Steven Sawyer

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Abstract.—A ship survey was conducted in summer and fall of 1991 to estimate the abundance of cetaceans in California waters between the coast and approximately 555 km (300 nmi) offshore. Line-transect methods were used from a 53-m research vessel. Approximately 10,100 km were searched, and 515 groups of cetaceans were seen. The estimated abundances and coefficients of variation (in parentheses) of the most common small cetaceans are the following: 226,000 (0.28) short-beaked common dolphins, *Delphinus delphis*; 78,400 (0.35) Dall's porpoises, *Phocoenoides dalli*; 19,000 (0.41) striped dolphins, *Stenella coeruleoalba*; 12,300 (0.54) Pacific white-sided dolphins, *Lagenorhynchus obliquidens*; 9,470 (0.68) long-beaked common dolphins, *Delphinus capensis*; and 9,340 (0.57) northern right whale dolphins, *Lissodelphis borealis*. The estimated abundances (and CV's) of the most common large cetaceans are 2,250 (0.38) blue whales, *Balaenoptera musculus*; 935 (0.63) fin whales, *Balaenoptera physalus*; 756 (0.49) sperm whales, *Physeter macrocephalus*; and 626 (0.41) humpback whales, *Megaptera novaeangliae*. Estimates are also made for other species and for higher-level taxa that could not be identified to species.

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The abundance of cetaceans in California waters. Part I: Ship surveys in summer and fall of 1991

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The abundance of cetaceans in California waters is poorly known for the majority of species found there. For small cetaceans, quantitative estimates of abundance with statistical confidence limits are available only for common dolphins, *Delphinus delphis* (Dohl et al., 1986) and for harbor porpoise, *Phocoena phocoena* (Barlow, 1988). For large cetaceans, such estimates are available for gray whales, *Eschrichtius robustus* (Reilly, 1984; Buckland et al., 1993a); humpback whales, *Megaptera novaeangliae* (Calambokidis et al., 1990a, 1993[1]), and blue whales, *Balaenoptera musculus*.[1] Estimates have been made for some of the other species (Dohl et al.[2,3]), but these estimates are more than 10 years old, and most lack information on statistical precision.

Many, and perhaps all, cetaceans in California waters are vulnerable to entanglement and death in gillnet fisheries. A program is now in place to estimate the incidental mortality of cetaceans in the California gillnet fisheries (Lennert et al., in press). It is difficult, however, to assess the impact of gillnet mortality on cetacean populations without knowing population sizes. Coordinated ship and aerial surveys were initiated recently to estimate the abundance of all cetacean species in the region of California gillnet fisheries. To evaluate the effect of seasonality on cetacean abundance, surveys were designed to cover both cold-water months (Feb–Apr) and warm-water months (Jul–Nov). A ship survey was conducted during the warm-water period of 1991; an aerial survey was conducted during the cold-water periods of both 1991 and 1992. Results from the ship survey are reported here; population estimates from the aerial surveys are reported in a companion paper (Forney et al., this issue).

Field methods

A line-transect survey was conducted from 28 July to 5 November 1991 with the 53-m National Oceanographic and Atmospheric Admin-

[1] Calambokidis, J., G. H. Steiger, and J. R. Evenson. 1993. Photographic identification and abundance estimates of humpback and blue whales off California in 1991–92. Final Contract Rep. 50ABNF100137, submitted to the Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038, 40 p.

[2] Dohl, T. P., K. S. Norris, R. C. Guess, J. D. Bryant, and M. W. Honig. 1978. Cetacea of the Southern California Bight. Part II of Summary of marine mammals and seabird surveys of the Southern California Bight area, 1975–78. Final Rep. to the Bureau of Land Management, 414 p. [NTIS Rep. No. PB81248189.]

[3] Dohl, T. P., R. C. Guess, M. L. Duman, and R. C. Helm. 1983. Cetaceans of central and northern California, 1980–83: status, abundance, and distribution. Final report to the Minerals Management Serv., Contract No. 14-12-0001-29090, 284 p.

istration (NOAA) vessel *McArthur* to assess the abundance of cetaceans in California waters. Primary cruise tracks were drawn for a unifirm survey of the 814,900 km^2 area between the 18-m (10-fathom) isobath and approximately 555 km (300 nmi) offshore (Fig. 1).

Primary observation team

The basic survey method was that which was developed and used to estimate the abundance of small cetaceans in the eastern tropical Pacific (Holt and Powers, 1982; Holt, 1987; Holt and Sexton, 1989; Wade and Gerrodette, 1993). The primary observation team consisted of three observers who searched from a viewing height of 10 m above the sea surface: two observers searched with 25× pedestal-mounted binoculars; the third observer searched with unaided eye, and (occasionally) 7× binoculars, and also served as data recorder. Observers rotated among these three duty stations every 1/2 hour, and two observer teams alternated work and rest periods every two hours. Sighting effort was maintained from dawn to dusk whenever weather conditions allowed, and searching covered the entire region from directly in front of the vessel to 90 degrees left and right and out to the horizon. Data were recorded on a lap-top computer that had direct input from the ship's GPS (Global Positioning System) navigation system. Recorded data included sighting conditions (sea state, cloud cover, sun position, etc.), observer positions, the beginning and end of effort, and information pertaining to sightings.

When a sighting was made, all observers were made aware of the animals' location. The perpendicular distance from the trackline to the center of the group was estimated from the initial bearing and distance. The initial bearing of a cue (a blow, a splash, or a sighting of animals) was measured relative to the bow of the vessel by means of a calibrated collar on the base of the yoke of the 25× binoculars. The initial distance was typically estimated from a calibrated reticle scale in the oculars of both the 25× and 7× binoculars with the formula derived by Smith (1982) and was calibrated by using radar-measured distances to inanimate objects (Barlow and Lee, 1994). If a shore horizon was closer than 11.1 km (6 nmi), distance was estimated by comparison with the radar-measured distance to shore. Occasionally, for very close animals seen only by the third observer, sighting distances and angles were estimated by eye. If a cue turned out to be a cetacean, effort was interrupted and the ship was typically diverted towards the animals in order to obtain estimates of species composition and group size. The vessel was not typically diverted for cetaceans that were greater than 5.55 km (3 nmi) perpendicular distance from the trackline.

Species identification was made collectively by the team, but quantitative estimates of species composition and group size were made independently by each observer. For estimation purposes, a group was defined as a collection of closely associated individuals (typically within several body lengths of each other) that exhibited cohesive behavior. In the field, however, a single distant sighting might prove to be two behaviorally distinct groups upon closer inspection. In such cases, when it was impossible to determine which was the original group sighted, both groups were pooled to estimate group size and species composition. For mixed-species groups, species composition was recorded as an observer's estimate of the percentage of each species present in the group. The observers recorded species composition and group-size data in confidential personal notebooks, and the data were transcribed at the end of the day into the computer data record by the cruise leader.

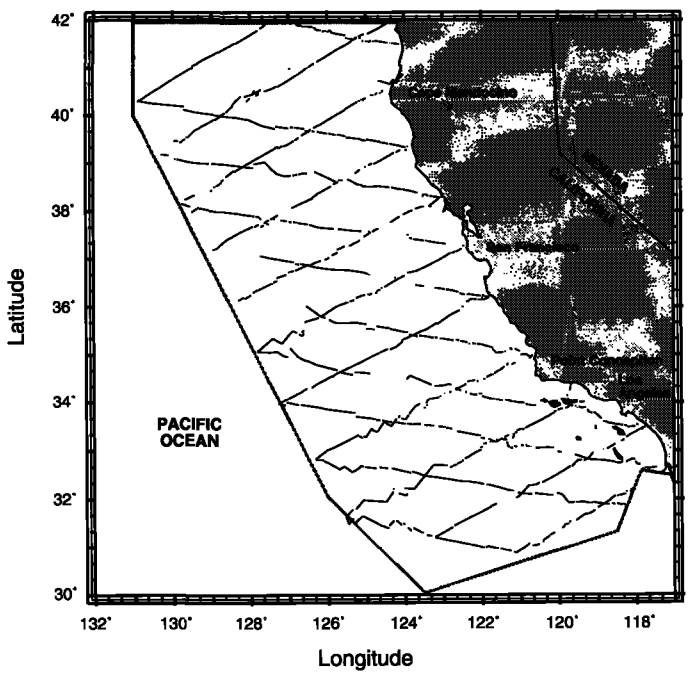

Figure 1

Transect lines (thin solid lines) completed during the survey. The bold polygon indicates the limit of the main study area.

Species identification

Observers attempted to classify all the species present in a group to the lowest possible taxonomic level (one member of each team was a cetacean identification expert with at least nine months of at-sea survey experience on prior marine mammal surveys). Several higher taxonomic groups were used in cases where species identification was not possible. These higher groups were beaked whales of the genus *Mesoplodon*; unidentified sei or Bryde's whales; unidentified beaked whales (including members of the genera *Mesoplodon* and *Ziphius*); unidentified large whales (including members of the species group "large whale" in Table 1 as well as the genera *Eschrichtius* and *Eubalaena*); unidentified baleen whales (including members of the genera *Balaenoptera*, *Megaptera*, *Eschrichtius*, and *Eubalaena*); unidentified small whales (including members of the species groups "small whales" and "large delphinids" in Table 1); unidentified delphinoids (including members of the species groups "small delphinids," "large delphinids," and "cryptic species" in Table 1); and unidentified cetaceans (which could include any of the species listed above or in Table 1). The number of sightings identified to these higher taxonomic levels is relatively small, and these animals were not included in the abundance estimates for individual species.

Conditionally independent observer

In addition to the primary observation team, a fourth observer was on duty 81% of the time and looked for cetaceans that were missed by the primary team. This conditionally independent observer was stationed immediately next to the other observers, searched with 7× binoculars and unaided eyes, and did not reveal the presence of cetaceans until after they were clearly missed by the primary observation team (i.e. after they had passed abeam of the vessel or were bow-riding). Nine different people served as independent observers during the survey, and all worked irregular schedules that overlapped with both primary teams. Independent observers did not work more than two consecutive hours. When a sighting was made by the independent observer, that person maintained their normal behavior so as to avoid drawing the attention of the primary observer team. Initial bearing and distance were estimated by eye or with the aid of reticles in the ocular of 7× binoculars and a hand-held protractor. After a group was clearly missed by the primary team, the independent observer announced the presence of the animals to the data recorder and gave the initial bearing and distance. Typically the vessel was diverted towards the group, and species composition and group size were estimated by the primary observation team.

Analytical methods

Cetacean abundance was estimated from survey data with line-transect methods (Buckland et al.,

Table 1

Number of groups of cetaceans which contained members of the indicated species and species groups. The sum of all species in a group may be greater than the total for that group because the latter contains mixed-species groups. Totals do not include off-effort sightings.

Species group and species	No. of sightings
Small delphinids	285
short-beaked common dolphin, *Delphinus delphis*	123
long-beaked common dolphin, *Delphinus capensis*	6
unclassified common dolphin, *Delphinus* spp.	8
striped dolphin, *Stenella coeruleoalba*	24
Pacific white-sided dolphin, *Lagenorhynchus obliquidens*	12
northern right whale dolphin, *Lissodelphis borealis*	16
unidentified delphinoid	21
Cryptic species	132
harbor porpoise, *Phocoena phocoena*	32
Dall's porpoise, *Phocoenoides dalli*	97
pygmy sperm whale, *Kogia breviceps*	3
Large delphinids	37
bottlenose dolphin, *Tursiops truncatus*	16
Risso's dolphin, *Grampus griseus*	29
killer whale, *Orcinus orca*	5
Large whales	127
sperm whale, *Physeter macrocephalus*	13
Baird's beaked whale, *Berardius bairdii*	1
Bryde's whale, *Balaenoptera edeni*	1
Bryde's or sei whale, *Balaenoptera edeni* or *B. borealis*	2
fin whale, *Balaenoptera physalus*	22
blue whale, *Balaenoptera musculus*	49
humpback whale, *Megaptera novaeangliae*	13
unidentified baleen whale	9
unidentified large whale	22
Small whales	48
unidentified beaked whale	7
mesoplodont beaked whale (*Mesoplodon* spp.)	5
Cuvier's beaked whale, *Ziphius cavirostris*	14
minke whale, *Balaenoptera acutorostrata*	4
unidentified small whale	11
unidentified cetacean	8

1993b). The basic equation for estimating abundance, N, for grouped animals with line transect is given by

$$N = \frac{AnSf(0)}{2Lg(0)}, \quad (1)$$

where A = size of the study area;
n = number of sightings;
S = mean group size;
$f(0)$ = sighting probability density at zero perpendicular distance;
L = length of transect line completed; and
$g(0)$ = probability of seeing a group directly on the trackline.

