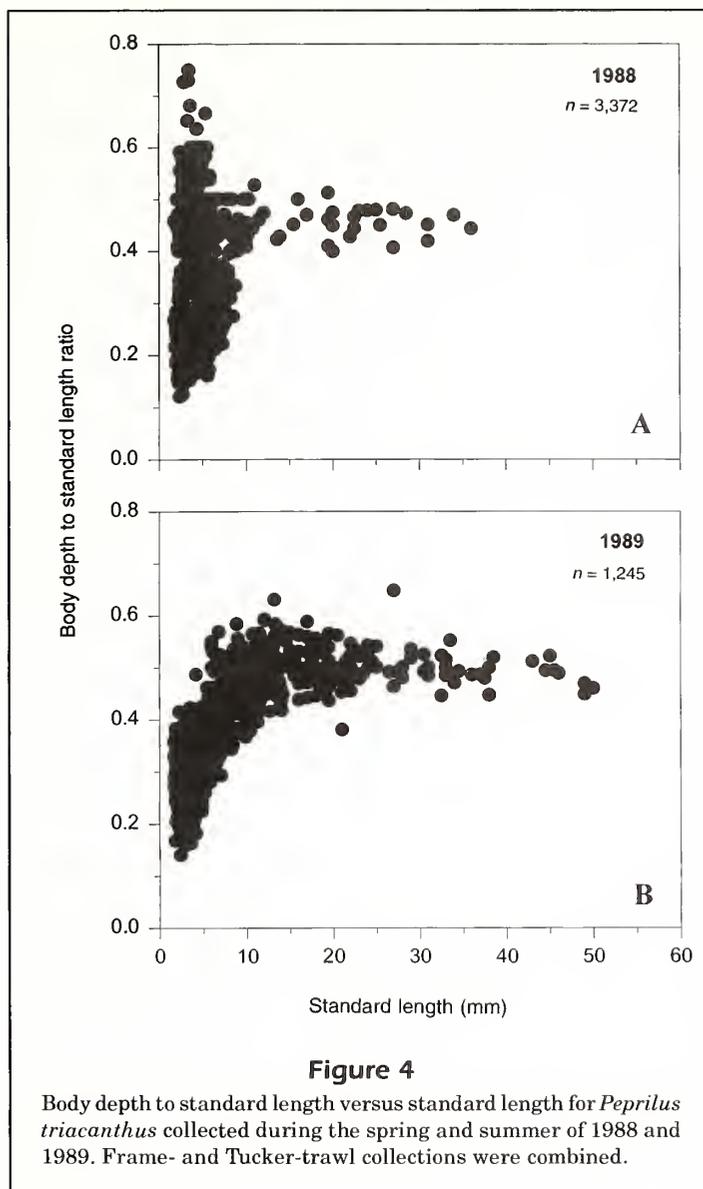
Otolith marking experiment

Daily increment formation was a valid indicator of age of *Peprilus* spp.. The presence of subdaily increments was also noted in these otoliths. The number of increments observed after the tetracycline mark regressed against the number of days since marking showed a 1:1 correspondence (Fig. 5). A y-intercept value of zero was assigned to the regression. The

slope of the regression (0.921) did not differ significantly from unity (t -test: $t=0.82$, $P=0.42$).

Growth and hatching date

Spring and summer growth rates were estimated from 1988 collections of *Peprilus* at 0.233 mm/day and 0.219 mm/day, respectively. These growth rates were not significantly different ($F=2.071$, $P=0.155$). Therefore, seasons were combined and an overall regression was computed that yielded an average growth rate of 0.225 mm/day (Fig. 6). The regression equation ($Age = 3.433(SL) + 8.270$, $r^2=0.93$) was used to backcalculate hatching dates from length frequencies. This age-length relation was also applied to 1989 collections for back-calculation purposes.

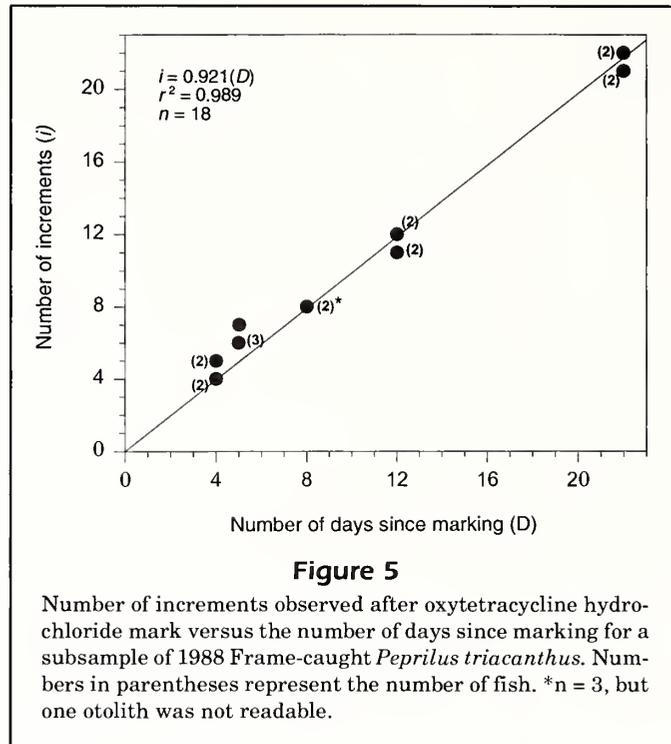


Hatching for *P. triacanthus* in our samples occurs from February through at least July and appears to be concentrated in two peaks that occur during early spring and summer (Fig. 7, A and B). The earliest hatching date recorded for fish caught in 1988 was 19 January 1988 and the latest was 22 July 1988. The winter-spring spawning appears to begin in January and continue through late April, with an apparent peak in March in the SAB (Fig. 7A). A decrease in spawning occurs at this time, although some spawning continues at a low level through May (Fig. 7A). Spring-summer spawning occurs during June and July in the MAB with a peak in late June. The relative strength of these two spawnings is not clear because sampling effort was not equivalent during each season.

Fish caught in 1989 had a similar spawning pattern to that of fish collected in 1988; the earliest hatching date calculated was 14 February 1989, the latest was 29 July 1989 (Fig. 7B). Spawning peaks occurred in late March to early April in the SAB and early to mid-June in the MAB. There appears to be a reduction in spawning during the month of May along the U.S. Atlantic coast.

Discussion

Peprilus triacanthus is the most common species of *Peprilus* found along the Atlantic coast of the United States. Within the New York Bight, spawning and larval presence for *P. triacanthus* is reported to oc-

**Table 2**

Body depth-standard length ratios reported by Horn (1970), Ditty and Truesdale (1983), and from our Frame and Tucker trawl surveys.

	Body depth-standard length range	Standard length range (mm)	n
Horn (1970)			
<i>P. burti</i>	0.460–0.640	7.80–167.00	232
<i>P. triacanthus</i>	0.364–0.600	10.60–198.00	202
<i>P. alepidotus</i>	0.565–0.877	18.22–222.00	205
Ditty (1981)			
<i>P. burti</i>	0.241–0.579	2.16–19.82	160
<i>P. triacanthus</i>	0.235–0.546	2.04–20.86	159
<i>P. alepidotus</i>	0.205–0.750	1.85–18.92	80
1988 and 1989 Frame and Tucker			
Spring	0.187–0.750	2.01–43.00	496
Summer	0.119–0.727	1.29–50.00	4,121
Spring and Summer	0.119–0.750	1.29–50.00	4,617

cur during summer only (Wilk et al., 1990). Fahay (1975) suggested however, on the basis of the range of larval lengths collected in 1967–68, that spawning of *P. triacanthus* may occur throughout the year in the SAB. The occurrence of larval and pelagic juvenile *Peprilus* within our spring samples collected in the northern SAB suggests two possible scenarios:

1) a species other than the most commonly found *P. triacanthus* spawns within the Atlantic (e.g. *P. burti*) or 2) *P. triacanthus* or *P. alepidotus* has a more protracted spawning season than previously thought. *Peprilus* larvae and juveniles in our samples proved to be *P. triacanthus*; therefore, our results demonstrate an extended spawning period for *P. triacanthus*

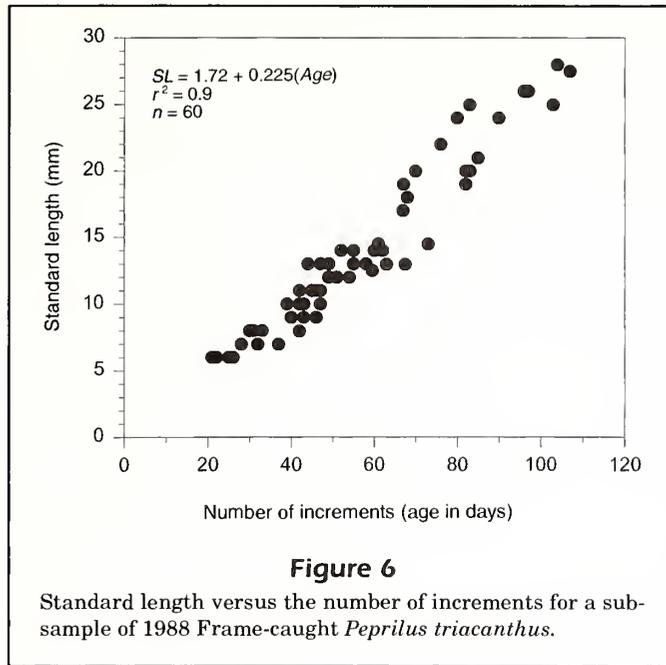


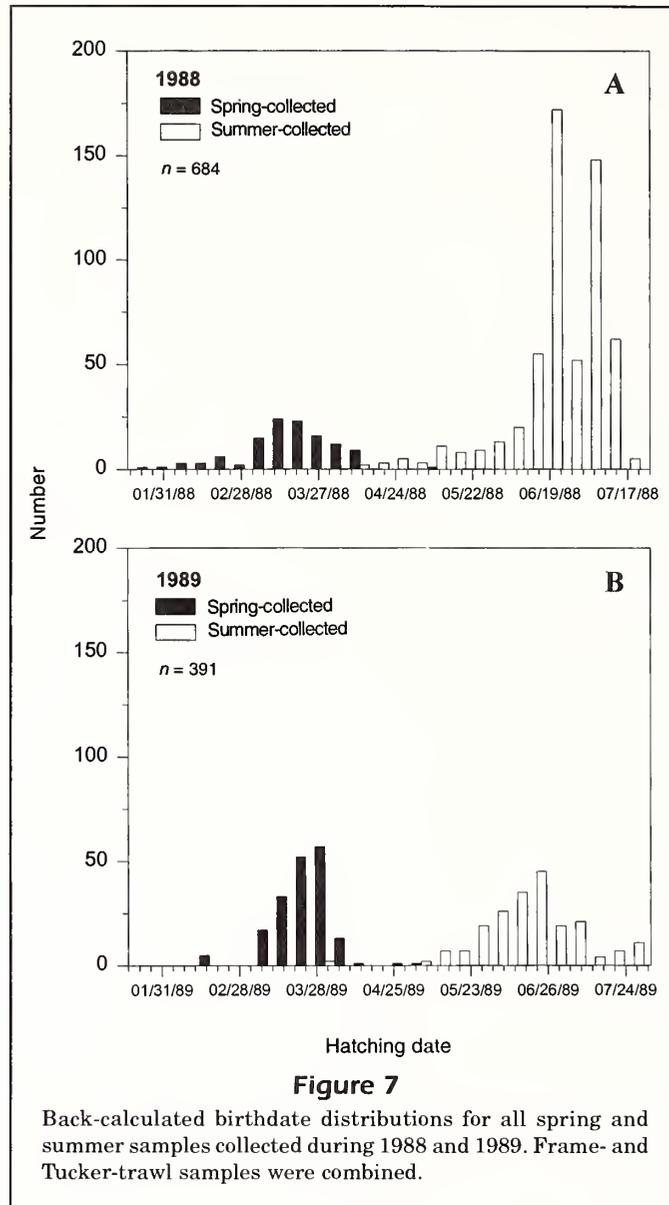
Table 3

Vertebral counts for *Peprilus* collected by Collette (1963), Horn (1970), Ditty (1981), and in this study (Frame).

	Standard length (mm) range	16	17	17-18	18	18-19	19	20	n
Collette (1963)									
<i>P. burti</i>	—	2	92	0	2	0	0	0	96
<i>P. triacanthus</i>	—	0	4	0	36	0	138	2	180
Horn (1970)									
<i>P. burti</i>	6.0-115.0	5	262	0	6	0	0	0	273
<i>P. triacanthus</i>	6.0-115.0	0	7	0	62	0	208	2	279
<i>P. alepidotus</i>	6.0-115.0	3	176	0	3	0	0	0	182
Ditty (1981)									
<i>P. burti</i>	7.14-14.45	0	13	9	0	0	0	0	22
<i>P. triacanthus</i>	7.14-14.73	0	0	0	1	8	10	0	19
<i>P. alepidotus</i>	7.74-11.01	0	5	0	0	0	0	0	5
Frame									
Spring 1988	8.0-26.0	0	0	0	4	0	48	0	52
Summer 1988	8.0-26.0	0	1	0	6	0	39	0	46
Spring 1989	8.52-37.5	0	0	0	2	0	28	0	30
Summer 1989	8.0-38.0	0	0	0	6	0	39	1	46
Total Frame	8.0-38.0	0	1	0	18	0	154	1	174

in the Atlantic. According to back-calculated hatching dates, *P. triacanthus* spawns from late January through at least July. We did not observe any seasonal differences in body depth. However, geographic

differences in body depth need to be further analyzed before discounting the existence of either a polymorphic *P. triacanthus* or a hybrid of *P. triacanthus* and *P. burti*.



Species identification

According to the reported ranges of body depth-standard length ratios (Horn, 1970; Ditty and Truesdale, 1983), our larval specimens could have been any one of the Atlantic or Gulf coast species of *Peprilus*. However, two points must be considered when interpreting these data. First, we found a strong allometric relation between body depth and standard length for individuals smaller than 15 mm SL. Because the collections of Horn (1970) include fish ranging in size from 6 to 222 mm SL, this allometric relation could have confounded his conclusions. Ditty and Truesdale (1983), however, apparently recognized this problem and therefore presented their data by size class. Sec-

ond, our other analyses (caudal vertebrae and melanophore counts) supported the contention that *P. triacanthus* was the dominant species of *Peprilus* in our samples. Our sample was predominantly composed of individuals with 19 caudal vertebrae, which was consistent with findings of previous authors for *P. triacanthus* (Collette, 1963; Horn, 1970; Ditty and Truesdale, 1983). The ventral midline melanophore counts were also similar to those used for *P. triacanthus* by Ditty (1981).

The overall results of the above morphometric, meristic, and pigment analyses lead us to conclude that *P. triacanthus* is the dominant and probably the only species of *Peprilus* collected in our samples. The two most definitive characters for identification were

the number of caudal vertebrae and ventral midline melanophores.

Age and growth

Ages of larval and juvenile *P. triacanthus* can be determined by counting otolith increments. Validation was necessary because of the prevalence of subdaily increments in this species. Secondary nuclei (multinucleation) were also noted in *Peprilus otoliths*. The cause and timing of the formation of secondary nuclei are not presently understood (Campana and Neilson, 1985), although these secondary nuclei have been demonstrated to form during metamorphosis in bluefish (Hare and Cowen, 1994). Secondary nuclei, in butterfish otoliths, do not seem to follow a consistent pattern in the development of the fish; we found that two sagittal bones from one fish frequently contained differing numbers of secondary nuclei. Although secondary nuclei may form during metamorphosis (Campana and Neilson, 1985; Hare and Cowen, 1994), we found secondary nuclei in larvae that were several millimeters smaller than the size at which metamorphosis occurs (16 mm).

Larval and early juvenile *P. triacanthus* from 6.0 to 28.0 mm SL grew at a rate of 0.227 mm/day. Although ages of young butterfish have not been recorded previously, Colton and Honey (1963) gave sizes of *P. triacanthus* from hatching to six days of age. Based on their estimates, growth rates ranged from 0.01 to 0.55 mm/day and decreased with the age of the fish. Specimens of young *P. burti* have been aged with modal length-frequency analysis; growth rates of *P. burti* ranged from 0.25 to 0.56 mm/day (Murphy and Chittenden, 1990). *Peprilus burti* may be expected to have a higher growth rate than *P. triacanthus* owing to the fact that it spawns in warmer waters of the Gulf of Mexico.

Our analysis of hatching-date distributions demonstrated that *P. triacanthus* has a more extensive spawning season than previously reported. Their spawning effort seems to be focused into two cohorts (spring: February–March; and summer: June–July) although evidence is presented that suggests at least some fish spawn during the interim period between seasonal peaks (i.e. late April to early June). Kawahara² speculated that *P. triacanthus* may begin spawning in April. It should be noted that Kawahara (1977) based his spawning estimate on adult growth

rates, which are higher than our estimate for larvae and juveniles and, therefore, would have underestimated the spawning duration.

A bimodal hatching-date distribution in *P. triacanthus* is similar to that reported for another north-south migrating species within the western Atlantic, the bluefish, *Pomatomus saltatrix* (Kendall and Walford, 1979; Nyman and Conover, 1988). However, Hare and Cowen (1993) and Smith et al. (1994) have proposed that *P. saltatrix* spawns continually during its north-south migration and that the apparent bimodal hatching date distribution may result from advective processes acting on the larval distributions and from sampling artifact.

The presence of an apparent bimodal spawning in *P. triacanthus*, with spring and summer peaks, may be an artifact of our sampling. Because we did not sample from April to June in each year and because our sampling locations were spatially distinct between spring and summer, it is possible that we did not collect larvae spawned during May and early June. However, we could have collected older fish in our samples that were spawned early in June. Data collected monthly by the National Marine Fisheries Services (NMFS) as part of their Monitoring, Assessment, and Prediction (MARMAP) surveys suggest that larvae are indeed present from April to August in the MAB, thus it is likely that spawning occurs continually (Fig. 8). Moreover, MARMAP data indicate a northward progression of larvae from near Cape Hatteras during March or April (or both) into the entire MAB by mid-summer and until October. This spatio-temporal pattern is consistent with the possibility of spawning associated with a seasonal northward migration of adult *P. triacanthus*. Horn (1970) has speculated that butterfish movements are highly influenced by temperature (and salinity to a lesser degree). Temperature-related movements by butterfish (and bluefish) would correspond with the observed northward progression of young larvae from the SAB in the spring into the MAB in the summer in association with seasonal warming. The extent of north-south migration by *P. triacanthus*, however, requires further study.

In conclusion, this study adds to our current knowledge of the early life history and spawning seasonality of butterfish, *P. triacanthus*. Our finding of a more protracted spawning season and of a seasonal difference between spawning locations should be of value in reassessing management plans for this species. Current management plans are based on conclusions that *P. triacanthus* spawns during summer months only. The apparent similarity of spawning periodicity of butterfish to that of bluefish (Cowen et al., 1993; Hare and Cowen, 1994, Smith et al., 1994) suggests

² Kawahara, S. 1977. Age and growth of butterfish, *Peprilus triacanthus* (Peck), in ICNAF Subarea 5 and Statistical Area 6. ICNAF Res. Doc. 77/VI/27. June 1977 Annual Meeting. Far Seas Fishery Laboratory, Shimizu, Japan.

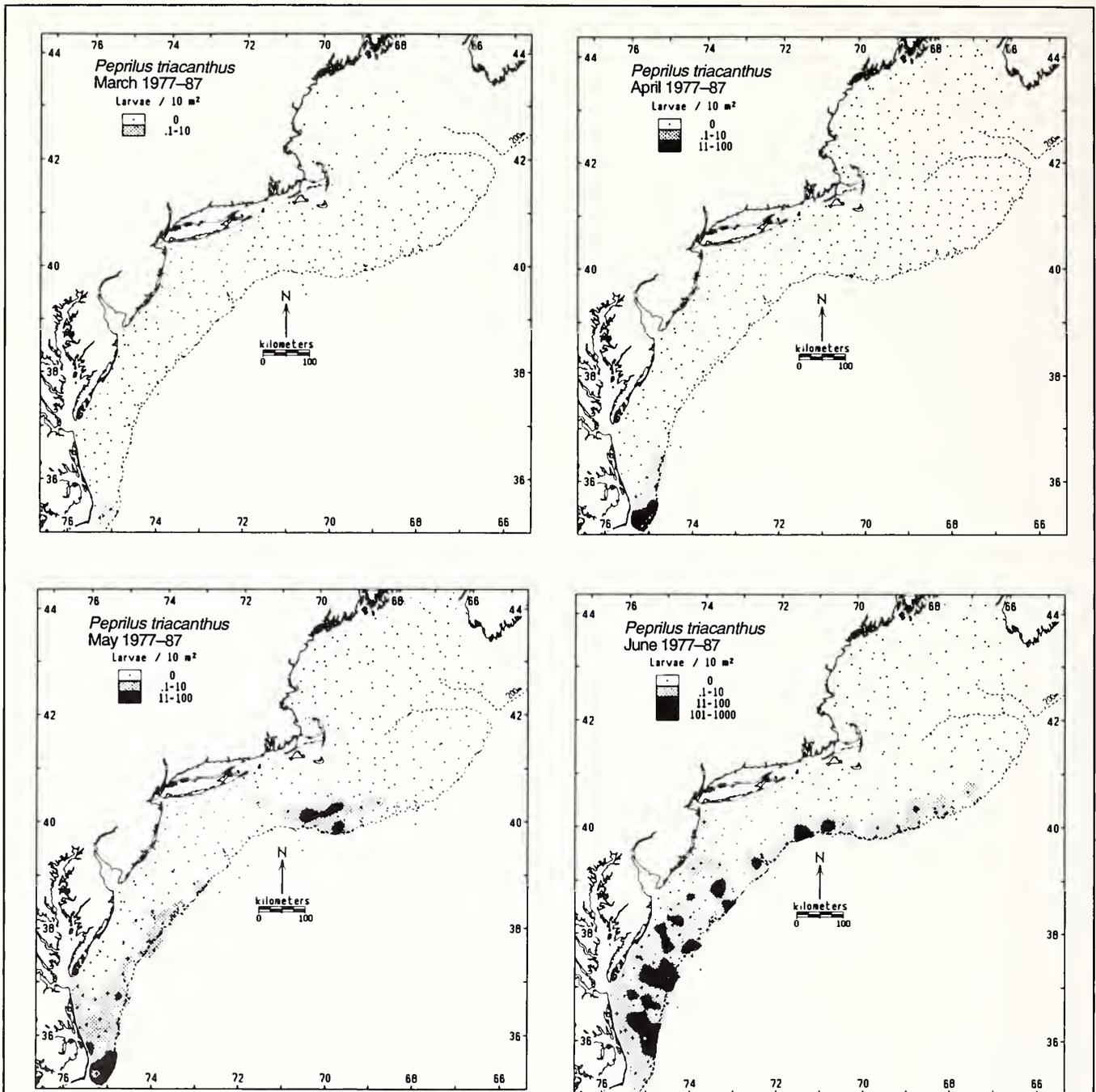


Figure 8

MARMAP monthly averaged collections (March through October) of larval *Peprilus triacanthus* during the years (1977-87).

that a possible adaptive strategy may be shared by these two seasonally migrating pelagic species. Perhaps with closer inspection, other seasonally migrating species may be found that share this spawning strategy (Hare and Cowen, 1996). Further study into the basis of this pattern is warranted.

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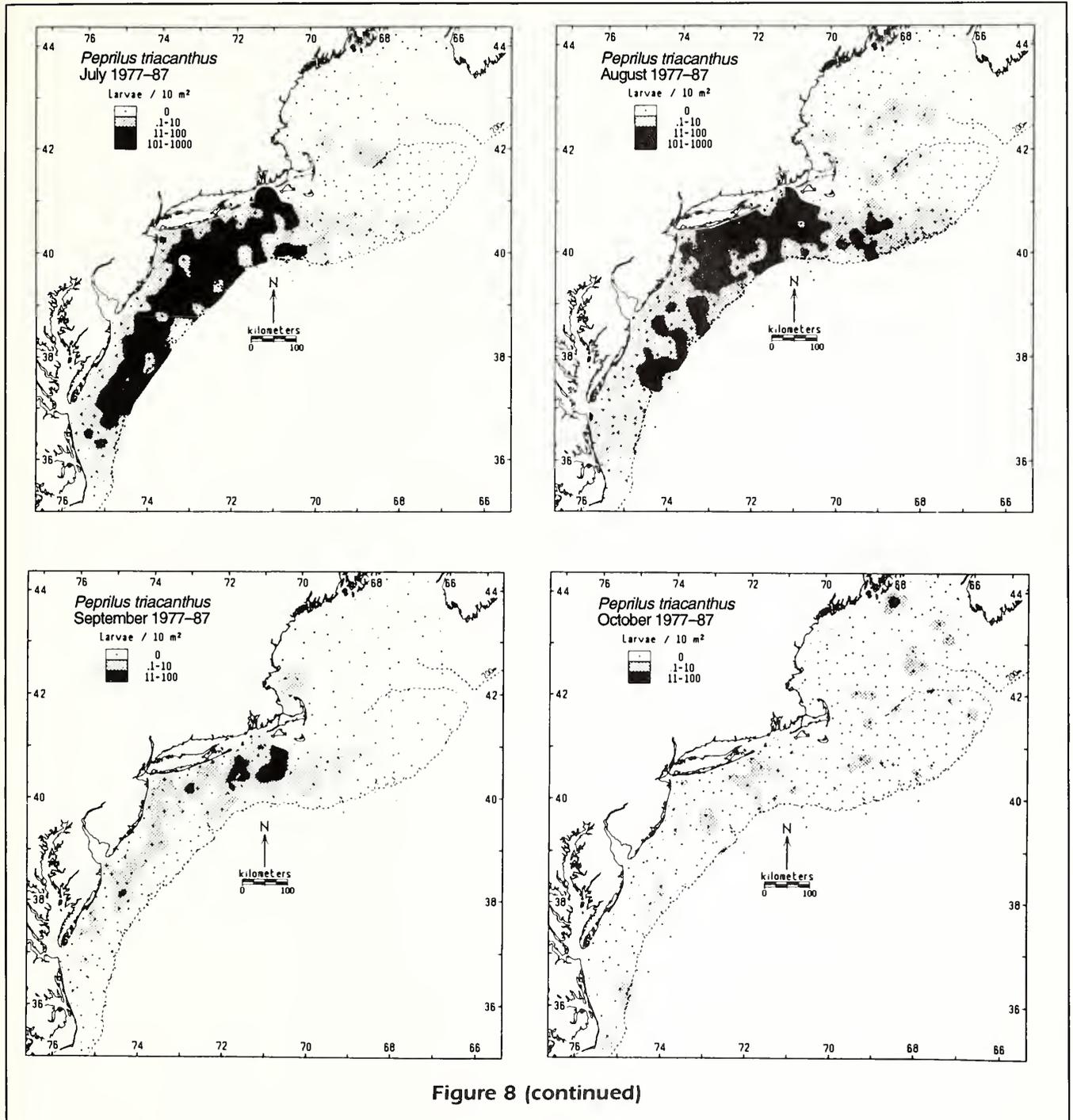


Figure 8 (continued)

and two anonymous reviewers. Jon Hare provided help with all phases of larval identification and otolith analysis. Mike Fahay generously provided Figure 8. This work is a result of research sponsored by the NOAA Office of Sea Grant, U.S. Department of Commerce, under Grants #NA86AA-D-SG045 and #NA90AA-D-SG078 to the New York Sea Grant Institute.

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Abstract.—Three types of genetic markers were used to determine genetic relations among four spawning populations of orange roughy off New Zealand. Eleven allozyme loci were tested in starch and cellulose acetate gels. Restriction fragment length polymorphisms were tested in two regions of the mitochondrial DNA amplified with the polymerase chain reaction. Random amplified polymorphic DNA (RAPD) products were generated with 10-base oligonucleotide primers and separated in agarose gels. There was a significant heterogeneity among all four populations, at 5 out of 11 allozyme loci, at 2 of 29 RAPD primer fragments, and in the frequency of mtDNA haplotypes. There was no significant difference between the two northern spawning populations for any marker, but there were significant differences between all other pairwise population comparisons with allozymes and RAPD's, indicating the presence of three genetic stocks. The mtDNA analysis revealed less genetic subdivision than did allozymes and RAPD's.

A comparison of three genetic methods used for stock discrimination of orange roughy, *Hoplostethus atlanticus*: allozymes, mitochondrial DNA, and random amplified polymorphic DNA

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The orange roughy, *Hoplostethus atlanticus*, is a deepwater species with wide distribution in the Atlantic, Indian, and South Pacific Oceans. Around New Zealand the species supports a fishery which peaked at 50,000 tons per annum in the mid 1980's but which has subsequently declined owing to quota restrictions. There are several geographically isolated spawning populations of orange roughy which are the major targets of fishing within the New Zealand Exclusive Economic Zone (EEZ).

A basic prerequisite of fisheries management is the identification of production units or stocks of a species; inadequate knowledge of stock structure may lead to over- or under-exploitation. Orange roughy occur at depths of about 1,000 m and therefore tag and release studies to estimate movements between areas are impracticable. There have been several other approaches to stock identification of orange roughy with differing results. Studies of parasite distribution (Lester et al., 1988), morphometric characters (Linkowski and Liwoch, 1986; Haddon and Willis, 1995), and trace element composition of otoliths

(Edmonds et al., 1991) have demonstrated regional subdivisions in Australasian orange roughy. An allozyme study revealed a high level of genetic variation but only marginally significant differences between the fishing areas around New Zealand (Smith, 1986). Genetic evidence for discrete stocks off South Australia and eastern Australia based on an allozyme survey (Black and Dixon¹) was not supported by a larger-scale study (Elliott and Ward, 1992). Restriction fragment length polymorphism (RFLP) analyses of mitochondrial (mt)DNA have indicated genetic subdivision of orange roughy around Australia (Smolenski et al., 1993) and New Zealand (Smith et al., 1996).

The development of the polymerase chain reaction (PCR), which amplifies DNA, enables genetic analyses to be carried out on small tissue samples and provides a range of methods for the population biolo-

¹ Black, M., and P. I. Dixon. 1989. Population structure of orange roughy (*Hoplostethus atlanticus*) in Australian waters. Internal Report, Centre for Marine Science, University of New South Wales, Kensington, Australia, 22 p.

gist without need for cloning and sequencing. PCR amplification of specific regions of mtDNA and digestion with restriction enzymes (PCR-RFLP) has been used as a fisheries tool for the differentiation of various fish species (Chow et al., 1993; Chow and Inoue, 1993) and for stock identification of albacore tuna (Chow and Ushiyama, 1995), anchovies (Bembo et al., 1995), and salmonids (Cronin et al., 1993; Hall and Nawrocki, 1995; O'Connell et al., 1995; Hansen and Loeschcke, 1996). Mitochondrial DNA is maternally inherited and has a higher evolutionary rate relative to protein coding loci (Brown, 1983) and consequently has become a useful stock discrimination tool.

Random amplified polymorphic DNA (RAPD) uses PCR to amplify fragments of DNA with primers with random nucleotide sequences (Welsh and McClelland, 1990; Williams et al., 1990). Most fisheries applications of RAPD's have been at the species level (Dinesh et al., 1993; Bardakci and Skibinksi, 1994; Takagi and Taniguichi, 1995), although Macaranas et al. (1995) used RAPD's to distinguish populations of the freshwater red claw crayfish, *Cherax quadricarinatus*, in northern Australia, and a population specific RAPD

marker was found in the marine shrimp *Penaeus vannamei* (Garcia et al., 1996).

In this paper we used three methods (allozymes, mtDNA, and RAPD's) to determine the genetic relations among orange roughy collected from four spawning sites off the east and south coasts of New Zealand.

Materials and methods

Tissue samples were collected on the RV *Tangaroa* from four spawning sites off the east and south coasts of New Zealand (Fig. 1). These sites were chosen because they are isolated by distances beyond the likely limit of larval drift (Zeldis et al., 1994). Each site supports significant fisheries, although the Waitaki fishery is relatively small and has declined quickly since development in the early 1990's (Annala and Sullivan²). Heart, liver, and muscle tissues were dis-

² Annala, J. H., and K. J. Sullivan. 1996. Report from the fishery assessment plenary, April–May 1996: stock assessments and yield estimates. Unpubl. Rep., Ministry of Fisheries, Greta Point Library, Wellington, New Zealand.

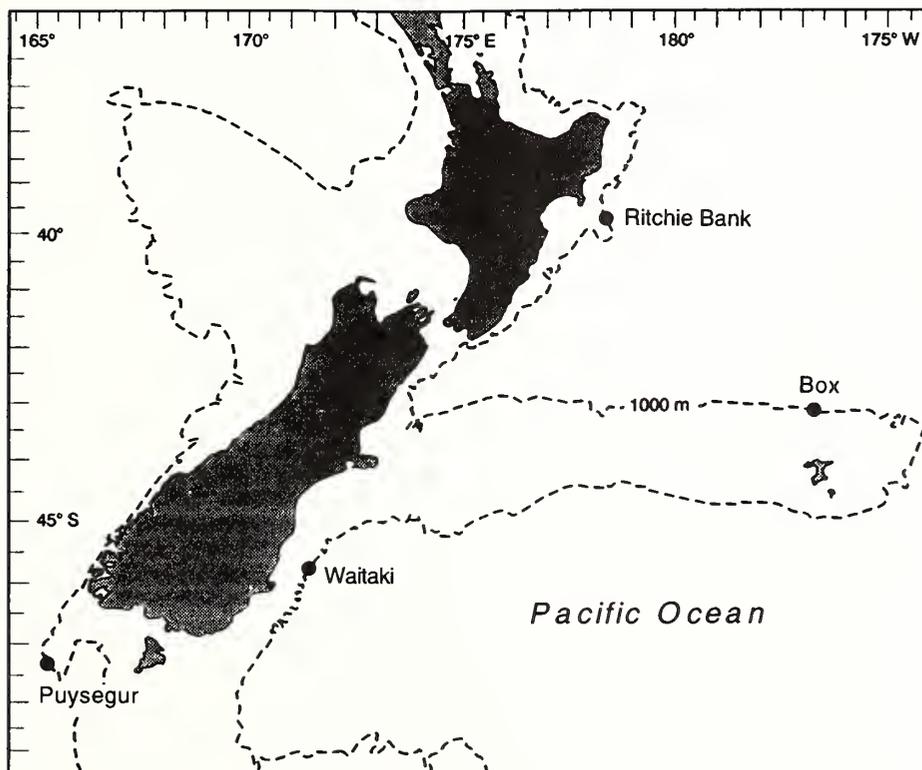


Figure 1

Location of orange roughy spawning sites around New Zealand sampled for genetic analyses. The dotted line represents the 1,000-m isobath.

sected from 100 specimens at three sites and from 50 specimens at Waitaki (Fig. 1). Tissue samples were frozen in liquid nitrogen at sea and stored at -70°C in the laboratory.

Allozyme electrophoresis

Eight enzyme systems were tested in heart, liver, and muscle tissues of orange roughy with cellulose acetate and starch gel electrophoresis following the methods in Smith (1986), except that BDH (British Drug House Chemicals Ltd, Poole, England) starch was substituted for ElectroStarch (ElectroStarch Company, USA).

DNA extraction

DNA was extracted from liver tissue of 50 orange roughy from each site. For each sample, 0.5 g of tissue was homogenized with 750 μL 4M guanidinium isothiocyanate in 8M urea and 2% sodium dodecyl sulfate (SDS) (Turner et al., 1989). DNA was extracted by mixing with an equal volume of phenol chloroform and centrifugation at 13,000 rpm for 5 min. The phenol-chloroform extraction was repeated and the aqueous fraction mixed with an equal volume of chloroform-isoamyl alcohol (24:1). Following centrifugation at 13,000 rpm, the aqueous fraction was mixed with two volumes of ethanol and the DNA allowed to precipitate at -20°C overnight. The DNA pellet was washed in 70% ethanol, air dried, and re-suspended in 40 μL of sterile deionised water.

mtDNA amplification and restriction enzyme digestion

Three primer pairs were used to amplify the mtDNA. Amplification reactions were performed in 50- μL volumes in a Perkin Elmer Cetus DNA thermocycler: protocols followed those of Palumbi et al. (1991) and Cronin et al. (1993). The nucleotide sequences of the primers were the following:

D-loop	5'-ATAGTGGGGTATCTAATCCCA-3' 5'-RCRCCCAAAGCTRRRRRTTCTA-3' (Palumbi et al., 1991);
cytochrome <i>b</i>	5'-CCCTCAGAATGATA- TTTGTCTCA-3' 5'-TGACCTGAARAACCA- YCGTTG-3' (Palumbi et al., 1991); and
ND 5/6	5'-AATAGTTTATCCA- GTTGGTCTTAG-3' 5'-TTACAACGATGGTTTTTCA- TAGTCA-3' (Cronin et al., 1993)

Twelve restriction endonucleases recognizing 4-base sites (*Bfa* I, *Bst* U I, *Cfo* I, *Hae* III, *Hpa* II, *Mse* I, *Msp* I, *Nla* III, *Rsa* I, *Sal* I, *Sau* 3A, and *Taq* I) were used to digest the D-loop primer amplification products. Eleven restriction endonucleases recognizing 4-base sites (*Alu* I, *Bfa* I, *Cfo* I, *Hpa* II, *Msp* I, *Nar* I, *Rsa* I, *Sal* I, *Sau* 3A, *Taq* I, and *Tru* I) were used to digest the cytochrome *b* primer amplification products. The ND 5/6 primers produced between 1 and 3 amplification products in different specimens, therefore no restriction digests were undertaken with the PCR products.

For each primer pair and restriction enzyme, 24 fish were tested, 6 from each area. The restriction enzymes that showed polymorphisms were used to test 50 fish from each site. The amplified and digested DNA products were separated in 1.4% agarose gels and detected with ethidium bromide under a UV light (312 nm).

RAPD amplification and separation

Six individuals from each sample site were amplified with 24 RAPD primers. Each sample was amplified separately with a 10-base oligonucleotide primer from Operon (Operon Technologies, Alameda, CA). These primers were randomly selected from Operon series A, D, E, and H primers, but all have a G+C content of 60–70%. Amplification reactions were performed in 50- μL volumes in a Perkin Elmer Cetus DNA thermocycler. Serial dilutions of DNA samples were tested initially to determine optimum DNA concentration for amplification (Fig. 2). The DNA concentration in each sample was estimated fluorometrically and appropriate volumes were used for amplification. Each reaction contained approximately 50 ng DNA in 10 mM Tris HCl (pH 8.3), 30 ng single 10-base primer, 50 mM KCl, 2 mM MgCl_2 , 100 mM each of *dATP*, *dCTP*, *dGTP*, and *dTTP*, and 1 unit *Taq* DNA polymerase in Perkin Elmer PCR buffer. The reaction was overlaid with mineral oil and amplified. The thermocycler was programmed for 40 cycles of 1-min duration at 94°C , 1 min at 36°C , and 2 min at 72°C . Amplification products were separated in 1.4% agarose gels and detected with ethidium bromide staining under a UV light (312 nm). A DNA size-ladder was included in each gel. Control samples were amplified without a DNA template. Those primers that yielded variable fragment patterns were retested in the same fish. Primers producing repeatable fragment patterns in the initial six fish from each site were tested in 50 fish from each site. Polymorphisms were scored by the presence or absence of an amplification product at specific positions in the gel.