Ideally, S, $f(0)$, and $g(0)$ would be estimated separately for each species. However, the presence of mixed-species groups and small sample sizes required pooling for the estimation of $f(0)$ and $g(0)$. The parameter $f(0)$ was estimated with the Hazard rate model (Buckland, 1985). This model was fitted by maximum likelihood with ungrouped perpendicular distances. Perpendicular distances were estimated from bearing and radial distance estimates made by observers.

Pooling and stratification for estimating f (0)

Pooled $f(0)$'s were estimated for five species groups: "small delphinids," "large delphinids," "small whales," "large whales," and "cryptic species." The five species groups were defined to include all of the species seen on the survey (Table 1) and were based on patterns of species cooccurrence in groups and on similarities in the physical and behavioral attributes that affect sightability from a ship. As an example, bottlenose dolphins, *Tursiops truncatus*, were never seen in a single-species group but were seen with Risso's dolphins, *Grampus griseus*, 13 times, with striped dolphins, *Stenella coeruleoalba*, one time, and with sperm whales, *Physeter macrocephalus*, three times. Bottlenose dolphins were pooled together with Risso's dolphins because they were seen most frequently with that species and because their sighting characteristics are more similar to Risso's dolphins (medium body size, prominent dorsal fin, occasional low puffy blow, small to medium group size) than to the other two species with which they were seen. Because killer whales, *Orcinus orca*, were never seen with other species but share the same sighting characteristics, these were also included in the species group "large delphinids." The other four groups are "small delphinids" which are of small body size (2–3 m) and are found in medium to large groups; "small whales" which are of medium body size (4–10 m), typically show no blow, often surface inconspicuously, and are typically found in small groups; "large whales" which are of large body size (10–30 m), almost always show a conspicuous blow, and are found in small to medium groups; and "cryptic species" which are small (1.5–4.0 m), show no blow, typically surface inconspicuously, and are found in small groups. The assignment of higher-than-species taxa to species groups is given in Table 1.

In estimating $f(0)$ for each species group, I explored stratification by two factors that are likely to affect sightability: sea state and group size. To avoid estimating more parameters than are justified by the data, I chose the most parsimonious stratification model by minimizing Akaike's Information Criterion (AIC) (Akaike, 1973), defined as 2 multiplied by the number of parameters used to estimate $f(0)$ *minus* 2 multiplied by the sum of the log-likelihoods of the fitted values of $f(0)$. Sea state was subjectively stratified into calm (Beaufort 0–2) and rough (Beaufort 3–5), based on the obvious degradation in sighting conditions that occurs with the presence of whitecaps at Beaufort 3. I stratified by group size by first finding the group size that divided the data into two samples with approximately the same number of sightings in each. If this stratification resulted in a lower AIC, I explored further stratification into three samples of approximately equal size.

The above approach to stratification resulted in different strata for each species group. For small delphinids, AIC was minimized by stratifying group size into the categories 1–20, 21–100, and >100. For large delphinids, optimal stratification was with group size categories of 1–20 and >20. For large whales, AIC was minimized by using group size strata of 1–3 and >3. Because "cryptic species" and "small whales" were seldom seen in rough conditions, I estimated abundance for these species by using only data from calm conditions and did not explore stratification by sea state. Group size stratification resulted in higher AIC values for "cryptic species" and "small whales," so these groups were not stratified by group size. Sea-state stratification was not chosen on the basis of AIC values for any species group.

In stratification by group size, estimates of density in the various strata are added together to give an overall density. The equation for estimating abundance of each species k is therefore given by

$$N_k = \sum_{j=1}^{3} \frac{A n_{j,k} S_{j,k} f_{j,k}(0)}{2L g_{j,k}(0)}, \quad (2)$$

where A = size of study area;

$n_{j,k}$ = number of sightings of species k in group size stratum j;
$S_{j,k}$ = mean group size of species k in group size stratum j;
$f_{j,k}(0)$ = sighting probability density at zero perpendicular distance for group size stratum j of the species group to which species k belongs;
L = length of transect line completed; and
$g_{j,k}(0)$ = probability of detecting a group directly on the trackline for group size stratum j of the species group to which species k belongs.

Perpendicular distance truncation

Sightings of distant groups add little to the estimation of trackline density and can introduce bias. Buckland et al. (1993b) recommend truncating to eliminate at least the most distant 5% of all sightings. In the current study, groups of cetaceans were typically not pursued for species identification and group size estimation if they were farther than 5.5 km (3 nmi) from the trackline. Therefore, by survey design, perpendicular distances must be truncated at no more than 5.5 km. I used a truncation distance of 3.7 km (2 nmi) for "small delphinids," "cryptic species," "large delphinids," and "small whales," which eliminated 8.8%, 2.4%, 4.6%, and 12.8% of all groups (respectively). A truncation distance of 5.5 km was used for "large whales," which eliminated 10.9% of groups.

Group-size estimation

The estimation of group size for cetaceans is difficult and can lead to bias in the estimation of abundance. To avoid bias, correction factors were developed for individual observers. The estimates of four of the six primary observers on the present survey had been previously calibrated by means of aerial photographic estimates to represent "true" group size.[4] The "best" estimates of two of these four were found to indicate group size with accuracy and did not require any correction factors. The other two required correction factors, and, for one, correction factors varied significantly from one year to the next. A helicopter was not available to make aerial photographic estimates of group size on the present survey, so correction factors for individual observers were estimated indirectly by comparison with the two observers who, in the previous study, did not require correction.

Linear regression was used to compare one observer's estimates of group size to another's for the subset of groups that were estimated by both. Group sizes were $\log_{10}$-transformed to normalize variances. For the two observers who did not require a correction factor in the previous study,[4] the slope of the regression was 1.009 (SE=0.017), indicating that, relative to each other, the observers were still estimating group size consistently. Correction factors for the other four observers were based on the slope and intercept of the regression of their "best" estimates against the mean of "best" estimates of the two who did not need calibration.

The group size for each species in a group was estimated as the average of all observers' corrected estimates of the size of the group multiplied by the average of all observers' estimates of the percentage of that species present (if in a mixed-species group).

Probability of detecting trackline groups

Estimating the probability that a group on the transect line will be seen, $g(0)$, is fraught with difficulties (see Buckland et al. [1993b] for a review of previous attempts). In the context of bias from missed groups of marine mammals, it is useful to think in terms of the dichotomy proposed by Marsh and Sinclair (1989): bias can result from groups that were available to be seen but were not (perception bias) and from groups that were not available to be seen either because they did not surface or because they surfaced behind a swell (availability bias). I will make a minimum estimate of perception bias based on data collected by the conditionally independent observer and on the approach given in the Appendix. Because the sample of sightings made by independent observers is small (only 37 cetacean groups), $f_2(0)$ in Equation 7 was estimated for all cetaceans pooled without stratification by group size or sea state. Perpendicular distance data were fitted with the Hazard rate model to estimate $f_2(0)$. (Groups are only available to the independent observer if they were missed by the other observers; therefore the distribution of perpendicular distances need not be monotonically decreasing. In this case, however, it was, and a more general model is not likely to have performed better than the Hazard rate model.) The analytical variances of $f_1(0)$ and $f_2(0)$ (from the information matrix method) were used in estimating the coefficient of variation of $g_1(0)$ from Equation 8, and the variances of n_1 and n_2 were estimated by assuming a Poisson distribution. Consideration of availability bias is deferred to the Discussion section.

[4] Gerrodette, T. D., and C. Perrin. 1991. Calibration of shipboard estimates of dolphin school size from aerial photographs. Admin. Rep. LJ-91-36, available from Southwest Fish. Sci. Cent., P.O. 271, La Jolla, CA 92038, 73 p.

Coefficients of variation and confidence intervals

Coefficients of variation (CV) and confidence intervals (CI) of the abundance estimates are based on the bootstrap method (Efron, 1977; Buckland et al., 1993b). The sightings associated with consecutive segments of search effort were combined to form a set of subsamples of 139 km (75 nmi) of search effort (corresponding to approximately one day of survey effort).[5] I drew subsamples randomly with replacement from this set of effort segments, and a pseudo-population size was estimated by using the same group size stratification as was used for the actual abundance estimates. For each bootstrap sample, the probability of detecting trackline groups, $g(0)$, was estimated as a random number between 0 and 1 drawn from the probability distribution of a binomial ratio with a mean and coefficient of variation equal to the estimated values. This process was repeated 1,000 times, and the CV of the estimated population size was calculated as the standard error of the 1,000 pseudo-population sizes divided by the estimated population size. Bootstrap 95% confidence intervals on the population estimates were based on the 25th and 976th ranked estimates from the bootstrap samples. Log-normal 95% confidence intervals were based on the method given by Buckland et al. (1993b) and used the bootstrap estimate of CV.

Results

During the survey approximately 10,100 km of searching effort were completed (Fig. 1), and 515 cetacean groups were seen during the sampling effort. Tracklines included 2,386 km in calm sea states (Beaufort 2 or less) and 7,696 km in rough sea states (Beaufort 3–5). During the survey, 18 cetacean species were identified (as well as at least one species that could only be identified to genus) (Table 1). More detailed data summaries for this survey are presented by Hill and Barlow (1992), including the positions and school sizes of all on- and off-effort sightings of cetaceans and pinnipeds, maps showing the distribution of sightings for each species, distributions of perpendicular distances for each species, patterns of association in mixed-species groups, summaries of searching effort completed under various conditions, and sighting rates of individual observers. The fit of the probability density functions to the distributions of perpendicular distances are illustrated by Barlow.[5]

Group-size estimation

Group-size correction parameters, the slopes and intercepts (in parentheses) of $\log_{10}$-transformed regressions, were 0.922 (0.03), 1.022 (–0.03), 0.886 (0.07), and 0.777 (0.11) for the four observers who required correction. Three of these observers appear to have underestimated group size, in some cases by a large amount (a group of 500 would have been, on average, estimated as 328, 534, 283, and 152 by these four observers, respectively).

Probability of detecting trackline groups

Independent observers searched a total of 8,190 km. Approximately 7% of groups were detected only by the independent observer; however, all groups that were detected only by the independent observer were groups of less than 20 individuals and accounted for only 0.7% of the individuals that were seen on the survey. Of all groups that had less than 20 animals and were seen while the independent observer was on duty, 347 were seen by the primary observers, and 40 were seen by the independent observer.

Abundance estimation

With estimated values of $f(0)$ and $g(0)$ (Table 2), density and abundance were calculated for 19 cetacean species and 9 higher taxonomic categories (Table 3). Common dolphins were the most abundant cetaceans by a large margin. Of the two recently recognized common dolphin species (Heyning and Perrin, 1994), the short-beaked variety was much more abundant than the long-beaked variety. Blue whales were the most abundant species of large whale.

Discussion

Distribution

The distributions of cetaceans seen during this survey (Figs. 2–6) are in general agreement with the results of other studies in this area (Leatherwood et al., 1982; Dohl et al., 1986; Smith et al., 1986; Barlow, 1988; Forney et al., this issue; Dohl et al.[2,3]). However, the observed distribution of some species contradicted results of previous studies. Striped dolphins were seen rather commonly in mixed groups with short-beaked common dolphins in southern and central California between 185 and 555 km (100–300

[5] Barlow, J. 1993. The abundance of cetaceans in California waters estimated from ship surveys in summer/fall 1991. Admin. Rep. LJ-93-09, available from Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038, 39 p.

Table 2

Estimated values of $f(0)$ and $g(0)$ for each of the species group stratifications which were chosen on the basis of Akaike's Information Criterion (AIC) minimization. Truncation distances for estimating $f(0)$ are 5.5 km for large whales and 3.7 km for all other species. Sample sizes include the total number of groups seen by the primary team, n, the number of groups seen by the primary team when an independent observer was on duty, n_1, and the number of groups seen by the independent observers but not by the primary team, n_2. NA indicates information that is not available because it could not be estimated. CV is the coefficient of variation.

Main stratum and substrata	Number of sightings			Primary observers		Secondary observers		Primary observers	
	n	n_1	n_2	$f(0)$ km^{-1}	CV $f(0)$	$f(0)$ km^{-1}	CV $f(0)$	$g(0)$	CV $g(0)$
Small delphinids (3.7 km truncation)									
group size 1–20	67	58	9	1.258	0.249	1.864	0.147	0.770	0.137
group size 21–100	58	51	0	0.944	0.336	1.864	0.147	1.000	NA
group size 101+	47	44	0	0.283	0.193	1.864	0.147	1.000	NA
Cryptic species (3.7 km truncation)									
calm seas	102	78	14	1.574	0.199	1.864	0.147	0.787	0.103
Large delphinids (3.7 km truncation)									
group size 1–20	15	14	1	0.504	0.306	1.864	0.147	0.736	0.391
group size 21+	17	17	0	0.352	NA	1.864	0.147	1.000	NA
Large whales (5.5 km truncation)									
group size 1–3	87	81	3	0.696	0.278	1.863	0.146	0.901	0.073
group size 4+	26	22	0	0.256	NA	1.863	0.146	1.000	NA
Small whales (3.7 km truncation)									
calm seas	23	19	1	0.614	0.488	1.864	0.147	0.840	0.218

nmi) from shore. Although striped dolphins were known to inhabit this area (Leatherwood et al., 1982), their frequency of occurrence was much greater than expected. Blue whales were seen primarily in southern California between 92 and 370 km (50–200 nmi) offshore. In previous years, this species was seen commonly in central California between the coast and 92 km (50 nmi) offshore (Calambokidis et al., 1990b). One species was surprising in its absence: short-finned pilot whales, *Globicephala macrorhynchus*, were previously common in southern California, especially around the Channel Islands in winter (Leatherwood et al., 1982). (Note: one group of pilot whales was seen and photographed by independent researchers between San Francisco and Monterey on 2 November 1991.[6])

Abundance

Abundance estimates from this study are also in general agreement with previous esti-

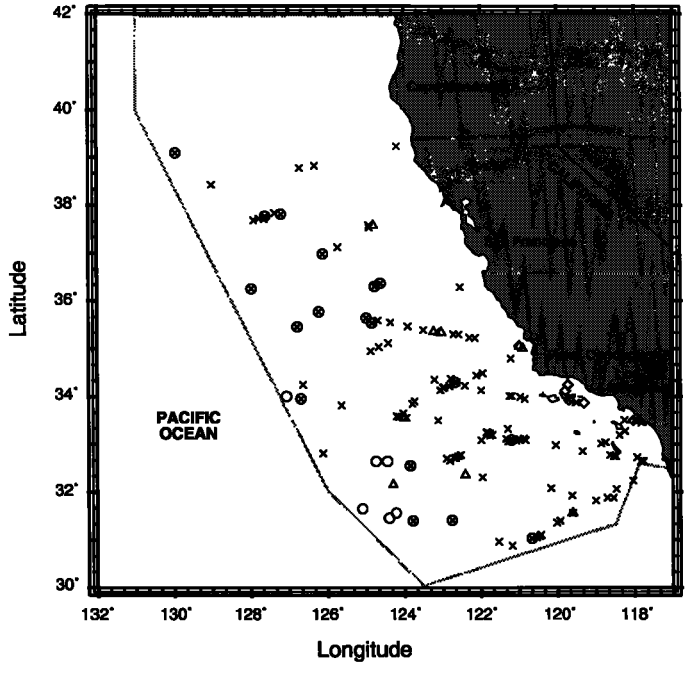

Figure 2

Locations of on-effort sightings of short-beaked common dolphins (×), long-beaked common dolphins (◇), unidentified common dolphins (△), and striped dolphins (○). Scientific names are given in Table 1.

[6] Jones, P. A., and I. D. Szczepaniak. 1992. Report on the seabird and marine mammal censuses conducted for the long-term management strategy (LTMS), August 1990 through November 1991, for the U.S. Environmental Protection Agency, Region IX, San Francisco. July 1992.

Table 3

Number of groups seen (n), mean group size (S), density of individuals, abundance estimates (N), 95% confidence intervals (CI) on those estimates, and coefficients of variation (CV) for all species and higher taxa that were identified. Density estimates are based on lengths of transect given in the text and estimates of $f(0)$ and $g(0)$ given in Table 2. Mean group size includes only the indicated species and can therefore be less than the minimum of the group size category (which is defined based on the total number of all species present). Scientific names are given in Table 1.

						Boot strap		Log-normal	
Species strata	Number of groups n	Mean group size S	Animal density km^{-2}	Pop. size N	CV	Lower 95% CI	Upper 95% CI	Lower 95% CI	Upper 95% CI
Small delphinids									
short-beaked common dolphin			3.248	225,821	0.279	143,026	419,911	132,139	385,918
group size 1–20	25	11.0	0.261						
group size 21–100	52	44.7	1.274						
group size 101+	39	267.3	1.713						
long-beaked common dolphin			0.136	9,472	0.683	0	27,029	2,817	31,842
group size 1–20	1	11.8	0.011						
group size 21–100	0	0.0	0.000						
group size 101+	4	190.2	0.125						
common dolphin (unclassified)			0.148	10,286	0.815	573	37,007	2,539	41,664
group size 1–20	6	5.4	0.031						
group size 21–100	1	15.1	0.008						
group size 101+	1	661.5	0.109						
striped dolphin			0.273	19,008	0.412	8,234	45,864	8,755	41,267
group size 1–20	2	7.7	0.015						
group size 21–100	5	29.3	0.080						
group size 101+	14	77.6	0.178						
Pacific white-sided dolphin			0.177	12,310	0.537	1,888	27,965	4,590	33,010
group size 1–20	7	11.5	0.076						
group size 21–100	3	46.2	0.076						
group size 101+	2	75.4	0.025						
northern right whale dolphin			0.134	9,342	0.567	2,125	21,488	3,322	26,272
group size 1–20	10	9.9	0.094						
group size 21–100	3	9.4	0.015						
group size 101+	2	75.7	0.025						
unidentified delphinoid			0.052	3,603	0.462	1,180	6,197	1,521	8,536
group size 1–20	17	3.2	0.052						
group size 21–100	0	0.0	0.000						
group size 101+	0	0.0	0.000						
Cryptic species									
harbor porpoise[1]	31	5.0	0.758	52,743	0.682	0	147,905	15,714	177,026
Dall's porpoise	69	3.3	1.127	78,422	0.354	33,462	150,487	40,026	153,649
pygmy sperm whale	2	1.3	0.013	870	0.796	0	2,741	220	3,433
Large delphinids									
bottlenose dolphin			0.022	1,503	0.481	499	3,819	615	3,674
group size 1–20	4	2.8	0.004						
group size 21+	10	8.3	0.017						
Risso's dolphin			0.122	8,496	0.415	4,236	21,676	3,890	18,555
group size 1–20	12	8.3	0.039						
group size 21+	16	25.2	0.082						
killer whale			0.004	307	1.196	0	2,340	48	1,947
group size 1–20	3	3.7	0.004						
group size 21+	0	0.0	0.000						
Large whales									
sperm whale			0.011	756	0.493	211	1,537	303	1,886
group size 1–3	4	1.2	0.002						
group size 4+	9	6.6	0.009						

Table 3 (Continued)

Species strata	Number of groups n	Mean group size S	Animal density km^{-2}	Pop. size N	CV	Boot strap Lower 95% CI	Boot strap Upper 95% CI	Log-normal Lower 95% CI	Log-normal Upper 95% CI
Baird's beaked whale			0.001	38	1.025	0	127	7	203
group size 1–3	0	0.0	0.000						
group size 4+	1	3.7	0.001						
Bryde's whale			0.001	61	1.078	0	242	11	339
group size 1–3	1	1.9	0.001						
group size 4+	0	0.0	0.000						
Bryde's or sei whale			0.001	63	1.093	0	232	11	355
group size 1–3	2	1.0	0.001						
group size 4+	0	0.0	0.000						
fin whale			0.013	935	0.635	130	2,607	299	2,925
group size 1–3	17	1.4	0.011						
group size 4+	4	4.7	0.003						
blue whale			0.033	2,250	0.381	899	4,131	1,093	4,632
group size 1–3	36	1.6	0.026						
group size 4+	13	3.3	0.007						
humpback whale			0.009	626	0.411	196	1,133	289	1,359
group size 1–3	7	1.8	0.006						
group size 4+	3	7.3	0.003						
unidentified baleen whale			0.003	214	0.631	26	530	69	665
group size 1–3	5	1.2	0.003						
group size 4+	1	2.1	0.001						
unidentified large whale			0.009	629	0.470	167	1,306	262	1,508
group size 1–3	15	1.3	0.009						
group size 4+	0	0.0	0.000						
Small whales									
unidentified beaked whale	3	3.5	0.019	1,322	0.892	0	4,541	295	5,921
mesoplodont beaked whale	2	1.0	0.004	250	0.834	0	746	60	1,040
Cuvier's beaked whale	7	1.9	0.023	1,621	0.823	186	5,555	396	6,637
minke whale	4	1.1	0.008	526	0.971	0	2,244	106	2,596
unidentified small whale	5	1.0	0.009	645	0.767	127	2,061	170	2,446
unidentified cetacean	3	1.7	0.009	620	0.879	0	2,026	141	2,731

[1] More precise estimates for harbor porpoise are recently available in Barlow and Forney (1994).

mates (Dohl et al., 1986; Barlow, 1988; Calambokidis et al., 1990a; Dohl et al.[2,3]). This is the first cetacean survey in California waters to include the region between 277 and 555 km (150–300 nmi) offshore. The studies of Dohl et al.[2,3] included only the inshore 185 km (100 nmi) of the present study area, making direct abundance comparisons difficult. The mark-recapture population estimates of blue and humpback whales by Calambokidis et al. (1990, a and b) were based on individuals sighted near the coast. Furthermore, the estimates of Dohl et al.[2,3] do not have associated statistical confidence intervals. Hence, accurate comparisons with previous studies can be made only for the more coastal species and meaningful statistical tests of differences can be made for even fewer species. Direct comparisons with the 1991 and 1992 aerial surveys (Forney et al., this issue) are planned for future publications.

The abundance of harbor porpoise estimated for 1984 and 1985 was approximately 9,576 (CV=0.51) (Barlow [1988] his regions 1–4), which is smaller than the present estimate of 52,700 (CV=0.68). This discrepancy may be due to the inappropriate design of the present survey for a coastal species such as harbor porpoise.

Humpback whale abundance in central California was estimated as 338 based on aerial surveys from August to November of 1980–83 (Dohl et al.[3]); however, this estimate does not include a correction factor for submerged whales. Based on mark-recapture methods, the abundance of humpback whales in 1991 and 1992 was estimated to be 581 (CV=0.03).[1] This estimate is

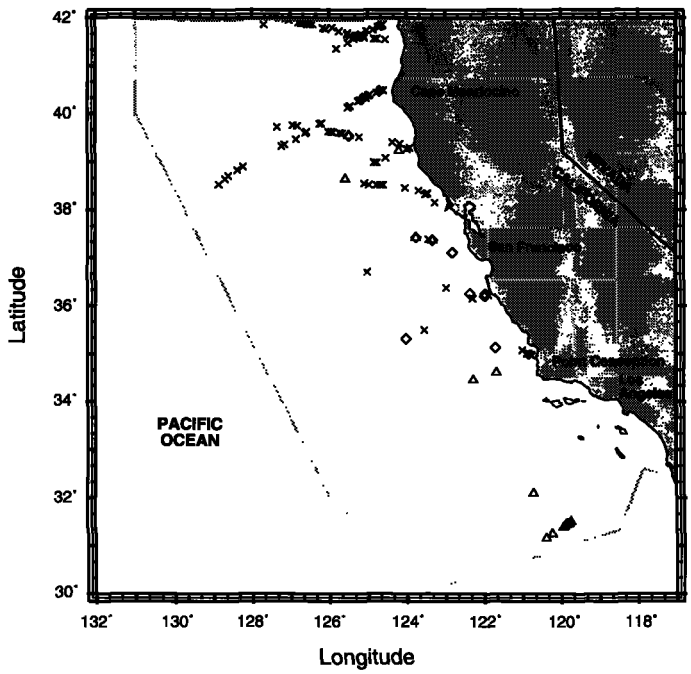

Figure 3

Locations of on-effort sightings of Dall's porpoise (×), northern right whale dolphins (△), and Pacific white-sided dolphins (◇). Scientific names are given in Table 1.