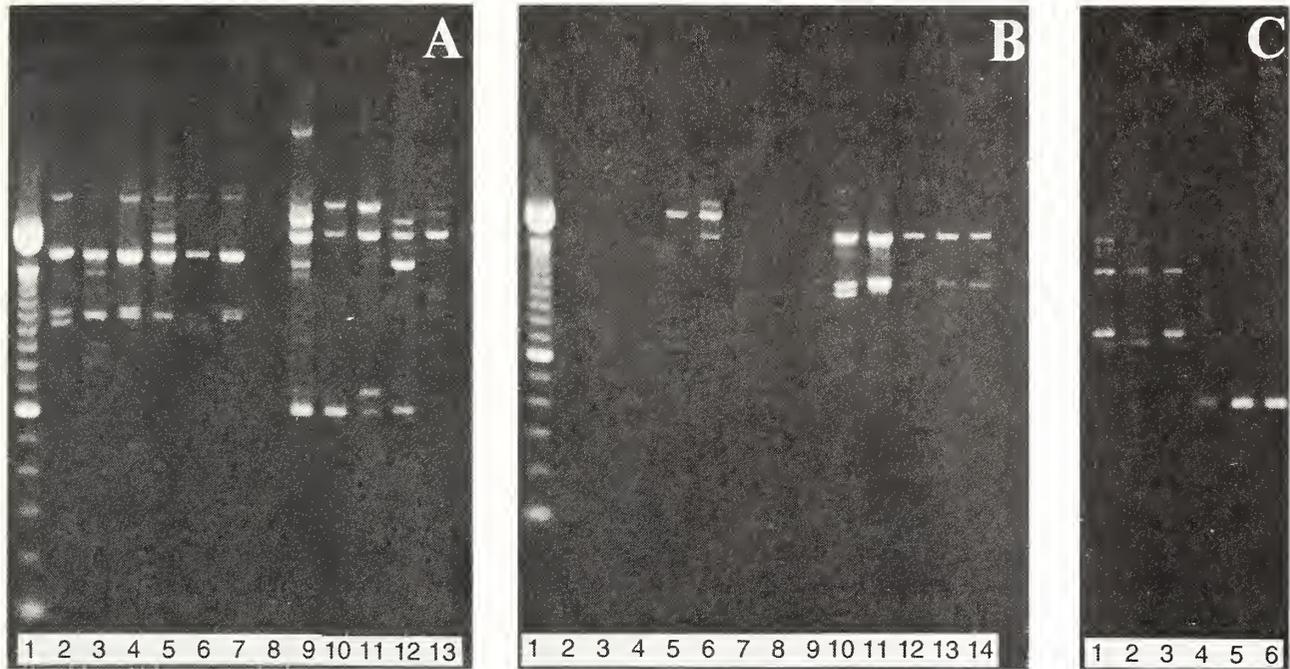


Figure 2

(A) Random amplified polymorphic DNA (RAPD) profiles in orange roughy generated with the primers A16 and E19. Lane 1 contains a DNA size-ladder (2,072–100 bp), lanes 2–7 represent orange roughy amplified with primer A16, lane 8 contains no DNA template, and lanes 9–13 represent orange roughy amplified with primer E19. Each amplified sample of orange roughy contained approximately 50 ng of DNA. (B) RAPD profiles in orange roughy generated with the primers A16 and E19 at different concentrations of DNA template. Lane 1 contains a DNA size-ladder (2,072–100 bp), lane 2 no DNA, lanes 3 and 4 contain 12.5 ng DNA amplified with E19, lanes 5 and 6 contain 50 ng DNA amplified with E19, and lanes 7 and 8 contain 200 ng DNA amplified with E19, lane 9 no DNA, lanes 10 and 11 contain 50 ng DNA amplified with A16, and lanes 12–14 contain 200 ng DNA amplified with A16. (C) RAPD profiles in orange roughy generated with the primer A14, lanes 1–3 contain 50 ng DNA, and lanes 4–6 represent the same samples at a concentration of 200 ng DNA.

Statistical analyses

Allozyme genotypes Genotypic frequencies were tested for Hardy-Weinberg equilibrium; weakly polymorphic loci (frequency of most common allele >0.95) were excluded. Rare heterozygotes were pooled with their nearest electrophoretic neighbor to reduce the number of cells with less than five observations. Allele frequencies were tested for heterogeneity among populations with contingency χ^2 tests with the BIOSYS software program (Swofford and Selander, 1981). To test for geographic structure, contingency χ^2 tests were undertaken on all pairwise combinations of populations. Probability levels were modified by the Bonferroni procedure for multiple tests according to Rice (1989).

The proportion of allozyme variation due to differentiation among populations was estimated with Nei's gene-diversity statistic G_{ST} (Nei, 1973), which is a multiallele estimator of Wright's F_{ST} statistics (Wright, 1951). Gene diversity is equal to

$$(H_T - H_S)/H_T,$$

where H_T = the total genetic diversity of all populations; and

H_S = the mean genetic diversity per population, calculated from the average expected heterozygosities.

Sampling error will produce differences in allele frequencies, even when samples are drawn from the same population, therefore a randomization test was used to test for differences due to sampling error (Elliott and Ward, 1992). One thousand randomizations were used, and the probability was estimated from the number of randomizations that were equal to or greater than the observed G_{ST} .

Gene diversity, G_{ST} , allows an estimation to be made of the number of migrants exchanged between populations per generation from the relation

$$N_e m = (1/G_{ST} - 1)/4,$$

where N_e = the effective population size; and
 m = the rate of gene flow per generation.

It is assumed that $m \ll 1$ and that population differentiation is due to genetic drift and migration with no selection. Gene diversity was corrected to a "true" estimate by subtracting the G_{STnull} due to sampling error, derived from a randomization test (Elliott and Ward, 1992).

mtDNA Heterogeneity in haplotype frequencies in the total data was tested by the χ^2 randomization test described by Roff and Bentzen (1989) with the REAP package (McElroy et al., 1992). This method overcomes the problem of a large number of observed haplotypes at low frequency, by comparing χ^2 values in 1,000 random rearrangements of the data. In addition the χ^2 randomization test was applied to pairwise comparisons of all populations to test for geographic structure. Probabilities were estimated from the number of randomizations that were equal to or greater than the observed χ^2 value. The proportion of haplotype variation due to differentiation between populations was estimated by G_{ST} from the haplotype frequencies, as for allozymes. The number of migrants exchanged per generation was estimated from the relation

$$N_e m_f = (1/G_{ST} - 1)/2,$$

where m_f = female migration, modified to account for the maternal inheritance of mtDNA.

RAPD Standard genetic calculations are not immediately applicable to RAPD data because the fragments are dominant: individuals carrying two copies of an allele cannot be distinguished from individuals carrying one copy of the allele. Black (1995) has provided a set of programs for analyzing RAPD population data but points out that a number of assumptions have to be made. First, the observed fragments are dominant alleles and the absent fragments are recessive alleles. Second, the genotypes are in Hardy-Weinberg equilibrium and each observed polymorphism is biallelic: all the absent observations are produced by the same recessive allele and all the present observations are produced by a single dominant allele with or without the recessive allele. Each primer was scored for the presence or absence of fragments in the gel. Each fragment, regardless of primer, was treated as an independent locus. In most RAPD studies, fragments have been found that vary in staining intensity; we scored only fragments that were intensely stained, following Black (1993).

Random amplified polymorphic DNA allele frequencies were calculated from the presence or ab-

sence observations with the RAPDBIOS software program (Black, 1995) and then used in the BIOSYS software program (Swofford and Selander, 1981) for calculation of heterogeneity in allele frequencies as for allozyme data. The gene-diversity statistic G_{ST} ($=F_{ST}$) was calculated with the RAPDFST software program (Black, 1995); probabilities were calculated according to Workman and Niswander (1970). An estimation of the number of migrants exchanged per generation, $N_e m$, was estimated as for the allozyme data.

Results

Allozymes

Eleven enzyme loci were resolved in the four populations and allele frequencies are given in Appendix Table 1. Eight loci were sufficiently polymorphic ($P < 0.95$) for Hardy-Weinberg tests. One out of a possible 32 tests (8 loci \times 4 populations) showed a significant departure from Hardy-Weinberg equilibrium when a Bonferroni modified probability level was applied (*Idh-1** Puysegur, $\chi^2 = 13.99$, 1 df, $P < 0.001$).

The polymorphic loci were tested with a contingency χ^2 test. There was a significant heterogeneity among all four populations at 5 loci, *Est-1**, *Gpi-2**, *Idh-1**, *Idh-2**, and *Ldh-1**, with a Bonferroni-modi-

Table 1

Results of comparisons of allele frequencies at eleven loci and mtDNA haplotypes in four populations of orange roughy. df = degrees of freedom; P = probability value; and G_{ST} = gene diversity. * = significant at the 5% level with a Bonferroni-modified P for multiple tests.

Locus	χ^2	df	P	G_{ST}	P
<i>Cck-1*</i>	7.93	6	0.243	0.006	0.277
<i>Est-1*</i>	63.09	12	<0.001*	0.030	<0.001*
<i>Gpi-1*</i>	4.70	9	0.860	0.002	0.889
<i>Gpi-2*</i>	25.09	6	<0.001*	0.021	0.002*
<i>Idh-1*</i>	26.91	9	0.001*	0.026	<0.001*
<i>Idh-2*</i>	46.08	9	<0.001*	0.065	<0.001*
<i>Ldh-1*</i>	19.02	3	0.003*	0.025	0.004*
<i>Ldh-2*</i>	12.09	6	0.061	0.008	0.153
<i>Mdh-1*</i>	11.20	6	0.082	0.012	0.066
<i>Mpi-1*</i>	7.56	9	0.581	0.003	0.653
<i>Pgm-1*</i>	2.58	6	0.860	0.001	0.839
all loci	226.2	81	<0.001	0.020	<0.001
mtDNA					
haplotypes	45.51		0.001	0.057	0.001

Table 2

Heterogeneity χ^2 pairwise comparisons for allozyme loci, mtDNA haplotypes, and random amplified polymorphic DNA (RAPD) fragments, among four populations of orange roughy. For the allozyme and RAPD data only those loci and fragments that were significant applying a Bonferroni-modified probability level are given.

Pair	Allozyme loci and probabilities	mtDNA haplotype probabilities	RAPD primer fragments and probabilities
Ritchie and Box	NS NS	NS	
Ritchie and Waitaki	<i>Est-1*</i> $P < 0.001$	0.001	E19-3 $P < 0.001$
Ritchie and Puysegur	<i>Gpi-2*</i> $P < 0.001$, <i>Idh-2*</i> $P < 0.001$	NS	A16-1 $P < 0.001$
Box and Waitaki	<i>Est-1*</i> $P < 0.001$, <i>Idh-1*</i> $P = 0.001$ <i>Idh-2*</i> $P < 0.001$	NS	E19-3 $P < 0.001$
Box and Puysegur	<i>Idh-2*</i> $P < 0.001$	NS	A16-1 $P < 0.001$
Waitaki and Puysegur	<i>Est-1*</i> $P < 0.001$	0.003	E19-3 $P < 0.001$

fied P for 11 loci (Table 1). To test for geographic structure, additional χ^2 tests were carried out on all pairwise combinations of populations. There was a significant heterogeneity for at least one locus between all population pairs, except Ritchie Bank and Box (Table 2).

The heterogeneity in the total data was confirmed by the gene diversity analysis (Table 1). When a Bonferroni-modified P is applied, the 5 loci show a G_{ST} significantly greater than that due to sampling error. Over all eleven loci G_{ST} was 0.020 (Table 1), indicating that around 2% of the observed genetic variation was due to differences among populations. From this estimate of G_{ST} , and by subtracting the G_{STnull} , the minimum number of effective migrants per generation ($N_e m$) was 13.2 (Table 3). Individual pairs of $N_e m$ varied from 15.7 (Box and Waitaki) to 124 (Ritchie and Box).

mtDNA

The estimated size of the PCR amplified D-loop was 1,500 base pairs and that of the cytochrome *b* was 500 bp. Four restriction enzymes, *Bst*U I, *Cfo* I, *Msp* I, and *Nla* III, produced two or more fragment patterns with the D-loop primers (e.g. Fig. 3) and were tested in all fish. For each area, a few fish samples failed to produce an amplification product; the same fish samples also failed to produce an amplification product with the RAPD primers. Four restriction enzymes, *Alu* I, *Bfa* I, *Rsa* I, and *Taq* I, showed variation in the first 24 fish tested with the cytochrome *b* primers, but the variation was limited to a single individual with each restriction enzyme. No further amplifications were undertaken with this set of primers. The numbers of haplotypes observed at each site are shown in Appendix Table 2. There is a significant heterogeneity in the total data ($P = 0.001$), with only 1 out of 1,000 randomizations exceeding the

Table 3

The estimated number of migrants exchanged per generation ($N_e m$) for allozyme, mtDNA, and random amplified polymorphic DNA (RAPD) data sets of orange roughy.

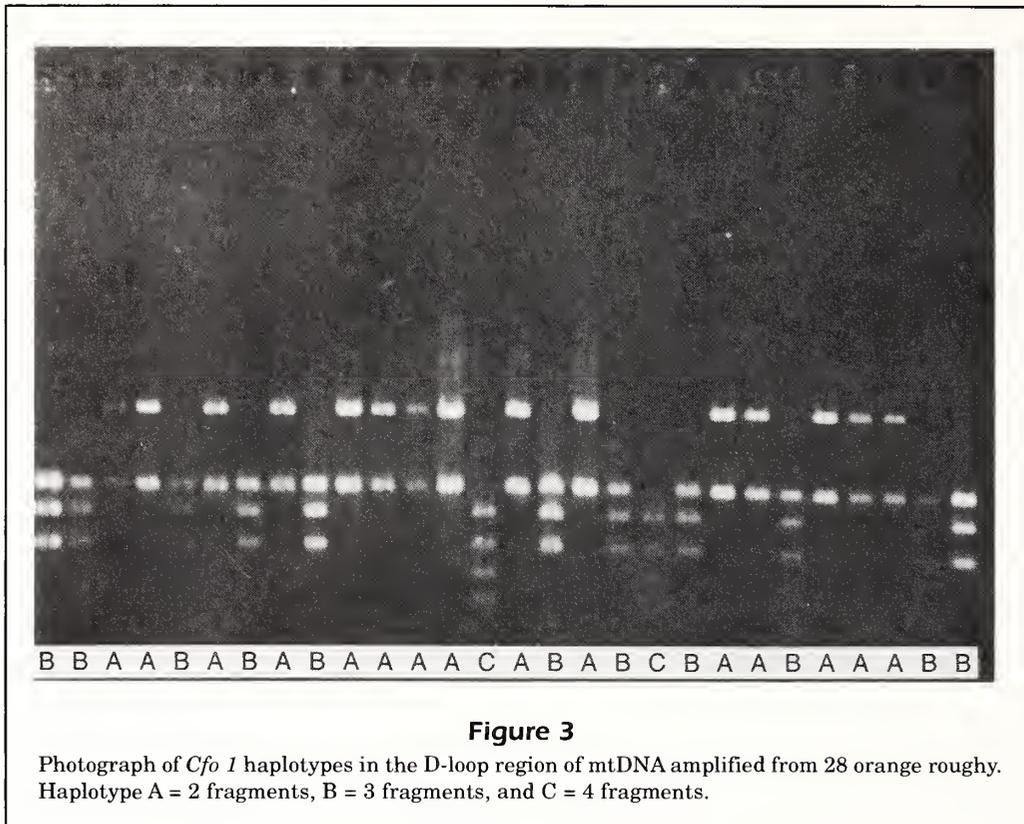
Population	Allozyme	mtDNA	RAPD
Ritchie and Box	124.0	277.8	75.0
Ritchie and Waitaki	14.7	7.2	7.7
Ritchie and Puysegur	19.4	35.7	18.0
Box and Waitaki	15.7	18.3	7.8
Box and Puysegur	25.3	36.5	16.0
Waitaki and Puysegur	75.5	9.6	6.5
Total	13.2	9.8	7.0

original χ^2 value (Table 1). In pairwise comparisons of the four spawning populations (Table 2), significant differences were found between Ritchie Bank and Waitaki ($P < 0.001$) and between Waitaki and Puysegur ($P = 0.001$), but not in the other pairwise comparisons.

Gene diversity was estimated to be 0.057 (Table 1), which is significantly greater than that due to sampling error, and indicates that around 6% of the observed genetic variation is due to differences among populations. From this estimate of G_{ST} , and by subtracting the G_{STnull} , the minimum number of female migrants per generation ($N_e m_f$) among the four populations was estimated to be 9.8 (Table 3). The pairwise values varied from 7.2 (Ritchie and Waitaki) to 277.8 (Ritchie and Box).

RAPD

Seven primers tested in 24 orange roughy produced clear DNA fragments and the same profiles in repeat tests. The primers (and their sequences 5' to 3')



were A14 (TCTGTGCTGG), A15 (TTCCGAACCC), A16 (AGCCAGCGAA), A17 (GACCGCTTGT), D15 (CATCCGTGCT), E19 (ACGGCGTATG), and H17 (CACTCTCCTC). The number of scored fragments varied from 1 to 6 per primer, and the size of the fragments from 0.6 to 2.8 kb. Fragments that could be scored were numbered in decreasing order of electrophoretic mobility (e.g. primer A14 fragment 1 = A14-1); each individual fish was scored for the presence or absence of each fragment. Repeat tests on some individuals did not produce repeatable patterns for some weakly staining fragments, therefore presence or absence of each fragment was not scored for these fragments. Omitting the DNA template from the PCR reaction (i.e. negative control) failed to produce fragments. The amount of DNA in the initial extractions varied tenfold between samples. Excess DNA, 250 ng, produced different fragment patterns with some primers (Fig. 2), therefore all amplifications were optimized to contain a 50-ng template of DNA.

The estimated allele frequencies are given in Appendix Table 3. Two out of 29 primer fragments (A16-1, E19-3) revealed a significant heterogeneity among populations when a heterogeneity χ^2 test with a modified probability for multiple tests was applied (Table 4). Pairwise comparisons showed significant differ-

ences between all pairs of populations except Ritchie Bank and Box at these two primer fragments (Table 2). The heterogeneity in the total data set was confirmed by the G_{ST} tests (Table 4). The effective number of migrants per generation was estimated to be 7.0 from the overall G_{ST} , minus G_{STnull} due to sampling error (Table 3), as described for allozymes. Pairwise values varied from 6.5 (Waitaki and Puysegur) to 75 (Ritchie and Box).

Discussion

There was significant heterogeneity in the allozyme data set at five loci (Table 1) which indicated that the population samples had not been taken from a single panmictic stock. Pairwise comparisons showed that there were significant differences between all pairs of spawning populations except the two northern populations at Ritchie Bank and Box (Fig. 1). The RAPD data also showed a significant heterogeneity that indicated that the population samples had been taken from more than one genetic unit stock. There were no area-specific RAPD fragments in orange roughy, as have been reported in marine prawns (Garcia et al., 1996) and freshwater crayfish (Macaranas et al., 1995), but there were differences in

frequencies of two primer fragments (A16-1, E19-3, Table 4). As with the allozyme data, there were differences between all pairwise comparisons, with the exception of those samples taken at Ritchie Bank and Box (Table 2).

The mtDNA data also showed a significant heterogeneity in the total data set but demonstrated less genetic differentiation than the allozyme and RAPD data sets, with only two pairwise comparisons showing a significant difference (Table 2). However all three methods, which have measured different parts of the genome, gave similar results of low genetic exchange among the four populations (Table 3). None of the estimates of $N_e m$ are true estimates because our data sets are biased in favor of polymorphic markers, which will tend to inflate the G_{ST} estimate; such estimates of $N_e m$ (Table 2) can be used to compare only relative levels of geneflow between areas (Ferguson, 1994). In this respect there is 8–10 times as much gene flow between Ritchie Bank and Box than between these sites and Waitaki, when measured with allozymes and RAPD's, and 15–38 times as much with mtDNA (Table 3). Significant genetic differences between spawning groups provides evidence of genetic isolation, and thus the data reveal three genetic groups: 1) Puysegur, 2) Waitaki, and 3) Ritchie Bank and Box (Table 2).

There are problems with RAPD analyses that may preclude them from use as stock markers for orange roughy. Because RAPD markers are dominant, a number of assumptions have to be made to analyze the data (Lynch and Milligan, 1994). Some of these assumptions, in particular that fragments with the same electrophoretic mobility are genetically identical and that absent fragments represent the same DNA fragment, may not be valid. Fragments that exhibited weak staining activity were not scored, so that there is a subjective element when scoring RAPD gels.

In the absence of breeding studies, the allelic nature of presence or absence of RAPD fragments may be suspect. Garcia and Benzie (1995) reported an extra RAPD fragment in prawn larvae that was absent in adults, although they found Mendelian inheritance of other RAPD markers. Unlike the other two genetic methods, there are no internal checks that can be used to fit RAPD phenotypes to a genetic model: with allozymes there is an expected gel phenotype for each enzyme and all alleles are equally expressed; with mtDNA the size of the restricted fragments should add up to the size of the undigested fragment.

Some primers produced weak fragments that were not repeatable in reamplifications. These weak fragments may be produced by excessive PCR cycles; Bell and DeMarini (1991) have shown that by increasing

Table 4

Heterogeneity χ^2 tests and gene diversity (G_{ST}) for seven random amplified polymorphic DNA (RAPD) primers in four populations of orange roughy. df = degrees of freedom; P = probability value; G_{ST} = gene diversity. (* = significant at Bonferroni-modified P for multiple tests).

Primer and fragment	χ^2 (3 df)	P	G_{ST} (3 df)	P
A14-1	2.820	0.422	0.010	0.415
A14-2	3.306	0.347	0.012	0.341
A14-3	9.089	0.028	0.032	0.031
A15-1	1.543	0.672	0.006	0.671
A15-2	8.189	0.042	0.029	0.044
A15-3	3.593	0.309	0.013	0.299
A15-4	2.138	0.544	0.008	0.540
A16-1	16.921	<0.001*	0.079	<0.001*
A16-2	1.473	0.688	0.005	0.685
A16-3	6.874	0.076	0.024	0.087
A16-4	5.072	0.167	0.019	0.156
A16-5	0.513	0.916	0.002	0.915
A17-1	2.138	0.544	0.008	0.540
A17-3	6.715	0.082	0.025	0.073
D15-1	5.436	0.143	0.018	0.178
D15-2	2.114	0.549	0.008	0.513
D15-3	3.862	0.277	0.014	0.280
D15-4	1.678	0.642	0.007	0.615
E19-1	8.080	0.044	0.300	0.043
E19-2	9.283	0.026	0.032	0.033
E19-3	23.079	<0.001*	0.082	<0.001*
E19-4	6.558	0.087	0.026	0.071
E19-5	2.680	0.444	0.010	0.423
E19-6	0.823	0.844	0.002	0.887
H17-1	3.824	0.281	0.014	0.268
H17-2	3.119	0.374	0.012	0.343
H17-3	0.776	0.855	0.003	0.863
H17-4	2.155	0.541	0.007	0.604
H17-5	0.500	0.919	0.002	0.913
Total (87 df)	164.66	<0.001	0.019	<0.001

the number of PCR cycles above 30, nonspecific DNA products can be obtained. However, in our preliminary amplifications in extracting DNA from frozen tissue samples, less than 40 cycles produced faint fragment patterns for most primers; thus 40 cycles were used as a standard. The RAPD technique has been shown to be very sensitive to changes in concentration of primer, concentration of template, annealing temperature, and the concentration of magnesium ions, all of which can affect the number and intensity of bands (Devos and Gale, 1992; Ellsworth et al., 1993; Patwary et al., 1993; Penner et al., 1993). We sought to avoid these problems by standardizing DNA quantities prior to amplification, performing all amplifications on the same thermocycler, and using the same batch of chemicals. Tissue samples from the four spawning sites were collected and stored under similar conditions.

Given the technical problems with RAPD's, we would recommend them only when other genetic methods have failed to reveal polymorphisms. Techniques such as PCR-RFLP of mtDNA, or allozymes, yielded fewer polymorphisms per unit of laboratory time than did RAPD's but still produced sufficient polymorphisms to detect population structure in orange roughy. Our allozyme data set indicated a higher level of genetic subdivision than that found with mtDNA in orange roughy. This result is surprising in view of the relatively higher rate of evolution of mtDNA (Brown, 1983), and it is possible that other regions of the mitochondrial genome, or use of additional restriction enzymes, might reveal more genetic variation. Several studies of marine organisms have detected greater genetic subdivision with mtDNA than with allozyme markers (e.g. Reeb and Avise, 1990), although there are examples of the reverse in the fisheries literature (Grewe et al., 1994; Ward et al., 1994). It is possible that the allozyme markers are under selection (Koehn et al., 1980) and are responding to short-term population events rather than to historical events due to reproductive isolation.

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Appendix

Appendix Table 1

Allele frequencies for 11 allozyme loci tested in four populations of orange roughy.

Allele frequencies for 11 allozyme loci tested in four populations of orange roughy.						Allele frequencies for 11 allozyme loci tested in four populations of orange roughy.						
Locus	Allele (n=no. of fish)	Ritchie	Box	Waitaki	Puysegur	Locus	Allele (n=no. of fish)	Ritchie	Box	Waitaki	Puysegur	
<i>Cck-1*</i>	1	0.494	0.500	0.596	0.551	<i>Idh-2*</i>	1	0.417	0.442	0.180	0.196	
	2	0.489	0.500	0.404	0.444		2	0.583	0.548	0.809	0.793	
	3	0.017	0.000	0.000	0.005		3	0.000	0.005	0.011	0.011	
	n	90	81	47	99		4	0.000	0.005	0.000	0.000	
<i>Est-1*</i>	1	0.051	0.160	0.093	0.152	<i>Ldh-1*</i>	1	1.000	0.983	0.979	0.931	
	2	0.222	0.229	0.372	0.250		2	0.000	0.017	0.021	0.069	
	3	0.709	0.606	0.430	0.585		n	96	94	47	94	
	4	0.006	0.005	0.006	0.013		<i>Ldh-2*</i>	1	0.000	0.000	0.011	0.000
	5	0.013	0.000	0.000	0.000			2	1.000	0.980	0.989	0.980
n	79	94	43	99	3	0.000		0.020	0.000	0.020		
<i>Gpi-1*</i>	1	0.515	0.551	0.553	0.517	n		96	99	47	99	
	2	0.232	0.253	0.245	0.265	<i>Mdh-1*</i>		1	0.625	0.729	0.656	0.745
	3	0.253	0.191	0.191	0.214		2	0.375	0.271	0.344	0.250	
	4	0.000	0.006	0.001	0.004		3	0.000	0.000	0.000	0.005	
	n	99	89	47	99		n	96	94	48	98	
<i>Gpi-2*</i>	1	0.015	0.033	0.042	0.058		<i>Mpi-1*</i>	1	0.037	0.027	0.052	0.057
	2	0.970	0.944	0.948	0.860	2		0.957	0.968	0.948	0.943	
	3	0.015	0.022	0.010	0.081	3		0.000	0.005	0.000	0.000	
	n	99	90	48	99	4		0.005	0.000	0.000	0.000	
	<i>Idh-1*</i>	1	0.030	0.011	0.106	0.083		<i>Pgm-1*</i>	1	0.116	0.144	0.117
2		0.970	0.979	0.883	0.897	2	0.879		0.850	0.883	0.874	
3		0.000	0.005	0.011	0.021	3	0.005		0.006	0.000	0.000	
4		0.000	0.005	0.000	0.000	n	99		90	47	99	
n		99	94	47	99							

Appendix Table 2

Numbers of composite mtDNA D-loop haplotypes observed in four populations of orange roughy. The composite haplotypes are based on the restriction enzymes *Bst*U I, *Cfo* I, *Msp* I, and *Nla* III.

Haplotype	Ritchie	Box	Waitaki	Puysegur
AABA	21	19	5	14
BBBA	11	18	21	7
ACBA	0	0	2	0
AAAA	2	0	0	0
AABB	1	1	1	3
AABC	1	0	0	0
AACA	1	0	0	0
ABBA	4	4	6	10
BABA	2	6	6	6

Appendix Table 3

Random amplified polymorphic DNA (RAPD) fragment frequencies, calculated by assuming a biallelic system in Hardy-Weinberg equilibrium, in four populations of orange roughy.

Locus	Allele (n=no. of fish)					Locus	Allele (n=no. of fish)				
	Ritchie	Box	Waitaki	Puysegur	Ritchie		Box	Waitaki	Puysegur		
A14-1	1	0.00	0.021	0.00	0.021	D15-2	1	0.426	0.542	0.500	0.489
	2	1.00	0.979	1.00	0.979		2	0.574	0.458	0.500	0.500
	n	44	48	42	40		n	44	48	42	40
A14-2	1	0.454	0.417	0.417	0.330	D15-3	1	0.629	0.708	0.583	0.745
	2	0.546	0.583	0.583	0.670		2	0.361	0.292	0.417	0.255
	n	44	48	42	40		n	44	48	42	40
A14-3	1	0.306	0.188	0.167	0.394	D15-4	1	0.083	0.063	0.042	0.043
	2	0.694	0.813	0.833	0.596		2	0.907	0.938	0.958	0.957
	n	44	48	42	40		n	44	48	42	40
A15-1	1	0.009	0.00	0.00	0.00	E19-1	1	0.269	0.292	0.142	0.330
	2	0.991	1.00	1.00	1.00		2	0.731	0.708	0.858	0.670
	n	44	48	42	40		n	43	48	42	38
A15-2	1	0.806	0.792	0.708	0.638	E19-2	1	0.148	0.271	0.042	0.149
	2	0.194	0.208	0.292	0.362		2	0.852	0.729	0.958	0.851
	n	44	48	42	40		n	43	48	42	38
A15-3	1	0.028	0.042	0.042	0.00	E19-3	1	0.639	0.646	0.125	0.521
	2	0.972	0.958	0.958	1.00		2	0.361	0.354	0.875	0.479
	n	44	48	42	40		n	43	48	42	38
A15-4	1	0.009	0.021	0.00	0.00	E19-4	1	0.093	0.021	0.083	0.021
	2	0.991	0.979	1.00	1.00		2	0.898	0.979	0.917	0.979
	n	44	48	42	40		n	43	48	42	38
A16-1	1	0.49	0.46	0.33	0.74	E19-5	1	0.056	0.042	0.00	0.021
	2	0.51	0.54	0.67	0.26		2	0.944	0.958	1.00	0.979
	n	43	48	42	38		n	43	48	42	38
A16-2	1	0.019	0.00	0.00	0.021	E19-6	1	0.769	0.708	0.708	0.745
	2	0.981	1.00	1.00	0.979		2	0.231	0.292	0.292	0.255
	n	43	48	42	38		n	43	48	42	38
A16-3	1	0.278	0.271	0.125	0.149	H17-1	1	0.046	0.00	0.00	0.021
	2	0.722	0.729	0.875	0.851		2	0.954	1.00	1.00	0.979
	n	43	48	42	38		n	44	48	42	38
A16-4	1	0.694	0.708	0.583	0.564	H17-2	1	0.806	0.708	0.708	0.713
	2	0.306	0.292	0.417	0.436		2	0.194	0.292	0.292	0.287
	n	43	48	42	38		n	44	48	42	38
A16-5	1	0.019	0.021	0.00	0.021	H17-3	1	0.769	0.792	0.708	0.745
	2	0.981	0.979	1.00	0.979		2	0.231	0.208	0.292	0.255
	n	43	48	42	38		n	44	48	42	38
A17-1	1	0.009	0.021	0.00	0.00	H17-4	1	0.731	0.708	0.708	0.638
	2	0.991	0.979	1.00	1.00		2	0.269	0.292	0.292	0.362
	n	43	48	42	38		n	44	48	42	38
A17-3	1	0.009	0.00	0.00	0.053	H17-5	1	0.019	0.021	0.042	0.021
	2	0.991	1.00	1.00	0.947		2	0.981	0.979	0.958	0.979
	n	43	48	42	38		n	44	48	42	38
D15-1	1	0.111	0.188	0.042	0.074						
	2	0.889	0.813	0.958	0.926						
	n	44	48	42	40						

Abstract.—To characterize the impact of spring floods on the survival of juvenile chinook salmon in the unstable, braided rivers on the east coast of New Zealand's South Island, I examined correlations between spring and summer flows in the mainstem of the Rakaia River and fry-to-adult survival for chinook salmon spawning in a headwater tributary. Flow parameters that were investigated included mean flow, maximum flow, and the ratio of mean to median flow (an index of flow variability), calculated during peak down-river migration of ocean-type juveniles (August to January). Survival was uncorrelated with mean or maximum flow but was positively correlated with the ratio of mean to median flow during spring (October and November). The correlation suggests that pulses of freshwater entering the ocean during floods may buffer the transition of fingerlings from fresh to saline waters and thus partly compensate for the lack of an estuary on the Rakaia River. A positive correlation between spring flow variability and the proportion of ocean-type chinook in relation to stream-type chinook is also consistent with this hypothesis. All correlations were relatively weak, reinforcing earlier results that production is primarily controlled by marine influences. These findings further demonstrate the considerable ability of chinook salmon to adapt to new habitats.

Survival of chinook salmon, *Oncorhynchus tshawytscha*, from a spawning tributary of the Rakaia River, New Zealand, in relation to spring and summer mainstem flows

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To understand the population dynamics of anadromous Pacific salmonids (*Oncorhynchus* spp.), it is important to isolate and characterize the influence of varying environmental factors on annual production. In the course of their life cycle salmon inhabit a succession of freshwater and marine environments, where prospects for survival depend on prevailing conditions. Spawning and incubation success may be adversely affected by substrate disturbance during floods; the suitability of riverine waters as habitat for rearing juveniles is dependent on both flow and temperature and may be reduced by flows that are too low or too high; and adult survival within the marine environment is at least partly determined by environmentally controlled factors such as oceanic water masses and the availability of suitable prey. Numerous studies have demonstrated significant correlations between environmental variables and indices of survival and growth, at scales ranging from local to global. Although correlation analysis in fisheries studies has been criticized for its potential for misuse and for a propensity to produce weak results of little practical value (Walters and Collie, 1988), other authors have noted that provided the method is used with discretion, biologically meaningful re-

sults can be derived (Kope and Botsford, 1990).

Despite the importance of in-stream habitats for rearing juvenile chinook salmon (*O. tshawytscha*), the relation between flow and brood year survival has received comparatively little attention. Interannual trends in the abundance of chinook salmon in the Fraser River, British Columbia, have been linked to flow variations in the mainstem (Beamish et al., 1994) and in the Nechako River tributary (Bradford, 1994). In the former study, annual production was inversely related to mean annual discharge, whereas in the latter study, juvenile survival in the upper Nechako appeared to decline as a result of flow diversion for hydroelectric generation, and the proportion of spawning fish using the upper river appeared to be negatively correlated with August flows. However, in the Nechako River study, as in some other studies linking downriver migration to river flows (e.g. Kjelson et al., 1982), low flows were often associated with increased water temperatures, making it difficult to differentiate between flow-related and temperature-related effects. Williams and Matthews (1995) found that survival of Snake River spring and summer chinook salmon juveniles was reduced during low flow conditions but concluded that these

losses were primarily due to problems with passage through hydroelectric dams rather than to low discharge per se. The effects of flow variability on survival have also received little attention. Increased downstream movement of newly emerged salmonid fry following sudden increases in discharge has been well documented (e.g. Irvine, 1986; Saltveit et al., 1995), but only rarely has flow variability been used as a predictor variable in population studies (Berggren and Filardo, 1993).

Whenever brood year survival is estimated from stock-recruitment or similar data, a search for correlations between river flow and survival will usually involve deriving a single flow index, such as the annual mean, for each cohort. Most such studies conducted to date have used flow averaged over periods from three months (Kope and Botsford, 1990) to one year (Beamish et al., 1994), but it is by no means obvious that these are the most informative or biologically meaningful parameters to use. A single catastrophic flood during the incubation period may cause large-scale destruction of redds and loss of alevins through bed scour (Montgomery et al., 1996) without having much effect on the mean annual flow. Prior to smolting, fry may be susceptible to short-term floods that carry them prematurely into seawater, when the same floods a few months later would have little impact. In addition, mean flow is not necessarily the most relevant statistic for characterizing flow regimes; it is possible that in the two examples given above, some other parameter (such as maximum flow or the coefficient of variation) might be more informative (e.g. Hvidsten and Hansen, 1988). For example, in New Zealand, where high flow variability is a defining characteristic of riverine ecosystems (Biggs, 1995), statistics such as the proportion of the time the flow exceeds three times the median (Clausen and Biggs, in press) and the ratio of mean flow to median flow (Jowett, 1990), have been successful in elucidating relations between flow regime and biological parameters. To explore fully the relation between flow and survival, therefore, it is necessary to consider not only the type of flow statistic that is likely to be of interest but also the duration and seasonal timing of the period over which the statistic is to be calculated.

Since the introduction of fall-run Sacramento River stock to New Zealand in the early 1900's (McDowall, 1994a; Quinn et al., 1996), chinook salmon have maintained self-sustaining populations in all major rivers on the east coast of the South Island (McDowall, 1990; Quinn and Unwin, 1993). Like most New Zealand rivers, these rivers (whose wide, braided shingle beds drain steeply mountainous catchments on the South Island main divide) are characterized by highly vari-

able flows (Jowett and Duncan, 1990), flooding quickly whenever snow and ice melt in the headwaters is augmented by heavy orographic rainfall. These floods occur at any time of year but are particularly common in spring. In rivers such as the Rakaia they cause massive bed movement (Ibbitt, 1979) and reduce the abundance and diversity of invertebrate fauna (Sagar, 1986) for up to one month afterwards. The impact of these events on seaward-migrating juvenile chinook has generated some debate. Several authors have remarked that survival of New Zealand chinook fry may be adversely affected during floods (McDowall, 1990; Flain¹). Other studies suggest that, although some fry may be lost during extreme floods, flow fluctuations in a more typical season do not have a serious negative impact on migration (Hopkins and Unwin, 1987).

Chinook salmon spawning populations in Glenariffe Stream, a headwater spawning tributary of the Rakaia River (Fig. 1), have been monitored since 1965 by means of an upstream counting fence (Quinn and Unwin, 1993). In this study I analyzed brood year survival, for chinook spawning in Glenariffe Stream, in relation to Rakaia mainstem discharge during spring and summer (August to January). My primary objectives were to examine various flow statistics as possible correlates with survival and to determine the sensitivity of any resulting correlations to changes in the interval used to calculate each statistic. A secondary objective was to examine evidence that spring floods were detrimental to brood year survival.

Chinook salmon in New Zealand

New Zealand chinook salmon are broadly similar to their Sacramento ancestors in terms of both their general life history (Unwin, 1986) and genetic make up (Quinn et al., 1996). Present day stocks comprise a mixture of ocean- and stream-type fish (Gilbert, 1913; Healey, 1983), corresponding to juveniles that spend 3–6 mo or 12–15 mo in fresh water before entering the ocean (Unwin and Lucas, 1993). In the Rakaia River, the most thoroughly studied of the major salmon producing rivers, ocean-type fish make up about two-thirds of the returning adults (Quinn and Unwin, 1993).

The migration patterns of age-0+ juvenile chinook salmon in the Rakaia River and a key spawning tributary, Glenariffe Stream (Fig. 1), have been studied in some detail, and are relatively well understood (Unwin, 1986; Hopkins and Unwin, 1987). From

¹ Flain, M. 1982. Quinnsat salmon runs, 1965–1978, in the Glenariffe Stream, Rakaia River, New Zealand. Occasional Publ 28, N.Z. Ministry of Agriculture and Fisheries, Fisheries Research Div., 22 p. [Copy held at NIWA, Christchurch, New Zealand.]

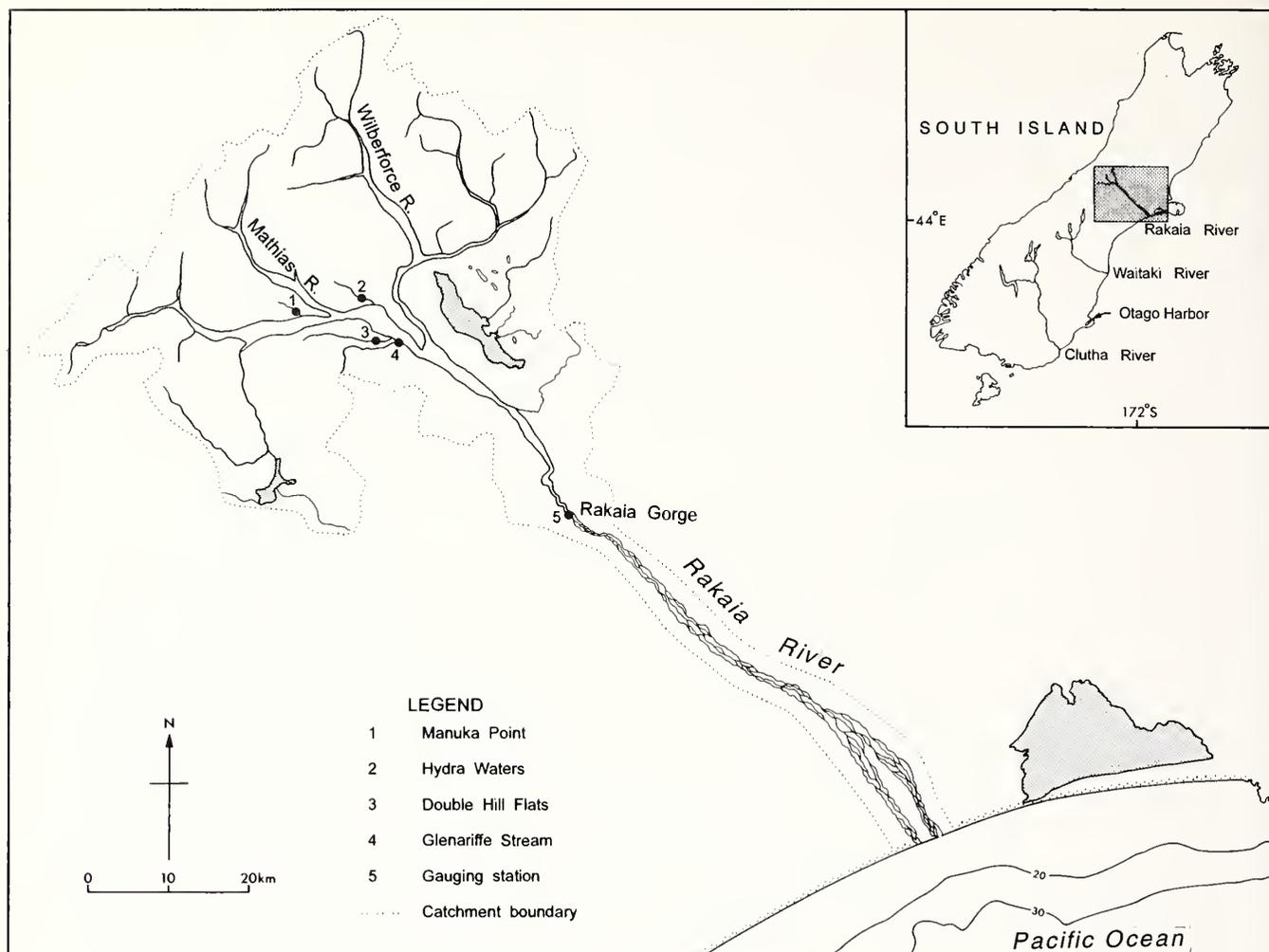


Figure 1

The South Island of New Zealand and the Rakaia River catchment, showing geographical features referred to in the text, the four main headwater tributaries used by spawning chinook salmon (1–4), and the 20-m and 30-m isobaths off the Rakaia mouth.

August to October (late winter to mid spring), large numbers of newly hatched fry emerge from the gravel in Glenariffe Stream and other spawning areas and begin to move downstream within 24 h of emergence. This migration appears to be driven by population pressure; the rearing capacity of Glenariffe Stream has been estimated at less than 100,000 fry, whereas annual fry production can exceed 3.7 million (Unwin, 1986). A second wave of larger fry, representing individuals remaining in their natal stream for up to 3 months, enters the upper river from November to January, but in Glenariffe Stream these fry represent less than 10% of the total production. This pattern appears to be typical for chinook populations within their native range (e.g. Lister and Walker, 1966; Reimers, 1973; Healey, 1991).

Within the upper reaches of the Rakaia River, fry quickly take up residence along the margins of the braided channels, where there is an abundance of

suitable rearing habitat (Glova and Duncan, 1985). Aquatic invertebrates, predominantly *Deleatidium* spp., are the primary prey in spring, but in summer the diet of fry is dominated by terrestrial species and chironomids (Sagar and Glova, 1987). From mid-August fingerlings gradually disperse downriver, growing steadily as the season progresses and reaching the lower river in mid-October at about 60–80 mm fork length (FL) (Hopkins and Unwin, 1987). Fingerlings remain abundant in the lower river until early February but show little tendency to increase in size; thus there appears to be a steady emigration of 90-day fingerlings into marine waters with continual replacement from upriver (Hopkins and Unwin, 1987). Similar patterns of movement have been observed in other New Zealand stocks (Davis and Unwin, 1989), in their ancestral Sacramento River (Kjelson et al., 1982), and elsewhere in North America (Healey, 1991). Mean FL at seawater entry

for these fingerlings is consistent with the back-calculated mean FL at seawater entry for ocean-type adults of Rakaia origin (Unwin and Lucas, 1993), confirming the importance of springtime mainstem rearing for ocean-type fry. Freshwater residence patterns of juvenile stream-type fish are less well understood, but there is some evidence that an initial period of tributary rearing lasting 3–6 mo is followed by mainstem rearing for the remainder of the first year (Unwin, 1986).

In the absence of a commercial marine fishery for salmon, very little is known about the marine phase of the salmon life cycle. Adult chinook are piscivorous and appear to feed opportunistically within the pelagic zone, although prey diversity is low and food availability is potentially limited by annual fluctuations in prey abundance (James and Unwin, 1996). Brood year survival rates for both naturally and hatchery-produced chinook of Rakaia origin vary by up to two orders of magnitude and appear to be predominantly related to marine influences (Unwin, in press). However, these results do not preclude the possibility that survival may also be partly influenced by conditions within the freshwater environment.

Data sources and methods

The Rakaia River

The Rakaia River is a large, braided, glacier-fed river draining a 2,910 km² catchment that spans 70 km of the Southern Alps and rises to 2,800 m. Apart from a gentle 5-km gorge where the flow is briefly confined to a single channel, the river occupies an unstable, highly braided shingle bed up to 5 km wide (see Fig. 2 of Glova and Duncan, 1985). After collecting water from two major headwater tributaries (the Mathias and Wilberforce), the lower section (90 km) of the river flows directly into the Pacific Ocean with no significant tributary input. All major salmon spawning waters are located upstream of the Wilberforce confluence (Fig. 1). River gradient is virtually constant below this point, averaging 4.5 m/km, and the river discharges into the ocean via a small freshwater lagoon extending inland from the open sea for less than 100 m. The term "lagoon" is used in preference to "estuary" because there is no ebb and flow of the tide (although there is a tidal backup of fresh water) and because the area supports few, if any, predominantly estuarine life forms.² A detailed de-

scription of the river and its catchment is given by Bowden.³

Continuous flow data for the Rakaia River have been collected since 1959 by means of recorders at the downstream end of the gorge, 62 km above the mouth. For the purposes of this study, all flow statistics were calculated from the daily mean discharge (Q). Discharge (annual mean 200 m³/s) shows a moderately seasonal pattern, monthly means varying from 127 m³/s in July to 265 m³/s in November.³ The mean annual flood (the average of the annual maximum flow) is 1 448 m³/s, with a peak instantaneous discharge of 5,600 m³/s (estimated to have a return period of 60 yr) recorded in January 1994. The bank-full discharge (the instantaneous flow which results in complete inundation of the river bed as individual braids coalesce) ranges from 800 m³/s just below the gorge to about 2,500 m³/s in the lower river. Flood waters move rapidly downriver, typically reaching the mouth 8–12 h after passing through the gorge, although peak velocity increases with flood intensity, and travel times as short as 3.5 h over 40 km have been observed.^{4,5} Over the months relevant to this study, daily mean water temperatures in the lower river (23 km above the mouth) range from 6°C in August to 16°C in January (Unwin, 1986).

Glenariffe Stream spawning runs

Glenariffe Stream is a spring-fed tributary joining the Rakaia River 100 km above its mouth at an altitude of 430 m (Fig. 1). The flow regime is exceptionally stable, with a mean discharge of 3.4 m³/s and a maximum recorded discharge (over a seven-year period) of 16 m³/s. Chinook salmon spawning runs in Glenariffe Stream have been monitored annually by means of a counting fence installed in 1965 (Quinn and Unwin, 1993; Flain¹). The modal age-at-maturity is three years, with smaller numbers of 2-year and 4-year-olds and very few 5-year-old fish. The angler interception rate varies little between years, typically ranging from 30% to 40%.^{6,7} Since 1980,

³ Bowden, M. J. 1983. The Rakaia River and catchment—a resource survey, vol. 2. North Canterbury Catchment Board and Regional Water Board, Christchurch, New Zealand, 101 p. [Copy held by NIWA, Christchurch, New Zealand.]

⁴ 1997. Unpubl. data, NIWA, Christchurch, New Zealand.

⁵ Horrel, G. 1997. Canterbury Regional Council, PO Box 345, Christchurch, New Zealand. Personal commun.

⁶ Unwin, M. J., and S. F. Davis. 1983. Recreational fisheries of the Rakaia River. Fisheries Environmental Report 30. New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Division, Christchurch, New Zealand. [Copy held by NIWA, Christchurch, New Zealand.]

⁷ Millichamp, R. 1997. North Canterbury Fish and Game Council, 3 Horatio Street, Christchurch, New Zealand. Personal commun.

² Eldon, G. A., and A. J. Greager. 1983. Fishes of the Rakaia Lagoon. Fisheries Environmental Report 30. N. Z. Ministry of Agriculture and Fisheries, Fisheries Res. Div., Christchurch, 65 p. [Copy held by NIWA, Christchurch, New Zealand.]

spawning stocks have been supplemented by hatchery releases, but scale-pattern analysis and coded-wire tag recoveries of spawning fish intercepted at the fence allow each run to be partitioned into hatchery-reared and naturally spawning components (Unwin and Glova, 1997). The stability of the flow regime ensures that pre-emergence mortality of ova and alevins is not flow-dependent and is reflected by the lack of interannual variation in egg to fry survival for naturally spawning fish (Unwin, 1986; Unwin, in press). Over five years (1973–76, and 1992) of record egg-to-fry survival ranged from 38 to 52% and averaged 48%. On this basis, annual production can be consistently expressed in terms of the number of fry leaving Glenariffe Stream (Unwin, 1997).

For this study, I used the data set in Table 1 of Unwin (1997), summarizing fry-to-adult survival (S) for the 26 years from 1965 to 1990, expressed as live adult spawners reaching Glenariffe Stream (summed over all year classes for each cohort) per 10,000 fry. These data are reproduced here as Table 1. Survival ranged from 1.3 (for the 1971 brood year) to 117 (for the 1973 brood year), with an annual mean of 8

spawners per 10,000 fry (0.079%). These data were log-normally distributed (Unwin, 1997); therefore I used log-transformed values for all calculations (see also Bradford, 1995).

Data analysis

For each year from 1965 to 1990, I calculated mean flows (\bar{Q}) for each calendar month, for the two three-month periods August–October (“spring”) and November–January (“summer”), and for the full six months. As indices of flow variability, I determined the maximum flow (\hat{Q}), and the ratio of the mean to the median flow (\tilde{Q}), for the same monthly, three-monthly and six-monthly intervals. Although other measures of flow variability are possible, such as skewness, coefficient of variation (CV), and baseflow index (which measures the ratio of the volume of base flow to the volume of total runoff), these all tend to be highly correlated and there is no one measure which represents the “best” index (Jowett and Duncan, 1990). I chose \tilde{Q} because it is more robust (i.e. insensitive to extreme outliers) than statistics

Table 1

Spawning population size, fry production, adult returns, and fry-to-adult survival (adults per 10,000 fry, rounded to the nearest integer) for naturally spawning Glenariffe Stream chinook, 1965–90. Fry production for 1973–76 was estimated from trapping records; all other figures are based on a mean egg-to-fry survival of 48% (Unwin, 1997).

Brood year	Number of female spawners	Estimated fry production (thousands)	Number of returning adults	Adults per 10,000 fry
1965	1,278	2,988	4,676	16
1966	573	1,513	1,334	9
1967	746	1,760	505	3
1968	1,781	4,310	2,642	6
1969	1,286	3,249	2,760	8
1970	248	655	474	7
1971	1,084	2,573	330	1
1972	1,618	3,418	1,731	5
1973	160	275	3,207	117
1974	173	426	1,242	29
1975	799	1,834	2,045	11
1976	1,522	3,436	2,943	9
1977	778	1,614	1,341	8
1978	863	1,810	1,787	10
1979	1,413	2,138	546	3
1980	481	826	548	7
1981	856	1,978	1,097	6
1982	276	643	2,815	44
1983	326	784	1,766	23
1984	772	2,037	3,037	15
1985	1,800	4,722	950	2
1986	970	2,136	493	2
1987	669	1,400	1,151	8
1988	838	2,074	526	3
1989	391	767	615	8
1990	295	676	504	7

such as CV or skewness, which involve raising flows to the second and third power, respectively. I also calculated several indices related to the incidence of flood peaks, including the number of days when the daily mean discharge exceeded 500 m³/s, 1,000 m³/s, and 1,500 m³/s, and the mean of the ten highest flows over the six months from August to January. The complete set of flow parameters used is summarized in Table 2.

For each parameter, I looked for evidence of a relation with the log-transformed Glenariffe Stream survival data by calculating the correlation coefficient for the paired data sets over the 26 years of record. I examined bivariate scatter plots and residual plots for any data sets showing a significant relation ($P < 0.05$). For these preliminary results I did not correct for the effect of multiple tests (i.e. the possibility of finding an artificially inflated correlation with one of the 32 flow parameters purely by chance); therefore P -values for each correlation over-estimated their true significance (Walters and Collicie, 1988; Kope and Botsford, 1990). For these parameters, my next level of analysis was to recalculate the appropriate flow statistic for periods ranging in duration from one week to four months, dating from 1 June to 31 January (representing 805 periods in total), and to recalculate the correlation with the survival data for each choice of date and duration. I then constructed contour plots depicting variations in the correlation coefficient as a function of starting date and duration and examined these "surfaces of correlation" for the presence of local extrema. My motivation for this analysis was not to identify a single period that maximized the correlation, but rather to gauge the sensitivity of the correlation to small changes in interval, and hence to identify seasonal periods for which significant correlations between flow indices and survival persisted over biologically meaningful time scales.

All statistical calculations were performed with version 6.0 of SYSTAT software (Wilkinson, 1996). Contour and surface fits were accomplished with version 6 of SURFER for Windows' implementation of Kriging smoothing (Keckler, 1994) applied to a grid of correlation coefficients calculated at 5-day intervals on both the date and period axes.

Results

River flows

Over the period covered by this study (August 1965 to January 1991), monthly mean discharge ranged from 146 m³/s to 306 m³/s (Table 2). Individual

Table 2

Flow parameters used for correlation analysis, together with their mean and range over the period 1965 to 1990.

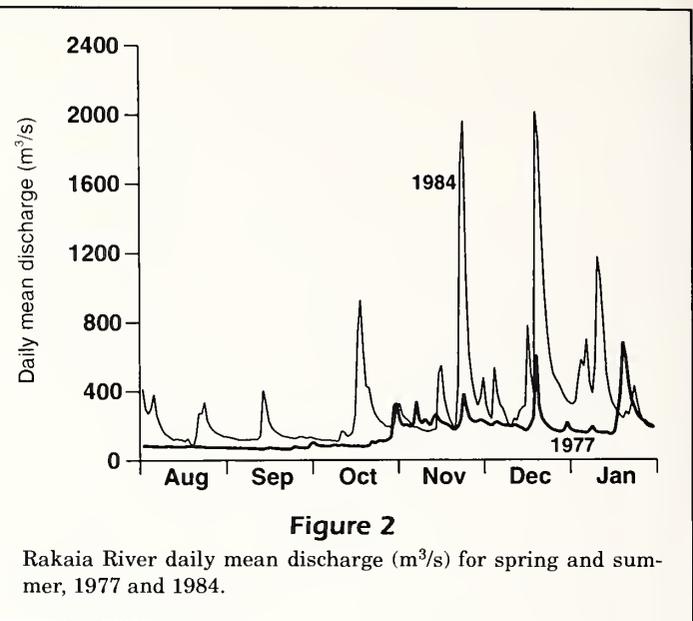
Parameter	Symbol	Mean	Range
Measures of flow volume (m ³ /s)			
Mean annual flow, Feb–Jan	\bar{Q}_{Annual}	209	156–277
Mean flow, Aug–Jan	$\bar{Q}_{\text{Spring/Summer}}$	237	157–329
Mean flow, Aug–Oct	\bar{Q}_{Spring}	190	86–348
Mean flow, Nov–Jan	\bar{Q}_{Summer}	283	186–456
Mean flow, Aug	\bar{Q}_{Aug}	146	80–293
Mean flow, Sep	\bar{Q}_{Sep}	181	71–570
Mean flow, Oct	\bar{Q}_{Oct}	243	106–493
Mean flow, Nov	\bar{Q}_{Nov}	282	131–457
Mean flow, Dec	\bar{Q}_{Dec}	306	160–589
Mean flow, Jan	\bar{Q}_{Jan}	262	148–416
Measures of flood peaks (flows in m ³ /s)			
Maximum flow, Aug–Jan	$\hat{Q}_{\text{Spring/Summer}}$	1,488	630–2,800
Maximum flow, Aug–Oct	\hat{Q}_{Spring}	975	167–2,470
Maximum flow, Nov–Jan	\hat{Q}_{Summer}	1,279	540–2,800
Maximum flow, Aug	\hat{Q}_{Aug}	385	86–2,470
Maximum flow, Sep	\hat{Q}_{Sep}	502	83–2,230
Maximum flow, Oct	\hat{Q}_{Oct}	755	133–2,030
Maximum flow, Nov	\hat{Q}_{Nov}	783	203–1,960
Maximum flow, Dec	\hat{Q}_{Dec}	1,006	282–2,800
Maximum flow, Jan	\hat{Q}_{Jan}	806	222–2,470
Mean of 10 highest flows, Aug–Jan	$\hat{Q}_{10\text{max}}$	854	443–1,410
Number of days $Q > 500$ m ³ /s, Aug–Jan	N_{500}	13	3–26
Number of days $Q > 1,000$ m ³ /s, Aug–Jan	$N_{1,000}$	2	0–8
Number of days $Q > 1,500$ m ³ /s, Aug–Jan	$N_{1,500}$	1	0–4
Measures of flow variability			
Mean/median, Aug–Jan	$\tilde{Q}_{\text{Spring/Summer}}$	1.33	1.04–1.73
Mean/median, Aug–Oct	$\tilde{Q}_{\text{Spring}}$	1.32	1.01–1.92
Mean/median, Nov–Jan	$\tilde{Q}_{\text{Summer}}$	1.29	1.09–1.52
Mean/median, Aug	\tilde{Q}_{Aug}	1.14	0.98–2.25
Mean/median, Sep	\tilde{Q}_{Sep}	1.15	1.00–1.91
Mean/median, Oct	\tilde{Q}_{Oct}	1.22	0.94–1.64
Mean/median, Nov	\tilde{Q}_{Nov}	1.23	1.02–1.75
Mean/median, Dec	\tilde{Q}_{Dec}	1.27	1.04–2.11
Mean/median, Jan	\tilde{Q}_{Jan}	1.27	1.02–2.03

monthly means varied from 71 m³/s (September 1977) to 734 m³/s (December 1979). The mean maximum August to January flow (effectively the mean annual spring and summer flood) was 1,488 m³/s; values for individual seasons ranged from 630 m³/s in 1980 to 2,800 m³/s in 1979. Flow variability was lowest during August and September, although highly variable flows ($\hat{Q} > 1.6$) were recorded in all months.

Hydrographs for 1977 (a low-flow season) and 1984 (an above average season) illustrate the sharp peaks and rapid recession typical of Rakaia floods (Fig. 2). In the November 1984 event, discharge increased by a factor of 10 (from 172 m³/s to 1,710 m³/s) over 48 h and then fell from 1,960 m³/s to 455 m³/s over 72 h. Despite the contrast between the two seasons, both hydrographs also show a common period of low and relatively stable base flows in August and September, followed by more frequent floods as the season progresses.

Correlation analysis

Of the 32 flow parameters listed in Table 2, 29 showed no correlation with survival rates for Glenariffe Stream chinook (Table 3). Correlation coefficients for these indices ranged from -0.223 to 0.283, none of which differed significantly from zero ($P > 0.16$ in all cases). The three exceptions were the mean flow \bar{Q} , the maximum flow \hat{Q} , and the ratio of the mean to median flow \tilde{Q} , for the month of November. All three measures were positively correlated with survival ($\bar{Q}_{\text{NOV}}, P = 0.045$; $\hat{Q}_{\text{NOV}}, P = 0.003$; $\tilde{Q}_{\text{NOV}}, P = 0.006$). By contrast, there was no correlation between sur-



vival and the same set of flow variables for the adjacent months of October and December.

The strongest and most consistent set of correlations involved the ratio of mean to median flow, calculated over periods of 30 to 90 d duration centered on or about November 1 (Fig. 3A). Over much of this range the correlation between \tilde{Q} and log S exceeded 0.5, with a maximum value of 0.667 for \tilde{Q} calculated over the 40-day period from 9 October to 17 November. More generally, survival tended to be high for broods corresponding to years when flow variability during October, November, and early December was high. For periods centered on the four weeks between

Table 3

Correlations between log-transformed brood year survival rates for Glenariffe Stream chinook and 32 indices of Rakaia mainstem flows, 1965–90. See Table 2 for definitions of symbols. Asterisks denote correlations significant at the 95% level (*) and 99% level (**).

Period	Flow parameter						
	\bar{Q}	\hat{Q}	\tilde{Q}	N_{500}	$N_{1,000}$	$N_{1,500}$	$\hat{Q}_{10\text{max}}$
February–January (year)	-0.091						
August–January (spring and summer)	-0.105	0.109	0.182	-0.062	0.261	0.165	0.164
August–October (spring)	-0.195	-0.140	-0.218				
November–January (summer)	0.046	0.205	0.269				
August	-0.068	-0.054	-0.066				
September	-0.082	-0.191	-0.159				
October	-0.223	-0.053	0.283				
November	0.397*	0.558**	0.520**				
December	-0.214	-0.112	-0.088				
January	-0.070	0.053	0.141				

18 October and 15 November, of five to nine weeks duration, the correlation between \bar{Q} and $\log S$ averaged 0.493. Taken as an isolated result, this correlation corresponds to an average significance level of $P < 0.01$ and an average coefficient of determination (r^2) of 0.243. There was some evidence of a weaker and more transient period of negative correlation between \bar{Q} and $\log S$ earlier in the season. For \bar{Q} calculated over periods of seven to nine weeks duration and centered on the fortnight from 6–19 September, the correlation with $\log S$ averaged -0.404 , corresponding to an r^2 of 0.16. The symmetric upright “V” shape apparent in the contours of Fig. 3A, centered on the beginning of November, is an artifact caused by the tendency for data sets representing \bar{Q} over periods of similar duration centered on the same date to be highly correlated.

Maximum flow (\hat{Q}) and mean flow (\bar{Q}) were generally only weakly correlated with survival, and the few periods during which correlations stronger than ± 0.4 were recorded showed little tendency to persist over temporal scales of more than a few days (Fig. 3, B and C). In addition, these correlations tended to become stronger at shorter time scales, suggesting that for \bar{Q} , and possibly for \hat{Q} , the correlations apparent in Table 3 were a transient effect of a fortuitous sequence of flood events. By contrast, the persistence of a positive correlation between \bar{Q} and $\log S$ for flows averaged over periods of up to 90 days suggests that the relation is much more robust and hence likely to be of biological significance. The correlations between \bar{Q} , \hat{Q} , and \bar{Q} are also consistent with this interpretation. Whereas \bar{Q}_{NOV} and \hat{Q}_{NOV} were highly correlated ($r=0.84$), \bar{Q}_{NOV} was only moderately correlated with both parameters ($r=0.61$ in both cases), confirming that \bar{Q} captured information on flow variation not measured by either \hat{Q} or \bar{Q} .

The relation between \bar{Q} and $\log S$ was moderately influenced by the 1973 brood (for which the survival rate was unusually high) but was not dependent on it. The 1965, 1974, 1982, and 1983 broods (for which survival was also relatively high) and the 1985, 1986, and 1988

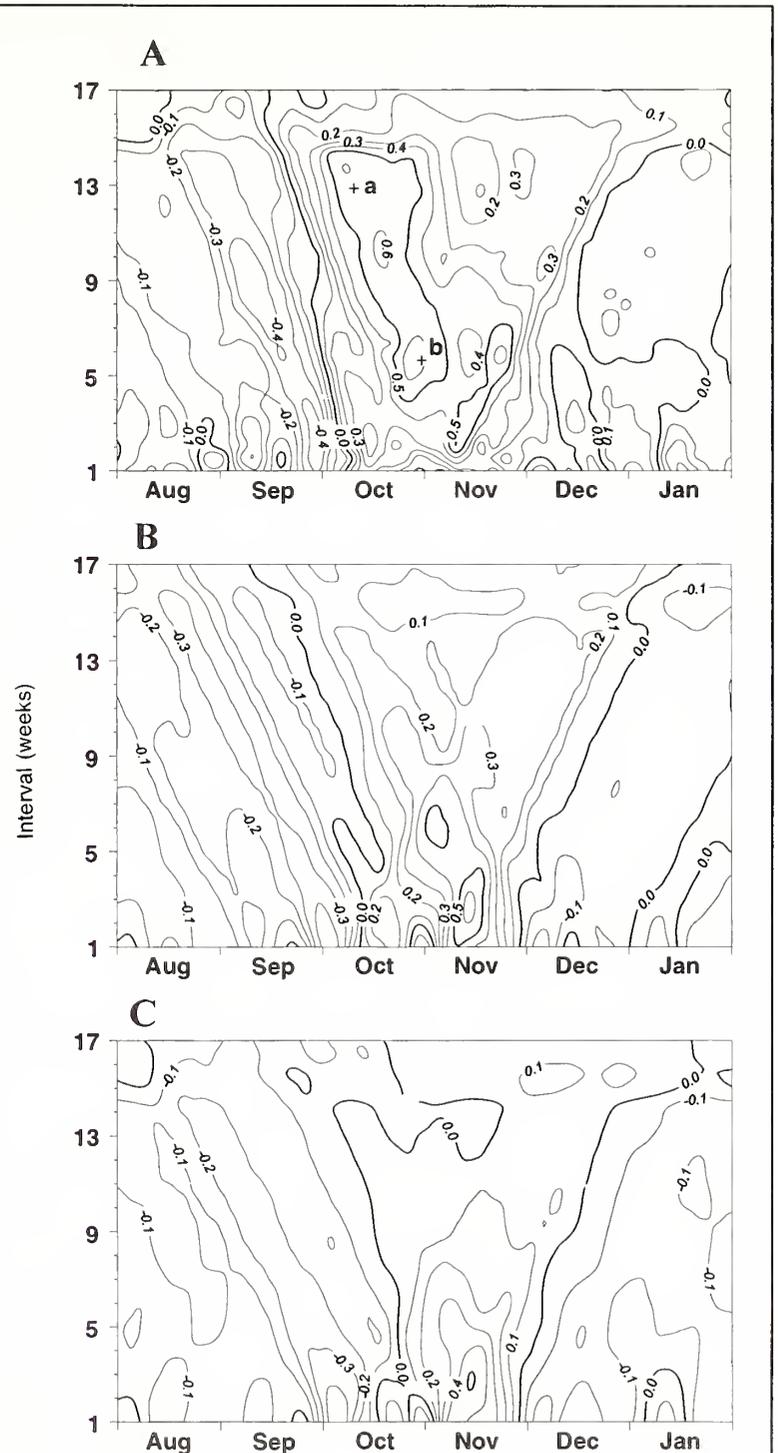


Figure 3

Correlations between log-transformed survival data for Glenariffe Stream chinook salmon and Rakaia River mainstem discharge expressed as the ratio of mean to median discharge (A), maximum discharge (B), and mean discharge (C), as a function of the period used to calculate each flow statistic. For each point, the locations on the x- and y-axes represent the mid-point of the period, and the duration, respectively. The points “a” and “b” correspond to the two intervals represented in Figure 4.

broods (for which survival was low) conform to the general trend irrespective of the duration of the period used to calculate \tilde{Q} (Fig. 4). With the exception of the 1969 brood, the value of \tilde{Q} during October and November was not highly sensitive to the choice of interval.

Discussion

Correlations and flow parameters

This study shows that, although fry-to-adult survival of Glenariffe Stream chinook salmon is correlated with the occurrence of springtime flood events in the Rakaia River, both the magnitude and the direction of the observed correlation depend strongly on the flow parameter used and the period over which this parameter is calculated. Survival was most strongly correlated with flow variability (as measured by the ratio of mean to median flow), the correlation being moderately negative for flows averaged over the period from mid-August to mid-October, and rather more strongly positive from mid-October to November. Similar but weaker correlations were apparent between survival and maximum flow, but mean flow was a poor predictor of survival irrespective of the time interval used.

The correlations reported here have two key features. First, although quite strong in a biological context, they are nevertheless relatively weak, accounting for at most 25–30% of the observed variation in

log survival. Even if the maximum positive correlation ($r=0.667$) is taken at face value, its predictive power allows years to be categorized only as “above average” or “below average,” at best (Prairie, 1996). This result is consistent with an earlier finding that annual survival rates for New Zealand chinook are primarily determined by marine rather than freshwater influences (Unwin, 1997; see also Bradford, 1995). Second, the tendency for survival to be positively correlated with flow variation but uncorrelated with mean flow suggests that increased flow variability (in the sense illustrated in Fig. 5) at the appropriate time of year is beneficial to survival. This is in sharp contrast to the generally held view that spring floods have a detrimental impact on chinook fry in the Rakaia and other New Zealand rivers (Waugh, 1980; McDowall, 1990; Flain¹).

The three key flow parameters used in this study—mean flow, maximum flow, and ratio of mean flow to median flow—are by no means the only ones possible and can only capture some of the information contained in the hydrograph for a given time period. Mean flow essentially measures the total volume of water passing through the river over the interval in question, without conveying any information about the magnitude or distribution of floods. For example, a 90-day mean of 200 m³/s could arise from 90 consecutive days at exactly 200 m³/s each, or from 89 days at 180 m³/s and one day at 1,980 m³/s. Maximum flow characterizes peak flood intensity, but not flow variability, so that a flow period with one 2,000 m³/s flood will outrank another period with ten 1,900 m³/s floods.

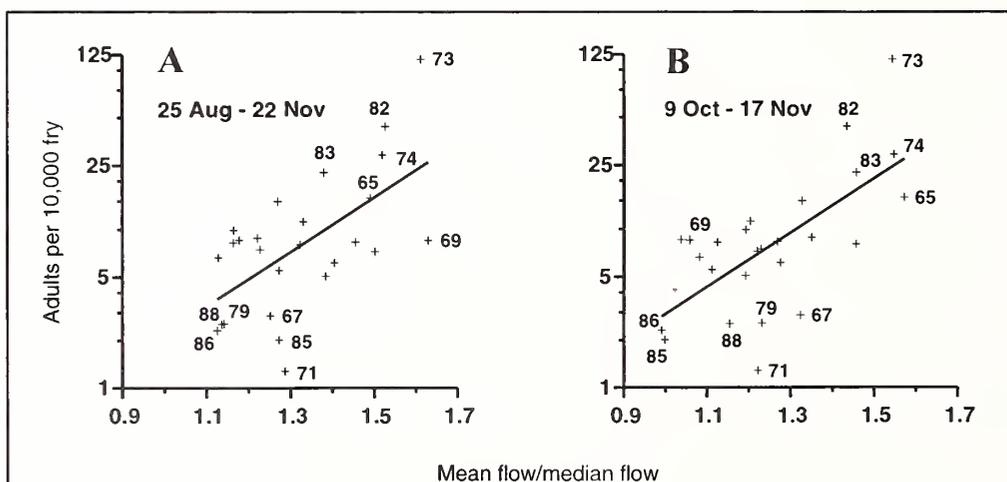
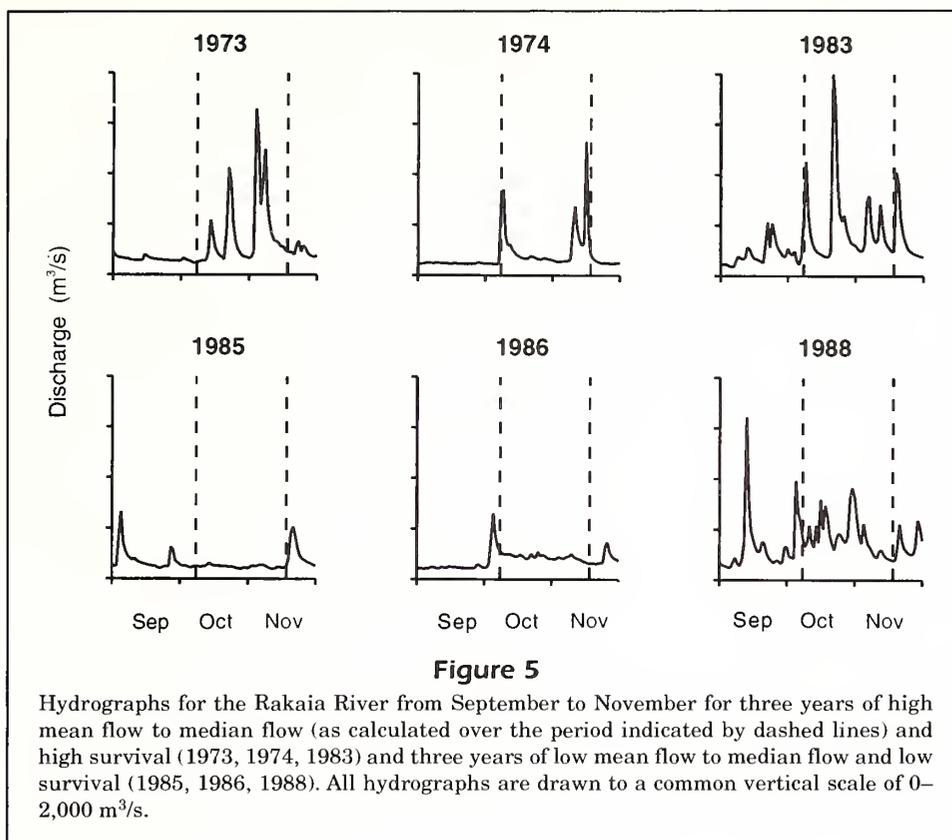


Figure 4

The relation between log-transformed survival data for Glenariffe Stream chinook salmon and the ratio of mean to median discharge in the Rakaia River mainstem for two periods near local maxima in Figure 3A. Twelve points corresponding to broods with extreme survival or flow indices for at least one of the two periods shown are identified by year.



The ratio of mean to median flow is a direct measure of flow variability, but it does not necessarily follow that low values of \bar{Q} correspond to low and stable flows. Flow regimes where \bar{Q} is close to one (i.e. mean flow differs little from the median) can arise in two different ways, only one of which corresponds to an extended period of low flows (Fig. 5). The other possibility is a period of highly variable flows superimposed on a high base flow, so that even though flows vary greatly from day to day, the flow distribution is only moderately skewed. By contrast, high values of \bar{Q} are more consistently associated with highly variable flows, tending to correspond to intervals when a lengthy period of low, stable base flows is punctuated by a relatively small number of short and sharp flood events. Both the 1973 and 1974 seasons ($\bar{Q}_{9 \text{ Oct} - 17 \text{ Nov}} = 1.54$ and 1.55 , respectively) were characterized by low and stable base flows during September, followed by two or three relatively short-lived flood events during October and November. The 1985 and 1986 seasons ($\bar{Q}_{9 \text{ Oct} - 17 \text{ Nov}} = 1.00$ in both cases) were characterized by uniformly low and stable flows, with no floods over the six weeks from 1 October. The effect of high base flows on flow variability is illustrated by comparing the 1983 and 1988 seasons ($\bar{Q}_{9 \text{ Oct} - 17 \text{ Nov}} = 1.46$ and 1.15 , respectively). Whereas base flows were low throughout 1983, so

that a 2,000 m³/s event in late October generated a high figure for \bar{Q} , the absence of a major flood during October and November 1988 produced a lower figure for \bar{Q} despite high and rapidly fluctuating base flows over most of the period shown.

The other flow parameters examined during the initial phase of this study, such as the number of days from August to January when flows exceeded a certain level, showed no correlation with survival. Although in principle it would have been possible to subject these parameters to the same level of analysis used for \bar{Q} , \bar{Q} , and \bar{Q} , this analysis becomes progressively less meaningful at shorter time scales. For example, given that $N_{1,000}$ ranged from 0 to 8 over a six month period (Table 2), the same statistic calculated over monthly intervals would typically take on only a few discrete integer values and would be inappropriate for correlation analysis.

Mechanisms

The topography of the correlations between \bar{Q} and survival, as illustrated by the qualitative features of Fig. 3A, coincides to a striking degree with several key events in the migration patterns of juvenile ocean-type fry in the Rakaia River. The period of highest positive correlation between flow variability

and survival, mid-October to November, coincides with the period when fingerlings first become abundant in the lower river and begin their transition to oceanic waters. The period centered on mid-September, when there is some evidence of a negative correlation between flow variability and survival, corresponds to the earlier time when fry are still migrating downriver and have yet to grow to the point where they are able to withstand the transition to salt water. Survival is not correlated, either positively or negatively, with flow variability at the beginning of the season (August, when most fry have yet to hatch) or at the end of the season (January, by which time most fingerlings have left the river). The correlation also tends to disappear when flow variability is averaged over more than about 100 days, a period that is consistent with the 90-day freshwater residence period of Rakaia fingerlings.

The tendency for survival to be positively correlated with flow variability rather than flow volume (as measured by \bar{Q}), and the short duration of each individual flood peak, suggest that these flood pulses must be an integral part of any plausible linking mechanism. Maximum survival appears to result when stable flows prior to mid-October are followed by a few (perhaps two or three) large floods over the next four to six weeks. By contrast, seasons when there are no major floods during October and November seem to result in poor survival irrespective of flows earlier in the season. Although any discussion based solely on the present results is speculative, I suggest that sudden increases in Rakaia discharge coinciding with peak emigration of fingerlings from the river mouth may increase survival by buffering the transition from fresh to saline waters in the vicinity of the offshore plume. If so, these pulses may help to compensate for the lack of an estuary at the Rakaia mouth and the low importance of the lagoon as a salmon rearing habitat,² one of the key features distinguishing the Rakaia (and other New Zealand salmon-producing rivers) from the extensive tidal basins below the Sacramento River mouth (Kjelson et al., 1982). The effect may be compounded by the well-documented tendency for downstream migration rates to increase with flow, both in New Zealand (Irvine, 1986) and North American populations (e.g. Kjelson et al., 1982; Berggren and Filardo, 1993), so that each flood pulse increases both the number of fingerlings leaving the river and their prospects for successful acclimation to salt water. Outflow of turbid flood waters may also increase survival by reducing visibility, and hence decreasing losses to inshore marine predators such as kahawai (*Arripis trutta*), although reduction in visibility is likely to be no more than a secondary effect (cf. St.

John et al., 1992). A positive correlation between survival of hatchery-reared Atlantic salmon (*Salmo salar*) and maximum river discharge during the first seven days after release has been attributed to reduced predation at higher flows (Hvidsten and Hansen, 1988).