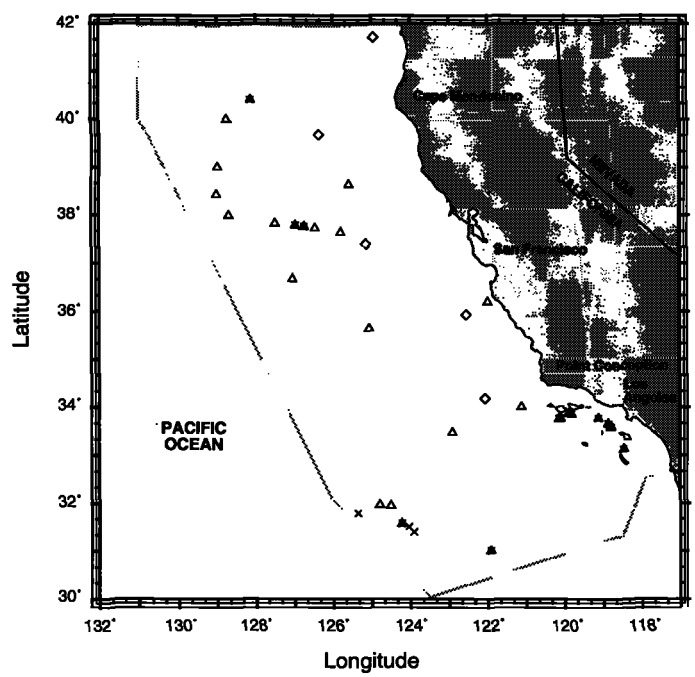

Figure 4

Locations of on-effort sightings of killer whales (◇), Risso's dolphins (△), and bottlenose dolphins (×). Scientific names are given in Table 1.

very close to the present estimate of 626 and is well within its 95% confidence interval.

For two species, new estimates of abundance appear to be substantially different from previous estimates. For the late 1970's, the combined summer and fall estimate of common dolphin abundance was 57,270 (CV=0.17) (Dohl et al., 1986). Although the methods used were very different and the area surveyed was smaller in that study, estimates for other small cetaceans are similar in the two studies. A large increase in common dolphin abundance is likely. This could have resulted as an effect of the 1991–92 El Niño. Although there were no surface temperature manifestations of El Niño in the study area at the time of the survey, it is possible that common dolphins were moving into California waters from farther south as a result of El Niño changes there. Since 1980, a decline has been noted in the abundance of the northern stock of common dolphins south of 30°N (Anganuzzi et al., 1993), and those authors hypothesize that this could have been caused by a general northward movement of that stock. This interpretation is consistent with the increases noted here, but the magnitude of the decrease in the south (from approximately 500,000 in 1980 to approximately 100,000 in 1991 [Anganuzzi et al. 1993]) is greater than the entire estimated population in California waters.

The abundance of blue whales, based on the current line-transect data (2,250), is also much higher than recent estimates made from individual-identification mark-recapture techniques (904 based on left-side photographs and 1,112 based on right-side photographs).[1] Although some mark-recapture estimates may be biased low because of geographic heterogeneity in habitat use by individual whales (Hammond, 1990), the methods used for mark-recapture should have minimized those effects.[1] South of the present study area, the abundance of blue whales was estimated to be 1,415 (CV=0.24) based on line-transect ship surveys in the eastern tropical Pacific from 1986 to 1990 (Wade and Gerrodette, 1993). The latter study included sightings made along the coast of Baja California (which probably belong to the California feeding population) as well as sightings made near the Costa Rica Dome and along the Equator (which are likely to be part of a different population; Reilly and Thayer [1990]).

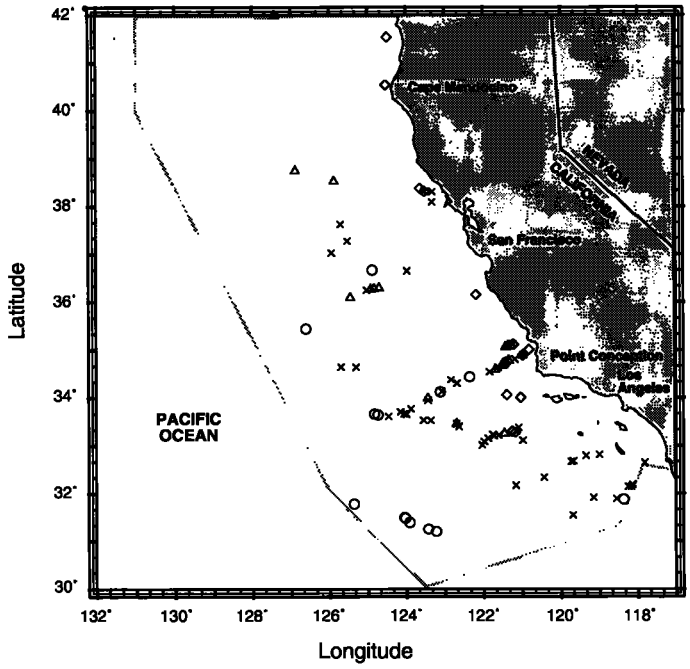

Figure 5

Locations of on-effort sightings of fin whales (△), humpback whales (◇), blue whales (×), and sperm whales (○). Scientific names are given in Table 1.

Probability of detecting trackline groups

The probability of detecting a trackline group of animals, $g(0)$, varied between 0.74 and 1.0 (Table 2). The data clearly indicated that small groups are much more likely to be missed than are large groups. This is intuitively obvious and justifies stratifying by group size when estimating $g(0)$ values. The fraction of trackline harbor porpoise seen in calm seas has been estimated previously to be 0.78 (with five observers on a similar platform in California, Barlow [1988] and 0.70 (with six observers in the Gulf of Maine, Palka [1993]). The higher value of $g(0)$ estimated here for "cryptic species" with only three observers (0.81) may be due to the inclusion of Dall's porpoise which may be easier to see or may simply be an artifact of small sample size.

These estimates of the fraction of animals seen include only animals that were available to be seen. Availability bias is likely to be large for species such as beaked whales, which have extremely long dive times, and harbor porpoise and Dall's porpoise, which have shorter dive times but seldom are seen more than 0.5 km from the ship and may therefore remain submerged during the entire time they are within visual range. Correcting for availability bias is more difficult than for perception bias. Attempts that have been made so far have involved detailed modeling of the surfacing behavior of the animal and the searching behavior of the researchers (Doi, 1971, 1974; Barlow et al., 1988; Stern, 1992; Kasamatsu and Joyce[7]). In addition, there are still problems with estimating perception bias because the methods used here assume that all animals are equally available to be seen if they surface. Heterogeneity in sightability (e.g. animals that splash vs. animals that do not) generally will result in an underestimate of the fraction missed. Additional work is needed to obtain complete estimates of the fraction of trackline animals seen for all species.

Previous studies of Dall's porpoise have shown that attraction to the vessel is a greater problem for estimating the abundance of this species than are missing trackline animals (Turnock and Boucher[8]). Turnock and Quinn (1991) estimated a correction factor of 0.2378 (CV=0.3391) to adjust Dall's porpoise abundance estimates for ship surveys (effectively then, g_0=4.2). That study was based, however, on a design that used only one observer who searched with 7× binoculars and unaided eyes. In the present study, very few Dall's porpoise appeared to be attracted to the vessel; of those sighted in calm conditions and used for abundance estimation, only 10% (9 of 88) of the Dall's porpoise groups approached the vessel to "ride the bow wave," and 89% (78 of 88) were exhibiting a "slow roll" surfacing behavior at the time they were first sighted. Because attraction to the vessel was less than in other studies and because most Dall's porpoise were sighted before showing any apparent reaction to the vessel (perhaps because 25× binoculars were used), the magnitude of bias is probably less than that estimated by Turnock and Quinn (1991).

Statistical precision

An attempt was made to account for most sources of sampling error in the bootstrap estimates of confidence intervals and coefficients of variation. However, several sources of variation could not be easily included. The process of selecting a stratification

[7] Kasamatsu, F., and G. G. Joyce. 1991. Abundance of beaked whales in the Antarctic. Int. Whaling Comm. working paper SC/43/O12.

[8] Turnock, B. J., and G. C. Boucher. 1990. Population abundance of Dall's porpoise, *Phocoenoides dalli*, in the western North Pacific Ocean. Int. Whaling Comm. working paper SC/42/SM10.

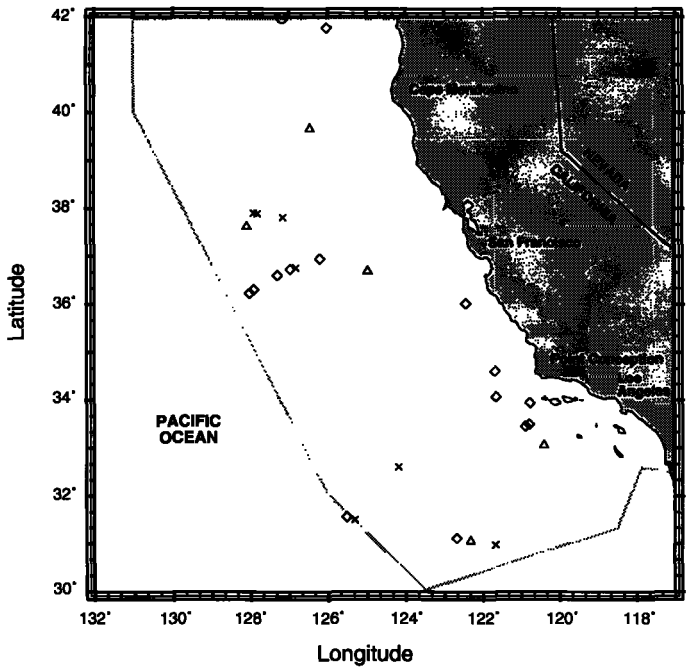

Figure 6

Locations of on-effort sightings of beaked whales of the genus *Mesoplodon* (△), Cuvier's beaked whales (◇), Baird's beaked whales (○), and unidentified beaked whales (×). Scientific names are given in Table 1.

model by minimizing AIC would have been too time consuming to include in the bootstrap procedure; hence, precision estimates are contingent on the chosen models being approximately correct. Variability in estimating mean group size was included implicitly in the Monte Carlo sampling, but it was assumed that the group size estimate for any given group was accurate. Pooling of data to estimate $f(0)$ and $g(0)$ introduces a bias (to the extent that individuals differ within a pooled group) which is not accounted for in precision estimates. All of these factors would tend to result in precision being overestimated. Overall, coefficients of variation are likely to be too small and true confidence intervals are probably wider than those reported.

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Appendix

To estimate the total fraction of trackline groups missed owing to perception bias requires that the survey be designed with two teams of completely independent observers. To be independent, both teams would have to search simultaneously, not notifying or cueing each other until a group of animals had passed abeam of the vessel and were clearly missed by the other team. This approach was deemed infeasible because of the need to approach groups to estimate group size and species composition. If the vessel was not turned until after all groups had passed abeam, a very large percentage of those groups would not be relocated. The probability of relocation would depend on group size and species composition. These factors would add considerably to the difficulty in interpreting such survey data.

Instead, the survey was designed to use a single, conditionally independent observer who was aware of sightings made by the primary team, but who did not reveal the presence of a group until that group was clearly missed by the primary team. Data from the conditionally independent observer are used to make an estimate of the probability that the primary survey team detected a trackline group.