A distinguishing feature of chinook salmon compared with other species of *Oncorhynchus* is their gradual acquisition of seawater tolerance while still in fresh water, without the sudden transition associated with smoltification in species such as coho (*O. kisutch*) or steelhead (*O. mykiss*) (Hoar, 1976). By early November, Rakaia fingerlings are of an age and size close to the generally accepted minima for successful transfer to seawater (Clarke and Shelbourn, 1985; Franklin et al., 1992), and water temperatures in the Rakaia River (12–15°C; Unwin, 1986) and at sea (12–14°C)⁸ appear to be within the optimal range for juvenile chinook salmon reported by these studies. However, acclimation to seawater also depends on the rate of transition. A gradual transfer to saline waters allows even very young fish to acclimatize successfully (Hoar, 1976), as evidenced by the abundance of chinook fry in low salinity estuarine waters in North America (Reimers, 1973; Healey, 1980; Levy and Northcote, 1981), including the lower Sacramento River (Kjelson et al., 1982). Changes in estuarine ecology during low-flow seasons in the Snake-Columbia River system have been suggested as a factor contributing to reduced survival of Snake River chinook (Williams and Matthews, 1995). In the Strait of Georgia, where the Fraser River plume forms a well-developed halocline at a depth of 5–10 m, juvenile salmonids showed a preference for surface waters of low salinity (10–15 ppt) in the plume, compared with the more saline waters (25–30 ppt) in other regions of the Strait (St. John et al., 1992). The Georgia Strait study also reported a tendency for plankton and larval fish to align with the plume boundary, providing enhanced feeding opportunities.

There have been no studies on salinity gradients off the Rakaia mouth, but nearshore salinity off Otago Harbour (on the east coast of the South Island 220 km south of the Rakaia) is inversely correlated with discharge from the Clutha River a further 100 km to the south (Jillett, 1969). The coastal shelf off the Rakaia River has a very gentle slope, with the 20-m isobath 5–10 km offshore (see Fig. 1). Consequently, peak Rakaia outflows should have a substantial impact on inshore salinity. For example, a daily mean discharge of 1 200 m³/s over 24 h (which is less than the mean annual spring flood) represents a total volume of fresh water of 0.1 km³, equivalent

⁸ 1997. NIWA, Christchurch, New Zealand. Unpubl. data.

to a 10 km² surface layer that is 10 m deep. Devolve- ment of the resulting halocline would presumably require considerable input of wave energy, and under calm conditions, a surface layer of low salinity water may persist for some days until dispersed to the north-east under the influence of the Southland current (Heath, 1972).

Implications

The analysis described in this study relates only to ocean-type fry. Because ocean-type fish make up approximately two thirds of the Rakaia adult population (Quinn and Unwin, 1993), fluctuations in their abundance would have a significant impact on brood year survival. However, one third of Rakaia adult chinook have a stream-type juvenile life history, and there is some evidence that the emergence of stream-type behavior in what was originally a fall-run stock represents an adaptive response to the lack of estuarine waters on New Zealand's salmon-producing rivers (Unwin and Glova, 1997). The freshwater habitat preferences and migration patterns of stream-type chinook in the Rakaia River are poorly understood, and their sensitivity to flow variations is unknown. However, the possibility that survival of ocean-type fry may increase in seasons of variable flow could provide a compensating selective force that would help to establish a balance between the incidence of the two phenotypes. If so, the ratio of ocean- to stream-type fry in any one annual cohort should also be positively correlated with the variability of spring flows into the Rakaia River during the first year of life.

To explore this hypothesis further, and hence to provide an independent test of the plausibility of the mechanisms outlined in the previous section, I examined archival material from NIWA's scale collections, aspects of which are summarized in Tables 2, 3, and 4 of Quinn and Unwin (1993). These records include scale samples from salmon taken in the Rakaia sports fishery for nine annual cohorts between 1965 and 1984. These scale samples permitted returning fish from each cohort to be classified according to juvenile life history. The incidence of ocean-type fish among 3-year-old adult chinook was positively correlated with mainstem flow variability over the period 9 October to 17 November ($r^2=0.54$, $P=0.025$; Fig. 6) during the year in which they emigrated as juveniles. Of particular interest is the high incidence of ocean-type fish in the 1973 and 1982 cohorts, which were also the broods for which survival was highest.

With regard to the New Zealand salmon fishery, which is managed purely for recreational anglers

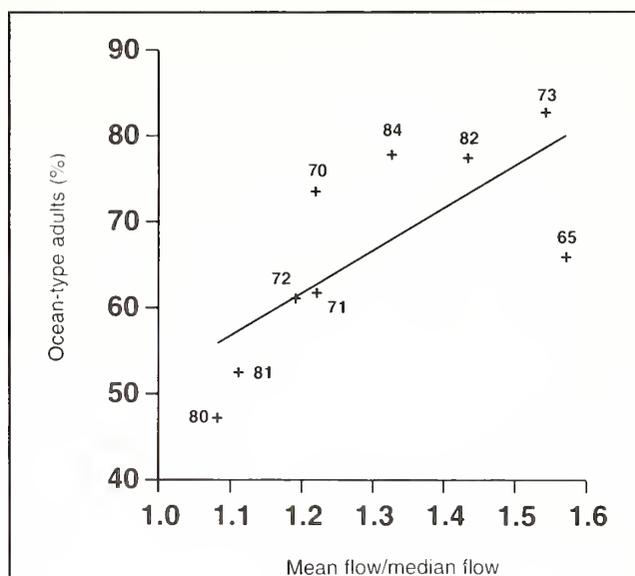


Figure 6

The relation between the incidence of ocean-type adults among 3-year-old chinook salmon caught by Rakaia River anglers over nine seasons from 1965 to 1984, and the ratio of mean to median discharge in the Rakaia mainstem for the corresponding juvenile cohort, for the same time interval (9 October to 17 November) as that represented in Figure 4B. Sample sizes averaged 127, and ranged from 36 to 373.

(McDowall, 1994b), the main conclusion to be drawn from this study is that despite the observed correlations between survival and flow variability, interannual variation in survival remains at best weakly predictable. However, spring flow variability is easy to analyze on a season by season basis, and the possibility of making at least a broad prediction identifying years of high or low survival up to two seasons in advance suggests the effort is worth making. The New Zealand Fish and Game Council (which is responsible for management of the sports fishery) have recently instituted annual monitoring programs for key spawning runs in all major salmon rivers,⁹ and these will eventually enable comparisons between survival and flows to be made for other major east coast catchments. My results also suggest that any reduction in flow variability resulting from development of storage impoundments for hydroelectric or irrigation purposes would have a significant negative impact on the fishery over and above any losses caused by barriers to upstream passage. The high bed load of major braided rivers such as the Rakaia makes them unattractive candidates for impoundment, but declines in salmon runs in two other riv-

⁹ Webb, M. 1997. Central South Island Fish and Game Council, PO Box 150, Temuka, New Zealand. Personal commun.

ers (the Clutha and Waitaki) following hydroelectric development (McDowall, 1990) may be partly linked to a reduction in the magnitude and frequency of spring floods. A positive association between salmon production and large offshore plumes is also consistent with the general distribution of salmon in east coast rivers (McDowall, 1990), with the largest populations confined to major rivers draining the main divide. Traditionally this distribution has been attributed to the presence of stable headwater spawning tributaries such as Glenariffe Stream, but this explanation is not fully convincing. Many minor east coast rivers support self-sustaining stocks of brown trout (Jowett, 1990; McDowall, 1990), and spawning requirements for chinook are not dissimilar.

From an evolutionary standpoint, the present results help to shed further light on the processes by which chinook salmon have been able to succeed in New Zealand waters. In addition to the emergence of stream-type fish as a significant component of modern New Zealand stocks, several other recent studies have noted differences between present-day New Zealand and Sacramento chinook at both phenotypic and genotypic levels (Quinn and Unwin, 1993; Quinn et al., 1996), suggesting that the process of adaptation may be ongoing. The somewhat unusual mechanisms which have apparently enabled New Zealand chinook salmon to establish the only self-perpetuating stocks outside their native range (Harache, 1992) underscore the great phenotypic plasticity of the species, and the value of the New Zealand populations as a laboratory for studying this plasticity.

Acknowledgments

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Abstract.—From the mid-1970's to the mid-80's, Stellwagen Bank was an important humpback whale feeding area with sand lance (*Ammodytes* spp.) as the major prey. Between 1988 and 1994, however, the number of humpback whales we identified each year on Stellwagen declined from a high of 258 (1990) to 7 (1994), and the mean number of whales identified per day fell from 17.7 (1988) to 0.9 (1994). Adult whales decreased steadily after 1988; juveniles decreased rapidly after 1991. Echo-sounder data from Stellwagen showed that prey trace levels declined from 19.1% of the vertical water column in 1990 to 2.8% in 1992 (no readings were taken in 1988–89, or 1993–94). Simultaneously, the number of whales identified on Jeffreys Ledge, north of Stellwagen Bank, increased dramatically beginning in 1992. Sixty-four percent of the whales identified on Jeffreys in 1992–94 were seen on Stellwagen Bank in 1988 and 1989. We hypothesize that humpback whales shift their distribution in order to prey upon recovering herring populations, their primary source of food.

A shift in distribution of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern Gulf of Maine

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Humpback whales, *Megaptera novaeangliae*, migrate seasonally between low-latitude breeding grounds and high-latitude feeding areas (Kellogg, 1929; Mackintosh, 1965; Katona, 1986). In the western North Atlantic, whales that winter in Caribbean waters migrate to feeding grounds in New England (the Gulf of Maine), in the Gulf of St. Lawrence, and in waters off Newfoundland, Greenland, Iceland, and Norway (Katona and Beard, 1990). The whales using each feeding area appear to consist of extended matriline (Baker et al., 1990; Clapham et al., 1992). Within feeding areas, prey distribution has been a primary influence on the local distribution and micro-movements of all baleen whales examined to date (Whitehead and Carscadden, 1985; Payne et al., 1986, 1990; Piatt et al., 1989).

Studies of humpback whale movement, ecology, demography, behavior, and social organization on their feeding grounds in the Gulf of Maine have been ongoing since the mid-1970's, (Payne et al., 1986; Clapham and Mayo, 1987, 1990; Weinrich, 1991; Weinrich and Kuhlberg, 1991; Clapham et al., 1992; Weinrich et al., 1992; Katona et

al.¹). During this period, several shifts in the distribution of humpback whales have been reported. Payne et al. (1986) showed that humpback whales in the late 1970's had moved from primary abundance on Georges Bank and in the waters of the northern Gulf of Maine to the inshore southwestern Gulf of Maine, especially Stellwagen Bank and the Great South Channel. They attributed this shift to a fishery-induced collapse of herring (*Clupea harengus*) populations (Anthony and Waring, 1980; Grosslein et al., 1980) and a corresponding increase in sand lance (*Ammodytes* spp.) (Meyer et al., 1979; Sherman et al., 1981, 1988; Sherman 1986; Sissenwine 1986). Both species are known prey for humpback whales (Mitchell, 1973; Overholtz and Nicholas, 1979; Kawamura, 1980). These fish species are potential ecological competitors (Reay, 1970; Meyer et al., 1979; Sherman et al., 1981); moreover, herring are known predators of

¹ Katona, S. K., P. Harcourt, J. S. Perkins, and S. D. Kraus. 1980. Humpback whales: a catalog of individuals identified by fluke photographs. College of the Atlantic, Bar Harbor, ME, var. pagination.

sand lance (Fogarty et al., 1991). Sightings of humpback whales off the Maine coast, where herring were the primary whale prey, decreased dramatically during the late 1970's (Payne et al., 1986; Mullane and Rivers²). Sand lance frequently use shallow areas with sandy bottoms, such as Stellwagen Bank in the southern Gulf of Maine (Meyer et al., 1979). This shift in distribution, and corresponding change in primary prey type, may have also led to changes in feeding behavior (Weinrich et al., 1992). Humpback whales remained abundant in the southwestern Gulf of Maine throughout the 1980's, with a brief decrease in some areas during 1986–87 (Payne et al., 1990; Cetacean Res. Unit³).

We documented a gradual but continuous decrease in the use of Stellwagen Bank by humpback whales during 1988–94. Our data suggest that whales have returned to a distribution similar to that documented until the late 1970's. We hypothesize that this return is due to the recovery of herring stocks in the Gulf of Maine and to a corresponding decrease in available prey for humpback whales on Stellwagen Bank and in other areas favored by sand lance in the southwestern Gulf of Maine.

Methods

Survey methods

From 1 May to 30 October, 1988 to 1994, daily shipboard surveys were carried out aboard commercial whale-watching boats. These departed from Gloucester and Boston, Massachusetts, and were typically 4–5 hours in duration. There were usually two cruises per vessel per day. A typical cruise included 90–120 minutes in areas where whales were often observed, as well as 2–3 hours of transit time. Whale watches usually emphasized the northern half of Stellwagen Bank. On occasion, whale watches surveyed the southern half of Jeffreys Ledge to the northeast of

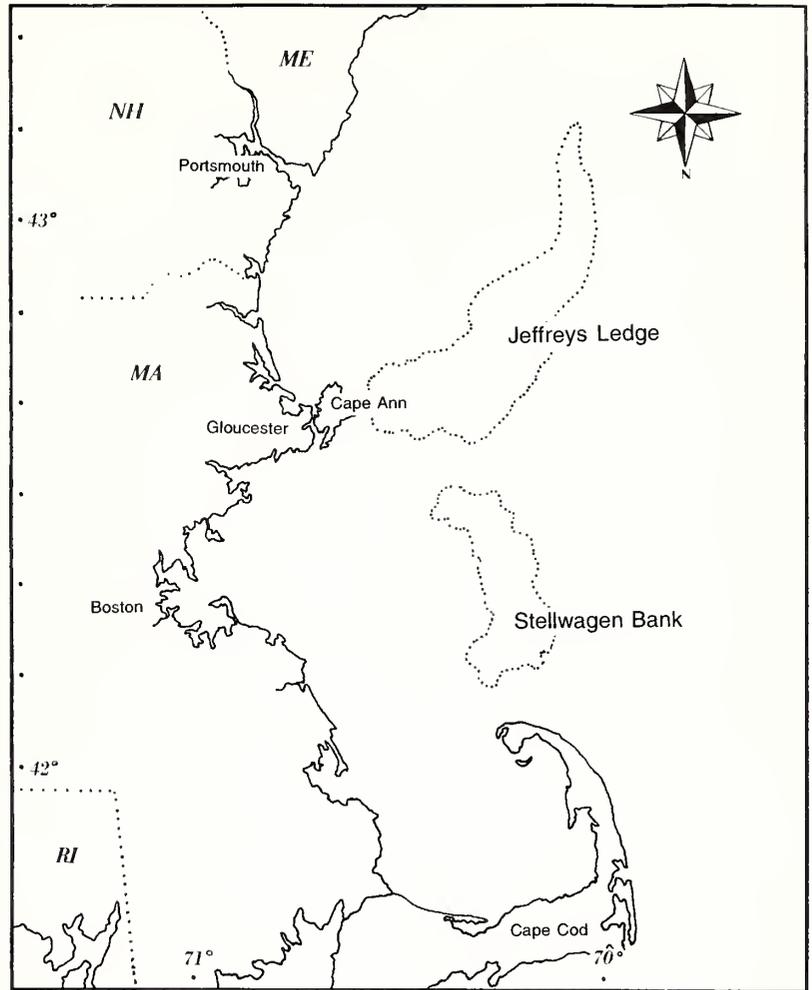


Figure 1

The study area in the Gulf of Maine.

Cape Ann (Fig. 1). This effort is detailed in Table 1. Within each whale-watching trip, protocol and typical amount of observation time were consistent on all vessels.

Whale-watching cruises were supplemented by occasional day-long (7–13 h) excursions on research vessels. These took place 1 April to 15 November of each year, with emphasis on April and October–November, as well as during periods of significant whale concentration from May to September. During each cruise, a specific attempt was made to conduct a comprehensive photo-identification survey of a specific area (i.e. northern Stellwagen Bank, southern Jeffreys Ledge, etc.). As time allowed, coverage was devoted to a larger portion of the entire geographic feature (either Stellwagen Bank or Jeffreys Ledge). Specific areas were determined by recent sightings of whale aggregations, reliable reports of whale sightings from local boaters, or a determination that an area had not been recently surveyed. Jeffreys

² Mullane, S. J., and A. Rivers. 1982. Mt. Desert Rock, Maine. Annual Report, 27 p. [Available from Allied Whale, College of the Atlantic, Bar Harbor, ME.]

³ Cetacean Research Unit. 1980–89. Cetacean Research Unit, PO Box 159, Gloucester MA 01930. Unpubl. data.

Table 1

Study effort by both number of survey days and number of survey trips for both Stellwagen Bank and Jeffreys Ledge. "JLSN days" represent the total number of survey days represented by the Jeffreys Ledge Sighting Network (JLSN), established after the 1992 season (see text for further details).

Year	Stellwagen days	Stellwagen trips	Jeffreys days	Jeffreys trips	JLSN days
1988	145	558	16	44	0
1989	151	550	17	20	0
1990	166	516	32	37	0
1991	160	460	31	36	0
1992	171	506	34	37	69
1993	106	364	48	79	119
1994	86	141	86	141	138

Ledge was the destination for just under half of the dedicated cruises from 1988 to 1992, all but four in 1993, and all but two in 1994.

Beginning in 1990, sighting and photo-identification data were also collected from a whale-watching boat operating out of Kennebunk, Maine, to obtain information from the northern end of Jeffreys Ledge. Observer coverage was for one trip per day, 3–5 days per week. Because of the unusually large number of whales first observed on our dedicated cruises to Jeffreys Ledge in 1992, a photo-identification network (consisting of three whale-watching boats working on Jeffreys Ledge for one trip per day) was formalized in fall 1992 (after the completion of field efforts), and existing 1992 data were obtained. Beginning in 1993, data collection from these vessels was standardized to be directly comparable with Stellwagen Bank whale-watching data. Because 1993 represented the first year in which Jeffreys Ledge data were collected in any kind of standardized fashion, occurrence and occupancy (defined below) were not calculated for Jeffreys Ledge humpback whale sightings.

Study areas

Stellwagen Bank, now a National Marine Sanctuary, is a sandy glacial deposit approximately 32 km long with depths from 18 to 37 m (Fig. 1). It borders the eastern margin of Massachusetts Bay and is located approximately halfway between Cape Ann and Cape Cod, Massachusetts. Jeffreys Ledge is a more complex, winding, shallow ledge, with typical depths of 45 to 61 m and with a length of approximately 54 km. Its substrate is a mixture of rocky and muddy bottoms. The southern edge of Jeffreys Ledge is 9 km northeast of Rockport, Massachusetts, whereas the northern end lies 36 km east of York, Maine.

Stellwagen Bank and Jeffreys Ledge are separated by 21.6 km at their closest point.

Field methods

Individual humpback whales were identified from photographs of distinctive pigment patterns on the ventral surface of their tail flukes or from the shape of and scarring on the dorsal fin (or by both features) (Katona and Whitehead, 1981). Two observers collected data on each whale or group of whales. One observer was responsible for photographing each whale, while the second recorded the whale's location (by means of LORAN-C), group affiliations, and behavior. This observer also recorded which photographs were taken of each whale, as dictated by the photographer. Each group of whales in an area was usually observed for 1–30 minutes; most, if not all, whales in a single location (3–5 km radius) were identified during each observation period. Field methods were consistent on all vessels.

Age class and sex determination

Individuals were identified by comparing photographs with those of a catalog of humpback whales maintained at the Cetacean Research Unit (CRU), Gloucester, MA. Details on cataloging methods and contents of the catalog were given in Weinrich (1991), Weinrich and Kuhlberg (1991), and Weinrich et al. (1992) and are based on procedures outlined by Katona and Whitehead (1981). Whales were sexed by photographing them while belly up at the surface (and by noting the presence or absence of a small lobe immediately posterior to the genital slit [Glockner, 1983]), by observing a female with calf, or by using molecular techniques (Baker et al., 1991). Individuals were assigned to age classes (juvenile or adult) based on known age (first observation as a calf) or based on the consensus among all experienced CRU observers of an animal's relative size at first sighting. The accuracy of the latter technique was confirmed by estimating the age class of animals of unknown identity in the field and by finding that these estimates matched (photographically) animals of known age. No incorrect classifications were made ($n=51$). For the purposes of this paper, an animal was classified as an adult if it was known to be at least five years old, an age at which 50% or more of the population is mature (Chittleborough, 1965; Clapham and Mayo, 1990).

Prey density

In 1990–92, a SITEX HE-358 50-kHz echo-sounder and chart recorder aboard a whale-watching vessel

were used to record prey density on Stellwagen Bank in the immediate area where whales had been observed. The echo-sounder was used for 83 days during 1990 (9 May to 20 October; 153 total hours), 98 days during 1991 (9 May to 28 September; 221 total hours), and 69 days during 1992 (24 April to 24 October; 60 total hours). Clear readings throughout the water column (i.e. with no interference present) were obtained for 69 hours in 1990, 166 hours in 1991, and 60 hours in 1992. An echo-sounder operating at this frequency is likely to detect the presence of fish but unlikely to detect plankton unless it is present in extreme densities (Dolphin⁴). The echo-sounder was started as the boat slowed to begin whale observations and turned off when the vessel left the observation area to return to port. Because echo-sounder tracings were obscured by noise when the vessel was moving at cruising speed (e.g. moving from one group of whales to the next), tracings performed at cruising speed were eliminated from analysis. A timing mark was placed simultaneously on both the echo-sounder chart and the data sheets by the second observer at 10-min intervals.

The echo-sounder chart was later sampled at 2-min intervals by interpolating between the 10-min marks. For each sampling point, prey presence was scored visually in 3.3 m (10 ft) vertical increments from the surface to the bottom, with a sliding score of zero (for no prey) to 10 (prey throughout that 3.3 m interval). From these readings mean values for vertical bait density were calculated for each quarter of the water column and the total water column. Mean depth in which readings were taken was 38.4 m (SD=15.1 m). No echo-sounder data were recorded on Jeffreys Ledge.

Although such data give an idea of the availability of prey in the immediate vicinity of whales, they do not reflect an area where whales were not present. Hence, there could have been very similar or different prey concentrations very nearby, without that information ever being recorded. However, since each year's data set came from numerous days and contained data points from several different locations (albeit within a 3–4 mile radius) within each day's observations, we feel they at least give a crude overview to overall prey densities in the vicinity of whales.

Data management and analysis

Both daily whale sighting data and prey density data were stored in PC-based computer files and analyzed with commercially available statistical software

(SPSS/PC+, Kinnear and Gray, 1992). For daily sighting data, an Xbase program was written to isolate the sightings of each whale and to calculate statistics summarizing that individual's within-year sighting history (including occurrence and occupancy—see below) in each part of the study area. These values were then stored in a separate data file and analyzed with the same statistical software. Temporal trends were analyzed with least-squares regression (Snedecor and Cochran, 1967) of individual data points with the year of observation as the independent variable, although only annual means are presented in our tables for occurrence and occupancy scores. The slope of the regression line (B) and the probability value (P) from a test of the null hypothesis that the slope did not differ from zero are presented for each test. Calves were eliminated from these analyses because we assumed that a calf is merely following the mother in her choice of habitat.

Definitions

"Occurrence" is defined as the number of days on which an individual whale was photographed in a single year. "Occupancy" is the number of days elapsed from the first to the last recorded sighting of an individual whale within a year. These definitions are consistent with those used by Clapham et al. (1992).

Results

Stellwagen Bank

Total number of humpback whales identified per year The number of humpback whales identified in any single year on Stellwagen Bank ranged from 258 (1990) to a low of 7 (1994), with a mean of 153.6 (SD=88.4) (Fig. 2). These values show a statistically significant declining trend ($B=-32.82$, $P=0.033$).

When the total number of whales was broken into age class, differences in annual trends were apparent. Numbers of adult whales identified on Stellwagen ranged from 173 (1990) to 3 (1994; mean=102.8, SD=60.4). These values also showed a statistically significant declining trend ($B=-0.84$, $P=0.018$). Number of juveniles identified in each year varied from 85 (1990) to 4 (1994; mean=50.71, SD=29.2). These also showed a downward trend, although not statistically significant ($B=-23.50$, $P=0.099$). The ratio of identified adult whales to identified juveniles varied from 2.5:1 (in 1988) to 0.75:1 (in 1994). Numbers of cow-calf pairs throughout the study period

⁴ Dolphin, W. F. 1994. Department of Biomechanical Engineering, Boston University, Boston, MA 02215. Personal commun.

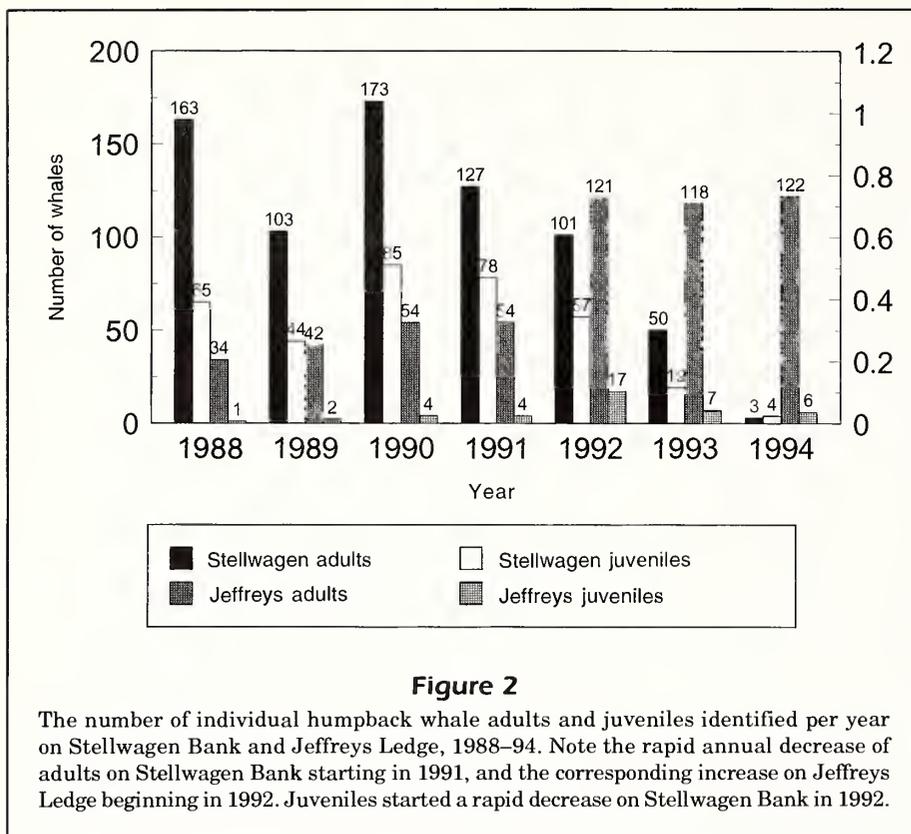


Figure 2

The number of individual humpback whale adults and juveniles identified per year on Stellwagen Bank and Jeffreys Ledge, 1988-94. Note the rapid annual decrease of adults on Stellwagen Bank starting in 1991, and the corresponding increase on Jeffreys Ledge beginning in 1992. Juveniles started a rapid decrease on Stellwagen Bank in 1992.

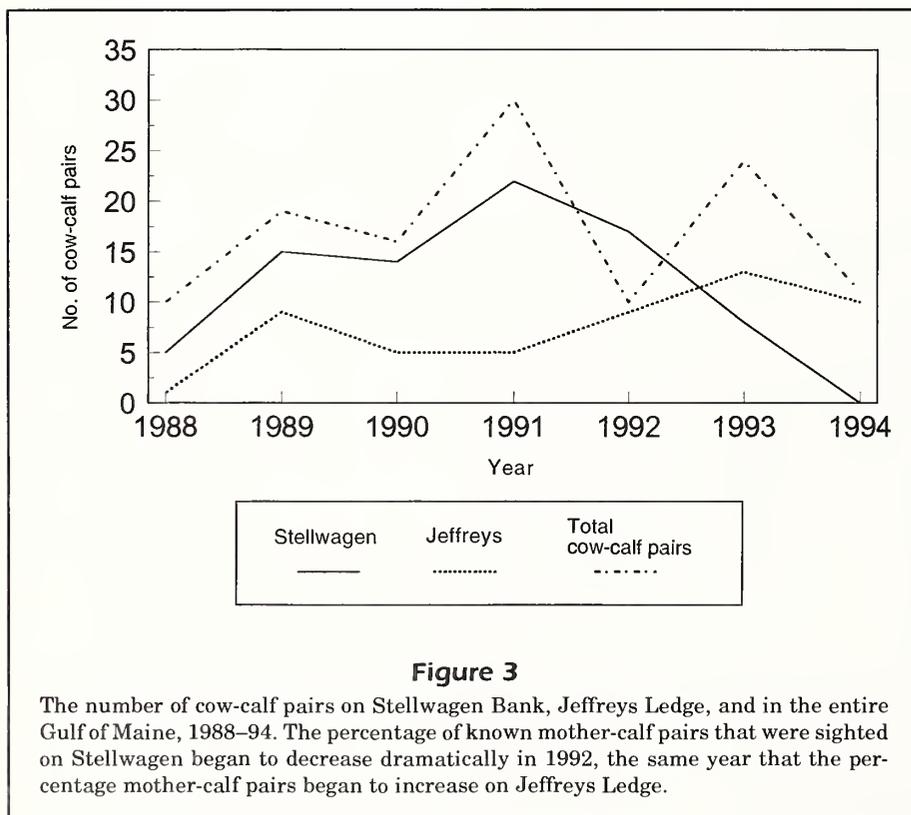


Figure 3

The number of cow-calf pairs on Stellwagen Bank, Jeffreys Ledge, and in the entire Gulf of Maine, 1988-94. The percentage of known mother-calf pairs that were sighted on Stellwagen began to decrease dramatically in 1992, the same year that the percentage mother-calf pairs began to increase on Jeffreys Ledge.

showed no significant trend in the absolute number seen on Stellwagen ($B = -1.214$, $P = 0.424$). Numbers of cows and calves began in 1991 to decline sharply, especially when compared with the total number of cow-calf pairs in the Gulf of Maine. By the last year of the study no cow-calf pairs were seen (Fig. 3).

Occurrence and occupancy

Mean occurrence of humpback whales on Stellwagen Bank within a single season ranged from 13.1 days (1989, $n = 147$) to 6.6 days (1993, $n = 69$) (Table 2; $B = -0.30$, $P = 0.501$). Adults showed a within-year mean occurrence of 6.4 days ($SD = 4.8$, $n = 720$), with a statistically significant declining trend through the study period ($B = -1.98$, $P < 0.001$). Compared with adults, juveniles showed a higher mean within-year occurrence (mean = 14.5 days, $SD = 4.2$, $n = 352$), which significantly increased throughout the study period ($B = 1.63$, $P = 0.030$).

Occupancy of individual whales within years declined significantly from a mean of 61.8 days (1989, $n = 147$) to 21.6 days (1994, $n = 7$) (Table 3; $B = -7.07$, $P = 0.002$). Again, age classes showed different trends. Adults had a mean occupancy period of 39.3 days ($SD = 23.56$, $n = 720$) throughout the study period, with a significant declining trend ($B = -10.65$, $P < 0.001$). In contrast, juveniles had a mean occupancy period of 55.0 days ($SD = 13.21$, $n = 352$), with no significant trend apparent ($B = -2.82$, $P = 0.296$).

Although juveniles showed no significant trend in occupancy and had occurrence values that actually increased throughout the period, a comparison of median values for

Table 2

The mean occurrence (in days) of humpback whales on Stellwagen Bank, 1988–94.

Year	Adults	Juveniles	Combined total
1988	13.5	7.2	11.2
1989	12.2	15.2	13.1
1990	7.9	12.5	9.6
1991	6.2	17.0	10.7
1992	7.2	19.6	12.0
1993	3.1	15.7	6.6
1994	1.3	19.8	11.9

Table 3

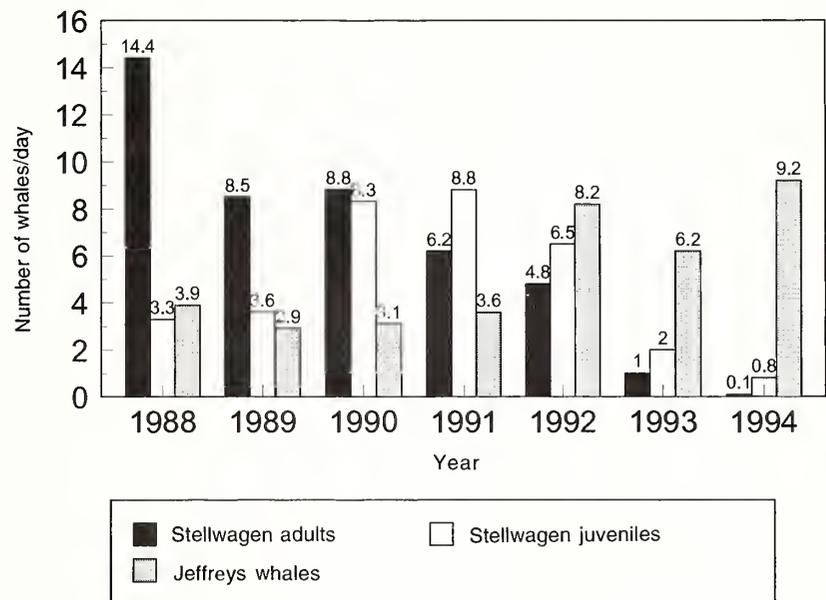
The mean occupancy (in days) of humpback whales on Stellwagen Bank, 1988–94.

Year	Adults	Juveniles	Combined total
1988	67.9	47.1	60.4
1989	56.5	71.6	61.8
1990	52.3	55.0	51.8
1991	47.5	73.1	54.6
1992	32.4	53.3	42.2
1993	17.2	48.4	25.7
1994	1.3	36.8	21.6

each of these variables portrays a trend more similar to that seen from adults. From 1992 through 1994, prolonged residency of a few juveniles skewed occurrence and occupancy values. During 1991–93, median occurrence of juveniles fell from seven days to three, whereas median occupancy periods fell sharply, from 59.5 days to 15 days. In 1994, so few juveniles were seen (four) that the relatively high values of two individuals severely skewed the results for that year. Median values of adult occurrence and occupancy showed the same trends as those portrayed from the regression analyses.

Number of whales per day

One of the clearest indicators of habitat use is the number of identified humpback whales sighted on Stellwagen Bank each day. This measure incorporates two of the above components—the number of whales identified as well as how often they were sighted in the area. Throughout the study period, a mean of 12.7 (SD=11.31, $n=1,072$) whales were identified per day, ranging from an annual high of 17.7 (SD= 15.30, $n=153$ days) in 1988 to a low of 0.9 (SD=0.76, $n=97$ days) in 1994 (Fig. 4). Adults and juveniles again showed different trends. Adults per day declined steadily from 14.4 in 1988 to 0.1 in 1994 ($B=-2.21$, $P<0.001$), whereas juveniles showed no clear trend, with a high of 8.8 in 1991 and a low of 0.8 in 1994 ($B=-0.44$, $P=0.501$). Juvenile values showed a clear peak in 1990–91 as compared with other years (Fig. 4).

**Figure 4**

The mean number of whales identified per day in each age class and year on Stellwagen Bank and Jeffreys Ledge, 1988–94. Jeffreys Ledge juveniles were not included because of their low numbers. Note the rapid decrease among adults on Stellwagen Bank beginning after 1988, and the decrease among juveniles on Stellwagen beginning in 1992. Jeffreys Ledge values were highest in the final three years, after the general decrease on Stellwagen Bank.

Vertical prey density Mean overall vertical prey density decreased from 19.1% with prey traces in 1990 to 2.8% with prey traces in 1992 ($B=-0.38$, $P<0.001$) (Table 4). Similar significant decreases were seen in each vertical quarter of the water column (Table 4).

Although it was impossible to determine prey type from traces alone, catches of groundfish (mainly Atlantic cod [*Gadus morhua*] and haddock [*Melanogrammus aeglefinus*]), and bluefish (*Pomatomus saltatrix*) in the immediate area of trace recordings

Table 4

Percentage of the water column with echo-sounder prey traces by year in each quarter. Mean depth was 38.4 meters.

Year	Quarter of the water column				Total
	Top 25%	2nd 25%	3rd 25%	4th 25%	
1990	17.2%	15.0%	16.8%	24.3%	19.1%
1991	3.1%	4.5%	7.3%	12.7%	7.9%
1992	1.4%	0.3%	0.8%	1.1%	2.8%

by party-fishing boats indicated that sand lance were the predominant fish prey in stomach contents of humpback whales; some small mackerel (*Scomber scombrus*) and herring were also observed in stomachs in much lower frequencies. Herring were more prominent in October during each field season, when only a small number of echo-sounder data points were recorded.

Jeffreys Ledge

Total number of humpback whales identified The number of humpback whales we identified on Jeffreys Ledge increased from a low of 35 (in 1988) to a high of 138 (in 1992) ($B=19.57$, $P=0.004$; Fig. 2). Although there was a generally increasing trend, there was a sudden increase from 58 in 1991 to 138 in 1992.

The increase among adult whales also showed a significant increase across years ($B=17.25$, $P=0.003$). Although juveniles increased steadily throughout the period, and suddenly from 1991 to 1992, they did not do so at a significant rate ($B=1.357$, $P=0.201$). (The same analysis without 1992 data, where there were an unusually high number of juveniles, does show a statistically significant increasing trend among juveniles [$B=0.914$, $P=0.006$]). Cow-calf pairs also showed a significantly increasing trend ($B=1.429$, $P=0.049$).

In each year, identified humpback whales on Jeffreys Ledge were biased toward adults. No more than 17 juveniles were photographed on Jeffreys Ledge in any year, and the number of juveniles photographed exceeded 10 in only a single season (1992). The ratio of adult to juvenile whales ranged from a high of 34.0:1 in 1988 to 7.1:1 in 1992, higher in all cases than the adult:juvenile ratios on Stellwagen Bank.

Number of whales per day The mean number of whales per day ranged from a low of 2.9 ($SD=1.9$, $n=22$) in 1989 to a high of 9.2 ($SD=7.7$, $n=138$) in 1994 (Fig. 4; $B=0.98$, $P=0.022$). In 1993 and 1994, the only years with coverage comparable to Stellwagen Bank levels, means of 6.2 ($SD=6.9$, $n=116$) and

9.2 ($SD=7.7$, $n=138$) whales were identified on each day of coverage, respectively.

The pattern of humpback abundance on Jeffreys Ledge showed surprising seasonal consistency throughout the study. Sightings were sporadic during May, June, and early July, with few, if any, concentrations of whales observed. In all years, concentrations increased from late July through September, with whales still abundant in three of the seven Octobers observed (1988, 1989, 1993).

Identification comparison To determine whether the whales using Jeffreys Ledge were the same as those previously inhabiting Stellwagen Bank, we examined how many of the 210 humpback whales identified on Jeffreys Ledge in 1992–94 had been previously sighted on Stellwagen Bank. Of this group, 123 (58.5%) were photographed on Stellwagen Bank during 1988–89. When the 17 animals that had not yet been born in 1988–89 were also discounted from the Jeffreys population, 63.7% of all animals were found to have been seen previously on Stellwagen. By comparison, only 35 (16.6%) of the Jeffreys Ledge whales were also seen on Stellwagen Bank during the 1992–93 period, or 16.6% of the total Jeffreys Ledge population.

Discussion

Humpback whales, especially adult and cow-calf pairs, decreased their use of Stellwagen Bank drastically between 1988 and 1994. The decreased use is reflected in decreased numbers of whales identified, decreased numbers of whales (regardless of age class) per day, and decreased adult occurrence and occupancy. The decline led to a virtual abandonment in 1994, when only seven humpback whales were seen on Stellwagen, and only two of those had occupancy periods longer than ten days. The decline in whale use corresponds with a decline in the amount of echo-sounder prey traces at the sites on Stellwagen Bank where whales were found over three years during the study. Although adults showed a clear decreasing trend on Stellwagen Bank, juvenile whales showed a less clear pattern. However, even juveniles showed a rapid decrease in use from 1991 to 1994.

The increase in juvenile whales on Stellwagen Bank during 1990–91 while adult use decreased may also be a more subtle indicator of a shift in habitat quality. Previous work has shown that juvenile humpback whales are often found in areas where prey density is lower than in areas where adults predominate (Weinrich and Kuhlberg, 1991; Belt et al.⁵), and may, therefore, be considered suboptimal

habitat for the species. The vertical distribution of prey has also been reported to be different between concentration areas of the two age classes. Adults are found where prey is concentrated in the upper reaches of the water column (Belt et al.⁵) where a humpback whale's bubble and cooperative feeding strategies are most effective (Hain et al., 1982; D'Vincent et al., 1985; Weinrich et al., 1992; Weinrich et al.⁶) or where foraging is most efficient because energy expenditures associated with diving are lowest (Dolphin, 1987). Juveniles appear to concentrate more often in areas where prey are predominantly subsurface, often feeding on or near the sea floor (Swingle et al., 1993; Hain et al., 1995; Belt et al.⁵; Weinrich et al.⁶). In the years where juvenile use increased while adult use decreased (1990–91), echosounder data showed that prey were most concentrated in the bottom 25% of the water column. Even within the year 1990, prey traces were found to be more common in the upper portions of the water column on days when more adult whales than juveniles were present (Belt et al.⁵).

These findings suggest that there are multiple ways of assessing habitat quality for whales. Past reports of population trends have included only the number of whales sighted per unit of effort as a guide to habitat quality (Payne et al., 1986, 1990; Piatt et al., 1989). However, indicators such as independent trends in occurrence and occupancy of individual whales, the number of individuals identified over a given time period, and even the age class of individuals, may also be important indicators of habitat quality. Although all of these measures (except the last) are factors of sightings per unit of effort, these individual components may be illuminating in detailed studies of a particular area. Prey type, for instance, could influence factors such as occurrence or occupancy (or both). In this case, a relatively nonmigratory prey species, such as sand lance (which are tied to areas of particular bottom substrate and topography) could lead to residency extremes (with whales staying in an area for prolonged periods or avoiding the area altogether), while a less habitat-restricted prey (such as herring) could lead to highly variable intraseason distribution patterns.

Although the number of whales on Stellwagen Bank showed a dramatic decrease, the number of whales photographed on Jeffreys Ledge more than doubled in the last three years of the study. The corresponding increase in observer effort during the same period no doubt had some effect on the dramatic increase in both the number of identified individuals and the mean number of whales identified per day. However, existing opportunistic data were collected following the 1992 season because of the increased use of the area suggested from our dedicated vessel surveys, where methods remained standard across years. Further, captains of whale watching boats and naturalists who had worked on Jeffreys Ledge since the mid-1980's unanimously agreed that there was a sudden, dramatic increase in daily whale sightings beginning in 1992. Therefore, we fully believe that an increase in effort is not the sole, or even the primary, cause for any increase in humpback whale numbers reported beginning in 1992.

Our data show that the sudden increase in humpback whale abundance on Jeffreys Ledge was primarily the result of whales seen on Stellwagen Bank earlier in the study relocating for much or all of their summer feeding season. What is perhaps more surprising is the relatively small number of whales that appeared in both areas during 1992 and 1993, despite the relative nearness of these areas to each other. Most of those whales photographed in both areas were seen on Stellwagen Bank for a brief period in October 1993, when herring stocks are known to migrate through the area (Fogarty and Clark⁷).

The consistent timing of whale aggregations on Jeffreys Ledge in each year (starting in early summer) corresponds with both the major influx of herring onto the Ledge and the start of their spawning season (USDC, 1991; Fogarty and Clark⁷). The biomass of the Georges Bank herring population (of which this is a segment—Stephenson and Kornfeld, 1990; Fogarty and Clark⁷) has increased dramatically over the past decade and, by 1991, was comparable to that of its pre-exploitation size (Stephenson and Kornfeld, 1990; Sherman, 1992; NMFS⁸). Echosounder data, observation of surface prey, and catches of local fishing boats all indicated that herring were common on Jeffreys Ledge at the same time and location as aggregations of

⁵ Belt, C. R., M. T. Weinrich, and M. R. Schilling. 1991. Effects of prey density on humpback whale (*Megaptera novaeangliae*) distribution in the Southern Gulf of Maine. P. 6 in Abstracts of the 9th biennial conference on the biology of marine mammals. Society for Marine Mammalogy, Chicago, IL.

⁶ Weinrich, M. T., C. R. Belt, M. R. Schilling, and M. E. Cappellino. 1985. Habitat use patterns as a function of age and reproductive status in humpback whales. Abstract in Abstracts of the 6th biennial conference on the biology of marine mammals. Society for Marine Mammalogy, Lawrence, KS.

⁷ Fogarty, M. J., and S. H. Clark. 1983. Status of herring stocks in the Gulf of Maine region for 1983. Woods Hole Laboratory Reference Document 83-46, NMFS, NOAA, 33 p. [Available from Northeast Fisheries Center, Woods Hole, MA.]

⁸ NMFS (National Marine Fisheries Service). 1992. Report of the thirteenth Northeast regional stock assessment workshop (13th SAW). Northeast Fisheries Science Center Document 92-02, Northeast Fisheries Center, NMFS/NOAA, Woods Hole MA. 71 p.

whales. The area is also a primary location for seine fishing for herring off New England. Herring seiners were observed fishing or transiting to or from areas of whale aggregation daily during summers 1992–94.

Although herring stocks were increasing, our data indicated that prey available for whales on Stellwagen showed a marked decrease, corresponding to a decrease in sand lance populations throughout the Northeast ecosystem (Sherman, 1992). This decrease in prey would be expected given the documented inverse relation between sand lance and herring or mackerel stocks, primarily due to direct predation (Fogarty et al., 1991). Although we cannot assign a definitive prey type to our echo-sounder traces from Stellwagen, the documented importance of sand lance as a prey for whales on Stellwagen Bank through observations of prey in the mouths of feeding whales (Hain et al., 1982; Weinrich et al., 1992), the direct observation of sand lance on Stellwagen Bank (Hain et al., 1995), prey in fish stomachs, and the lack of other suitable prey records throughout the years suggest that sand lance remained the predominant prey type for whales in that location.

We propose that humpback whales feeding in the Gulf of Maine ecosystem have shifted from their primary distribution of the mid-1970's through the late-1980's as a result of a shift in the abundance of available prey. Although we have considered only a small portion of the Gulf of Maine habitat, our findings correspond with other data from the same period. In the western side of the Great South Channel (an important area for whales from 1979 to 1991 where sand lance were the primary prey [Kenney and Winn, 1986; Payne et al., 1990]) humpback whale sightings were sporadic after July 1991 (Francis⁹; Clapham¹⁰; Mattila¹¹). Off Mt. Desert Rock, Maine, where humpbacks were virtually absent throughout the 1980's, numbers of whale sightings increased to levels far above those of the mid-1970's (Fernald¹²). Surveys conducted in 1993 on Georges Bank by researchers from the YONAH (Years of the North Atlantic Humpback) project also sighted large numbers of humpbacks, including many animals photographed on Stellwagen Bank in previous years (Clapham¹⁰).

If a resurgence of herring is responsible for shifts in distribution and in primary prey type, it suggests that the distribution of humpback whales through the late 1970's and 1980's may have been a human-

induced consequence. The "explosion" of sand lance in the mid- to late 1970's is thought to be primarily the result of the virtual elimination of herring due to overfishing. If this is true, we hypothesize that our observed distribution of whales from 1992 to 1994 should remain relatively stable over the course of a fairly long period because the current situation would be closer to a "natural" ecosystem.

Alternatively, fluctuations in primary prey may occur naturally, and may take place regardless of human interference. If this is true, we hypothesize that whale distributions will show fluctuations that may be cyclical. New England ground-fishermen have for years talked of regular cycles in sand lance abundance, although there are no scientific data to support this often-made contention.

Regardless of which hypothesis, if either, proves true, our data show a shift in both distribution and primary prey type for humpback whales in southern New England waters in recent years. Because this shift has been so complete, it will be interesting and illustrative to see whether, and how, other potentially prey-dependant humpback whale life history parameters, such as reproductive patterns, social behavior, and demographics of whales, all well-documented during a period of explosive sand lance abundance (Clapham and Mayo, 1990; Weinrich, 1991; Weinrich and Kuhlberg, 1991; Clapham et al., 1992), change in response to these ecosystem alterations.

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¹⁰ Clapham, P. 1995. Smithsonian Institution, Washington, DC. Personal commun.

¹¹ Mattila, D. 1995. Center for Coastal Studies, PO Box 1036, Provincetown, MA 02657. Personal commun.

¹² Fernald, T. 1995. Allied Whale, College of the Atlantic, Bar Harbor, ME 04609. Personal commun.

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Abstract.—Percentages of mature male and female vermilion snapper, *Rhomboplites aurorubens*, based on total length (TL) and age were calculated for five three-year periods during 1979–93. Males and females collected during 1982–87 became sexually mature at a smaller size and younger age than individuals collected during 1979–81. The median TL at maturity for females decreased from 160 mm in 1979–81 to 151 mm in 1985–87. The median TL at maturity for males was 145 mm during 1979–81. During 1985–87 all males were mature at 140 mm. The temporal shift toward a smaller size at maturity was more pronounced in males than in females. The percentage of mature males at age 1 significantly increased from 63.6% in 1979–81 to 100% in 1985–87 and afterwards. More than twice as many females at age 1 were mature in 1985–87 (48.6%) as in 1979–81. The decline in size and age at maturity may have been caused by fishing pressure that gradually increased during the 1980's.

The sex ratio of vermilion snapper was dependent upon latitude and gear type but was generally independent of water depth, fish length, and sampling years. Although the sex ratios were significantly different among latitudes, there were no trends among latitudes 31°N, 32°N, and 33°N. The percentage of females was 72.1%, 68.0%, and 59.9% for vermilion snapper caught by trap, hook-and-line, and trawl, respectively. Reasons for the difference in sex ratio among gear types are unclear, suggesting that caution must be used when interpreting sex ratios estimated for any fish species collected by various gear types.

Temporal variation in sexual maturity and gear-specific sex ratio of the vermilion snapper, *Rhomboplites aurorubens*, in the South Atlantic Bight*

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The spawning potential ratio (SPR) has been widely used by U.S. fishery management councils to define overfishing of a fish stock (Goodyear, 1993; Rosenberg et al., 1994; SAFMC¹). To estimate SPR, life history characteristics (e.g. growth and reproduction) are required and are generally assumed constant among years (Gabriel et al., 1989). However, these parameters, particularly maturity schedules, are not static. They can change in response to fishing pressure, predator and prey abundance, stock composition, and other biotic and abiotic environmental factors (Wootton, 1990). Ignorance of temporal changes in life history parameters may result in the use of incorrect data by fishery managers and therefore may be a reason why fish stocks fail to be protected from overfishing (Rosenberg et al., 1994).

Vermilion snapper, *Rhomboplites aurorubens*, from the South Atlantic Bight (SAB) occur in shelf and upper-slope waters between depths of 26 and 183 m (Grimes, 1978). This species spawns multiple times during a prolonged spawning season (April through September: Grimes and Huntsman, 1980; Cuellar et al., 1996). Vermilion snapper have been of extreme commercial and recreational importance along southeast-

ern states since the early 1980's. Total landings in this region have increased over the years with a peak in 1991 (Zhao and McGovern²). However, recent studies have suggested that vermilion snapper are overfished. The stock abundance estimated by virtual population analysis (VPA) has declined since 1984 (Zhao and McGovern²). The relative abundance represented by catch per unit of effort (CPUE) markedly declined during 1988–93. There has also been a significant decrease in mean length of vermilion snapper caught by fishery-independent surveys and by the headboat and commercial fishery (Zhao and McGovern²). Changes in life history characteristics induced by intense harvesting have been reported for vermilion snapper. Zhao et al. (1997) validated the ageing

* Contribution 391 of the South Carolina Marine Resources Center, 217 Fort Johnson Rd., Charleston, South Carolina 29412.

¹ SAFMC (South Atlantic Fishery Management Council). 1993. Amendment 6, regulatory impact review, initial regulatory flexibility analysis and environmental assessment for the snapper grouper fishery of the south Atlantic region. South Atlantic Fishery Management Council, Charleston, SC, 155 p.

² Zhao, B., and J. C. McGovern. 1996. Population characteristics of the vermilion snapper from the southeastern United States. In preparation

method of otolith sections and demonstrated that size-at-age decreased with time. Collins and Pinckney (1988) reported preliminary evidence that vermilion snapper caught in 1978–80 from SAB became reproductively mature earlier in life than those caught in 1972–74. Grimes and Huntsman (1980) determined that vermilion snapper were gonochorists, females (62.5%) significantly outnumbered males, and the sex ratio was dependent on fish length. However, Nelson (1988) reported that the sex ratio of vermilion snapper from the Gulf of Mexico differed from 1:1 in favor of males (54.5%). He also reported that area and season had a significant effect on this ratio. Although what may have caused the difference in sex ratios of two studies was unknown, limited sample sizes made their comparisons among areas, lengths, or seasons less convincing (Grimes and Huntsman, 1980: $n=874$; Nelson, 1988: $n=881$).

In this paper, we investigated the percentage of mature vermilion snapper at each length class and age for each sex and examined the temporal change in maturity schedules during 1979–93. We also determined the sex ratio of vermilion snapper according to depth and latitude of sampling sites, fish length, sampling period, and types of fishing gear used.

Materials and methods

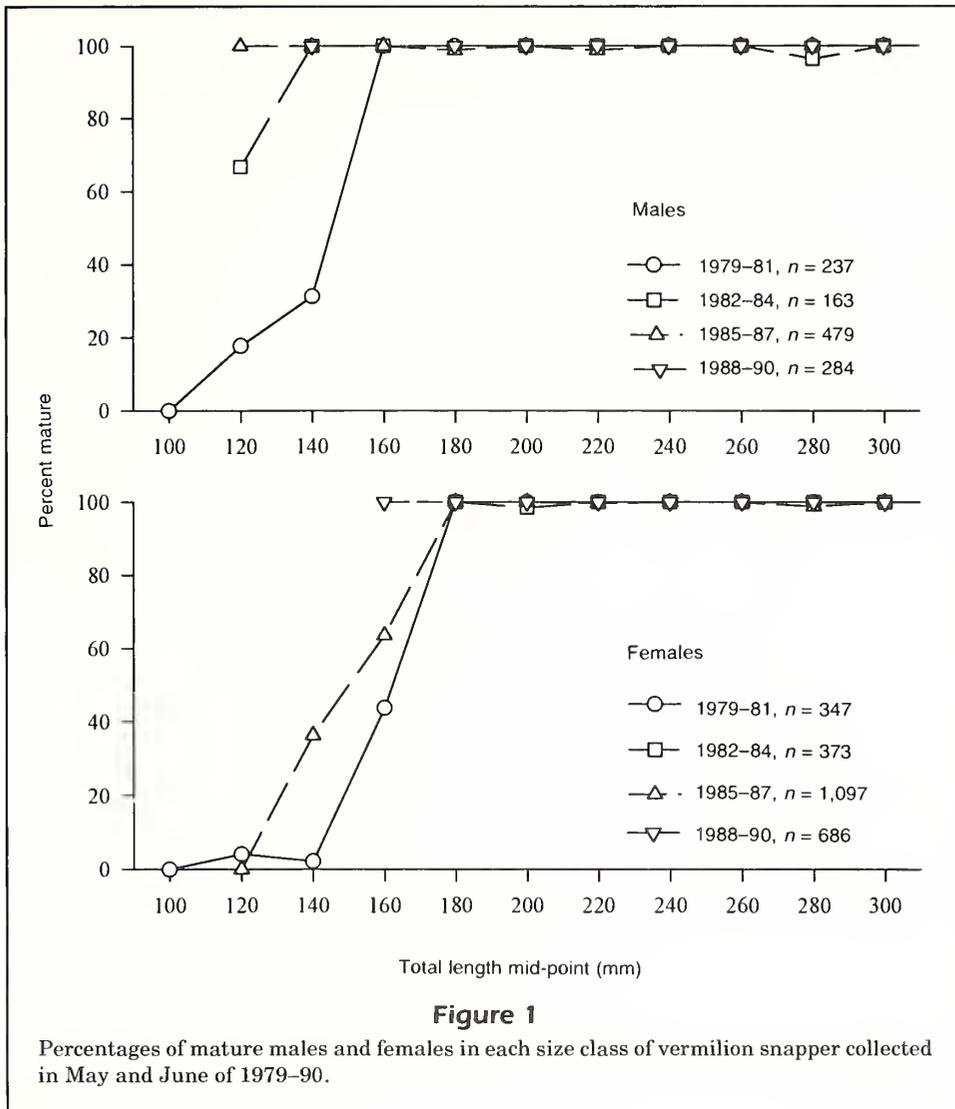
Data were collected from the SAB during 1979–93 by reef fish surveys of the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program. Most vermilion snapper were captured by standardized hook-and-line and trapping gear during the spring and summer of 1979–93 (Collins, 1990; Collins and Sedberry, 1991). In addition, many vermilion snapper were obtained from the MARMAP trawling program that was terminated in 1988. In the field, fish were measured to the nearest mm (TL and FL) and weighed to the nearest gram (whole body weight). Water depth, latitude, and longitude of sampling sites were recorded. The posterior portion of the gonad was removed and preserved in 10% formalin buffered with seawater. In the laboratory, sex and maturity stages were determined by examining the stained gonad sections according to standard MARMAP histological criteria (Cuellar et al., 1996). All gonad samples taken in 1987–93 were examined with histological methods. During 1979–86, sex of specimens was determined and a reproductive condition was assigned in the field by using clearly defined visual staging criteria. The definitions of maturity stages by gross visual inspection were confirmed to be accurate by histological examination during 1978–80 (Collins and

Pinckney, 1988). The codes used for defining maturity stages were consistent between histological and macroscopic methods. Seven reproductive stages were used: 1) immature, 2) developing, 3) running ripe, 4) spent, 5) resting, 6) developing with evidence of spawning in the previous week, and 7) mature, but stage-unknown. Mature fish included those in stages 2–7.

Percentages of mature males and females based on total length (TL) and age were calculated for five periods, each corresponding to a three-year interval, i.e. 1979–81, 1982–84, 1985–87, 1988–90, and 1991–93. Because the monthly distribution of samples was not necessarily similar among periods, it was essential to define a standard month(s) if comparison of maturity schedules among years was to be meaningful. In addition, the reproductive condition was most discernible and the sizes and ages at first maturity could be determined during and immediately prior to the spawning season. Therefore, we used the data only from May and June that corresponded to the time of slow somatic growth. Age assignments of vermilion snapper were based on the number of annuli on otolith sections (Zhao et al., 1997). We took into consideration knowledge of the time of annulus formation, the relative growth of the otolith margin, the date of sampling, and used a January 1 hatching date. Because only a part of the samples was aged, some sexed and maturity-determined samples did not have age information.

Although the variation in gear type, latitude, and depth of sampling sites should have been included in the maturity analysis before the data were pooled, limited sample sizes of small (TL < 170 mm) and young (age-1) vermilion snapper prevented us from comparing maturity schedules by area (latitude) or by gear type. However, 97% of the males and females smaller than 170 mm were collected by trawl in consistent depth ranges during 1979–90. A majority of these small fish were collected from similar areas, with 88% males and 82% females from latitude 31°N, and 12% males and 18% females from 32°N. Thus, gear selectivity and geographical distribution can be disregarded as sources of bias in comparison of maturity schedules among periods.

As recommended by Trippel and Harvey (1991), the *G*-test was used to compare maturity schedules of each sex among periods with the same length class or the same age (e.g. age 1). Maturity schedules between sexes at age 1 were compared for the periods of 1979–81 and 1985–87 respectively, when sample sizes of both sexes were sufficient. When conditions of the *G*-test were not met, Fisher's exact test was used (Zar, 1984). When the percentages of mature fish of each sex in 20 mm TL intervals exhibited a successive increase with length, the median length



at sexual maturity (TL_{50}) was calculated by probit analysis following the recommendation of Tripple and Harvey (1991). The likelihood ratio test at a significance level of 0.10 was used to determine if the probit model could be fitted to the observations of maturity-at-length (SAS Institute, 1990).

Because sex ratio may change with water depth and latitude of sampling sites, fish length, sampling year, gear, or season (Grimes and Huntsman, 1980; Nelson, 1988), all sexed samples, including mature and immature individuals between 1979 and 1993, were split into the same five periods as described above for maturity analysis. The time frame was increased to May through August to increase the sample size. We compared the percentages of females among varying water depths (midpoints: 25, 35, 45, and 55 m), latitudes (31°N, 32°N, and 33°N), length classes (TL=100 – 450 mm, with 50-mm intervals),

periods, and gear types (traps, hook-and-line, and trawl). Latitudes of 31°N, 32°N, and 33°N refer to 31°00'–31°59'N, 32°00'–32°59'N, and 33°00'–33°59'N, respectively. When the independence between sex ratio and one of above factors was tested, other factors were kept consistent. The chi-square test and Fisher's exact test were used to decide the independence. As a reference, Bonferroni's method was used to adjust the significance level, i.e. $\alpha'=0.05/m$, where m = the number of cases (Sokal and Rohlf, 1995). First, we compared the percentage of female vermilion snapper taken from varying depths with the same length classes (TL=200–249 mm and TL=250–299 mm respectively), same latitude (32°N), same periods, and same gear type. Seventy-three percent of the vermilion snapper were collected from latitude 32°N during 1979–93, and eighty percent of them were between 200 and 299 mm TL. If the hypothesis

of independence between sex ratio and depth was not rejected, the data from all depth classes were pooled to compare further the percentage of females among latitudes, other factors (length, period, and gear) being consistent. If the hypothesis was rejected, data from a certain depth class were chosen for further comparison. In a similar fashion, we compared the percentage of females among length classes, periods, and gear types.

The statistical methods available in SAS were used to analyze data of maturity and sex ratio (SAS Institute, 1990). Rejection of the null hypothesis was based on a significance level of 0.05, unless otherwise noted.

Results

Maturity schedules

Males and females collected in 1982–84 and 1985–87 became sexually mature at a smaller size than individuals collected in 1979–81 (Fig. 1). For instance, 31% of male vermilion snapper collected in 1979–81 were mature at 140 mm. However, 100% of males taken at the same size during 1982–90 were mature. All fish taken in May and June of 1991–93 were larger than 180 mm and mature, and therefore were not included in our analysis. There was a significant temporal increase in the percentage of mature males among 1979–81, 1982–84, and 1985–87 at 120 mm (Fisher's exact test: two-tailed $P < 0.01$), and at 140 mm (two-tailed $P < 0.005$). The percentage of mature females also showed a significant in-

crease with time for 140-mm individuals collected between 1979–81 and 1985–87 (two-tailed $P < 0.005$). The observed differences in the percentage of mature females at 160 mm collected during 1979–81, 1985–87, and 1988–90 were not statistically significant (Fig. 1). Males larger than 140 mm and females larger than 160 mm were not tested because all fish were mature.

The likelihood ratio tests indicated that the probit model could be used to describe the maturity at length during 1979–81 for both males (likelihood ratio $\chi^2 = 2.721$, $P > 0.10$) and females (likelihood ratio $\chi^2 = 1.407$, $P > 0.10$), and for females during 1985–87 (likelihood ratio $\chi^2 = 4.647$, $P > 0.10$). The median TL at maturity of males was 145 mm (95% limits: 135–203 mm) during 1979–81. The TL_{50} of females was 160 mm (95% limits: 155–164 mm) in 1979–81 and 151 mm (95% limits: 143–156 mm) in 1985–87.

There was a significant increase in the percentage of mature age-1 males with time between 1979–81, 1982–84, and 1985–87 (Fisher's exact test: two-tailed $P = 0.013$) (Table 1). The percentage of mature age-1 females increased ($G = 5.318$, $P = 0.021$) between 1979–81 and 1985–87. More than twice as many age-1 females were mature in 1985–87 (48.6%) as in 1979–81 (23.1%). The median age at sexual maturity could not be calculated because of the abrupt transition from immature to mature.

Males matured at a smaller size and younger age than females (Fig. 1; Table 1). During 1979–81, TL_{50} for males (145 mm) was smaller than that for females ($TL_{50} = 160$ mm). Although TL_{50} for males in 1985–87 could not be calculated, it was observed that the TL_{50} of males declined with time faster than that of fe-

Table 1

Percentages of sexually mature vermilion snapper caught in May and June of 1979–93. Numbers of fish in each category are given in parentheses. Blanks indicate no data available for that category. There were significant ($P < 0.05$) differences in percent mature of age-1 fish among periods for each sex.

Period	Age 1	Age 2	Age 3	Ages 4+
Males				
1979–81	63.6 (11)	100.0 (15)	100.0 (12)	100.0 (13)
1982–84	85.7 (7)			100.0 (28)
1985–87	100.0 (19)	100.0 (12)	100.0 (10)	100.0 (55)
1988–90	100.0 (2)	100.0 (4)	100.0 (4)	100.0 (47)
1991–93			100.0 (1)	100.0 (32)
Females				
1979–81	23.1 (39)	91.3 (23)	100.0 (9)	100.0 (9)
1982–84		100.0 (4)	100.0 (6)	100.0 (67)
1985–87	48.6 (35)	95.8 (24)	100.0 (18)	100.0 (135)
1988–90	100.0 (2)	100.0 (8)	100.0 (10)	100.0 (104)
1991–93			100.0 (3)	100.0 (86)

males (Fig. 1). During 1979–81 and 1985–87, the percentage of mature males at age 1 was significantly larger than that of females at the same age (Table 1; 1979–81: Fisher's exact test, two-tailed $P=0.024$; 1985–87: $G=20.252$, $P<0.001$).

Sex ratios

More vermilion snapper were caught by traps and hook-and-line in the depth range of 40–49 m than in other depth classes (Table 2). The trawl was generally deployed in shallower water (20–39 m) than were

traps and hook-and-line. These three gear types were deployed most often in latitude 32°N than in other areas (Table 2). To exclude the effects on sex ratios from varying latitude, fish length, years, and gear types, we used the data collected from the same latitude (32°N), length (200–249 mm or 250–299 mm TL), period, and gear when the independence between sex ratio and depth was tested. Sample sizes in all categories were not always sufficient for a chi-square test. If the expected frequency of a depth-class was unacceptably low, that data was discarded from the contingency table. When sample sizes of depth

Table 2

Numbers of sexed vermilion snapper collected from May through August during 1979–93 by depth and latitude of sampling sites. Blanks indicate that no samples were available for that category.

Period	Depth midpoint (m)	Traps					Total	Hook-and-line				Trawl		
		30°N	31°N	32°N	33°N	34°N		31°N	32°N	33°N	Total	31°N	32°N	Total
1979–81	15												3	3
	25		26				26	27	10		37	5	97	102
	35			1			1	5	10	27	42	242	120	362
	45			8			8		326		326			
	55													
	65													
	Total		26	9			35	32	346	27	405	247	220	467
1982–84	15													
	25			21			21	6	42		48	29	217	236
	35			50			50		31		31		28	28
	45			298			298		214		214			
	55			100			100		27		27			
	65								7		7			
	Total			469			469	6	321		327	19	245	264
1985–87	15		129				129							
	25							13			13	283	22	305
	35								1		1		173	173
	45		20	367			387		145		145			
	55			95			95	17	114		131			
	65													
	Total		149	462			611	30	260		290	283	195	478
1988–90	15													
	25		44	111	80		235	50	53	27	130			
	35	3	13	70			86	22	12		34			
	45			406	23		429		226		226			
	55	2		153			155		118		118			
	65			1			1							
	Total	5	57	741	103		906	72	409	27	508			
1991–93	15			9			9							
	25		155	69	81	10	315	1			1			
	35		104	84	155	6	349		10	4	14			
	45	3		124			127		35		35			
	55	18		286			304		14		14			
	65			4			4							
	Total	21	259	576	236	16	1,108	1	59	4	64			

classes were similar to one another and were small relative to the size of a contingency table, Fisher's exact test was used instead of a chi-square test (Zar, 1984). All tested cases supported the null hypothesis of independence between sex ratio and depth, except for the samples of 200–249 mm TL fish caught

with traps during 1982–84 (Table 3). After allowance for multiple-testing ($\alpha' = 0.05/18 = 0.0028$), none of the cases was statistically significant.

Since there were no significant differences among depth classes, we pooled the data from all depth classes to compare the percentage of females among

Table 3

Comparison of percentages of females among water depth-classes with the same latitude (32°00'–32°59' N), length ranges (TL=200–249 mm and 250–299 mm), period, and gear type. % = female percent. *n* = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of depth. Blanks indicate no or few samples available for comparison. df = degrees of freedom.

Period	Depth midpoint (m)	Traps				Hook-and-line				Trawl			
		TL=200–249		TL=250–299		TL=200–249		TL=250–299		TL=150–199		TL=200–249	
		%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
1979–81	25									54.6	55	53.9	39
	35									66.7	48	59.7	62
	chi-square									1.572		0.333	
	<i>P</i>									0.210		0.564	
	df									1		1	
	Reject H_0									No		No	
1982–84	25	83.3	18	100.0	2 ¹	66.7	15	57.7	26			58.9	112
	35	91.7	36	84.6	13	64.7	17	80.0	10			65.2	23
	45	67.1	152	69.1	97	74.4	43	71.6	109				
	55	80.0	45	75.6	41	75.0	8	40.0	15				
	chi-square	11.28		1.708		Fisher's ²		Fisher's ²				0.314	
	<i>P</i>	0.010		0.426		0.859		0.056				0.575	
	df	3		2								1	
	Reject H_0	Yes		No		No		No				No	
1985–87	25											57.9	19
	35											62.2	135
	45	86.9	206	72.4	134	68.6	51	63.9	72				
	55	76.7	60	82.4	34	61.4	44	71.2	59				
	chi-square	3.727		1.414		0.550		0.783				0.132	
	<i>P</i>	0.054		0.234		0.458		0.376				0.716	
	df	1		1		1		1				1	
	Reject H_0	No		No		No		No				No	
1988–90	25	82.7	81	73.7	19	61.8	34						
	35	77.1	48	79.0	19								
	45	72.5	189	67.1	176	65.1	126	60.0	45				
	55	64.9	74	75.0	76	70.0	60	71.8	39				
	chi-square	6.808		2.484		0.745		1.286					
	<i>P</i>	0.078		0.478		0.689		0.257					
	df	3		3		2		1					
	Reject H_0	No		No		No		No					
1991–93	25	80.0	30	84.6	13 ¹								
	35	74.5	47	80	20								
	45	70.0	30	77.9	68								
	55	64.4	160	73.5	102								
	chi-square	3.910		0.649									
	<i>P</i>	0.271		0.723									
	df	3		2									
Reject H_0	No		No										

¹ The row was discarded from the contingency table because of its excessively low expected frequency.

² When conditions for a chi-square test were not met, Fisher's exact test was used.

latitudes with other factors (length, period, and gear) remaining consistent. Six of the 14 tested cases indicated that sex ratio was dependent on latitude (Table 4). Even after allowance for multiple-testing ($\alpha'=0.05/14=0.0036$), there were still two cases indicating significant difference (1979–81, trawl, 150–199 TL and 1988–90, traps, 200–249 TL). Because the latitudinal distribution of samples was not similar among periods for any gear type (Table 2), we used only data from the latitude of 32°N in subsequent analyses.

There were no significant differences in percentage of females caught by traps among length classes 200–249, 250–299, and 300–349 mm during 1982–84, 1988–90, or 1991–93 (Table 5). During 1979–81, the hypothesis of independence between sex ratio and

length was rejected for fish caught by hook-and-line within the length range of 150–449 mm. However, it was not rejected within 200–299 mm (Table 5). Thus, the common TL range of vermilion snapper caught by hook-and-line was 200–299 mm, within which the sex ratio was independent of length during 1979–93. There were no significant differences in percentages of females caught by trawl within 150–249 mm during 1979–81 and 1985–87 (Table 5). After allowance for multiple-testing ($\alpha'=0.05/12=0.004$), none of the 12 cases showed significant difference.

We compared the percentage of females among periods by pooling data for each gear type within the common TL range and periods when the sex ratio was independent of length. There were no signifi-

Table 4

Comparison of percentages of females among latitudes with the same length ranges (TL=200–249 mm and TL=250–299 mm), period, and gear type. All data were pooled from various water depth classes. % = female percent. *n* = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of latitude. Blanks indicate no or few samples available for comparison.

Period	Latitude (°N)	Traps		Hook-and-line				Trawl					
		TL=200–249 %	TL=250–299 <i>n</i>	TL=200–249 %	TL=250–299 <i>n</i>	TL=200–249 %	TL=250–299 <i>n</i>	TL=150–199 %	TL=200–249 <i>n</i>	TL=150–199 %	TL=200–249 <i>n</i>		
1979–81	31			57.1	14	87.5	8	36.5	115	57.1	14		
	32			73.6	106	67.6	105	60.2	103	57.4	101		
	33			87.5	16	50.0	4						
	chi-square			Fisher's ²		Fisher's ²		12.205		0			
	<i>P</i>			0.178		0.352		<0.001		0.984			
	df							1		1			
	Reject H_0			No		No		Yes		No			
1985–87	31	82.6	115	50.0	20	72.7	11	93.3	15	39.4	221	52.3	44
	32	84.6	266	74.4	168	65.6	96	67.2	131	58.3	36	61.7	154
	chi-square	0.234		5.258		Fisher's ²		Fisher's ²		4.571		1.260	
	<i>P</i>	0.629		0.022		0.747		0.039		0.033		0.262	
	df	1		1						1		1	
	Reject H_0	No		Yes		No		Yes		Yes		No	
	1988–90	31	63.9	36	100.0	4 ¹							
32		73.7	392	70.5	291								
33		91.8	61	76.7	30								
chi-square		11.96		0.511									
<i>P</i>		0.003		0.475									
df		2		1									
Reject H_0		Yes		No									
1991–93	31	80.0	235	57.1	7								
	32	68.8	276	76.8	207								
	33	77.7	206	60.0	20								
	chi-square	9.509		3.925									
	<i>P</i>	0.009		0.141									
	df	2		2									
	Reject H_0	Yes		No									

¹ The row was discarded from the contingency table because of its excessively low expected frequency.

² When conditions for a chi-square test were not met, Fisher's exact test was used.

Table 5

Comparison of percentages of females among length classes with the same latitude (32°00'–32°59' N), period, and gear type. All data were pooled from various depth classes. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of length. Blanks indicate no or few samples were available for comparison.

Period	TL (mm)	Traps		Hook-and-line		Trawl				
		%	n	%	n	%	n			
1979–81	90–149					$\chi^2 = 14.079$	78.6	14	$\chi^2 = 2.293$	
	150–199			38.9	18	$P = 0.015$	60.2	103	$P = 0.318$	
	200–249			73.6	106	df = 5	57.4	101	df = 2	
	250–299			67.6	105		100.0	2 ¹		
	300–349			54.6	77					
	350–399			72.4	29					
	>399			54.6	11					
	Reject H_0					Yes			No	
1982–84	150–199	66.7	3 ¹	$\chi^2 = 1.597$	80.0	5 ¹	$\chi^2 = 0.449$	41.0	100	$\chi^2 = 8.847$
	200–249	74.1	251	$P = 0.450$	71.1	83	$P = 0.930$	60.0	135	$P = 0.012$
	250–299	72.6	153	df = 2	67.1	161	df = 3	40.0	10	df = 2
	300–349	65.3	49		67.3	52				
	350–399	80.0	10 ¹		66.7	18				
	>399	100.0	3 ¹		100.0	2 ¹				
	Reject H_0			No			No			Yes
1985–87	90–149	100.0	1 ¹	$\chi^2 = 6.844$	0	1 ¹	$\chi^2 = 0.515$	66.7	3 ¹	$\chi^2 = 0.138$
	150–199	100.0	5 ¹	$P = 0.033$	75.0	4 ¹	$P = 0.773$	58.3	36	$P = 0.710$
	200–249	84.6	266	df = 2	65.6	96	df = 2	61.7	154	df = 1
	250–299	74.4	168		67.2	131		100.0	2 ¹	
	300–349	81.0	21		73.1	26				
	350–399	100	1 ¹		100.0	2 ¹				
	>399									
	Reject H_0			Yes			No			No
1988–90	90–149			$\chi^2 = 1.048$	33.3	3 ¹	$\chi^2 = 1.547$			
	150–199	100.0	5 ¹	$P = 0.592$	59.7	62	$P = 0.461$			
	200–249	73.7	392	df = 2	67.1	228	df = 2			
	250–299	70.5	291		68.8	93				
	300–349	75.0	44		41.2	17 ¹				
	350–399	57.1	7 ¹		25.0	4 ¹				
	>399	50.0	2 ¹		100.0	2 ¹				
	Reject H_0			No			No			
1991–93	150–199	50.0	4 ¹	$\chi^2 = 6.035$	100	2 ¹	Fisher's ²			
	200–249	68.8	276	$P = 0.110$	64.5	31	$P = 1.0$			
	250–299	76.8	207	df = 3	64.3	14				
	300–349	63.4	71		25.0	4 ¹				
	350–399	71.4	14		60.0	5 ¹				
	>399	50.0	4 ¹		100.0	3 ¹				
	Reject H_0			No			No			

¹ The row was discarded from the contingency table because of its excessively low expected frequency.

² When conditions for a chi-square test were not met, Fisher's exact test was used.

cant differences in percentages of females among periods for either gear type (Table 6). The overall chi-square test indicated a significant lack of independence between sex ratio and gear type (Table 7A). We subdivided the data into 2×2 contingency tables formed by any two gear types. Significant differences in the percentage of females were found between

trawl and traps ($\chi^2=22.642$, $P<0.001$), between trawl and hook-and-line ($\chi^2=8.424$, $P=0.004$), and between traps and hook-and-line ($\chi^2=5.166$, $P=0.023$). Therefore, we concluded that traps caught more females than did the other two gear types, and hook-and-line caught more females than trawl. This conclusion was supported by additional analysis with various length

Table 6

Comparison of percentages of females among periods with the same latitude (32°00'–32°59' N) and gear type. All data were pooled from various depth classes. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of period. Blanks indicate few samples available for comparison or the null hypothesis of independence between sex ratio and length was rejected in Table 5. df = degrees of freedom.

Period	Traps (TL=200–349)		Hook-and-line (TL=200–299)		Trawl (TL=150–249)	
	%	n	%	n	%	n
1979–81			70.6	211	58.8	204
1982–84	72.6	453	68.4	244		
1985–87			66.5	227	61.1	190
1988–90	72.5	727	67.6	321		
1991–93	71.1	554	64.4	45		
chi-square	0.382		1.199		0.204	
P	0.826		0.878		0.652	
df	2		4		1	
Reject H_0	No		No		No	

Table 7

Comparison of percentages of females among gear types with the same latitude (32°00'–32°59' N). All data were pooled from various depth classes. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of gear type. Data were pooled from periods that were used in Table 6. Data with different length ranges were used in A, B, and C. (A) TL ranges were the same as used in Table 6 for each gear; (B) TL = 200–249 mm for all gear types; (C) TL = 186–540 mm, mean TL = 254 mm for traps, TL = 142–560 mm, mean TL = 261 mm for hook-and-line, and TL = 112–256 mm, mean TL = 203 mm for trawl.

Gear	A		B		C	
	%	n	%	n	%	n
Traps	72.1	1734	72.4	919	72.1	1786
Hook-and-line	68.0	1048	68.6	544	66.2	1395
Trawl	59.9	394	60.0	255	61.0	415
chi-square	23.460		14.558		24.938	
P	<0.001		0.001		<0.001	
df	2		2		2	
Reject H_0	Yes		Yes		Yes	

ranges (Table 7B: a single TL range for all gear types; Table 7C: all data available were used with full TL ranges). Vermilion snapper caught by all gear types had an unequal sex ratio that was female-biased (traps and hook-and-line: $P < 0.001$, trawl: $P < 0.005$).