The expected number of groups, n, seen very close to the transect line, say within distance δ, can be estimated as

$$n_\delta = \frac{n_\omega \int_0^\delta g(x)h(x)dx}{\int_0^\omega g(x)h(x)dx}, \quad (3)$$

where n_ω is the total number of groups seen within the truncation distance ω, $g(x)$ is the probability of seeing a group that is at perpendicular distance x, and $h(x)$ is the probability that a group will be at perpendicular distance x (usually assumed to be 1.0 for primary observers at all x). As δ approaches zero distance, the above equation can be reexpressed as

$$n_\delta = \frac{n_\omega g(0)h(0)\delta}{\int_0^\omega g(x)h(x)dx}, \quad (4)$$

which, from the line-transect definition of $f(0)$ (Burnham et al., 1980), can be simplified to

$$n_\delta = n_\omega f(0)\delta. \quad (5)$$

The probability of a trackline group being seen by the primary observers can be expressed as

$$g_1(0) = \frac{n_{1\delta}}{n_{1\delta} + n_{2\delta}/g_2(0)}, \quad (6)$$

where the subscript 1 refers to sightings made by the primary observers and subscript 2 refers to sightings missed by the primary observers but seen by the independent observer. Combining Equations 5 and 6 and simplifying results in

$$g_1(0) = \frac{n_{1\omega} f_1(0)}{n_{1\omega} f_1(0) + n_{2\omega} f_2(0)/g_2(0)}. \quad (7)$$

Because there were three primary observers and only one independent observer, $g_1(0)$ should be greater than or equal to $g_2(0)$. Thus

$$g_1(0) \le 1 - \frac{n_{2\omega} f_2(0)}{n_{1\omega} f_1(0)}. \quad (8)$$

This equation was applied (substituting = for $\le$) to the subset of data collected while an independent observer was on duty to estimate the probability that a group on the trackline would have been seen by the primary observer team. This quantity will be biased and overestimated to the extent that $g_1(0)$ is greater than $g_2(0)$.

The coefficient of variation for $g_1(0)$ can be approximated as

$$CV\left(g_1(0)\right) = \frac{m\,CV(m)}{1-m}, \quad (9)$$

given

$$m = \frac{n_{2\omega} f_2(0)}{n_{1\omega} f_1(0)}, \quad (10)$$

and

$$CV(m) = \sqrt{CV^2(n_{1\omega}) + CV^2(n_{2\omega}) + CV^2\left(f_1(0)\right) + CV^2\left(f_2(0)\right)}. \quad (11)$$

Abstract.—Two aerial line-transect censuses of cetaceans were conducted along the California coast during March–April 1991 and February–April 1992. The two surveys were designed to provide a combined estimate of cetacean abundance for winter and spring (cold-water) conditions; they complemented a summer and fall ship survey in 1991. The study area (264,270 km^2) extended about 278 km (150 nmi) off the coast of southern California, and 185 km (100 nmi) off the coast of central and northern California. A primary team of two observers searched for cetacean species through bubble windows that allowed an unobstructed view to the sides and directly beneath the aircraft. A third, conditionally independent observer searched through a belly window and reported animals that were missed by the primary team. Approximately 7,069 km and 5,973 km were searched in 1991 and 1992, respectively, resulting in 253 sightings of at least 18 cetacean species (some animals could only be identified to higher taxa). Estimates of abundance and coefficients of variation (in parentheses) for the most common small cetaceans are the following: 306,000 (0.34) common dolphins, *Delphinus* spp.; 122,000 (0.47) Pacific white-sided dolphins, *Lagenorhynchus obliquidens;* 32,400 (0.46) Risso's dolphins, *Grampus griseus*; and 21,300 (0.43) northern right whale dolphins, *Lissodelphis borealis*. Abundance estimates (and CV's) for the most common whales are the following: 892 (0.99) sperm whales, *Physeter macrocephalus*; 392 (0.41) beaked whales, genera *Mesoplodon* and *Ziphius*; 319 (0.41) humpback whales, *Megaptera novaeangliae*; and 73 (0.62) minke whales, *Balaenoptera acutorostrata*.

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The abundance of cetaceans in California waters. Part II: Aerial surveys in winter and spring of 1991 and 1992

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California coastal waters are a productive and highly variable oceanographic region with a diverse marine fauna. Coastal fisheries, primarily gillnet fisheries, cause the incidental death of a variety of marine mammal species (Barlow et al., in press). However, the impact of this mortality can only be evaluated if estimates of population size are available for the affected species. In the late 1970's and early 1980's, abundance estimates were obtained based on aerial surveys,[1,2] but estimates of precision were not obtained for most species. Because of the age and uncertainty of these estimates, the National Marine Fisheries Service conducted aerial and shipboard surveys during 1991 and 1992. Based on evidence of seasonality in the abundance and distribution of some cetaceans (Leatherwood and Walker, 1979; Dohl et al., 1986), separate abundance estimates were obtained for winter and summer conditions. Two aerial surveys (March–April 1991 and February–April 1992) were completed during cold-water conditions, and one ship survey (July–November 1991) was conducted during warm-water conditions (Barlow, this issue). The survey periods were chosen based on climatic atlases of the California coast which show that, on average, March and April have the coldest, and September and October the warmest sea-surface temperatures (U.S. Navy, 1977). Standard line-transect methods (Burnham et al., 1980; Buckland et al., 1993a) were used from both platforms. Preliminary abundance estimates were calculated after completion of the first aerial survey in 1991 (Forney and Barlow, 1993), but confidence limits were large. In this paper, we present combined abundance estimates for the 1991 and 1992 aerial surveys.

Survey methods

The methods used during the 1991–92 aerial surveys are described in detail by Forney and Barlow (1993) and Carretta and Forney (1993), and only a summary is presented below. The study area (264,270 km^2)

[1] Dohl, T. P., K. S. Norris, R. C. Guess, J. D. Bryant, and M. W. Honig. 1978. Cetacea of the Southern California Bight. Part II of Summary of marine mammal and seabird surveys of the Southern California Bight area, 1975–1978. Final Report to the Bureau of Land Management, 414 p. [NTIS Rep. PB81248189.]

[2] Dohl, T. P., R. C. Guess, M. L. Duman, and R. C. Helm. 1983. Cetaceans of central and northern California, 1980–1983: status, abundance and distribution. OCS Study MMS 84–0045. Minerals Management Service contract No. 14-12-0001-29090, 284 p.

encompasses California waters out to a distance of 185–278 km (100–150 nmi) from the coast and roughly a depth of 3,000–4,000 m (Fig. 1). It was defined on the basis of the distribution of fisheries that are known to take marine mammals and does not reflect a distributional boundary for any marine mammal population. Surveys were conducted along transect lines forming two nearly uniform, overlapping grids (Fig. 1). The resulting overall grid lines were spaced 41–46 km (22–25 nmi) apart. The location of the transect grid was chosen without reference to specific areas or topographical features. To avoid potential differences in regional coverage, an attempt was made in each year to complete all transects of the first grid, providing coarse coverage of the entire study area, before beginning the second grid. However, in both years, poor weather conditions prevented the completion of both survey grids. In 1991, 85% (5,326 km) of transect grid 1 and 27% (1,739 km) of grid 2 were completed, and in 1992, 81% (5,065 km) of transect grid 1 and 14% (890 km) of grid 2 were completed. The relative proportions of survey effort in different sea state and cloud cover conditions were similar for the two years (Table 1).

The survey platform was a twin-engine turbo-prop DeHavilland Twin Otter, flown approximately at an altitude of 213 m (700 ft) and an airspeed of 165–185 km/h (90–100 knots). All cetacean and sea turtle sightings were recorded, but because of the high densities of pinnipeds near rookeries, these species were recorded only when seen farther than 10 km from land. Two "primary" observers searched through bubble windows on the left and right sides of the aircraft. These windows allowed observers to view to the side and directly beneath the aircraft with at least 10° of overlap between sides. To achieve higher sighting efficiency near the transect line, observers searched for cetaceans only out to a declination angle of 12° (1,004 m perpendicular distance). An additional "secondary" observer monitored the trackline area out to 55° declination angles (on both sides) through a round 45-cm (18-in) viewing hole in the belly of the aircraft and reported sightings missed by the primary team. A fourth person recorded all sighting, effort, and environmental data. To minimize observer fatigue, all observers rotated between these four active positions and one resting position roughly every 30 minutes. All observers had previous experience in identifying cetacean species from aerial or shipboard platforms, or both.

All survey data were recorded on a laptop computer connected to a LORAN or GPS (Global Positioning System) navigational receiver, providing a continuous record of position (updated every few seconds), altitude, air speed, and survey conditions. Environmental conditions, such as Beaufort sea state, percent cloud cover, and glare, were updated whenever changes occurred. Conversation in the aircraft was recorded on a central cassette recorder as a backup to the computer record. Observers also recorded individual sighting information into personal notebooks. Surveys were conducted only in Beaufort sea states 0–4.

Following the methods described in Forney and Barlow (1993) and Carretta and Forney (1993), the aircraft circled for each sighting to obtain species identifications and school size estimates

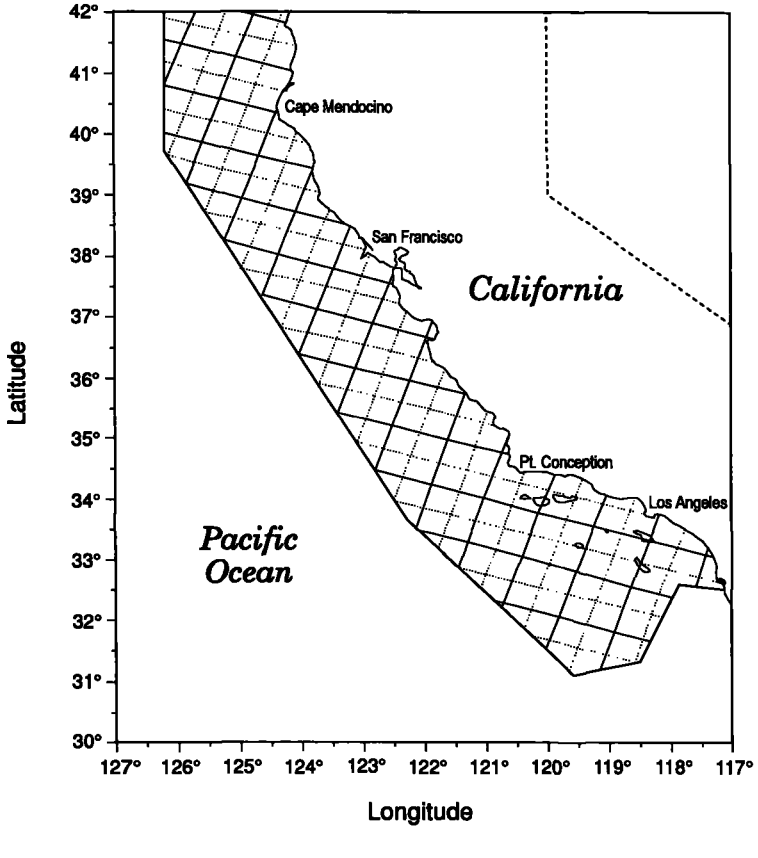

Figure 1

Study area with two overlapping transects grids. The solid line represents grid 1, the dotted line grid 2.

Table 1

Survey effort (in km) stratified by sea state and percent cloud cover.

	Beaufort sea state				
% Cloud cover	0 and 1	2	3	4	Total
1991					
0–24	212	913	1,932	1,346	4,403
25–49	26	66	96	85	273
50–74	45	58	331	241	676
75–100	76	129	980	532	1716
Total	359	1,166	3,338	2,205	7,069
1992					
0–24	406	933	1,349	1,220	3,908
25–49	0	8	141	113	262
50–74	2	43	192	47	284
75–100	78	251	758	433	1,519
Total	486	1,235	2,440	1,813	5,973
Both years combined					
0–24	618	1,846	3,280	2,566	8,311
25–49	26	74	238	199	536
50–74	47	101	523	288	960
75–100	154	380	1,737	965	3,235
Total	845	2,401	5,778	4,018	13,042

(each observer made a confidential record of best, high, and low estimate into a personal field notebook). Any additional schools sighted while the aircraft was diverted from the transect were recorded as 'off-effort' sightings. Only sightings made during active searches on predetermined transect lines ('on-effort') were included for abundance estimation. The secondary observer only reported sightings missed by the primary observer team; these secondary sightings were used to estimate the fraction of animals missed on the transect line.

Analytical methods

Stratification

Because we were not able to complete both grids in all regions of the coast, the study area was divided into four a posteriori geographic areas to approximate uniform coverage within each stratum (Fig. 2). Environmental conditions such as sea state and percent cloud cover were recorded throughout the survey, as they have been shown to influence cetacean sighting rates (Holt and Cologne, 1987; Forney et al., 1991). However, because of the small number of sightings made during each combination of environmental conditions, it was not possible to evaluate their effect quantitatively.