Discussion

Maturity schedules

Although data used for maturity analysis were limited to those collected in the same season (May and June) of each period, growth may occur, and stages of maturity may change, within two months. An immature fish in May may become mature in June. If more fish were collected in June of recent years than in 1979–81, the percent mature at a certain age would be overestimated for recent years. The monthly distribution of observations, however, was similar among periods with more than 80% of the fish smaller than 170 mm being collected in May. Relative differences in maturity schedules among periods remained valid throughout the study.

The essential underlying assumption of the maturity analysis is that length, age, and reproduction conditions are correctly measured or determined. In 1985, 1986, 1987, and 1988, only fork lengths (FL) were measured. These FL were converted to TL with $TL \text{ (mm)} = 1.115FL - 0.254$ (Zhao et al., 1997). For

other years, observed TL was available. Because the method for ageing vermilion snapper by means of otolith sections has been validated by Zhao et al. (1997) and because the persons who read otoliths in Zhao et al.'s study also read otoliths in our study, incorrect ageing of vermilion snapper is not considered a source of bias. During 1979–86, gonads were examined macroscopically by experienced biologists by means of clearly defined gross morphological staging criteria. These criteria were confirmed to be accurate by histological examination during 1978–80. All gonads, since 1987, were examined by using reliable histological techniques (Cuellar et al., 1996). Therefore, it is believed that sex and maturation were correctly determined. In general, sex and maturity stages can be more reliably determined during the spawning season than in off-seasons. Data used for maturity analysis were only from May and June, the first part of the spawning season, during which errors in maturity determination were not expected. Furthermore, in the present study, all maturity stages of mature fish were pooled in only one maturity state, i.e. mature. As long as immature and mature fish could be distinguished, inaccurate classification of mature substage would not introduce a bias in estimates of age and size at maturity.

This study indicated that both age and length at sexual maturity of vermilion snapper declined over time. This decline may have resulted from increased fishing pressure, because the total landings consis-

tently increased during the 1980's (Zhao and McGovern²). The demonstration that the harvest of a fish stock can lead to declines in length or age at maturity has been reported for many fishes, including northeast Arctic cod (Jørgensen, 1990), Pacific salmon (Ricker, 1981), and California halibut (Love and Brooks, 1990). Changes in size or age at maturity may be the result of a density-dependent response to decreased stock abundance, selective removal and incomplete replacement of later-maturing fish by the fishery, or genetic change within a population (Nelson and Soulé, 1987). Jørgensen (1990) attributed a decline in median age-at-maturity in northeast Arctic cod to an increase in length-at-age (i.e. faster growth) coincident with declining stock density, an idea that implicitly assumes a minimum threshold for size-at-maturity. If the scenario of Jørgensen (1990) is correct, declines in length and age should not occur concurrently. Furthermore, Zhao et al. (1997) indicated that the size-at-age of vermilion snapper has decreased with time. Therefore, changes in maturity schedules of vermilion snapper are not part of a density-dependent compensatory response to harvesting, but quite likely a result of the selective removal and incomplete replacement of faster-growing, later-maturing fish by the fishery. If intensive fishing pressure continues, and the early-maturing trait is heritable, length and age at maturity in the population will decrease with time. Life history theory predicts that genetic changes in life history characteristics will occur following increased mortality (Roff, 1992). Harvesting can reverse the relative fitness of genotypes, because an inferior genotype (e.g. slow-growing and early-maturing) in an unexploited population may be more fit under increased fishing pressure (Bergh and Getz, 1989). Early-maturing genotypes reproduce before being fully recruited to the fishery, whereas genotypes that mature at larger sizes or older ages tend to be removed before reproduction. This process would explain the decreasing abundance of larger, immature fish with time and would account for declines in both size and age at maturity. The long-term impacts of size-selective fish harvests may have caused the decline in size-at-age of vermilion snapper through disproportionate harvesting of fast-growing individuals (Zhao et al., 1997). Similarly, it may be that late-maturing genotypes were removed from the vermilion snapper population in the 1980's when fishing pressure was intensive.

Maturity schedules of vermilion snapper collected during 1972–74, prior to heavy exploitation, were investigated by Grimes and Huntsman (1980). They used a gonadosomatic index and indicated that "most fish attain sexual maturity during their third or

fourth years of life (186–256 and 256–324 mm TL), but a few precocious individuals may mature in their second year (100–186 mm TL) at about 150 mm TL." It is not rigorous to compare the percent mature, based on age, between Grimes and Huntsman (1990) and the present study because an obvious discrepancy in size-at-age exists between Grimes (1978) and Zhao et al. (1997). It is meaningful, however, to compare maturity schedules based on length between these two studies. The maximum-likelihood estimates from the probit analysis of data from the present study predicted that 50% of males and 15% of females matured by 150 mm during 1979–81 and that 50% females at 150 mm matured during 1985–87. All males and females at 180 mm were mature in the present study. Differences between previous (Grimes and Huntsman, 1980) and present results could be partially due to differences in methods used to determine maturity (Collins and Pinckney, 1988) or may truly reflect the changes in maturity that occurred in the 1970's. The increase in percentage of mature females at 150 mm was faster during the 1980's than during the 1970's (i.e. an increase of 35% in six years from 1979–81 to 1985–87, versus an increase of less than 15% in seven years from 1972–74 to 1979–81). The degree of exploitation may account for the differing rates of change in maturity while the fishery for vermilion snapper was initiated in the 1970's, but heavy exploitation did not occur until the 1980's.

Sex ratios

The chi-square analysis did not suggest significant differences in percentages of females among months (May–August) for any gear type. This information supported the notion that pooling data between May through August would not bias the comparison of sex ratios. Seasonal comparisons of sex ratios could not be done because little sampling was done in fall or winter.

This study showed that the sex ratio of vermilion snapper was dependent on area (latitude) and gear type, but independent of depth of sampling sites, fish length, or sampling years. The reason for the significant differences among latitudes is unknown. However, only 2 of the 14 cases showed a significant difference according to Bonferroni's method (Table 4), and no trend was observed between latitudes. In addition, relatively small sample sizes collected from latitudes other than 32°N may have induced errors in comparison. Therefore, we attribute the difference in sex ratio between latitudes to chance.

Although significantly different, the percentages of females of vermilion snapper collected by traps

and hook-and-line were similar to each other (traps: 72.1%; hook-and-line: 68.0%) but differed from that for trawl capture (59.9%). Trawls caught smaller fish from shallower waters when compared with traps and hook-and-line (Tables 2 and 7C). However, present results indicated that sex ratios were not affected by water depth or fish length. With traps and hook-and-line gear, baits were used to attract fish. If female vermilion snapper were more aggressive in pursuing bait than males, the percentage of females in the catch of traps and hook-and-line could be higher than that in the population. In contrast, no baits were used for trawling, and therefore males and females might be caught with the same probability. If the difference in feeding behavior between sexes can account for the difference in sex ratio between gear, then the sex ratio of vermilion snapper in the population may be correctly represented by the trawl catch. Watanuki et al. (1993) reported that basket traps caught the greatest ratio of female cuttlefish among three types of gear (basket traps, jigs, and trammel nets). More females may be attracted to traps for spawning, but Watanuki et al. indicated that there are probably other unknown factors governing the entry of cuttlefish into traps. Because information on spawning behavior of vermilion snapper is unavailable, we cannot evaluate how the spawning activity of vermilion snapper may affect its vulnerability to different gear types.

We pooled data from all gear types and calculated the overall sex ratio by period. The percentage of females gradually increased from 62% in 1979–81 to 70% in 1991–93. The temporal increase in the percentage of females proved to be an artifact of unequal distribution of catch by gear among periods. Reasons for the difference in sex ratios among gear types are unknown. Caution must be used when evaluating the sex ratios of any fish species collected by various gear types.

Our conclusion of independence between sex ratios and lengths differs from previous studies. Grimes and Huntsman (1980) concluded that the sex ratio of vermilion snapper was dependent on fish length, with the percentage of females increasing in larger size classes. However, the percentage of females within the range of 551–600 mm TL (89.3%, $n=32$) was obviously higher than those for other length ranges. Thus, it is suspected that the significant chi-square calculated by Grimes and Huntsman (1980) was probably due to this length range. We used the original data published in Table 4 of Grimes and Huntsman (1980) but excluded the data with length greater than 550 mm TL ($n=32$). We found that sex ratio was independent of length ($\chi^2=13.105$, $P=0.108$, $n=841$, $df=8$, TL=101–550 mm) and thus was in

agreement with the conclusion of the present study. A further 2×2 contingency table analysis formed by the TL range of 551–600 mm versus all other length ranges rejected the null hypothesis of independence between sex ratio and length ($\chi^2=11.732$, $P=0.001$, $n=873$, $df=1$). Thus, we confirmed that the sex ratio within 551–600 mm TL is significantly different from those of other length ranges. Because our data had relatively few vermilion snapper larger than 450 mm TL, the conclusion of independence between sex ratio and length may be limited to 450 mm TL or less. However, the similar size-at-age and the same longevity of male and female vermilion snapper do not suggest the percentage of females would increase with length even beyond 450 mm TL (Zhao et al., 1997).

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A polyphasic growth function for the endangered Kemp's ridley sea turtle, *Lepidochelys kempii*

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The Kemp's ridley, *Lepidochelys kempii*, is the smallest of the seven extant species of sea turtle (Marquez, 1994) and is endemic to the Gulf of Mexico and Atlantic coast of the United States (Pritchard, 1989). It has been subject to extensive human exploitation and is the most endangered sea turtle species in the world (Marquez, 1994). Seasonal trawl and pound-net fisheries are major hazards, posing a serious risk to the long-term population viability of the Kemp's ridley (Epperly et al., 1995; Caillouet et al., 1996). Although the Kemp's ridley sea turtle is endangered, the somatic growth and population dynamics of this species are not well known (Chaloupka and Musick, 1997) despite several important growth studies that have been carried out for captive or head-started stocks (Caillouet et al., 1986; Caillouet et al., 1995b). We propose a new growth model for the endangered Kemp's ridley sea turtle that is based on a skeletochronological data set derived recently by Zug et al. (1997) from wild stock sea turtles stranded along the Atlantic Bight and Gulf coasts of the United States. The growth model presented provides a basis for improving our understanding of sea turtle growth dy-

namics in general and for modeling Kemp's ridley population viability.

Materials and methods

Data set

The data set used here comprised 70 size-at-age records for Kemp's ridley sea turtles—69 records from stranded turtles plus the inclusion of known mean hatchling size (see Marquez, 1994). The data set ($n=70$) also comprised growth records spanning the postnatal development phase (from 4 to 72 cm straight carapace length, SCL) and including the mature adult phase, but the records were not distributed evenly over this size range. The age estimates were derived from a skeletochronological analysis of wild Kemp's ridley sea turtles stranded along the Atlantic coast of the United States and in the Gulf of Mexico (see Zug et al., 1997). Straight carapace length (SCL) was measured to 0.1 cm and age to 0.1 yr. The original sample of stranded turtles comprised 73 individuals, but age estimates for 4 individuals were not possible because of either 1) a lack of discernible growth rings or 2) uninterpretable irregular

growth. Records for these 4 individuals were discarded, yielding the 69 individual turtles used in this study.

The data set also included stranding location, with 79% of the sample comprising turtles stranded on the Atlantic coast. Sex was recorded for 37% of the strandings; no proportional difference was evident between the Atlantic and Gulf of Mexico subsamples. Further details of the strandings data set and the skeletochronological methods used for age estimation can be found in Zug et al. (1997).

The limitations of skeletochronological ageing techniques and the need for caution in interpreting such age estimates for sea turtles have been well discussed elsewhere (Zug et al., 1986; Zug, 1990; Zug et al., 1997). Chaloupka and Musick (1997) have also provided a critical review of sea turtle skeletochronological studies and have discussed the limitations of such studies in terms of age validation, length back-calculation, growth estimation, layer loss adjustment protocols, and implications of the specific time-dependent sampling design implicit in the data set. For instance, the implicit sampling design in the current study was mixed cross-sectional because only the terminal age-size estimate was available for each of the 69 stranded turtles. This sampling design confounds age and cohort effects and thus only an expected or mean growth function can be estimated (see Chaloupka and Musick, 1997).

Statistical modeling approach

The functional relation between size (cm SCL) and estimated age for the 70 Kemp's ridley sea turtles was modeled with a two-stage approach: 1) exploratory data visualization including nonparametric smoothing (see Cleveland, 1993) to

evaluate the implicit functional form of the growth model without having to specify an explicit and perhaps invalid nonlinear function; and 2) a polyphasic parametric growth function fitted to the size-at-age data on the basis of the functional form implied by the nonparametric smooth. Polyphasic growth means that there is more than one growth phase or cycle in postnatal development, suggesting ontogenetic shifts in growth rates manifested by at least two growth spurts between birth and the onset of adult maturity (see Gasser et al., 1984). The polyphasic growth function used in our study was the Peil and Helwin (1981) parameterization comprising a summation of logistic functions as follows:

$$y_t = \sum_{i=1}^j \left\{ \alpha_i \left[1 + \tanh(\beta_i(t - \delta_i)) \right] \right\} + \varepsilon_{ti} \quad (1)$$

where y_t = mean length at age t ;
 α_i = (asymptotic mean)/ j length in phase i ;
 β_i = growth coefficient in phase i ;
 δ_i = age at the inflection point of phase i ;
 $\tanh(z) = (e^z - e^{-z})/(e^z + e^{-z})$ and $z = (\beta_i(t - \delta_i))$;
 j = number of growth phases; and
 ε_{ti} = an appropriate random error structure.

Parameters of the standard logistic function (monophasic with skewed symmetric inflexion and suggesting one growth spurt) are well known to have excellent statistical properties (Ratkowsky, 1990). It was

assumed that the polyphasic form (Eq. 1) used here also has sound statistical properties. In principle, Equation 1 was fitted by heteroscedasticity-robust nonlinear least-squares (HRNLS) with a heteroscedasticity-consistent covariance matrix estimator (HCCME) to account for growth variability and measurement error (see Davidson and MacKinnon, 1993). In practice, Equation 1 was fitted with RATS (Doan, 1992), which implements HRNLS with White's HCCME. Otherwise, the generalized method of moments (GMM) approach can be used for robust nonlinear regression estimation (Davidson and MacKinnon, 1993). The age-specific growth-rate function for the Kemp's ridley sea turtle was derived analytically by taking the first derivative of the fitted Equation 1 with the software program MATHEMATICA (Wolfram Research, 1993).

Results

The size and estimated age data for the 70 Kemp's ridley sea turtles presented in Zug et al. (in press) are shown in Figure 1A with a locally weighted regression smoothing known as LOWESS (see Cleveland, 1993) superimposed to reveal the implicit functional form. The LOWESS procedure can be implemented by using S software (Becker et al., 1988). The nonparametric smooth (Fig. 1A) implies a polyphasic function with two sequential growth phases, with the first decelerating around 30 cm SCL and the second

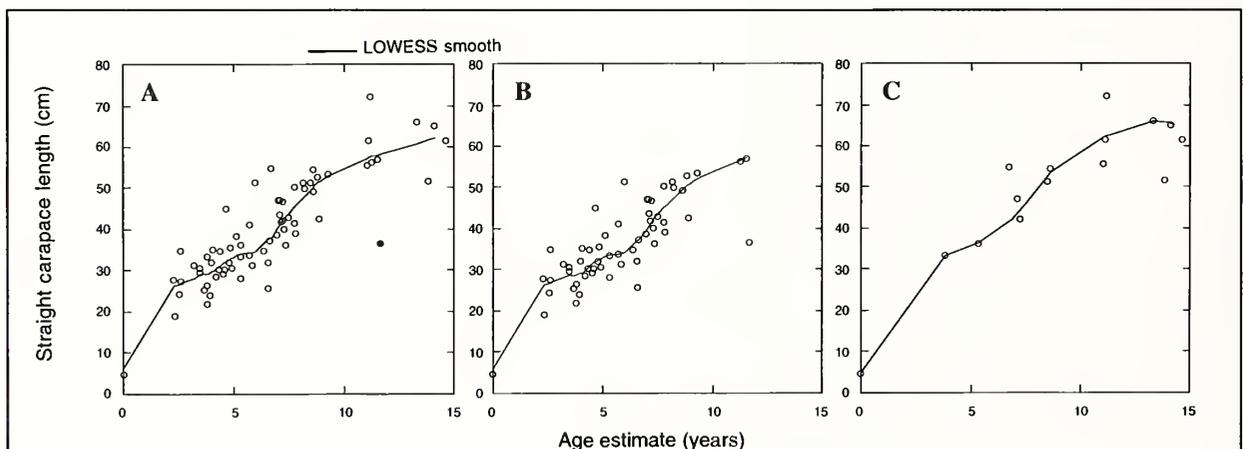


Figure 1

(A) Scatterplot of size-at-age estimates for the 69 Kemp's ridley sea turtles stranded along the Atlantic Bight and Gulf coasts of the United States, with an additional estimate of mean hatchling size (age=0 yr). Open circles and solid dot are the original data estimates ($n=70$) from Zug et al. (1997). Solid dot is the outlier discounted in the parametric model (Table 1). The curve in (A) is a LOWESS (locally weighted robust regression) smooth superimposed to highlight the underlying size-at-age function without presuming the functional form. (B) Scatterplot of the Atlantic Bight subsample estimates ($n=55$), with hatchling size included and a LOWESS smooth superimposed. (C) Scatterplot of the Gulf of Mexico subsample estimates ($n=14$), with hatchling size included and a LOWESS smooth superimposed.

at ≥ 60 cm SCL. It is proposed that a polyphasic growth model might be a better mathematical description of growth than the monophasic (monotonic) von Bertalanffy (Caillouet et al., 1995b; Schmid, 1995; Zug et al., 1997) or the monophasic (non-monotonic) Gompertz functions (Caillouet et al., 1986) proposed for this species. A similar polyphasic growth function comprising two phases is also evident for the Atlantic Bight subsample (Fig. 1B) and is suggested for the Gulf subsample (Fig. 1C) despite a very sparse data field in the latter case.

Figure 1 also highlights the considerable variability (heterogeneity) inherent in sea turtle growth and why heteroscedasticity-robust estimation procedures (e.g. HCCME, GMM) should be used to derive regression parameter estimates for growth model fits. There is also a major outlier in Figure 1A indicated by a solid dot—this value was discounted in the explicit parametric model fit because no parametric model could be as robust in respect to this outlier as the nonparametric smooth displayed in Figure 1A. Growth variability in sea turtle studies is a complex function of demographic (sex, maturity status) and geographic factors as well as a function of the time-dependent nature of the implicit sampling design (confounding year and cohorts effects) and instrumental measurement error. For instance, Caillouet et al. (1986) have shown conclusive evidence of somatic growth variability due to cohort (year-class) effects for captive reared Kemp's ridley sea turtles. The small sample size, mixed cross-sectional sampling design, and insufficient data on demographic and geographic covariates precluded any reliable estimate of these additional sources of growth record variability in the current study.

The parametric growth curve proposed here to match the nonparametric smooth (Fig. 1A) for the Kemp's ridley data comprises separate logistic growth functions for each of the two inferred growth phases integrated into a single explicit polyphasic function—Equation 1. The statistical fit of this function to the growth data (Fig. 1A) is shown in Table 1. The growth model with robust estimation and with elimination of the extreme outlier (see Fig. 1A) fitted the data well with significant parameter estimates even allowing for family-wise error-rate adjustment, small parameter estimate standard errors, and no aberrant residual behavior (see Judge et al., 1985, or Ratkowsky, 1990, for a discussion of nonlinear regression fitting and goodness-of-fit criteria). Despite the good fit, significant growth variability, probably due to instrumental measurement error and confounding of year and cohort sampling effects, was not accounted for by the model (residual variance: $\sigma^2=29.1$).

Table 1

Parameter estimates for the polyphasic logistic growth function (Eq. 1) fitted to the Kemp's ridley sea turtle size-at-age growth data in Zug et al. (1997). See Equation 1 for definitions of parameters.

Parameter	Estimate	Asymptotic standard error	t-ratio	Inference
α_1	13.6467	2.7463	4.97	$P < 0.001$
β_1	0.7901	0.2989	2.64	$P < 0.008$
δ_1	1.1169	0.4303	2.59	$P < 0.009$
α_2	17.6595	3.9288	4.49	$P < 0.001$
β_2	0.3059	0.1274	2.40	$P < 0.016$
δ_2	7.6361	0.5407	14.12	$P < 0.001$

The expected polyphasic size-at-age function is shown in Figure 2A (age=skeletochronological age estimate) and presented numerically in Table 2 for comparative purposes. The explicit size-at-age growth function (Fig. 2A) was then differentiated with respect to estimated age by an analytical solution to Equation 1 to derive the age-specific growth rate function (Fig. 2B). The expected age-specific growth rate function (Fig. 2B) displays an initial posthatchling growth rate >5 cm SCL/year, increasing to 11 cm SCL/year ≥ 1 year of age (Δ_1) or 13 cm SCL, slowing to 2 cm SCL/year by 3–4 years of age (ca. 27 cm SCL), marking the end of the first growth phase (i.e. $2\alpha_1=27.3$ in Table 1; mid-curve asymptote in Figs. 1A and 2A). The growth rate then rises to 6 cm SCL/year near 8 years of age (δ_2) or to 46 cm SCL before declining slowly to negligible growth approaching adulthood ≥ 15 years of age at a size ≥ 62 cm SCL, marking the end of the second growth phase (i.e. $2(\alpha_1+\alpha_2)=62.6$ in Table 1; upper asymptote in Figs. 1A and 2A).

Discussion

Monophasic von Bertalanffy growth functions have been proposed for the Kemp's ridley sea turtle by Caillouet et al. (1995b), Schmid (1995), Zug et al., (1997), and others (Marquez, 1994, and references therein). With the von Bertalanffy growth function, however, a monotonic decreasing growth-rate function is implied and hence no growth spurt at any age or size. The statistical validity of that function fitted to a limited data span and of the Fabens mark-recapture analogue used by Schmid (1995) and Zug et al. (1997) has been reviewed critically by Chaloupka and Musick (1997). It is questionable whether a monophasic von Bertalanffy function fits the mean growth profile for the complete postnatal

Table 2

Comparison of size-at-age growth functions for three Kemp's ridley sea turtle growth models. Age = known age for the Caillouet et al. (1995b) model, whereas age = skeletochronological age estimate for the Zug et al. (1997) model and the polyphasic model presented here. SCL = straight carapace length.

Age (years)	Size-at-age estimate (cm SCL)			Age (years)	Size-at-age estimate (cm SCL)		
	Caillouet et al. (1995b)	Zug et al. (1997)	This study (Fig. 2A)		Caillouet et al. (1995b)	Zug et al. (1997)	This study (Fig. 2A)
0 (hatchling)	2.79	8.86	4.32	13	61.30	59.49	61.33
1	18.95	14.85	12.99	14	61.57	61.63	61.91
2	30.72	20.39	22.96	15	61.76	63.62	62.23
3	39.29	25.50	27.93	16	61.90	65.45	62.40
4	45.53	30.23	30.46	17	62.00	67.14	62.50
5	50.08	34.60	33.11	18	62.07	68.70	62.55
6	53.39	38.63	36.77	19	62.13	70.15	62.58
7	55.80	42.36	41.56	20	62.17	71.48	62.59
8	57.56	45.81	46.91	21	62.19	72.72	62.60
9	58.84	48.99	51.92	22	62.21	73.86	62.61
10	59.77	51.94	55.88	23	62.23	74.91	62.61
11	60.45	54.65	58.61	24	62.24	75.89	62.61
12	60.94	57.17	60.32	25	62.25	76.79	62.61

development phase of any sea turtle species (see Chaloupka and Limpus, 1997; Chaloupka and Musick, 1997).

On the other hand, the monophasic form of the Gompertz growth function used by Caillouet et al., (1986) in a single cohort growth study (weight gain) of 10 Kemp's ridley sea turtles held in captivity

clearly fitted the data well at least for the observed range (ca. 2–7 years old). In the Gompertz function, a nonmonotonic growth-rate function is assumed with a growth spurt in early development similar to the first growth spurt in our study (see Fig. 2B). Whether growth in Caillouet et al.'s (1986) study might have been better fitted by using a polyphasic

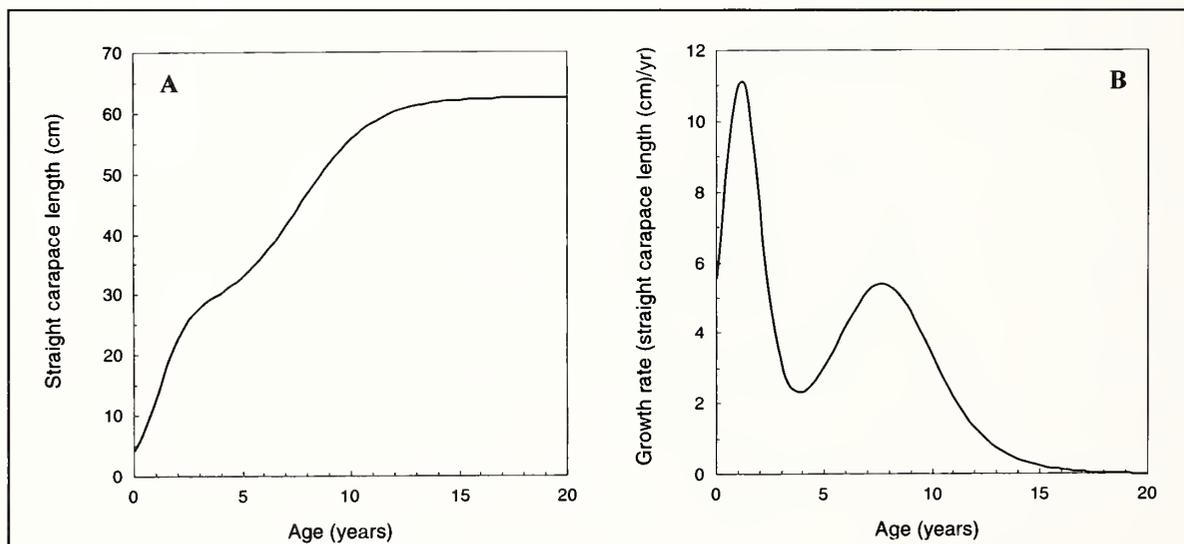


Figure 2

(A) Kemp's ridley sea turtle size (SCL cm) plotted as a function of the correction-factor age estimates derived from Zug et al. (1997). Solid curve shows the polyphasic logistic growth Equation 1 fitted to the growth data shown in Figure 1A, excluding the single outlier. (B) The age-specific growth-rate function for the Kemp's ridley sea turtle growth function shown in Panel A represented by the first derivative of Equation 1, which is $y'_{(t)} = \sum (\alpha_i \beta_i \text{sech}^2(\beta_i(t - \delta_i)))$ with the same parameters defined for Equation 1 and with sech (hyperbolic secant) = $(1 - \tanh)$.

function is inconclusive because the data span was incomplete, missing not only the first growth cycle (if it occurred at all) but also the onset of adult maturation. By the end of the study the remaining 8 turtles were still growing and below estimates of adult size (weight) recorded for wild stocks. Moreover, growth in captivity might well bear little similarity to the growth dynamics of wild stock Kemp's ridley sea turtles, which seem to grow much slower at a given size (Caillouet et al., 1986).

The nonparametric smooth shown here in Figure 1A fitted to a more complete age and size range for wild stock Kemp's ridley sea turtles implied that growth comprised two consecutive phases and that an explicit polyphasic model (Table 1; Fig. 2) might be a better parametric description of growth than monophasic models proposed previously for this species. Nonetheless, two major cautions are warranted prior to drawing further conclusions from Figure 2 about Kemp's ridley growth dynamics. These cautions relate to the implications for growth inferences due to 1) data sparsity in the early growth years for this data set and 2) the size composition anomaly between stranding subsamples for this data set.

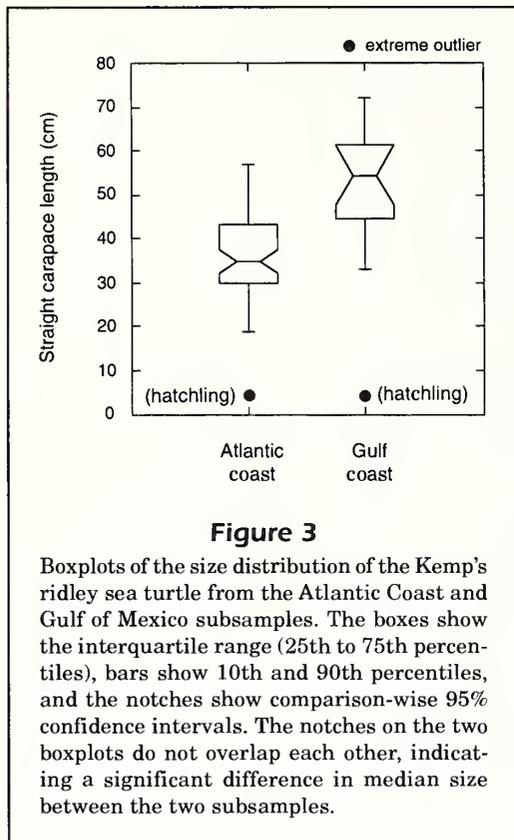
The data were sparse in the lower region of the first inferred growth spurt (see Fig. 1). The growth-layer loss protocols used in deriving the skeletochronological age estimates provided differing coverage of this growth region (see Zug et al., 1997). The age estimates used in our study were based on the correction-factor protocol that was considered more reliable than ranking protocol estimates (Zug et al., 1997) despite providing no coverage of the first growth year except for hatchling size. The model that was fitted (Fig. 2A) interpolated between known hatchling age and the end of the first year on the basis of the explicit form implied by the specified parametric function (Eq. 1). Although the conclusion of the first growth phase completed by ca. 25–30 cm SCL (see Fig. 1A) is firm despite sparse data during early growth, a specific growth spurt ≥ 1 year of age is tenuous. Given the lack of data during the first year, maximum growth might just as feasibly occur immediately following hatching, resulting in a monotonic decreasing age-specific growth-rate function for the first cycle and not the nonmonotonic function seen in Figure 2B. On the other hand, a growth spurt might occur a little later after hatching, resulting in a nonmonotonic age-specific growth-rate function for the first cycle similar to that proposed in Figure 2B but with the spurt occurring at say 3 or 6 months rather than at 12 months of age. Because of a sparsity of data during the early growth years, all these growth scenarios for the first growth cycle are feasible; therefore data for the first 12 months of life

following hatchling dispersal from the nesting beach are essential to resolve this important issue.

Nonetheless, other sources of information corroborate the growth profile proposed for the first phase in Figure 2B. First, the polyphasic function described by Equation 1 fitted the growth data well, including an estimated mean adult size (upper asymptote = $2(\alpha_1 + \alpha_2) = 62.6$ cm SCL from Table 1) consistent with empirical estimates of mean nesting female size of 64–65 cm SCL (Marquez, 1994). Moreover, the polyphasic function also predicted a mean hatchling size of 4.3 cm, which is consistent with the empirical estimate of mean hatchling size of 4.4 cm (Marquez, 1994). No other growth model has come close to predicting both the mean upper and lower size asymptotes of the postnatal development phase for the Kemp's ridley sea turtle. It is worth noting here that it is a common misconception in growth studies (particularly sea turtle growth studies) involving more than one animal that the upper asymptote of a parametric growth function estimates maximum adult size rather than the correct interpretation of mean adult size (see Ricker, 1979).

Second, a growth spurt ≥ 12 months of age and a growth phase completed by ca. 27 cm SCL (30–36 months of age) is coincident with developmental changes to the blood oxygen system of the Kemp's ridley sea turtle prior to acquisition of an adult blood system by 28 months of age (see Davis, 1991)—at least this was the case for captive-reared Kemp's ridley sea turtles. Davis (1991) also found that the oxygen capacity of the blood had increased substantially during the first 12 months of growth. The size range and timing of the first growth cycle is also consistent with apparent dietary and habitat shifts around 20 cm SCL (ca. 18 months of age; Fig. 2A; Eq. 1) from a presumed epipelagic habit to a coastal benthic habit (see Shaver 1991; Burke et al., 1994; Musick and Limpus, 1997).

The second major caution relates to a lack of informative cofactors (sex, geographic subsample) being included in the model because of insufficient records or small subsamples. For instance, sex was recorded for only 37% of the strandings, whereas the Atlantic coast subsample (cf. Gulf coast) accounted for 79% of the strandings data (see Fig. 1, B and C). Moreover, the Atlantic subsample comprised a significantly different size composition compared with that of the Gulf of Mexico (see Fig. 3). The apparent size composition anomaly might be due to 1) differential and inadequate spatial sampling of strandings and 2) developmental migration of Kemp's ridley sea turtles ≥ 40 cm SCL from the Atlantic coast to the Gulf of Mexico (see Collard and Ogren, 1990; Morreale et al., 1992; Epperly et al., 1995; Musick and Limpus,



1997). If the Atlantic and Gulf coast subsamples in the Zug et al., (1997) data set represent two discrete populations with population-specific growth behaviors, then the growth model here (Table 1; Fig. 2) is applicable to the Atlantic group only although a similar polyphasic model is apparent for both subsamples despite a sparsity of data for the ≥ 50 cm SCL group of the Atlantic subsample (Fig. 1B) and ≤ 40 cm SCL group of the Gulf subsample (Fig. 1C). The inclusion of the Gulf subsample serves to provide sufficient data to derive the upper asymptote for estimating mean adult size (see Fig. 1C). The Atlantic subsample comprised only immature Kemp's ridley sea turtles consistent with recorded size distributions for populations resident in various habitats along the US Atlantic coast (see Burke et al., 1994, Epperly et al., 1995; Schmid, 1995).

If the Zug et al. (1997) data set is representative of a single panmictic interbreeding stock displaying some form of staged developmental migration, then the model presented here is a reasonable approximation of the growth dynamics of the endangered Kemp's ridley sea turtle. There is compelling support for this view given current knowledge of Kemp's ridley sea turtle movement patterns (Musick and Limpus, 1997). Further support comes from the dis-

covery of a Kemp's ridley sea turtle (70 cm CCL, 67 cm SCL) nesting at Rancho Nuevo in 1996 (116 eggs laid) that had been tagged as a juvenile (51 cm CCL, 49 cm SCL) seven years earlier in Chesapeake Bay (Musick¹). Growth for this nesting ridley was consistent with the polyphasic growth function (Fig. 2A) although clearly a single record is not sufficient to provide conclusive evidence. Nonetheless, if the Atlantic and Gulf subsamples represent a single panmictic interbreeding stock, then a juvenile growth spurt at 46 cm SCL (ca. 8 years old, Fig. 2B) would indicate an ontogenetic shift associated with developmental migration from juvenile foraging habitats in the South Atlantic Bight (Musick and Limpus, 1997) and from within the Gulf of Mexico (Collard and Ogren, 1990) to foraging grounds in habitats along the Gulf coast prior to the onset of sexual maturity.

It is also conceivable, given the dispersal scenarios proposed by Collard and Ogren (1990), that the Kemp's ridley sea turtle is a single panmictic interbreeding stock that comprises two distinct post-hatchling developmental groups. One group remains within the Gulf of Mexico displaying relatively rapid growth owing to the warmer water (see Caillouet et al., 1995b). The second group represents the posthatchlings swept from the Gulf of Mexico that settle as juveniles (ca. 20 cm SCL) in the inshore developmental habitats of the mid-Atlantic (Morreale et al., 1992; Burke et al., 1994) and South Atlantic Bights (Epperly et al., 1995; Schmid, 1995). In this case the polyphasic growth model presented here (Table 1; Fig. 2) would be applicable to describing the mean stochastic growth dynamics of the cohorts swept each year from the Gulf of Mexico and undergoing growth in the Atlantic Bights prior to migrating back to the Gulf of Mexico. A separate growth model would need to be derived for the Gulf of Mexico developmental group although polyphasic growth behavior is also apparent for that subsample in our study (see Fig. 1C).

Clearly, a better understanding of the dispersal and developmental dynamics of the Kemp's ridley sea turtle based on a mark-recapture program with a high recapture likelihood is needed to resolve these complex issues. Although several local tagging programs have been undertaken (e.g. Caillouet et al., 1995a; Schmid, 1995; Burke et al., 1994, and references therein) a more comprehensive spatial and sampling-intensive program spanning the distributional range of this species is needed.

¹ Musick, J. 1997. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA. Personal commun.

Meanwhile, it is common practice to use somatic growth functions to estimate mean age at sexual maturity. The difficulty in using growth functions for this purpose is that there are no conclusive growth criteria to indicate onset of sexual maturity. Minimum or mean female nesting size, or an arbitrary size set slightly below mean nesting size, is a commonly used criterion. Using an arbitrary size criterion based on reasonable biological considerations, Caillouet et al., (1995b) proposed that head-started Kemp's ridley sea turtles irrespective of sex, took 10 years to reach sexual maturity at ca. 60 cm SCL. Zug et al. (1997) estimated 11–16 years for age-at-maturity for wild stock Kemp's ridley sea turtles on the basis of mean female nesting size. The upper asymptote of a parametric growth function is the correct estimate of mean adult size, if the correct growth function was used (see Ricker, 1979). By using the upper asymptote metric, it is then apparent that sexual maturity could be reached at ≥ 20 years of age for the current study (see Fig. 2B; Table 2) compared with 30 years of age for the Caillouet et al. (1995b) growth function (see Table 2).

But as Caillouet et al., (1995b) point out, mean adult size (nesting females) is a questionable criterion for estimating age at sexual maturity. That is why Caillouet et al. (1995b) defined an arbitrary size criterion to estimate age-at-maturity. However, the correct function for estimating mean age at maturity is an age-specific maturity-rate function conditioned on time-varying age, year, and cohort effects derived from a mixed longitudinal sampling study (see Chaloupka and Musick, 1997, for time-dependent demographic sampling issues). In the absence of such a complex function, a useful growth criterion for estimating age-at-maturity might be negligible growth derived from the age-specific growth-rate function indicating the onset of maturity. It is increasingly apparent that growth for sea turtles becomes negligible approaching the onset of sexual maturity (see Chaloupka and Limpus, 1997). Although this is a study-dependent and subjective metric, it is clear that negligible growth in the current study occurs ≥ 15 years of age or ≤ 0.25 cm SCL/year (see Fig. 2B and Table 2). Growth was imperceptible by 21 years of age (Table 2); thus the age range of 15–20 years appears to be a reasonable interval estimate of expected age at sexual maturity for the Kemp's ridley sea turtle.

It is therefore noteworthy that the Kemp's ridley sea turtle tagged in Chesapeake Bay as a juvenile (ca. 49 cm SCL) and discovered nesting seven years later at Rancho Nuevo (see "Discussion" above) was estimated by reference to Figure 2 to be about 9 years old when tagged and therefore 16 years old at the

first recorded nesting. The nesting turtle was ca. 67 cm SCL, which is larger than the estimated upper asymptote of ca. 63 cm SCL (Table 1: $2(\alpha_1 + \alpha_2)$ cm SCL). Recall, however, that the upper asymptote here represents mean adult size (or mean nesting size, assuming growth is not sex-specific); therefore 50% of a random sample of adult or nesting Kemp's ridley sea turtles would be >63 cm SCL, whereas 50% of the sample would be smaller.

Despite sampling design constraints, cautions about skeletochronological methods, small sample size, and perhaps nonequivalent geographic subsamples, the data set presented in Zug et al. (1997) is of considerable importance for helping to improve our understanding of the growth dynamics of the endangered Kemp's ridley sea turtle. The re-analysis of these data with exploratory nonparametric smoothing suggested that expected age-specific growth for the Kemp's ridley sea turtle was polyphasic and could be modeled with a sequence of parametric curves. A parametric model comprising a summation of logistic functions fitted the data well, implying growth spurts at ≥ 1 year of age (mean size=13 cm SCL) and ca. 8 years of age (mean size=46 cm SCL) followed by negligible growth approaching the onset of maturity ca. 15–20 years of age (mean size=63 cm SCL). Polyphasic growth behavior is therefore one of many reasons why a monophasic growth function cannot fit the entire postnatal developmental phase of the Kemp's ridley sea turtle, let alone for any other sea turtle species (see Chaloupka and Musick, 1997).