Because of the difficulty in identifying beaked whales to species level during aerial surveys, only a combined abundance estimate was obtained for this group. In the preliminary analyses of the 1991 aerial survey data, Forney and Barlow (1993) assigned other unidentified species based on a 'nearest identified neighbor' approach. In the analyses presented here, unidentified cetacean sightings were treated separately as either 'unidentified dolphin or porpoise,' 'unidentified small whale,' or 'unidentified large whale,' because they represented only a small fraction of the total animals seen.

The small number of sightings for each species made it necessary to pool distributions of perpendicular sighting distances for line-transect calculations. Forney and Barlow (1993) created preliminary species groups based on considerations of school size, body size and behavior, and pooled distributions for groups that were not statistically different from one another. The same procedure was used for this analysis, resulting in the same three species/group-size categories: 1) small cetacean groups with 1–10 animals; 2) small cetacean groups with more than 10 animals; and 3) medium and large cetaceans (Table 2).

Table 2

Estimates of $f(0)$ and $g(0)$, and number of sightings (n) for the three species/group-size categories used in the analysis.

Small cetaceans	Group size	n	$f(0)$	$g(0)$
	1–10	99	4.70	0.67
	> 10	53	2.85	0.85
Species				
Harbor porpoise, *Phocoena phocoena*				
Dall's porpoise, *Phocoenoides dalli*				
Pacific white-sided dolphin, *Lagenorhynchus obliquidens*				
Risso's dolphin, *Grampus griseus*				
Bottlenose dolphin, *Tursiops truncatus*				
Common dolphins *Delphinus delphis* and *D. capensis*				
Northern right whale dolphin, *Lissodelphis borealis*				

Medium and large cetaceans	Group size	n	$f(0)$	$g(0)$
	1–22	57	2.49	0.95
Species				
Killer whale, *Orcinus orca*				
Small beaked whales, *Ziphius cavirostris* and *Mesoplodon* spp.				
Sperm whale, *Physeter macrocephalus*				
Right whale, *Eubalaena glacialis*				
Gray whale, *Eschrichtius robustus*				
Minke whale, *Balaenoptera acutorostrata*				
Blue whale, *B. musculus*				
Fin whale, *B. physalus*				
Humpback whale, *Megaptera novaeangliae*				

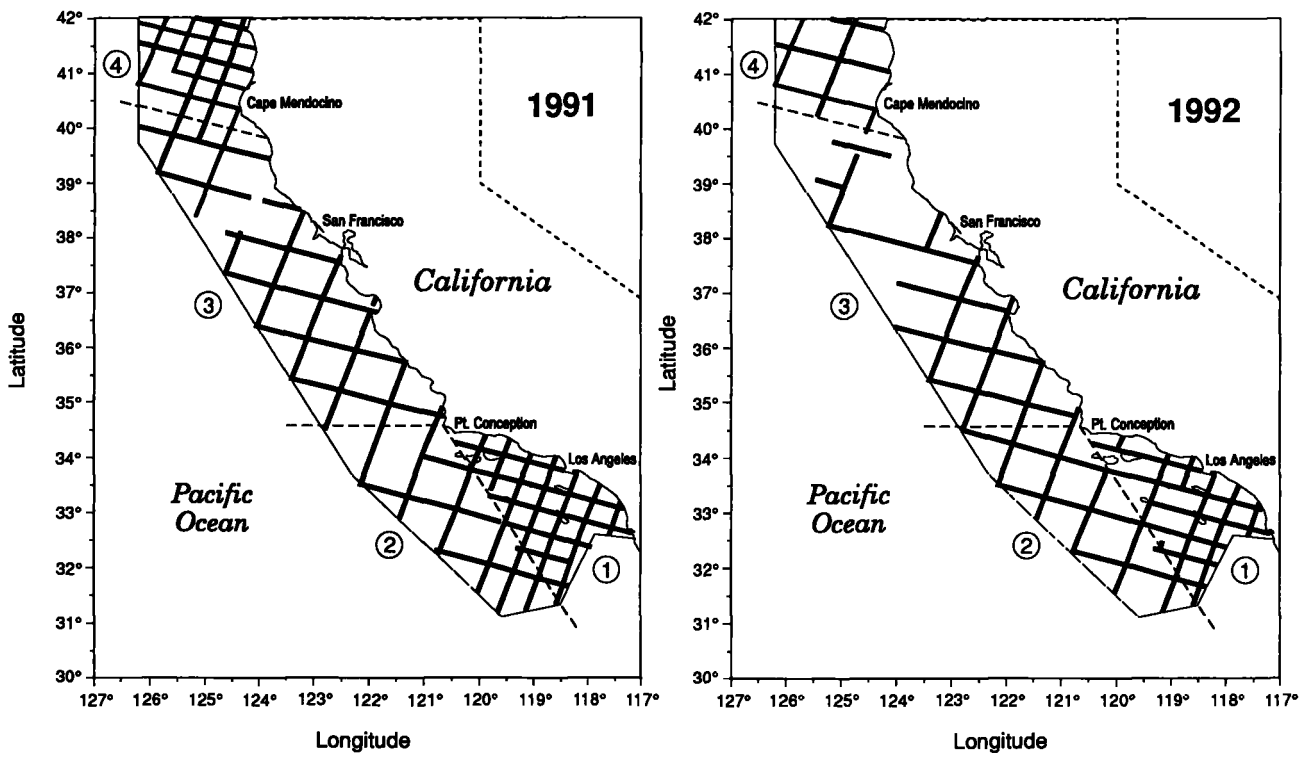

Figure 2

Completed transects (solid lines) for 1991 and 1992, and a posteriori geographic strata (separated by broken lines) used in the analysis. Area numbers are shown in circles.

Abundance estimation

Line transect methods (Burnham et al., 1980; Buckland et al., 1993a) were applied to estimate abundances separately for each species in each stratum:

$$N_k = \sum_{j=1}^{3} \sum_{i=1}^{4} \frac{A_i \, n_{i,j,k} \, S_{i,j,k} \, f_j(0)}{2 L_i \, g_j(0)}, \qquad (1)$$

where

N_k = estimated total number of animals of species k in the study area;

$n_{i,j,k}$ = number of sightings of species k in area i and species/group-size category j;

$s_{i,j,k}$ = average group size of species k in area i and species/group-size category j, calculated as the total number of animals in all groups divided by the number of groups sighted;

$f_j(0)$ = the probability density function evaluated at zero perpendicular distance for species/group-size category j;

$g_j(0)$ = the probability of detecting a group of animals on the transect line for species/group-size category j;

L_i = the length of transect surveyed in area i (in km); and

A_i = the size of area i (in km^2).

Values for $f(0)$ were obtained for each species/group-size category by fitting the distribution of all perpendicular sighting distances (primary and secondary; measured in km) to the Hazard rate model with the statistical software program HAZARD (Buckland, 1985). A value for $g(0)$ was estimated following the methods described in Forney and Barlow (1993), but because of small sample sizes, it was not possible to estimate the variance in $g(0)$. This should result in a downward bias in the variance of the abundance estimates, but bias in the abundance estimates themselves will be reduced. The lengths of transect lines flown, L_i (and total sizes, A_i), for the four areas are 3,715 km (46,300 km^2) for area 1; 2,831 km (63,772 km^2) for area 2; 4,461 km (120,108 km^2) for area 3; and 2,035 km (34,090 km^2) for area 4.

Variance estimation

Variance in estimated abundance was calculated with bootstrap techniques applied to the complete data

set. The data were subdivided by area into effort segments of equal length, and the segments were then drawn randomly with replacement until the total number of kilometers actually surveyed in each area was reached. This process was replicated 1,000 times. Forney and Barlow (1993) demonstrated that the choice of segment lengths between 5 km and 20 km did not influence the resulting estimates of precision. In this analysis we also performed bootstrap simulations for 50 km and 100 km segments and again found that segment length did not affect estimates of variance. For the bootstrap analysis, we chose a segment length of 50 km, which roughly reflects the degree of sampling variability for these surveys (i.e. the dimension of actual gaps in the sampling grid in Figure 2).

Each of the 1,000 bootstrap replicates was treated and analyzed as a separate survey: sightings were first stratified into the three species/group-size categories given above. Individual values for n and s were calculated, and $f(0)$ was estimated with the program HAZARD. The estimated value of $g(0)$ was treated as a correction factor known without error. The variance, coefficient of variation, and 95% confidence intervals were obtained from the distribution of the 1,000 bootstrap abundance estimates with standard formulae. Because the bootstrap method (Buckland, 1984) of obtaining confidence intervals can result in the lower 95% confidence intervals being smaller than the actual number of animals seen (or even zero) we also calculated log-normal confidence intervals based on the bootstrap coefficient of variation.

Results

Detailed results of the survey, including sighting information and plots of sighting locations for all species sighted are presented elsewhere (Carretta and Forney, 1993). Results relevant to the analyses presented in this paper are given below. A total of 253 cetacean sightings were made (Fig. 3): 213 on effort (while actively searching), and an additional 40 off effort (24 while in transit, 8 beyond 12° declination angle, 7 while circling over another group of animals, and 1 by an off-effort observer). Twenty eight on-effort sightings could not be positively identified to the

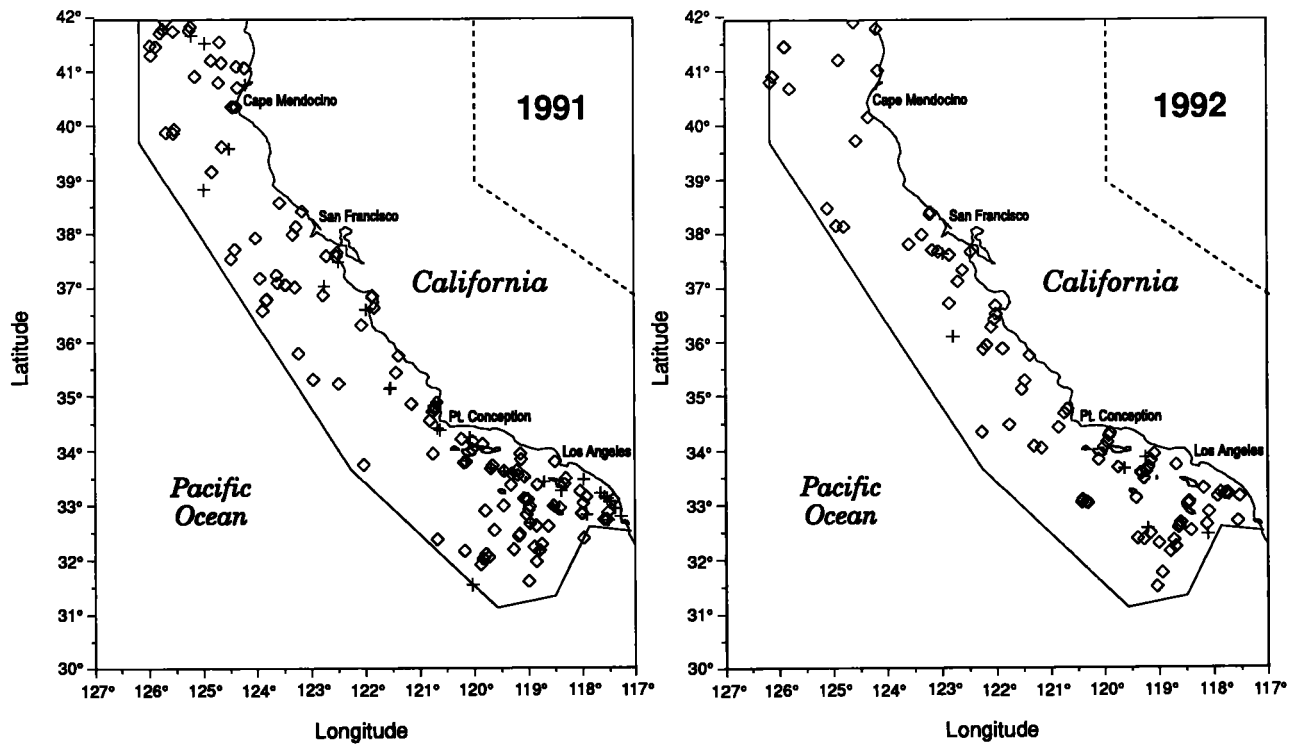

Figure 3

Locations of all 253 cetacean sightings made during the 1991 and 1992 surveys. The 213 on-effort sightings (used in the abundance estimation) are shown by diamonds, and the 40 off-effort sightings (e.g. made while circling or in transit) are shown with plus signs.

species level. Four of these sightings were identified as ziphiid whales, for which a combined abundance estimate was calculated. The remaining 24 sightings were treated separately in the analyses.

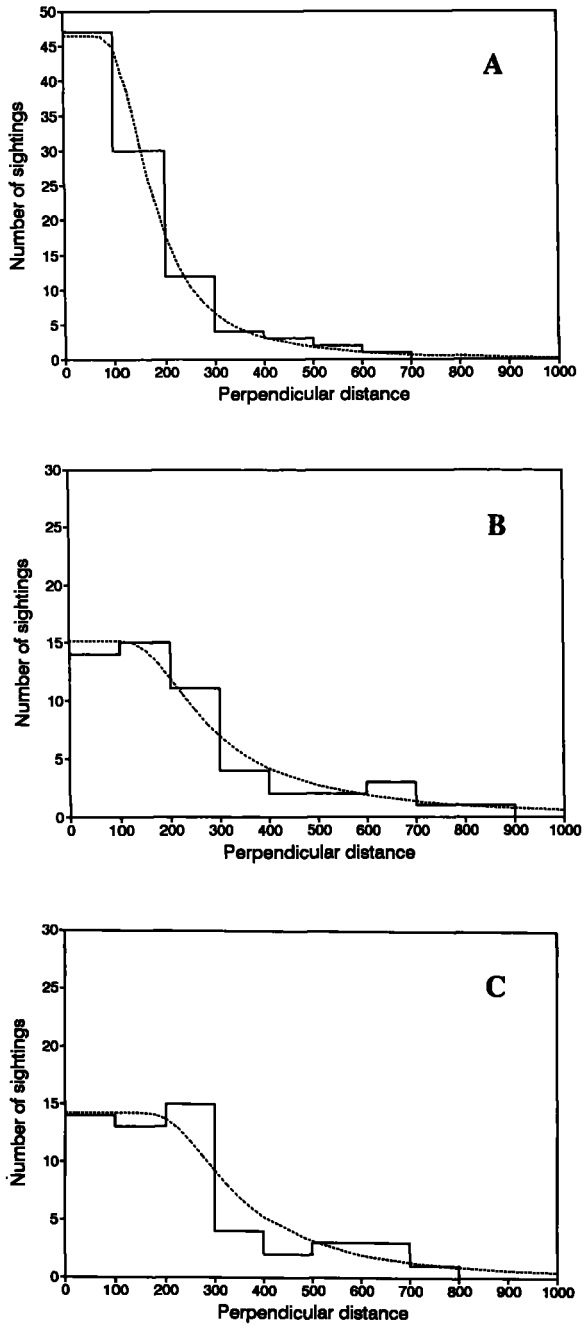

Figure 4

Distribution of perpendicular sighting distances (100-m intervals; solid line) and Hazard model fit (dotted line) for (A) small cetaceans in groups ≤10, (B) small cetaceans in groups >10, and (C) medium and large cetaceans.

The Hazard model provided adequate fits to the perpendicular distance distributions for the three species/group-size categories (Fig. 4). Estimates of $f(0)$ and $g(0)$ are given for each group in Table 1. Although the full transect grid was not completed in either year because of poor weather, the resulting estimates of abundance (Table 3) are the most precise that have been produced to date for this area and season. CV's range from 0.24 to 0.49 for small cetaceans and from 0.35 to 1.11 for large cetaceans.

Discussion

Comparisons with previous abundance estimates

Our abundance estimates (Table 3) can be compared directly with estimates based on 1975–83 aerial surveys,[1,2] which are likely to have similar biases. The estimate of 8,460 Dall's porpoise, *Phocoenoides dalli*, is similar to previous aerial survey estimates of 3,000–4,000 in winter and spring.[1,2] The current estimate of 122,000 Pacific white-sided dolphins,[3] *Lagenorhynchus obliquidens*, is greater than the combined estimates of 26,000 (spring) to 33,500 (winter) for central and northern California[2] and 5,300 (Jan–Jun) for southern California.[1] Our estimate of 21,300 northern right whale dolphins is less than the combined estimates of 29,000 (spring) to 61,500 (winter) for central and northern California[2] and 5,900 (Jan–Jun) for southern California.[1] The prior studies do not give estimates of statistical precision for any of the above species, but given the CV's of our estimates, the above differences are not likely to be statistically significant.

In contrast to the species above, common dolphins, *Delphinus* spp., appear to be much more abundant at present than during the period 1975–83. The current winter estimate (306,000; CV=0.34) is more than an order of magnitude larger than the previous value of 15,488 (CV=0.36; Dohl et al., 1986), and the 99% log-normal confidence limits for these two estimates do not overlap. Preliminary comparisons (Barlow, unpubl. data) of 1979 and 1980 ship surveys with the 1991 ship survey (Barlow, this issue) also show a significant increase in common dolphin abundance. Based on these two separate lines of evidence for winter and summer conditions, the abundance of common dolphins in California appears to have in-

[3] Although estimates for Pacific white-sided dolphins based on the combined 1991 and 1992 survey data are over twice the preliminary estimate of 46,000 from only the 1991 data (Forney and Barlow, 1993), the new estimate lies well within the 95% confidence limit of the previous value.

Table 3

Number of groups seen, mean group size, density of individuals, and abundance estimates for cetaceans in the entire California study area, and subdivided by geographic stratum (See Fig. 2). Coefficients of variation (CV) and 95% confidence intervals (CI) for the overall abundance estimates are also given. Unid.=unidentified.

Species and area	Number of groups	Mean group size	Animal density km^{-2}	Population size N	CV	Bootstrap CI		Log-normal CI	
						Lower 95%	Upper 95%	Lower 95%	Upper 95%
Harbor porpoise[1]	18	1.2	0.0060	1,599	0.345	664	2,915	829	3,085
Area 1	0	0.0	0.0000	0					
Area 2	0	0.0	0.0000	0					
Area 3	10	1.0	0.0079	949					
Area 4	8	1.4	0.0191	650					
Dall's porpoise	38	3.1	0.0320	8,460	0.240	5,203	13,361	5,320	13,453
Area 1	9	4.0	0.0342	1,582					
Area 2	2	4.5	0.0112	716					
Area 3	19	2.6	0.0395	4,744					
Area 4	8	3.0	0.0416	1,418					
Pacific white-sided dolphin	21	151.6	0.4605	121,693	0.466	35,404	261,524	51,041	290,144
Area 1	5	24.6	0.0573	2,654					
Area 2	7	69.4	0.2945	18,779					
Area 3	7	237.1	0.6218	74,678					
Area 4	2	457.0	0.7505	25,583					
Risso's dolphin	19	47.6	0.1225	32,376	0.456	10,255	65,984	13,812	75,891
Area 1	14	28.5	0.2029	9,396					
Area 2	1	8.0	0.0100	636					
Area 3	4	124.3	0.1860	22,343					
Area 4	0	0.0	0.0000	0					
Bottlenose dolphin	8	17.9	0.0123	3,260	0.487	618	6,783	1,320	8,052
Area 1	7	20.3	0.0684	3,165					
Area 2	0	0.0	0.0000	0					
Area 3	1	1.0	0.0008	95					
Area 4	0	0.0	0.0000	0					
Common dolphins	27	514.9	1.1568	305,694	0.340	124,730	539,319	159,864	584,552
Area 1	22	592.7	5.8769	272,101					
Area 2	4	176.0	0.4161	26,535					
Area 3	1	157.0	0.0588	7,058					
Area 4	0	0.0	0.0000	0					
Northern right whale dolphin	31	18.9	0.0807	21,332	0.428	9,151	42,629	9,548	47,658
Area 1	18	12.3	0.1378	6,381					
Area 2	4	56.5	0.1395	8,895					
Area 3	6	11.8	0.0341	4,091					
Area 4	3	22.7	0.0577	1,966					
Killer whale	2	1.0	0.0002	65	0.689	0	133	19	220
Area 1	0	0.0	0.0000	0					
Area 2	1	1.0	0.0005	30					
Area 3	1	1.0	0.0003	35					
Area 4	0	0.0	0.0000	0					
Beaked whales[2]	8	1.9	0.0015	392	0.408	151	774	182	845
Area 1	0	0.0	0.0000	0					
Area 2	3	1.0	0.0014	89					
Area 3	2	1.5	0.0009	106					
Area 4	3	3.0	0.0058	197					
Sperm whale	3	10.0	0.0034	892	0.990	0	2,798	176	4,506
Area 1	0	0.0	0.0000	0					
Area 2	2	14.5	0.0134	857					

Table 3 (Continued)

Species and area	Number of groups	Mean group size	Animal density km^{-2}	Population size N	CV	Bootstrap CI Lower 95%	Bootstrap CI Upper 95%	Log-normal CI Lower 95%	Log-normal CI Upper 95%
Area 3	1	1.0	0.0003	35					
Area 4	0	0.0	0.0000	0					
Northern right whale	1	1.0	0.0001	16	1.110	0	59	3	95
Area 1	1	1.0	0.0004	16					
Area 2	0	0.0	0.0000	0					
Area 3	0	0.0	0.0000	0					
Area 4	0	0.0	0.0000	0					
Gray whale[3]	25	4.2	0.0108	2,844	0.347	1,187	5,270	1,469	5,507
Area 1	12	3.4	0.0145	669					
Area 2	0	0.0	0.0000	0					
Area 3	11	5.3	0.0170	2,043					
Area 4	2	3.0	0.0039	132					
Minke whale	3	1.0	0.0003	73	0.616	0	181	24	223
Area 1	1	1.0	0.0004	16					
Area 2	0	0.0	0.0000	0					
Area 3	1	1.0	0.0003	35					
Area 4	1	1.0	0.0006	22					
Blue whale	1	1.0	0.0001	30	0.990	0	100	6	149
Area 1	0	0.0	0.0000	0					
Area 2	1	1.0	0.0005	30					
Area 3	0	0.0	0.0000	0					
Area 4	0	0.0	0.0000	0					
Fin whale	2	1.5	0.0002	49	1.012	0	57	9	254
Area 1	2	1.5	0.0011	49					
Area 2	0	0.0	0.0000	0					
Area 3	0	0.0	0.0000	0					
Area 4	0	0.0	0.0000	0					
Humpback whale	8	1.6	0.0012	319	0.407	114	622	148	688
Area 1	1	1.0	0.0004	16					
Area 2	0	0.0	0.0000	0					
Area 3	2	1.5	0.0009	106					
Area 4	5	1.8	0.0058	197					
Unid. large whale	5	1.2	0.0006	160	0.457	40	348	68	376
Area 1	1	2.0	0.0007	33					
Area 2	0	0.0	0.0000	0					
Area 3	3	1.0	0.0009	106					
Area 4	1	1.0	0.0006	22					
Unid. small whale	3	1.0	0.0003	68	0.676	0	188	20	226
Area 1	2	1.0	0.0007	33					
Area 2	0	0.0	0.0000	0					
Area 3	1	1.0	0.0003	35					
Area 4	0	0.0	0.0000	0					
Unid. dolphin or porpoise	15	4.4	0.0180	4,766	0.331	2,050	8,368	2,533	8,966
Area 1	2	1.5	0.0028	132					
Area 2	5	4.2	0.0223	1,419					
Area 3	7	5.7	0.0258	3,096					
Area 4	1	2.0	0.0035	118					

[1] More appropriate estimates for harbor porpoise are recently available in Barlow and Forney (1994). (See Discussion section.)

[2] This category includes beaked whales of the genus *Mesoplodon* and Cuvier's beaked whale, *Ziphius cavirostris*. No Baird's beaked whales, *Berardius bairdii*, were seen during the surveys.

[3] A more accurate estimate of the entire population of California gray whales is presented in Buckland et al., 1993. (See Discussion section.)

creased dramatically since the early 1980's. The causes of this increase are not known, but it is possible that long-term oceanographic changes (Roemmich, 1992; Roemmich and McGowan, 1994) have resulted in a shift in the distribution of common dolphins into this area. This hypothesis is consistent with the observed decline in population size of the northern common dolphin south of our study area (Anganuzzi and Buckland, 1994).