Acknowledgments

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Age determination of larval strombid gastropods by means of growth increment counts in statoliths

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The queen conch, *Strombus gigas* Linnaeus, and the milk conch, *S. costatus* Gmelin, are important gastropods of the Caribbean region (Appeldoorn and Rodríguez, 1994). To age strombid larvae by means of their statoliths would be useful in order to study aspects of their larval life histories and ecology. Statoliths, like fish otoliths, are formed of aragonitic calcium carbonate deposited on a protein matrix and exhibit periodic growth increments (Radtke, 1983). Research on statolith microstructure has been limited primarily to age determination of commercially important cephalopods (e.g. Jackson, 1994). D'Asaro (1965) observed statocysts that appeared in four-day-old embryos of *S. gigas* and that were fully functional by day six; he also noted growth increments or rings on these structures. These increments were confirmed by Salley (1986). Our objective is to validate the use of statolith microstructure in *S. gigas* and *S. costatus* to provide information on age, growth, and length of larval life.

Materials and methods

Egg masses from eight *Strombus costatus* and one *S. gigas* were col-

lected from ovidepositing females at a site 7 km south of La Parguera, southwest coast of Puerto Rico (17.92°N, 67.05°W). Egg masses were held in 75-L aquaria subjected to the natural light-dark cycle. Culture methods of Ballantine and Appeldoorn (1983) were used. Aquaria were cleaned daily, after which one liter of Tahitian *Isochrysis* (10⁶ cells/mL) was added. A minimum daily sample of ten individuals was removed from each aquarium and preserved in 70% ethanol. We examined the statolith microstructure of larvae from the longest surviving cultures. Since no veligers reared in our laboratory developed through metamorphosis, we obtained preserved (5% buffered formalin, pH 8.0) *S. gigas* veligers and juveniles of known age from the Trade Wind Industries' hatchery in the Turks and Caicos Islands.

Preserved veligers were examined with a dissecting microscope, their larval shell length (apex to siphonal canal) was measured, and their shell removed. A drop of 60% solution of alizarin red in glycerin was added to increase contrast between stained soft tissues and the unstained statolith. Coverslips were added, sealed with Permount, and samples were inspected under a compound scope at 1,000×. Sta-

tolith diameters were measured with an ocular micrometer. Increments on statoliths were counted by focusing up and down through the statolith. For each day of age, counts were made from one statolith from each of 20 veligers; all counts were made by the same reader in a blind manner. General physical structure was observed and described, with emphasis placed on the periods preceding and following hatching, and, for *S. gigas* juveniles, preceding and following metamorphosis to determine the presence and nature of any transitional marks associated with these events.

Statolith diameter, number of growth increments, and shell length were averaged for each day and arranged with age (in days after hatching). Linear least-squares regressions were calculated to determine the relations among these three variables. To determine the precision (or reproducibility) of counts of increments (i.e. verification, Wilson et al., 1983), repeated counts for both statoliths were made on subsamples. The number of increments in these representative samples were counted three separate times (double-blind), and the results were averaged for individual veligers. Standard deviations (SD) were calculated for each individual; standard error of the means (SE) was calculated as appropriate. A nested analysis of variance (ANOVA) was done for each species to determine if variability in incremental counts was due to errors in measurement or to natural variability in increment deposition (Sokal and Rohlf, 1981). Data were grouped at four levels: 1) all

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individuals across age groups, 2) between individuals within age groups, 3) between statoliths within individuals, and 4) within statoliths.

For one culture of eight-day-old veligers of *S. costatus*, feeding was suspended for two consecutive days to induce change in statolith structure and to determine if changes in feeding regimen affected increment deposition. Statolith-increment numbers and statolith diameters ($n=10$) were compared with those of nonstarved larvae ($n=10$) of equivalent age with two-sample *t*-tests (Sokal and Rohlf, 1981).

Results

Statoliths from *Strombus costatus* and *S. gigas* veligers were similar in size, shape, and pattern of increment formation and were translucent in appearance. They have either a circular or elliptical appearance from a longitudinal view and a biconvex structure in transverse section. On the basis of changes in size and shape, three regions are apparent (Fig. 1). At the very center is a primordial granule, around which all other increments grow; newly hatched veligers show five increments (including the primordial granule). This five-increment region (region 1) is quite distinct because of its lighter color, greater width, and seemingly dome-like nature. Prehatching increments in *S. costatus* and *S. gigas* had mean widths of $1.11\ \mu\text{m}$ and $1.22\ \mu\text{m}$, respectively. Deposited around region 1 is a second, slightly darker, region. Thinner and smaller in width, this region (region 2) is composed of increments formed between hatching and completion of metamorphosis. Increment widths corresponding to the first day after hatching averaged $0.33\ \mu\text{m}$ for both *S. costatus* and *S. gigas*; over the first six days after hatching the average increment width was $0.24\ \mu\text{m}$ for both species. A third region (region 3), observed only in juveniles of *S. gigas*, appears immediately after completion of metamorphosis. A darker band visible at the outer edge of region 2 results from the even smaller spacings between five or six increments deposited just before metamorphosis. Increments corresponding to the last day before metamorphosis (age 20 days) measured $0.09\ \mu\text{m}$ on average, whereas increments corresponding to the first day after metamorphosis had a mean of $0.43\ \mu\text{m}$. Region 3 appears lighter than region 2, because of the wider increments.

In both species, most veligers hatched on the sixth day after egg mass deposition, defined as age 0. The mean number of increments on the first day after hatching was 6.00 for *S. costatus*, 6.70 for *S. gigas* (Table 1). Statoliths in *S. costatus* show a deposition pattern of 1.11 increments/day ($\text{SE}=0.59$) over days

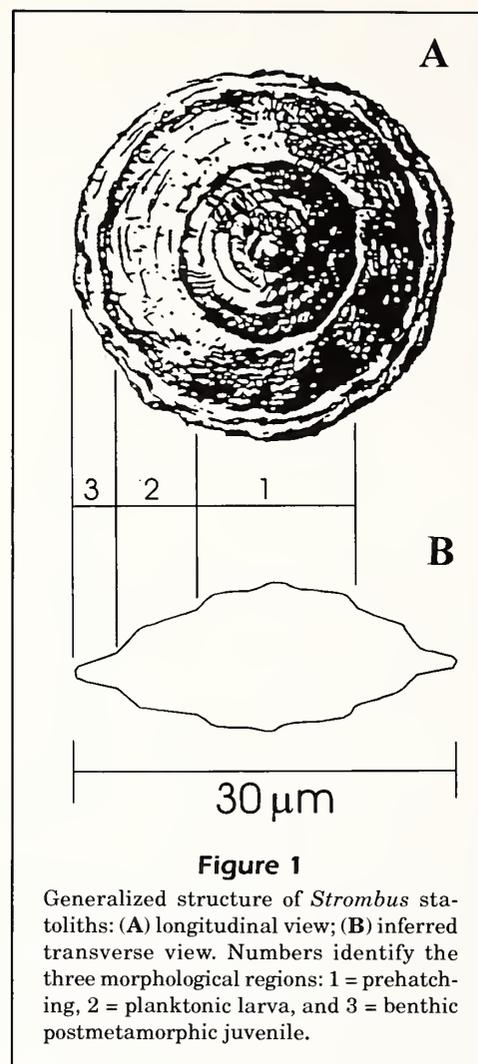


Figure 1

Generalized structure of *Strombus* statoliths: (A) longitudinal view; (B) inferred transverse view. Numbers identify the three morphological regions: 1 = prehatching, 2 = planktonic larva, and 3 = benthic postmetamorphic juvenile.

0–11; in *S. gigas* the deposition rate was 1.13 increments/day ($\text{SE}=0.59$) over days 0–9 (Table 1). In *S. gigas* this pattern continued until metamorphosis. For the day preceding metamorphosis (age 20 days), mean number of increments was 26.05; two days after metamorphosis (age 23 days) mean increment number was 29.40 (Table 1).

Significant regressions ($P<0.05$) were found between age (A, in days) and mean increment number (I) (*S. costatus*: $I = 6.08 + 0.986A$, $r^2=0.98$; *S. gigas*: $I = 6.17 + 0.984A$, $r^2=0.99$; data from Table 1). For analysis of *S. gigas*, we pooled locally-reared larvae with those brought from the Turks and Caicos. Separate regressions for these two sets of larvae were not significantly different. In the regression equations for both species, the slope did not differ from 1 significantly and the intercept did not significantly differ from 6 (*t*-test, $P<0.05$). Thus, the equations can be generalized to predict strombid veliger age from the number of statolith increments: $A = I - 6$.

Table 1

Mean statolith diameter ($\mu\text{m} \pm \text{SD}$), mean number of increments ($\pm \text{SD}$) and mean shell length ($\mu\text{m} \pm \text{SE}$) by age (days after hatching) for *Strombus costatus* and *S. gigas*. $n = 20$ for each day. META = day of metamorphosis, data not available.

Age (d)	<i>Strombus costatus</i>			<i>Strombus gigas</i>		
	Stolith diameter	Number of increments	Shell length	Stolith diameter	Number of increments	Shell length
0	13.35 \pm 0.48	6.00 \pm 0.65	345.00 \pm 32.60	14.65 \pm 0.80	6.70 \pm 0.73	325.00 \pm 35.36
1	14.05 \pm 0.22	7.06 \pm 0.64	390.00 \pm 13.69	15.05 \pm 0.59	7.30 \pm 0.66	375.00 \pm 40.82
2	15.30 \pm 0.56	8.80 \pm 0.70	440.00 \pm 13.69	15.70 \pm 0.71	7.25 \pm 0.79	387.50 \pm 17.68
3	15.50 \pm 0.50	8.75 \pm 0.50	470.00 \pm 18.71	16.45 \pm 0.50	8.00 \pm 1.03	408.25 \pm 14.43
4	15.93 \pm 0.46	9.57 \pm 1.28	625.12 \pm 17.83	—	—	—
5	—	—	—	16.35 \pm 0.51	10.72 \pm 0.46	443.00 \pm 18.32
6	16.14 \pm 0.64	11.71 \pm 0.73	625.80 \pm 21.77	17.40 \pm 0.97	12.35 \pm 1.26	458.25 \pm 28.87
7	15.65 \pm 0.91	12.65 \pm 1.04	635.00 \pm 15.69	17.15 \pm 0.57	13.45 \pm 1.28	461.35 \pm 15.22
8	16.50 \pm 0.67	14.85 \pm 0.99	641.75 \pm 30.28	—	—	—
9	—	—	—	18.10 \pm 0.30	15.55 \pm 2.63	466.75 \pm 14.43
10	16.35 \pm 0.57	15.15 \pm 2.03	650.00 \pm 14.42	17.93 \pm 0.46	17.07 \pm 1.59	475.80 \pm 13.67
12	17.33 \pm 1.55	18.33 \pm 1.15	700.67 \pm 24.32	—	—	—
19	—	—	—	27.60 \pm 0.82	24.35 \pm 0.75	1160.00 \pm 31.75
20	—	—	—	27.90 \pm 0.55	26.05 \pm 0.83	1177.50 \pm 40.00
21	—	—	—	META	META	META
22	—	—	—	28.15 \pm 1.39	26.75 \pm 4.28	1340.00 \pm 44.50
23	—	—	—	30.45 \pm 1.10	29.40 \pm 1.10	1655.00 \pm 83.25

Individual statolith increment counts and the magnitude of corresponding standard deviations (Tables 2 and 3) indicate that observed variability may be due to errors in measurement, not to variability in increment deposition. Nested ANOVA of subsamples of each species supported this hypothesis (Table 4), showing significant variability only at the level of readings between age groups.

Within each species, the relation between age (A) and statolith diameter (D, μm) was more variable than that between age and increment count (*S. costatus*: $D = 14.21 + 0.26A$, $r^2 = 0.80$; *S. gigas*: $D = 14.93 + 0.34A$, $r^2 = 0.93$). Similarly, the relation between age and shell length (L, μm) was more variable than that between age and increment count but was similar to that between statolith diameter and age (*S. costatus*: $L = 397.6 + 29.2A$, $r^2 = 0.83$; *S. gigas*: $L = 356.7 + 13.7A$, $r^2 = 0.89$).

Significant regressions occurred between shell length and statolith diameter (*S. costatus*: $L = -1015 + 100.4D$, $r^2 = 0.85$; *S. gigas*: $L = -237 + 39.9D$, $r^2 = 0.90$). Data for *S. gigas* obtained from the Turks and Caicos hatchery did not, however, fit this relation, suggesting that 1) environmental or genetic factors influence the relative growth of these structures, or 2) the relation is not linear over the entire larval and postmetamorphic period.

Larvae of *S. costatus* subjected to starvation showed no unusual pattern in region 2; mean number of increments between seven-day-old starved

(12.09 ± 0.74 SD) and nonstarved (12.65 ± 1.04 SD) larvae were not significantly different ($t_{18} = 0.262$; $P > 0.05$). Mean statolith diameter was also similar in the two groups (15.65 ± 0.91 SD μm for nonstarved larvae; 14.83 ± 0.75 SD μm for starved ones) ($t_{18} = 1.414$; $P > 0.05$).

Discussion

Statoliths of strombid larvae have a distinctly recognizable structure at hatching. Region 1 consists of a primordial granule surrounded by four increments. Three regions within the statolith result from changes in density of increments caused by abrupt changes in increment width at times of hatching and metamorphosis. Large transitions in incremental width may be caused by differences in metabolism during normal larval growth and development, including variable mineral deposition in the larval shell (Maeda-Martínez, 1987).

In both *S. costatus* and *S. gigas*, the rate of increment formation is constant after hatching. Variability found in incremental deposition was due largely to errors in measurement, not variation in depositional rate. A two-day period of starvation did not produce any noticeable structural change or precise mark. Starved veligers may have continued growing on stored energy reserves (Rodríguez Gil, 1995), negating differences between treatments. That starved

veligers still produced statolith rings without structural change implies that age estimates of veligers from statolith increment counts are robust. Periodicity of statolith growth in larval *S. costatus* and *S. gigas* is sufficiently reliable to be considered a better tool for age determination than diameter of statolith or measurement of shell length. Counts of increments were measurably less variable with age than were measurements of statolith diameter, or shell length.

In fishes, otoliths have been used to address questions regarding larval dispersal (Thresher and Brothers, 1985); settlement dynamics (Victor, 1983); growth rates (Radtke and Dean, 1982); mortality rates (Essig and Cole, 1986); and larval patch-size estimation (Victor, 1984). Statolith-based age and growth determination, however, has not been used in early life history studies of mollusks; characteristics such as size, shell structure, and distance off-

shore have been used to infer relative age or length of planktonic life (e.g. Scheltema, 1978; Jablonski and Lutz, 1980, 1983; Pechenik et al., 1984; Pechenik, 1986). Our results here indicate a more highly quantitative method for ageing larvae.

Acknowledgments

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Table 2
Variability in statolith increment counts within laboratory-reared larval *Strombus costatus*. Age = days after hatching.

Age (d)	Statolith A					Statolith B				
	Counts			Mean	SE	Counts			Mean	SE
	1	2	3			1	2	3		
0	6	6	6	6.00	0.00	6	5	5	5.33	0.58
0	6	6	6	6.00	0.00	5	5	5	5.00	0.00
0	6	7	7	6.67	0.58	7	7	6	6.67	0.58
(average)				6.22	0.44				5.67	0.87
1	6	6	6	6.00	0.00	7	7	7	7.00	0.00
1	7	7	8	7.33	0.58	8	6	8	7.33	1.15
(average)				6.67	0.82				7.17	0.75
2	8	8	9	8.33	0.58	9	9	9	9.00	0.00
2	10	8	9	9.00	1.00	9	9	9	9.00	0.00
2	9	9	9	9.00	0.00	10	10	8	9.33	1.15
(average)				8.78	0.67				9.11	0.60
4	10	10	10	10.00	0.00	10	9	9	9.33	0.58
6	11	12	11	11.33	0.58	12	13	12	12.33	0.58
6	11	11	11	11.00	0.00	11	12	11	11.33	0.58
(average)				11.17	0.41				11.83	0.75
7	10	10	11	10.33	0.58	11	11	12	11.33	0.58
7	13	11	13	12.33	1.15	12	10	13	11.67	1.53
7	14	14	12	13.33	1.15	15	13	13	13.67	1.15
7	14	14	15	14.33	0.58	15	13	13	13.67	1.15
(average)				12.58	1.73				12.58	1.51
8	15	14	15	14.67	0.58	14	13	16	14.33	1.53
8	13	15	14	14.00	1.00	12	14	13	13.00	1.00
(average)				14.33	0.82				13.67	1.37
10	15	14	14	14.33	0.58	16	15	15	15.33	0.58
10	14	16	15	15.00	1.00	15	14	16	15.00	1.00
(average)				14.67	0.82				15.17	0.75

Table 3

Variability in statolith increment counts within laboratory-reared larval *Strombus gigas*. Age = days after hatching.

Age (d)	Statolith A					Statolith B				
	Counts			Mean	SE	Counts			Mean	SE
	1	2	3			1	2	3		
0	6	6	6	6.00	0.00	6	6	7	6.33	0.58
0	8	8	7	7.67	0.58	8	8	7	7.67	0.58
0	7	7	7	7.00	0.00	7	6	7	6.67	0.58
(average)				6.89	0.78				6.89	0.78
1	8	7	7	7.33	0.58	8	7	6	7.00	1.00
1	8	7	7	7.33	0.58	9	8	7	8.00	1.00
1	7	8	7	7.33	0.58	8	8	8	8.00	0.00
(average)				7.33	0.50				7.67	0.87
2	8	6	7	7.00	1.00	7	7	7	7.00	0.00
2	7	7	6	6.67	0.58	7	6	7	6.67	0.58
(average)				6.83	0.75				6.83	0.41
3	7	7	6	6.67	0.58	7	7	7	7.00	0.00
5	11	11	11	11.00	0.00	11	11	11	11.00	0.00
5	10	11	10	10.33	0.58	10	10	11	10.33	0.58
(average)				10.67	0.52				10.67	0.52
6	13	15	13	13.67	1.15	12	14	14	13.33	1.15
6	10	11	11	10.67	0.58	11	12	12	11.67	0.58
(average)				12.17	1.83				12.50	1.22
7	14	14	12	13.33	1.15	14	12	11	12.33	1.53
7	12	12	12	12.00	0.00	12	13	13	12.67	0.58
7	14	16	15	15.00	1.00	16	13	14	14.33	1.53
(average)				13.44	1.51				13.11	1.45
9	18	17	15	16.67	1.53	16	20	16	17.33	2.31
9	16	15	17	16.00	1.00	16	18	16	16.67	1.15
9	14	14	14	14.00	0.00	13	15	13	13.67	1.15
(average)				15.55	1.51				15.89	2.20
10	16	18	17	17.00	1.00	20	20	19	19.67	0.58

Table 4

Nested ANOVA of statolith increment counts for subsamples of laboratory-reared larval *Strombus costatus* and *S. gigas*. SS = sum of squares, df = degrees of freedom, MS = mean square, P = probability of error, $S = P \leq 0.05$, $NS = P > 0.05$.

Source	SS	df	MS	F-ratio	P
<i>Strombus costatus</i> :					
Among age groups	6,868.3	7	981.2	103.3	$P < 0.05$ S
Among individuals	171.5	18	9.5	5.3	$P > 0.05$ NS
Between statoliths	68.1	37	1.8	0.2	$P > 0.05$ NS
Within statoliths	1,063.4	123	8.7		
Total	8,171.3	185	44.2		
<i>Strombus gigas</i> :					
Among age groups	6,732.5	8	841.6	195.7	$P < 0.05$ S
Among individuals	81.7	19	4.3	10.8	$P > 0.05$ NS
Between statoliths	14.1	39	0.4	0.7	$P > 0.05$ NS
Within statoliths	74.8	119	0.6		
Total	6,885.2	185	37.2		

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Bias in Chapman-Robson and least-squares estimators of mortality rates for steady-state populations

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When age-frequency data are insufficient for fisheries scientists to estimate year- or age-specific mortality, they are often pooled to provide a single estimate for all fully recruited age groups. The accuracy of a pooled estimate depends largely on whether or not the sampled population is in a steady state, i.e. a state in which the rates of recruitment and mortality are relatively constant with respect to time and age. Departures from this condition introduce known biases to the estimate of mortality (Ricker, 1975; Jensen, 1984). These departures may be difficult to detect because trends in time-specific recruitment or time- and age-specific mortality can result in a population age structure that is quite similar to that for a steady-state population. For instance, a long-term increasing trend in recruitment could result in a stable age frequency that would indicate a higher mortality rate than was actually occurring (for various scenarios see Ricker, 1975).

Pooled-data estimation techniques that have been applied to age-frequency data for fish populations include "catch curve" least-squares regression analysis (Seber, 1973; Ricker, 1975) and nonregression-based methods developed by Heincke (1913), Jackson (1939), and Chapman and Robson (1960). Of the nonregression-based estimators, the Chapman and Robson estimator is preferred because it is

the least sensitive to sampling error (Robson and Chapman, 1961). Despite the restrictive steady-state requirements, these techniques have been applied to a wide variety of marine animals; recent examples include Atlantic croaker, *Micropogonias undulatus* (Barbieri et al., 1994); blue rockfish, *Sebastes mystinus* (Adams and Howard, 1996); red drum, *Sciaenops ocellatus* (Ross et al., 1995); red porgy, *Pagrus pagrus* (Pajuelo and Lorenzo, 1996); and deep-water shrimp, *Aristeus antennatus* (Ragonese and Bianchini, 1996).

The Chapman-Robson (CR) estimator is based on the probability density function of the geometric distribution and provides a unique minimum-variance, unbiased estimate of survival (S),

$$S = \frac{\sum_{i=1}^N x_i}{N + \sum_{i=1}^N x_i - 1},$$

where x_i = the number of years the i th fish is older than the age at full recruitment; and

N = the total number of fully recruited fish.

The underlying assumption is that the age of each fish sampled represents a random, independent age observation from a steady-state

population. For age-frequency data that have been truncated to eliminate some older age groups, a slightly biased maximum likelihood estimator of survival (CRt) that can be solved by iteration is

$$\frac{\sum_{i=1}^N x_i}{N} = \frac{S}{1-S} - (K+1) \frac{S^{(K+1)}}{1-S^{(K+1)}},$$

where $K+1$ = the number of fully recruited age groups used (Chapman and Robson 1960).

The least-squares regression (LS) estimator provides an unbiased estimate of $-\log S$ (denoted as Z , the instantaneous total mortality rate) and is based on a linear fit to a log-transformed exponential decay model

$$E(\log N_j) = \log(pN_0) - Zj,$$

where N_j = the number of age j fish in the sample;

N_0 = the original number of fish in the population; and

p = the probability that a fish in the population is included in the sample (Seber, 1973).

As required for linear regression, log-abundance data are assumed to be independent and normally distributed with constant variance along the regression line. Concern about violating these assumptions led Chapman and Robson (1960) to recommend that when the LS method is used, the age-frequency data should be truncated to exclude less abundant age groups.

Although both the CR and LS estimator returned very accurate estimates of Z for a suite of exact steady-state age frequencies (Jensen, 1985), the effect of random variation within the sample age frequencies

has not been investigated. Jensen (1996) found that the CR method was less biased and more precise than the LS method when used to estimate mortality from the age structure of pooled, simulated net-hauls of lake whitefish, *Coregonus clupeaformis*. A random sample drawn from a known geometric distribution of ages will have an age distribution that varies stochastically from the true distribution. In this study, I evaluate the effect of sample size, mortality rate, and an age-frequency truncation scheme on the accuracy and precision of the CR (and CRt) and LS estimators when the sample age frequency is drawn randomly from a population of geometrically distributed ages.

Materials and methods

I used a stochastic model that allowed for random departures from the exact age distribution of the population to generate the simulated sample age frequencies. Under a known, constant survival rate, a geometric distribution function defines the cumulative probability of a fish from a fully recruited cohort being less than age j as

$$P(\text{age} < j) = \begin{cases} 0 & j < 1 \\ \sum_{m=1}^j (1-S)S^{m-1} & j \geq 1, \end{cases}$$

where S = the annual survival rate.

For this simulation, age-0 fish are defined as those in their first year of full vulnerability to capture. I sampled individual aged fish from this distribution by choosing a random, uniform number (probability) within the interval from 0 to 1 and determining the age corresponding to this value of the cumulative distribution function. By repeating this process, I was able to draw randomly a specified number of aged fish from a known geometric distribution defined by S . Each generated sample consisted of 100–1,000 individuals drawn independently from geometric distributions defined by Z values between 0.20 and 2.00. One thousand simulations were run for each combination of sample size and Z . For each simulation, a CR estimate of S and an LS estimate of Z were calculated from the sample age frequency. Means of the Chapman-Robson estimates of S were converted to Z so that they could be compared to the means of the LS estimates of Z .

The effect of constraining the right-hand limb of the sample age frequency was investigated by truncating each age-frequency distribution and recalculating mortality. The CRt and the LS estimates were

calculated with these data, and the mean CRt estimates of S were converted to Z . Each truncated age frequency was a subset of a simulation from the complete age-frequency simulations in which all fish that were older than the oldest age group meeting or exceeding a threshold abundance of 5 fish were removed. Although this truncation scheme reduced the effective sample size within each simulation, it accurately reflected the application of a truncation scheme to a real sample.

Results and discussion

Simulations indicated that mean CR estimates of mortality for the complete age frequencies were essentially unbiased. At all Z 's and sample sizes examined, the mean CR estimator agreed closely with the true value of Z . All differences between estimated mean Z 's and true Z 's (relative to the true Z) were <1% (Table 1).

The maximum likelihood estimator developed for use with truncated age frequencies (CRt) showed a negative bias that was greatest when sample size was low. With a 5-fish threshold rule, the mean CRt estimate of instantaneous total mortality was biased –12% at $Z = 0.2$ for a random sample of 100 fish (Fig. 1). At sample sizes of 300 fish or more, bias was reduced to less than about –4% for all Z 's (Fig. 1).

The mean LS estimates of Z for complete age frequencies were consistently less than the true instantaneous total mortality rate. This bias was greatest at low levels of Z when sample sizes were small (Table 2). At $Z = 0.2$, the difference between the mean estimated Z and true Z ranged from –16% for samples of 1,000 individuals to –37% for samples of 100. Deviations were much less, –4% to –8%, for all sample sizes when the true Z was 2.0. Bias in the LS estimator was reduced by truncating the sample age frequency. When I used a minimum threshold abundance of five, the negative bias was reduced to less than about 5% at sample sizes of at least 200 fish (Fig. 1).

Precision of the CR and CRt estimators was generally better than that of the LS estimator, especially at low Z 's. Although precision improved for all estimators as sample sizes became larger, the coefficient of variation (CV) for the CR and CRt estimators approached 1% for large samples at $Z = 0.2$, whereas the CV for the LS estimator approached only 6–9% (Fig. 2). For all given sample sizes, the precision of the CR and CRt estimators deteriorated as Z increased. The precision of the LS estimator changed little as Z increased, except when the estimator was based on samples of only 100 fish. In general, the CV's for the CR or CRt estimators were less than the

Table 1

Percent deviation from true instantaneous total mortality rate (Z) for the mean of 1,000 Chapman-Robson estimates of Z for each of the given combinations of sample size and true Z . Frequencies for all age groups were used in calculating mortality rates.

True Z	Sample size									
	100	200	300	400	500	600	700	800	900	1,000
0.20	-0.2	-0.1	-0.2	0.1	-0.0	-0.0	0.1	0.2	0.1	-0.0
0.40	-0.1	0.0	0.2	-0.1	0.3	-0.1	0.1	0.2	-0.2	0.2
0.60	-0.3	-0.2	0.0	0.0	-0.1	-0.0	-0.2	0.0	-0.2	0.1
0.80	-0.1	-0.2	0.2	-0.1	0.0	0.2	0.1	-0.0	-0.1	0.0
1.00	0.4	0.2	0.4	-0.1	-0.0	0.1	0.1	0.1	0.0	-0.2
1.20	-0.5	0.2	0.1	-0.0	0.1	0.0	0.2	-0.0	-0.2	-0.1
1.40	-0.3	0.3	-0.1	0.1	0.0	-0.0	-0.1	-0.1	0.0	-0.1
1.60	0.6	-0.1	0.2	0.2	0.2	-0.2	0.1	-0.1	-0.1	-0.1
1.80	-0.2	0.1	0.1	-0.1	0.1	-0.2	-0.1	0.1	-0.2	0.2
2.00	-0.1	-0.0	0.3	-0.1	0.0	-0.2	-0.2	-0.1	0.2	0.2

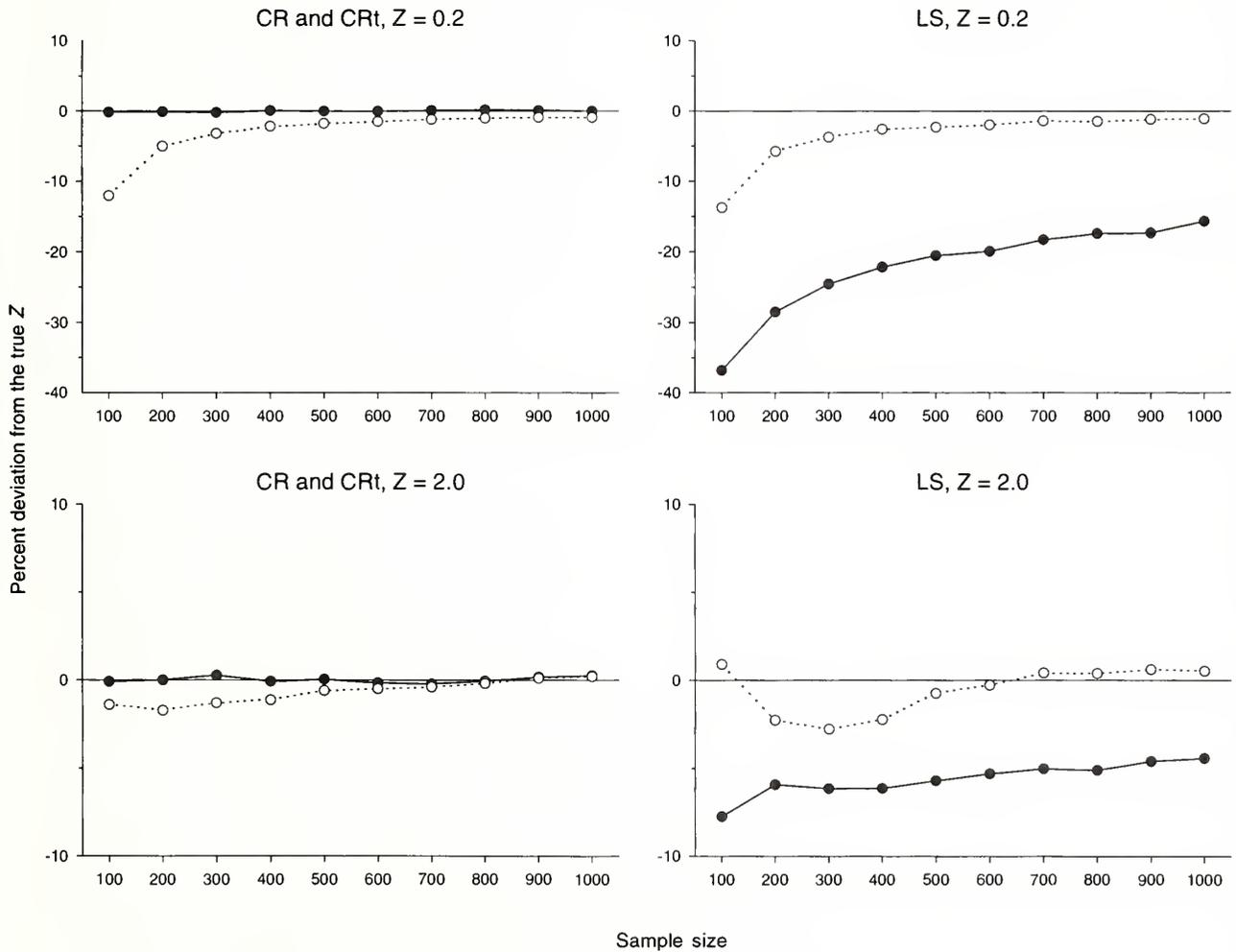


Figure 1

Percent deviation from true instantaneous total mortality (Z) for the mean of 1,000 Chapman-Robson (CR) or Chapman-Robson-for-truncated-data (CRt) estimates of survival or least-squares regression (LS) estimates of equivalent Z for different sample sizes when true Z is 0.2 or 2.0. The threshold levels, representing the minimum acceptable abundance for the oldest age used in the calculation of mortality were one fish (—●—) and five fish (—○—).

Table 2

Percent deviation from true instantaneous total mortality rate (Z) for the mean of 1,000 least-squares regression estimates of Z for each of the given combinations of sample size and true Z . Frequencies for all age groups were used in calculating mortality rates.

True Z	Sample size									
	100	200	300	400	500	600	700	800	900	1,000
0.20	-36.8	-28.5	-24.6	-22.1	-20.5	-19.9	-18.2	-17.4	-17.3	-15.6
0.40	-25.2	-20.4	-18.3	-16.9	-14.7	-14.3	-14.3	-13.2	-13.2	-12.3
0.60	-19.6	-17.1	-14.0	-12.9	-12.9	-11.9	-11.5	-11.3	-10.7	-10.6
0.80	-15.8	-14.1	-11.3	-11.0	-10.3	-9.8	-9.6	-9.3	-9.2	-9.7
1.00	-13.6	-10.7	-9.5	-9.3	-8.7	-9.1	-8.3	-7.8	-7.9	-7.9
1.20	-13.0	-9.1	-9.2	-8.4	-7.3	-8.2	-7.5	-7.2	-7.3	-6.8
1.40	-10.8	-9.1	-7.5	-7.9	-6.6	-6.8	-6.6	-6.5	-5.9	-7.1
1.60	-8.8	-7.6	-6.9	-6.2	-6.0	-7.0	-5.9	-5.6	-5.7	-6.1
1.80	-8.3	-6.7	-7.2	-6.4	-5.5	-5.1	-4.4	-5.6	-4.8	-4.9
2.00	-7.7	-5.9	-6.1	-6.1	-5.7	-5.3	-5.0	-5.1	-4.6	-4.4

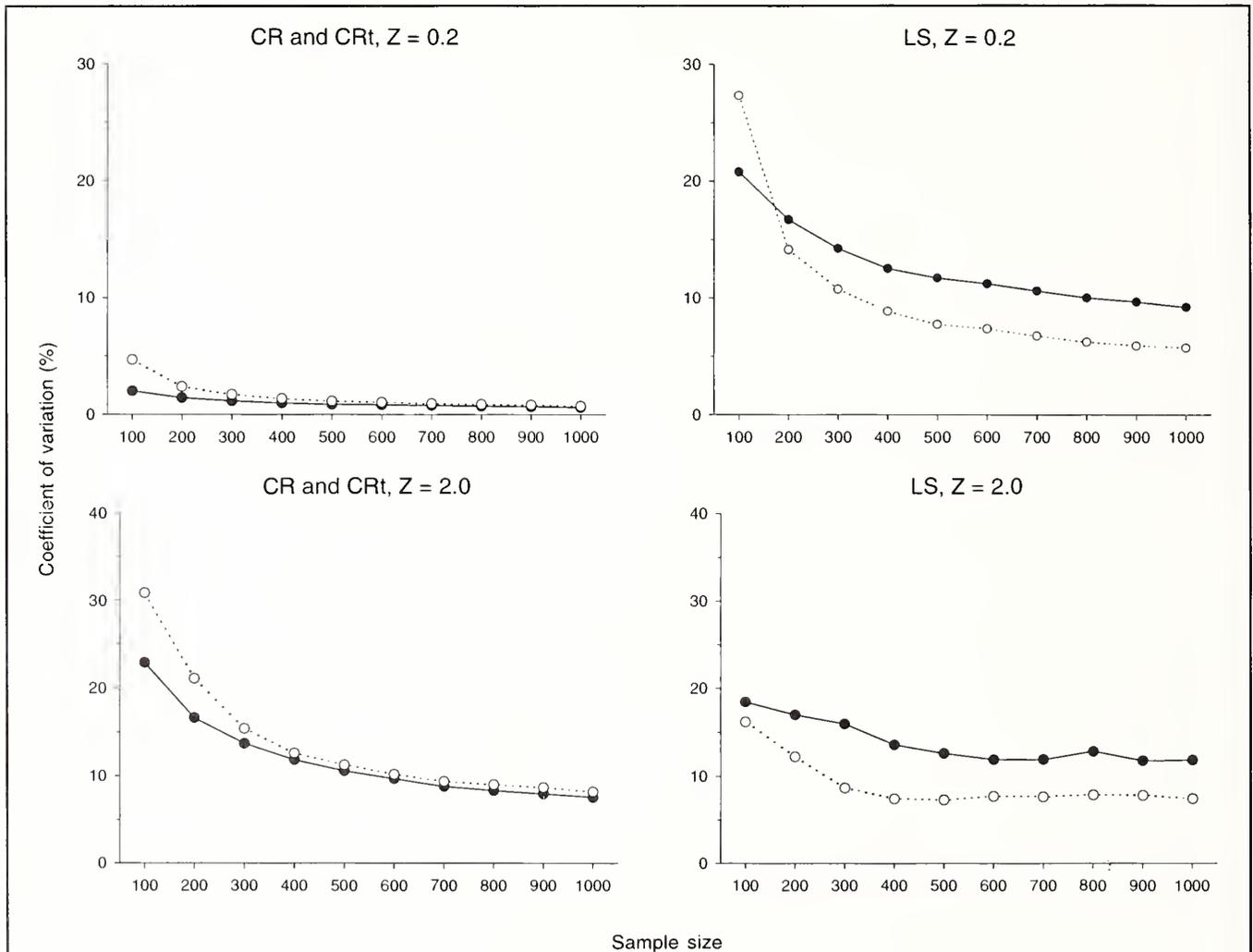


Figure 2

Coefficients of variation for Chapman-Robson (CR) and Chapman-Robson-for-truncated-data (CRT) estimates of survival or least-squares regression (LS) estimates of equivalent instantaneous total mortality (Z) made from samples of 100 to 1,000 ages generated stochastically under $Z = 0.2$ or $Z = 2.0$. Complete age frequencies (—●—) or those truncated using a 5-fish threshold (—○—) were used.

CV's for the LS estimator when Z was low but were similar or higher when Z was high.

When all fully recruited fish are equally available to a sampling gear, the CR estimator can provide a more accurate estimate of mortality than the LS estimator can. Applying the least-squares estimator to these data clearly violates the linear-regression assumption of equal variances among age groups. When a population is subjected to a low Z , the frequency distribution of log-abundances for older age groups in a sample becomes skewed to the right because log-abundance reaches a lower limit at zero (log of 1; Fig. 3). The frequency distribution of log-abundance then becomes truncated (undefined) past some distance to the left of its mean when zero abundances occur in the untransformed frequencies. The variances of the log-abundances appear to be positively related to age until the log-abundance frequencies become truncated when zero abundances appear in the samples for older age groups.

Empirical evidence led Chapman and Robson (1960) to conclude that haul data (catch rates for each age group) had an approximately constant variance when log transformed. However, the results from my simulations indicate that variances for the log-abundances are likely to differ among age groups. The assumption of constant variance is likely to be met only when the sampling gear operates on a few abundant age groups, in which there is no chance of only

periodically encountering an older age group. This led Chapman and Robson (1960) to suggest that these data should be truncated to eliminate the age frequencies beyond the oldest age with a minimum abundance of five fish. Although my findings concur with those of Chapman and Robson, the use of this threshold rule to eliminate older age groups does not completely eliminate all bias in the LS estimator—bias that can be attributed to violations of the assumptions on which the linear regression is based.

For truncated age-frequency data, both estimators gave biased results when small samples were drawn from a population of many age groups ($Z=0.2$). In these cases, truncation generally resulted in smaller samples that had far fewer age groups than were in the original complete age frequency. At high Z 's, age-frequency truncation reduced bias in the LS estimator to less than 5% at all sample sizes and reduced bias in the CRt estimator to less than 2%.

Violations of steady-state assumptions probably impart the most serious biases to pooled estimators of mortality. By simply inspecting a plot of log-abundance versus age for evidence of concavity or for a trend in the linear regression residuals, one can detect gross violations to these assumptions. Subtle biases inherent when the assumptions required by linear regression are not met are more difficult to detect. Both the CR and LS methods can provide very accurate and precise estimates of Z for age frequencies that follow an exact geometric distribution (Jensen, 1985). However, the LS estimator is biased when sample ages are drawn randomly from a steady-state, geometrically distributed population, whereas the CR estimator is not. The LS estimator may be more robust when age samples are not taken randomly (Chapman and Robson, 1960). The CRt and LS estimators generally showed similar levels of bias when the sample age structure is truncated with a minimum frequency criterion of 5 fish. In summary, the CR estimator will provide a more accurate and at least as precise an estimate of mortality as the LS estimator will when a random and complete age-frequency sample can be obtained from a population in steady-state.

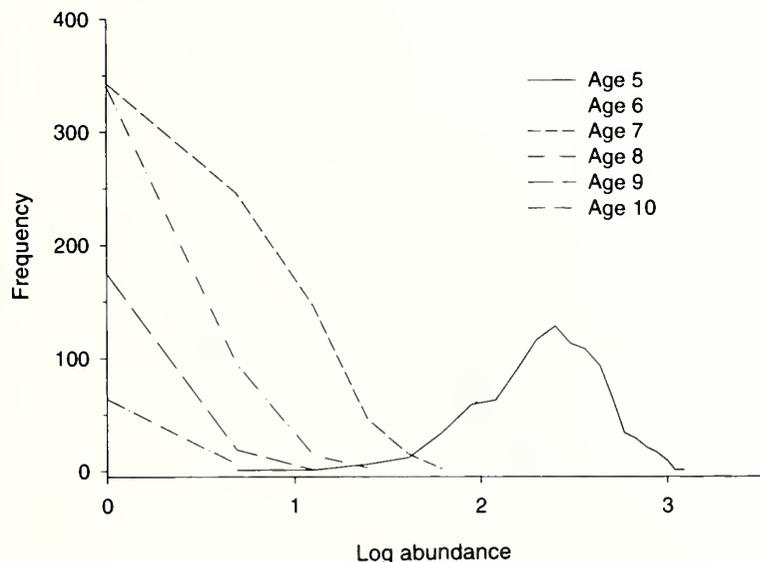


Figure 3

Frequency distributions of log-abundance for ages 5–10 generated stochastically with $Z = 1.0$. Log-abundance of each age group was taken from 1,000 simulations in which samples of 1,000 ages were drawn during each simulation.

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The effects of formalin and freezing on ovaries of albacore, *Thunnus alalunga*

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In almost every biological sampling program, tissue samples are collected and preserved for further examination. In this study, the effects of freezing and 10% buffered formalin on albacore, *Thunnus alalunga*, ovaries are compared to examine how each method of preservation affects ovarian weight and oocyte diameter. Formalin is frequently used to preserve ovaries for histological studies but, due to its toxicity, it may not be a good choice in all cases, and alternative methods, such as freezing, should be investigated. There is limited information on the effects of preservation on tuna gonads and, specifically, on albacore gonads. We investigated the effects caused by freezing and 10% buffered formalin on weight and oocyte diameter, because weight and other measurements (such as oocyte diameter) from fresh samples are not considered interchangeable with those from preserved samples (Lagler, 1968).

The purpose of our investigation was to compare fresh ovarian weights with weights of frozen ovaries and formalin-preserved ovaries from albacore as well as to determine how the diameters from oocytes are affected by differing methods of preservation.

Materials and methods

Albacore are seasonal spawners, spawning mainly during summer

months (Otsu and Uchida, 1959; Ramon and Bailey, 1996). Ovaries were collected from albacore caught from 1990 to 1993 (Table 1) with longline gear in the South Pacific (group A) and in waters off Hawaii (group B) and with trolling gear in the North Pacific (group C). In group B, samples were labeled as one of three subgroups (B1, B2, or B3) on the basis of the method of preservation used (Table 1).

In the South Pacific, ovaries from each collected fish were dissected and preserved; a total of 150 pairs were collected. In the North Pacific, sampling took place at two sites: 1) between latitude 42°33'N and 52°02'N and from longitude 129°00'W to 145°52'W and 2) in the waters off Hawaii. Table 1 lists the methods of preservation used for all samples.

To investigate the effects that freezing and 10% buffered formalin have on oocyte diameter, we examined oocyte diameters from 58 immature North Pacific albacore from 70 cm to 89 cm fork length (FL) in group C. Right-side ovaries were preserved in 10% buffered formalin; left-side ovaries were frozen until processed two months later. The diameters of the most developed oocyte for each side of the ovary were measured to the nearest 0.01 mm and compared statistically with Student's *t*-test.

To compare differences in oocyte diameter and weight between the two methods of preservation, we used ovaries from subgroup B,

which consisted of large, mature albacore (>95 cm FL). The mean diameter of oocytes in the most developed mode was measured from each side of the ovary and compared statistically with Student's *t*-test. The most developed mode of oocytes was determined with the criteria and method described by Schaefer (1987).

The effect of preservation on ovarian weight was examined for all samples collected in Hawaii (group B). Ovaries in group B were weighed fresh to the nearest 0.1 g and were then either preserved in 10% buffered formalin or were frozen. The samples were then reweighed two to three months later; samples preserved in 10% buffered formalin were placed on a paper towel, and excess moisture was patted off before they were weighed to the nearest 0.1 g on a Mettler PM3000 electronic balance. Frozen samples were thawed before being placed on a paper towel, and excess moisture was patted off before they were weighed.

The preserved weights of ovaries were compared with fresh weights by means of Student's *t*-test.

Results and discussion

Effect of preservation on oocyte diameter

Because measurements of oocyte diameter were not made on fresh oocytes, we assumed that left and right ovaries develop at the same rate. This assumption was tested with preserved specimens. Mean oocyte diameters of oocytes in the most developed mode in the right and left ovaries in group A were compared with mean oocyte diameters of oocytes in subgroups B2 and B3. The results indicated no

Table 1

Summary of albacore ovaries collected in the Pacific Ocean and preservation treatment used. MFL = Mean fork length.

Group	Location	Date	Number of samples	Collection purpose	Preservation method
A—South Pacific	New Caledonia lat. 21–23°S long. 164–166°E	May 1990–Feb 1992	105	Control group for oocyte diameter MFL = 90 cm (78–103 cm)	Formalin
	Tonga lat. 16–29°S long. 171–177°W	Jan 1990–Feb 1992	45	Control group for oocyte diameter MFL = 88 cm (82–102 cm)	Formalin
B—North Pacific	Hawaii within 200-mi EEZ	Jun 1991–Aug 1992	95	Preservation effects on weight and oocyte diameter MFL = 103 cm (96–116 cm)	
B1			16	Left and right ovary of each pair treated differently	Formalin or Frozen
B2			64		Formalin
B3			15		Frozen
C—North Pacific	U.S. jigboat fishery lat. 42–53°N long. 129–146°W	Aug 1990–Sep 1990	60	Preservation effects on oocyte diameter MFL = 82 cm (78–87 cm) Left and right ovary of each pair treated differently	Formalin or Frozen

Table 2Mean oocyte diameter (mm) data by ovary weight (g) and preservation method for albacore collected in North Pacific. *n* = number of fish in sample.

Ovary weight (g)	<i>n</i>	Mean oocyte diameter (mm)				Percent difference (formalin vs. frozen)
		Formalin		Frozen		
		\bar{x} +/-SE	Range	\bar{x} +/- SE	Range	
10–19	19	0.10 ± 0.004	0.07–0.14	0.09 ± 0.003	0.07–0.11	10.0
20–29	27	0.11 ± 0.002	0.09–0.13	0.10 ± 0.002	0.08–0.13	9.1
30–39	11	0.11 ± 0.004	0.08–0.13	0.09 ± 0.032	0.08–0.12	18.1
40–49	2	0.11 ± 0.000	0.11–0.11	0.11 ± 0.002	0.10–0.11	0.0
>50	1	0.11		0.11		0.0
Total	60	0.11 ± 0.002	0.07–0.13	0.10 ± 0.002	0.07–0.13	9.1

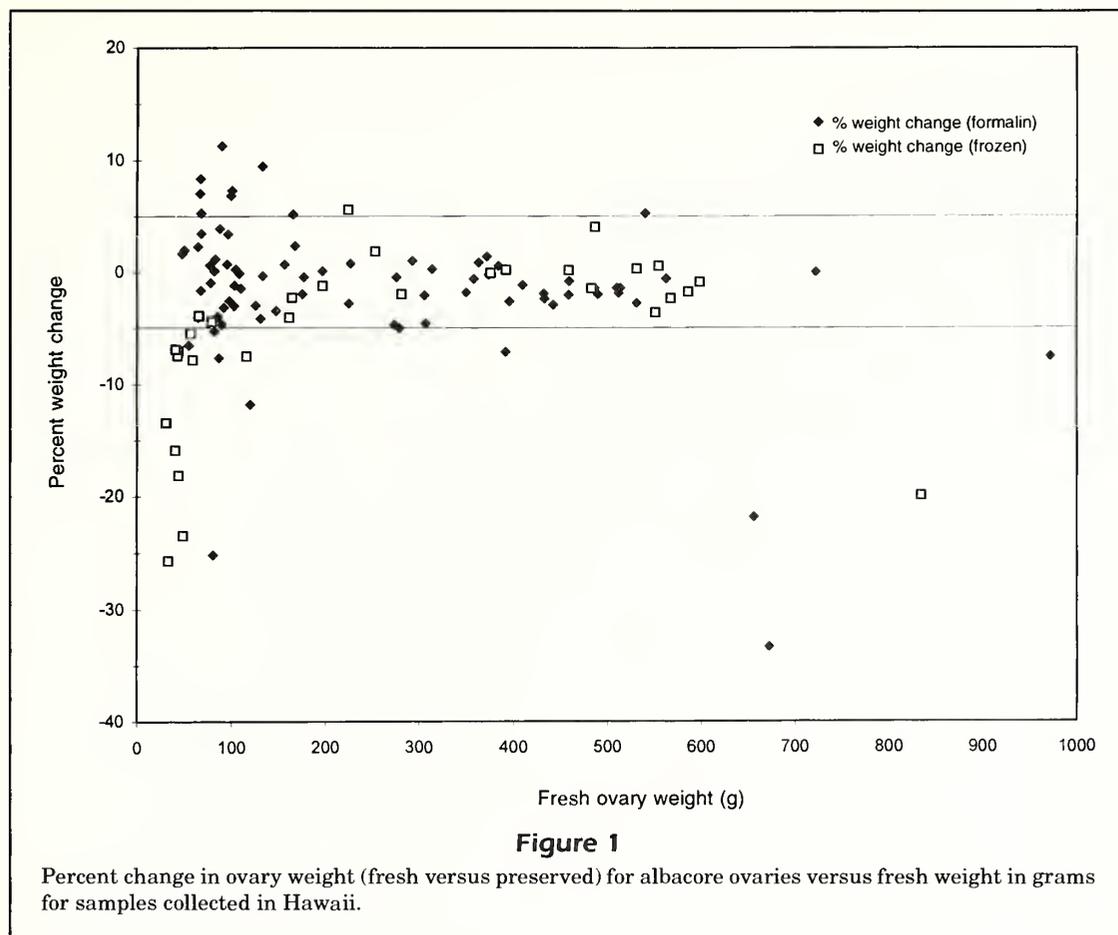
significant difference in oocyte diameter ($t=0.601$, $df=225$, $P>0.05$) within method of preservation, and we feel the effects of preservation are largely the source of any differences in measurements.

Ovaries from immature albacore (<88 cm FL) in group C, which had been preserved in 10% formalin, were found to have oocytes in the most developed mode with a significantly larger mean diameter in comparison with those from frozen samples ($t=4.614$, $df=59$, $P<0.05$). The mean diameter of oocytes preserved in 10% buffered formalin was, on average, 9.1% larger than the mean diameter of frozen oocytes (Table 2).

In mature albacore >95 cm FL, the mean diameter of oocytes in the most developed mode within

an ovary was measured for each side of the ovary and compared statistically within group B1. Oocytes preserved in 10% buffered formalin were found to have a significantly larger diameter ($t=3.581$, $df=14$, $P<0.05$)—7.1% greater, on average, than the oocyte diameter in frozen ovaries (Table 3).

Thus the mean diameter of oocytes in the most developed mode suggested that mean oocyte diameters of frozen ovaries shrank more than those preserved with 10% formalin. Differential preservation effects were reported by Joseph (1963), who looked at the effects of Gilson's fluid (Simpson, 1951) versus 4% formalin on oocyte diameter in yellowfin and skipjack tuna ovaries. He found that the diameters

**Table 3**

Mean oocyte diameter (mm) data by ovary weight (g) and preservation method for albacore collected near Hawaii. n = number of fish in sample.

Ovary weight (g)	n	Mean oocyte diameter (mm)				Percent difference (formalin vs. frozen)
		Formalin		Frozen		
		$\bar{x} \pm \text{SE}$	Range	$\bar{x} \pm \text{SE}$	Range	
<200	11	0.19 ± 0.031	0.12–0.48	0.17 ± 0.027	0.11–0.43	5.3
200–299	1	0.37		0.33		10.8
>300	3	0.59 ± 0.049	0.50–0.67	0.55 ± 0.042	0.48–0.62	6.8
Total	15	0.28 ± 0.049	0.12–0.67	0.26 ± 0.045	0.11–0.62	7.1

of oocytes preserved with Gilson's fluid shrank an average of 24% in comparison with those preserved in 4% formalin. This finding is in contrast with that of Schaefer and Orange (1956) who also examined the effects of Gilson's fluid versus formalin on oocyte diameter. They found that size frequencies for oocytes were similar with both methods for oocytes in the 5–63 μ size range. The strength of formalin used

by Schaefer and Orange was greater than that used by Joseph and may be the cause of the different results. Itano¹ examined the effects of brine, refrig-

¹ Itano, D. 1994. Progress report on a large-scale investigation on the reproductive biology of yellowfin tuna in the central and western Pacific region. Fourth meeting of the western Pacific yellowfin tuna research group; Koror, Palau, 9–11 August 1994.

eration, freezing, and 10% formalin on the histological quality of samples of ovary from yellowfin tuna. He reported that histological quality was best for those samples preserved fresh in 10% buffered formalin, whereas samples that had been merely refrigerated could not be used for histology (Itano¹).

Effect of preservation on weight

The preserved weight of the ovaries from mature fish in group B caught in Hawaii was compared with the fresh weight of ovaries from mature fish in group B ($t=2.565$, $df=94$ and $P<0.05$) and found to have significantly different means at the 95% confidence level. Preserved ovaries averaged a loss of 2% of their fresh weight. Our observations ranged from a loss of 33% to a gain of 11%.

Samples that were frozen ($n=31$) lost, on average, 6% of their weight and ranged from a loss of 26% to a gain of 6% (Fig. 1). In comparison, those that were preserved in 10% buffered formalin lost, on average, 1% of their weight and ranged from a loss of 33% to a gain of 11%. The greatest difference in albacore ovary weight was observed for ovaries weighing less than 200 g and which had been frozen, as well as for those greater than 600 g and which had been frozen (Fig. 1). The greater percent weight change observed in the smaller ovaries may be a result of processing method. The percentage of weight change for samples greater than 200 g, but less than 600 g, was within 5%. Of the limited number of samples ($n=5$) greater than 600 g, three of the ovaries that displayed a large loss of weight had oocytes that were hydrating and had mean oocyte diameters near 1 mm.

Conclusion

Freezing was found to have a greater effect on ovarian weight and oocyte diameter than 10% buffered formalin. Consequently, the different methods of preservation used in comparative studies should be evaluated cautiously. Furthermore, a single method of preservation or protocol should be used in a given study.

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Short-term retention of coded wire and internal anchor tags in juvenile common snook, *Centropomus undecimalis*

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Common snook, *Centropomus undecimalis*, are popular gamefish in southern Florida (Bruger and Haddad, 1986) and throughout their range in the southeastern United States and Central America. Snook populations in Florida declined during the 1970's and 1980's despite increasingly strict limits on the fishery (Taylor¹). In an effort to enhance snook populations, the Florida Department of Environmental Protection has considered developing a stocking program to supplement depleted wild snook stocks. To evaluate a stocking program's success or impact on native populations, hatchery-released fish must be marked to distinguish them from wild fish. Mark retention rates must be known to correctly interpret catch records and to make inferences about the stocking program or the wild population (Wallin and Van Den Avyle, 1994).

Coded wire tags (CWT's) are common in fish stocking programs because they can be applied quickly and economically to small, juvenile fish (<100 mm standard length, SL). Although retention rates of CWT's vary considerably among different species because of morphological differences (Heidinger and Cook, 1988; Szedlmayer and

Howe, 1995), retention rates are generally very good (>95%) if appropriate tagging tissues are identified and used (Dunning et al., 1990; Pitman and Isaac, 1995).

A disadvantage with using CWT's is that they cannot be detected by recreational or commercial fishermen; therefore, recovery of CWT data must be obtained independently. Internal anchor-external streamer tags with imprinted information allow recapture information to be obtained from recreational or commercial fisheries. However, these tags are generally restricted for use on fish >110 mm SL. As with CWT's, retention rates of these tags may vary because of morphological differences (Vogelbein and Overstreet, 1987; Waldman et al. 1990).

In this study, we evaluated retention of CWT's and two types of internal anchor-external streamer tags in age-0 common snook. The fish sizes in this study were similar to sizes that would be produced in a large-scale stocking program. We also evaluated the effects of tagging on growth and mortality. Retention of coded wire tags inserted in the cheek musculature was evaluated in common snook 60–115 mm SL for approximately 60 days after tagging. Retention of internal

anchor-external streamer tags with disk- or T-style anchors was evaluated in snook 110–180 mm SL for 30 days after tagging. The major differences between the two types of internal anchor tags were the shape of the anchor and the size of incision needed to apply the tags, either of which could affect retention or mortality. This study provides baseline information on tag retention rates in common snook that can be used to interpret catch records correctly and to evaluate common snook stocking programs.

Methods

Coded wire tag retention

We evaluated retention of CWT's and the effects of tagging on growth and mortality in 60–115 mm SL common snook. Equal numbers of fish were randomly assigned to one of three treatment groups: 1) tagged fish, 2) untagged fish that were handled in the same manner as tagged fish but were not tagged, and 3) control fish that were not tagged or handled. The cheek muscle was chosen for tag implantation because of the high CWT retention rates for this location in red drum and striped bass.

Tagged and untagged snook were anesthetized (100 ppm MS-222) just prior to treatment. One person applied all tags. Tags (1-mm-long, 0.25-mm-diameter) were injected vertically, 2 mm deep into the left adductor mandibularis muscle, posterior to the eye with a Northwest Marine Technology (Shaw Island, WA) Mark IV tagging machine.

¹ Taylor, R. 1997. Florida Marine Res. Inst., Florida Dep. of Environmental Protection, 100 Eighth Ave. SE, St. Petersburg, FL 33701-5095. Personal commun.

Fish were passed through a quality control device (QCD) to ensure tag presence. Fish in the untagged treatment were handled and passed through a QCD in the same manner as tagged fish but were not impaled on a tagging needle. Tagged and untagged fish were placed in separate 1,300-L tanks. Control fish were transferred directly to a 1,300-L tank with minimal disturbance.

The three tanks were aerated and had sand, diatomaceous earth, ultra-violet light, and biological filters. To prevent fish from jumping out, half of each tank was covered with 5-mm nylon mesh net and the other half was covered with opaque black plastic. Water temperatures averaged 24°C (range: 17–30°C); salinity averaged 26 ppt (range: 22–30 ppt); dissolved oxygen averaged 6.4 ppm (range: 4.0–7.4 ppm), and pH averaged 7.8 (range: 7.7–7.9). Fish were fed baitfish or commercially prepared fish chow daily.

Fish in the tagged treatment were checked for tag retention at 3, 30, and 60 days after tagging. At each tag check, fish were anesthetized (100 ppm MS-222), checked for tag presence with a field sampling de-

tector (Northwest Marine Technology), and measured. Fish in the untagged treatment were similarly anesthetized and measured at 3 and 30 days after tagging. Dead fish were removed from the tanks and checked for tag presence.

We assumed that mortality associated with tagging or handling would occur within 30 days of tagging (Szedlmayer and Howe, 1995). Therefore, after 30 days, fish in the untagged and control groups were combined and then randomly divided into two groups that received either the tagged or untagged treatment. This created a second trial of the experiment to evaluate CWT retention. Fish in the second trial were checked for tag retention at 3 and 30 days after tagging.

The entire experiment was repeated three times with fish from different culture facilities, resulting in three trials in which tag retention was evaluated for 30 days and three trials in which tag retention was evaluated for 30 and 60 days. Mean initial fish sizes varied among trials from 62 to 115 mm SL, and numbers of fish per treatment varied among trials from 24 to 76 (Table 1).

Table 1

Tag (coded wire) retention rates and fish survival rates at 3, 30, and 60 d after tagging for each treatment (tagged fish, untagged fish, and control fish) and fish sizes at the time of tagging. Starting no. = number of fish at the beginning of the experiment. Survival rates are from the start of the experiment until 3, 30, or 60 d after tagging. Standard length at the time of tagging is given as the mean with standard deviation in parentheses.

Trial	Treatment	Starting no.	Standard length (mm)	Tag retention rates (%)			Survival rates (%)		
				3-day	30-day	60-day	3-day	30-day	60-day
1	Tagged	26	92 (6.8)	100	100	100	100	92.3	92.3
	Untagged	24	95 (5.9)	—	—	—	92.3	92.3	—
	Control	26	94 (6.4)	—	—	—	100	100	—
2	Tagged	24	115 (9.7)	100	100	—	100	95.8	—
	Untagged	24	117 (9.6)	—	—	—	100	100	—
3	Tagged	76	62 (8.3)	98.6	92.0	85.4	98.7	67.1	63.1
	Untagged	76	59 (8.3)	—	—	—	100	93.1	—
	Control	75	59 (8.2)	—	—	—	100	81.3	—
4	Tagged	62	63 (9.2)	100	87.1	—	100	100	—
	Untagged	61	63 (9.2)	—	—	—	100	100	—
5	Tagged	74	74 (7.8)	100	95.8	95.8	98.6	98.6	98.6
	Untagged	75	71 (8.4)	—	—	—	98.7	98.7	—
	Control	75	75 (8.7)	—	—	—	100	100	—
6	Tagged	74	82 (10.1)	100	98.6	—	100	97.3	—
	Untagged	75	81 (9.4)	—	—	—	100	100	—
Overall	Tagged	—	71 (14.5)	99.8	95.6	93.7	99.6	91.9	84.7
	Untagged	—	73 (16.6)	—	—	—	98.5	97.4	—
	Control	—	72 (17.3)	—	—	—	100	93.8	—

Retention of internal anchor tags with external streamers

We evaluated retention of internal anchor tags with external streamers (disk and T-style) in 110–180 mm SL common snook. Tags with disk anchors (Model FM-89SL, Floy Mfg., Seattle, WA) consisted of a plastic 5 × 15 mm imprinted elliptical disk and 50-mm imprinted streamer. T-anchor tags (IEX tags, Hallprint Ltd., Holden Hill, Australia) consisted of an 18-mm T-shaped anchor and a 42-mm imprinted streamer. Equal numbers of fish were randomly assigned to one of three treatments: 1) fish tagged with disk anchor tags, 2) fish tagged with T-anchor tags, and 3) untagged fish that were handled in the same manner as tagged fish.

All fish were anesthetized (100 ppm MS-222) and measured just prior to treatment. To apply disk anchor tags, we used a scalpel to make an approximately 6-mm vertical incision into the body wall and then inserted the disk into the incision. To apply the T-anchor tags, we used a sharpened tag-applicator needle to make an approximately 2-mm diameter puncture and then inserted the T-anchor into the opening. Incisions were made on the left ventral side of the fish, anterior to the vent and posterior to the pectoral fin. Anchors were dipped in betadyne prior to insertion to minimize infection. Fish in the tag treatments were distinguished by fin clips: disk anchor-tagged fish received a left pectoral fin clip and T-anchor-tagged fish received a right pectoral fin clip. Fish in the untagged treatment were anesthetized, measured, and handled in the same manner as tagged fish but did not receive an incision or finclip. All fish were transferred immediately after treatment to a 13,300-L tank containing approximately 9,000 L of water. The tank was aerated and had sand, diatomaceous earth, and biological filters. Water temperatures averaged 27°C (range: 24–29°C); salinity averaged 26 ppt (range: 11–30 ppt); dissolved oxygen averaged 6.5 ppm (range: 4.9–8.4 ppm), and pH averaged 7.8 (range: 7.7–7.9 ppm). Fish were fed live baitfish daily.

Fish were checked for tag retention at 14 and 30 days after tagging. At each tag check, fish were anesthetized (100 ppm MS-222), checked for tag and finclip presence, measured, and weighed. The entire experiment was repeated twice; numbers of fish per treatment varied between trials from 61 to 78 fish per treatment (Table 1). During the first trial, necropsies were performed on three to ten fish from each treatment after 14 days to evaluate a bacterial infection. Six of ten T-anchor-tagged fish examined had anchors that were inserted into the swim bladder, whereas all disk-anchor-tagged fish examined ($n=3$)

had anchors that were correctly placed in the peritoneal cavity. Because of the potential for misapplication with the T-anchor tag, during the second trial we applied T-anchor tags by making a 3-mm scalpel incision rather than by making a puncture with a tag applicator needle. At the end of the second trial, ten randomly selected fish from each tag treatment were dissected and examined for tag implant locations and tissue healing.

Analyses

Estimates of the rates of tag retention and survival were arcsine-transformed prior to analysis (Sokal and Rohlf, 1981). Fish size at the time of tagging differed significantly among trials in both the CWT experiments (ANOVA, $df=5$, $F=517.6$, $P<0.01$) and in the internal-anchor-tag experiments (ANOVA, $df=1$, $F=6.7$, $P<0.01$). Therefore, mean size at tagging was used as a covariate in analysis of covariance (Sokal and Rohlf, 1981; SAS, 1989) to compare rates of tag retention, survival, and growth among time periods and treatment groups. Post hoc comparisons were conducted with the method of least-square means (SAS Institute, Inc., 1989).

Results

Overall, retention rates of coded wire tags averaged 99.8%, 95.6%, and 93.7% at 3, 30, and 60 days after tagging, respectively (Table 1). At 3 days, tag retention rates for all sizes of snook ranged from 98.6 to 100% (Fig. 1). Fish size at the time of tagging significantly affected tag retention rates ($F=12.5$, $P<0.01$); larger fish had higher retention rates, particularly during the 30- to 60-d period after tagging (Fig. 1). Tag retention of common snook >70 mm SL at the time of tagging was ≥95% at 30 and 60 days after tagging, whereas tag retention in snook <65 mm SL was 92.0% and 85.4% at 30–60 days after tagging, respectively (Table 1; Fig. 1). Tag retention rates decreased between 3 and 30 days after tagging (LSMEANS, $P=0.02$) but did not change significantly between 30 and 60 days (LSMEANS, $P=0.89$; Fig. 2).

Survival rates of CWT fish were not significantly different from those of the untagged or control fish ($df=2$, $F=0.5$, $P=0.61$). Survival rates of fish in all treatments averaged 99.6%, 91.9%, and 84.7% at 3, 30, and 60 days after tagging, respectively (Table 1). Poor survival of fish in the third trial (63%, Table 1) is attributed to parasitic infection. Growth rates of CWT fish were also not significantly different from those of untagged or control fish ($df=2$, $F=0.87$, $P=0.42$).

Overall, retention rates of T-anchor and disk-anchor tags averaged 100% and 99.2%, respectively, after 30 days (Table 2). Fish size at the time of tagging did not significantly affect internal anchor tag retention rates ($df=1, F=0.3, P=0.64$). Retention rates did not differ significantly between disk- and T-an-

chor-tagged fish or among time periods (for both comparisons, $df=1, F=0.8, P=0.43$). There were also no significant differences in survival ($df=2, F=0.7, P=0.55$) or growth ($df=2, F=0.03, P=0.10$) among treatments. Survival rates of T-anchor- and disk-anchor-tagged fish averaged 97.0 and 91.9% at 14 and 30 days after tagging, respectively (Table 2).

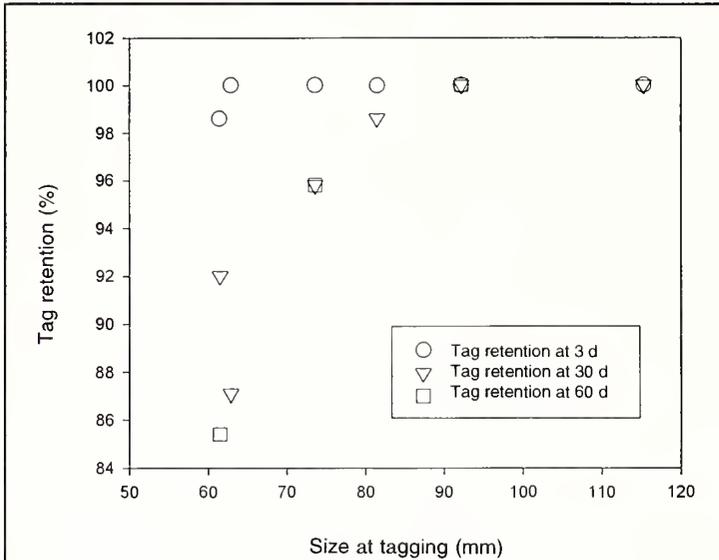


Figure 1

Retention rates of coded wire tags and average size (standard length) of juvenile snook at the time of tagging.

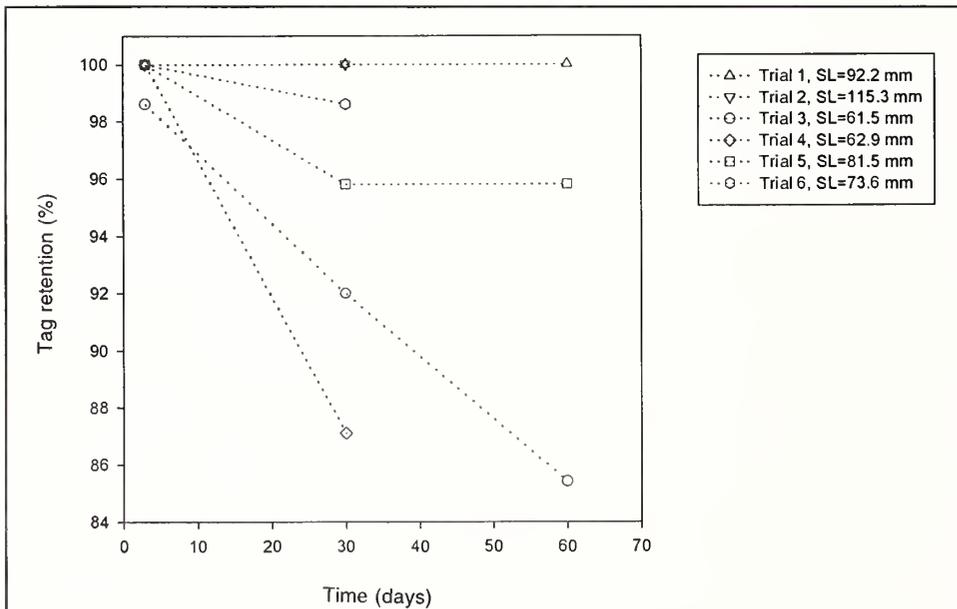


Figure 2

Retention rates of coded wire tags in fish 3, 30, and 60 days after tagging. The key shows mean initial size (SL) of fish in each trial.

Discussion

The high retention rates of CWT's reported in this study (85–100%) indicate that CWT's are effective for marking age-0 common snook and that the cheek musculature is appropriate for tagging. CWT's did not affect snook survival

or growth during the first 30–60 days after tagging, indicating that CWT's have negligible adverse effects during this time period. CWT retention rates increased with initial fish size (Fig. 1) from 87–92% for snook with an initial mean size of 62 mm SL to 95–100% for snook with initial mean sizes of 71–117 mm SL. Several authors have noted the importance of fish size or target tissue size in the retention of CWT's (Heidinger and Cook, 1988; Szedlmayer and Howe, 1995). Our study also shows a relation between initial tagging size and CWT retention.

Most tag loss occurred between 3 and 30 days (Fig. 2). Other studies have noted

Table 2

Internal anchor tag retention rates and fish survival rates at 14 and 30 d after tagging for each treatment (t-bar-tagged fish, disk-tagged fish, and control fish) and fish sizes at the time of tagging. Starting no. = number of fish at the beginning of the experiment. Survival rates are from the start of the experiment until 14 or 30 d after tagging. Standard length at the time of tagging is given as the mean with standard deviation in parentheses.

Trial	Treatment	Starting no.	Standard length (mm)	Tag retention rates (%)		Survival rates (%)	
				14-day	30-day	14-day	30-day
1	T-bar-tagged	78	139 (13.1)	100	100	93.6	93.6
	Disk-tagged	78	138 (13.0)	100	100	91.0	75.6
	Control	78	137 (13.7)	—	—	97.4	82.1
2	T-bar-tagged	61	135 (11.3)	100	100	100	100
	Disk-tagged	61	136 (10.4)	100	98.4	100	100
	Control	61	134 (10.7)	—	—	100	100
Overall	T-bar-tagged	—	136 (12.5)	100	100	96.8	96.8
	Disk-tagged	—	137 (11.9)	100	99.2	95.5	87.8
	Control	—	137 (12.6)	—	—	98.7	91.1

that most CWT loss in juvenile fish occurs within two to four weeks after tagging, the time period corresponding with the time required for the tagging puncture wound to heal (Dunning et al., 1990). Although there was no significant change in retention rates after 30 days, tag retention rates in the smallest fish (mean SL 62 mm) continued to decline between 30 and 60 days (Fig. 2), providing further evidence of the importance of fish size for tag retention.

Thirty-day retention rates of both types of internal anchor-external streamer tags were very high (>99%), indicating that these tag types are effective tools for marking >110 mm common snook. However, other studies have suggested that retention of disk- and T-anchor tags may decrease over months or years and should therefore be evaluated for longer periods of time (Collins et al., 1994). Although the incisions required to apply disk tags are larger than incisions required for T-anchor tags, there was no difference in survival or growth rates of fish with either tag type. Both tag types caused similar incidences of irritation at the tag insertion site. Similar irritation has been noted in other fish species and can eventually result in tag loss (Mattson et al., 1990; Collins et al., 1994). After 30 days, disk anchors were more frequently encapsulated and attached to the inside of the body wall than were T-anchors. Both tag types were equally likely to be incorrectly inserted in the swim bladder or gastrointestinal tract when the incision was made with a scalpel; overall, incorrect insertions were noted in 10–20% of the fish examined. We recommend using scalpels to insert the T-anchor tags; when a tag applicator needle was used, incidences of incorrect insertion increased to 60%, prob-

ably because of difficulty in controlling puncture depth.

In conclusion, because CWT retention rates were significantly improved for fish >70 mm SL, we recommend tagging snook at this size whenever possible. We also recommend that CWT retention in snook be evaluated for 30 days after tagging so that accurate estimates of tag-loss rates can be calculated. For snook >110 mm SL, both the T-anchor and disk internal anchor-external streamer tags were effective marking techniques. For all types of tags and all sizes of fish in our study, tagging did not significantly affect snook survival or growth.

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Announcement

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Fishery Bulletin

Guide for Contributors

Content

Articles published in *Fishery Bulletin* describe original research in fishery marine science, engineering and economics, and the environmental and ecological sciences, including modeling. Articles may range from relatively short to extensive; notes are reports of 5 to 10 pages without an abstract and describing methods or results not supported by a large body of data.

Although all contributions are subject to peer review, responsibility for the contents of papers rests upon the authors and not upon the editor or the publisher. It is therefore important that the contents of the manuscript are carefully considered by the authors.

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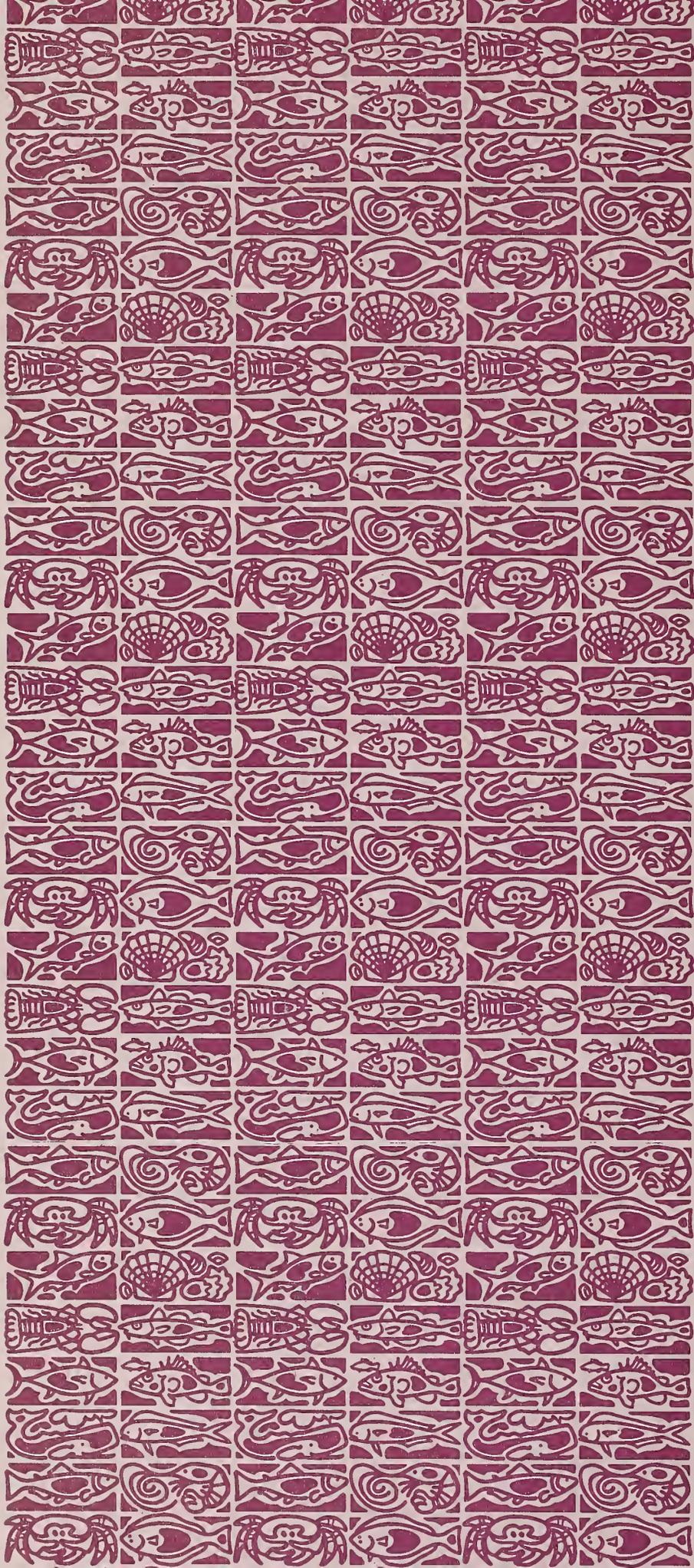
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