Similarly, an apparent decrease in abundance was seen in short-finned pilot whales, *Globicephala macrorhynchus*. This species was commonly seen in the Southern California Bight on surveys during the late 1970's and early 1980's,[1,2] but only one off-effort sighting of four animals was made during our surveys.

Our estimate of 304 humpback whales is roughly half the recent estimate obtained from photo-identification studies.[4] This is quite surprising because humpback whales, *Megaptera novaeangliae*, in the California feeding population are expected to be in waters off Mexico during the winter and spring season. However, it is possible that some animals had already moved north into California at the time of the sightings. Alternatively, the sighted animals may have been part of the southeastern Alaska feeding population that migrates southward to breed in Mexican waters in spring (Baker et al., 1986).

Previously published estimates for harbor porpoise, *Phocoena phocoena* (Barlow, 1988; Barlow et al., 1988; Barlow and Forney, 1994) and gray whales, *Eschrichtius robustus* (Reilly, 1984; Buckland et al., 1993b), are substantially higher than the estimates presented here. This is probably because the defined study area is not appropriate for the range of these animals. Gray whales have a much larger range and migrate through California waters (southward and then northward) from roughly November to May. Our estimate represents that portion of the population which was migrating through California in March and early April. Harbor porpoise are limited to a narrow coastal band, and our transect lines only overlapped with this region at specific points. More appropriate abundance estimates for harbor porpoise are published in Barlow (1988) and in Barlow and Forney (1994).

Comparisons with 1991 ship surveys

Although a statistical comparison between these winter and spring aerial survey estimates and the 1991 summer and fall ship survey estimates (Barlow, this issue) is precluded at this time because of differences in the sizes of the two study areas, a few patterns are noteworthy. Despite the differences in seasonal timing and areal coverage, estimates of abundance are very similar for several species. Similar estimates of abundance were obtained for total common dolphins (306,000 vs. 246,000), northern right whale dolphins, *Lissodelphis borealis* (21,300 vs. 9,340), bottlenose dolphins, *Tursiops truncatus* (3,260 vs. 1,500), and sperm whales, *Physeter macrocephalus* (892 vs. 756) (aerial vs. ship estimates, respectively). More disparate estimates were obtained for Pacific white-sided dolphins (122,000 vs. 12,300), Risso's dolphins, *Grampus griseus* (32,400 vs. 8,500), harbor porpoise (1,600 vs. 52,700), Dall's porpoise (8,460 vs. 78,400), and total beaked whales, *Ziphius cavirostris* and *Mesoplodon* spp. (392 vs. 3,230).

It may be important to note that all cases in which the ship estimates are substantially larger than the aerial estimates are for species which spend a large fraction of their time diving (harbor porpoise, Dall's porpoise, and beaked whales). Such species could be more easily missed by aerial observers owing to availability bias. In the case of Pacific white-sided dolphins and Risso's dolphins, the winter and spring aerial estimates may be larger because of a seasonal movement of animals out of Oregon and Washington in winter.[5] Additional analyses, which account for differences in geographic extent of the aerial vs. ship surveys, are planned in the future.

Bias

There are several sources of potential bias in this study. First, abundance estimates may be biased low because animals are missed by aerial observers (perception bias; Marsh and Sinclair, 1989). This is most likely to be a problem with poor observation conditions (high sea state or overcast conditions, or both). We have attempted to estimate the magnitude of perception bias in this study through the use of a conditionally independent observer and have corrected abundance estimates to reduce this effect. A second source of downward bias, availability bias (Marsh and Sinclair, 1989), is introduced because animals that are submerged when the aircraft passes overhead are not available to be seen. This effect is

[4] Calambokidis, J., G. H. Steiger, and J. R. Evenson. 1993. Photographic identification and abundance estimates of humpback and blue whales off California in 1991–92. Final Contract Report 50ABNF100137 to Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038, 67 p.

[5] Green, G. A., J. J. Brueggeman, R. A. Grotefendt, C. E. Bowlby, M. L. Bonnell, and K. C. Balcomb III. 1992. Cetacean distribution and abundance off Oregon and Washington, 1989–1990. Ch. 1 *in* J. J. Brueggeman (ed.), Oregon and Washington marine mammal and seabird surveys. Minerals Management Service Contract Report 14-12-0001-30426 prepared for the Pacific OCS (Outer Continental Shelf) Region.

expected to be smallest for species which tend to occur in large groups, such as common dolphins, and largest for species which spend relatively little time at the surface, such as porpoise, beaked whales, and sperm whales.

Dive studies (Barlow et al., 1988) may provide information on the magnitude of availability bias, but each species requires a separate assessment of the average proportion of time it spends at the surface (and hence is 'available'), and adequate estimates are not currently available for most species in California waters. Rough estimates can be made for Dall's porpoise and humpback whales based on prior studies. Dall's porpoise have similar sighting characteristics to those of harbor porpoise (both have a small body size and generally are found in small groups); thus, assuming that dive patterns are similar and applying the correction factor of 3.1 (CV=0.17) for harbor porpoise,[6] one would obtain a corrected estimate of approximately 26,200 Dall's porpoise. Based on a very small sample, a correction factor of 2.7 has been estimated for humpback whales.[7] This would yield a corrected abundance estimate of 861 humpback whales. Clearly, given the magnitude of these correction factors, availability bias can be substantial.

Potential upward bias in line-transect analysis can result if factors other than distance to the trackline affect the probability of seeing a school. School size has been shown to affect the probability of detection (Drummer, 1985; Holt and Sexton, 1989), and this can lead to an upward bias in the abundance estimate (Quinn, 1985; Drummer and McDonald, 1987; Buckland et al., 1993a). To counteract this effect, we have stratified small cetacean sightings by group size and estimated abundances separately for small and large groups of the same species. This is an artificial separation, but it reduces potential biases that are due to large variation in group size within a single species, such as common dolphins or Pacific white-sided dolphins. Within each stratum, correlations of perpendicular sighting distance with group size are weak and not significant at α=0.05 (r=0.195 for small cetaceans in groups of 1–10 animals; r=0.169 for small cetaceans in groups of greater than 10 animals; and r=0.183 for whales in groups of all sizes).

[6] Calambokidis, J., J. R. Evenson, J. C. Cubbage, P. J. Gearin, and S. D. Osmek. 1993. Development of a correction factor for aerial surveys of harbor porpoise. Draft Final Contract Report to the National Marine Mammal Laboratory, NMFS, NOAA, 7600 Sand Point Way NE, BIN C-15700, Seattle, WA 98115. 36 p.

[7] Calambokidis, J., G. H. Steiger, J. C. Cubbage, K. C. Balcomb, and P. Bloedel. 1989. Biology of humpback whales in the Gulf of the Farallones. Final report for Contract CX-8000-6-0003 to Gulf of the Farallones National Marine Sanctuary, NOAA, Fort Mason Center, Bldg. 201, San Francisco, CA 94123, 93 p.

In summary, we have attempted to correct for perception bias by estimating the fraction of animals missed during these surveys and have minimized potential upward bias with a poststratification by school-size range. However, species-specific availability bias cannot currently be estimated, and overall our abundance estimates are likely to be biased downward.

Precision

Estimation of variance for line-transect abundance calculations can be difficult. We have attempted to include most of the sources of sampling error in the bootstrap procedure, which reestimates n, s, and $f(0)$ (in Eq. 1) for each replicate. Our analysis revealed that the choice of segment length used for the bootstrap did not affect the resulting estimates of precision within the range of appropriate segment lengths for this study (5–100 km; longer segments would not be appropriate because surveys extended only 100–150 km offshore). However, potential heterogeneity due to the pooling of different species and group sizes for estimation of $f(0)$ and $g(0)$ was not accounted for in precision estimates. Furthermore, we did not include the variance in $g(0)$ or in the estimation of group size for each school encountered (however, the variance in the estimated mean group size for the survey was included in the bootstrap procedure). Thus, the coefficients of variation for the abundance estimates (Table 3) are likely to be underestimated and the confidence intervals are likely to be too narrow.

Considerations for future aerial surveys

Two species of common dolphins, short-beaked and long-beaked, are recognized in California waters (Rosel, 1992; Dizon et al., 1994; Heyning and Perrin, 1994). Although clear differences in color pattern, size, and beak length exist between these two forms, it is not currently possible to differentiate them during aerial surveys; therefore the abundance estimate here is a combined estimate. Unless reliable means of identifying the two species from the air are developed, aerial surveys will not be adequate for future assessments requiring separate estimates of short-beaked and long-beaked common dolphins.

Similarly, it was difficult to distinguish between the smaller species of beaked whales during our aerial surveys. The estimates presented for the beaked whales as a group are therefore a combined estimate for *Ziphius cavirostris* and *Mesoplodon* spp. All unidentified beaked whale sightings could be narrowed down to these two genera. The only other beaked whale species known to occur in this region, *Berardius bairdii*, can be readily distinguished based

on its size and was not sighted during this survey. It is likely that the categorization of "small beaked whales" will be necessary on future aerial surveys.

The survey grid used here was not designed for species which are restricted to a narrow coastal region. Harbor porpoise are found primarily in waters inshore of the 50-fathom (92-m) isobath (Barlow, 1988). Two distinct populations of bottlenose dolphins are found in California; the inshore form is found only within about 1 km of shore (Hansen, 1990; NMFS[8]). All of the bottlenose dolphins seen during this aerial survey were at least several miles from the mainland; therefore our estimate is assumed to represent the population of offshore animals. Precise estimates of abundance for harbor porpoise and inshore bottlenose dolphins will require dedicated aerial surveys designed for those species. Work is currently in progress on both of these projects.[8]

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Larval development of King George whiting, *Sillaginodes punctata*, school whiting, *Sillago bassensis*, and yellow fin whiting, *Sillago schomburgkii* (Percoidei: Sillaginidae), from South Australian waters

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Abstract.—The larval development of *Sillaginodes punctata*, *Sillago bassensis*, and *Sillago schomburgkii* is described based on both field-collected and laboratory-reared material. Larvae of the three species can be separated based on a combination of pigment and meristic characters, including extent and appearance of dorsal midline pigment, lateral pigment on the tail, presence or absence of pigment above the notochord tip, myomere number, extent and timing of gut coiling, and size at flexion. The most useful meristic character across the range of specimens was number of myomeres. *Sillaginodes punctata* with 42–45 myomeres are easily distinguished from *Sillago schomburgkii* with 36–38, and from *S. bassensis* with 32–35. The timing of gut coiling and its subsequent effect on anus position differed both among the three species examined here and from that previously reported for sillaginid larvae in general. Timing of gut coiling and extent of anus migration are not useful characters for the identification of temperate Australian sillaginids at the family level but are useful on a specific level. Possible implications of the development of the gut to diet are discussed.

Based on the presence of larvae, all three species spawn in South Australian waters. No larvae of a fourth sillaginid species, *S. flindersi*, were found during the study. South Australia is the western distributional limit for *S. flindersi* and it does not appear to spawn in the area.

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The perciform family Sillaginidae (whiting and sand smelts) consists of three genera, three subgenera, and thirty-one species of small to moderately sized fishes found primarily in shallow coastal waters of the Indo-Pacific (McKay, 1992). Sillaginids are highly valued food fishes in many tropical and temperate waters. The Sillaginidae are related to the Percidae, Sciaenidae, and, to a lesser extent, the Haemulidae (McKay, 1985) although their sister group is yet to be determined (McKay, 1992). The most speciose of the three sillaginid genera (*Sillago*) includes twenty-nine species. The remaining two genera, *Sillaginodes* and *Sillaginopsis*, are monotypic. The taxonomy of the family is approaching stability; only a few species remain undescribed (McKay, 1992).

Two genera and thirteen species of sillaginids are found in Australian waters. Four species inhabit the waters off South Australia: the King George or spotted whiting, *Sillaginodes punctata*; yellow fin whiting, *Sillago schomburgkii*; western school whiting, *Sillago bassensis*; and eastern school whiting, *Sillago flindersii*. The latter two species were, until recently, considered subspecies of *S. bassensis* (McKay, 1992). All four species are widely distributed in southern Australia and form the basis for important commercial fisheries across their range (McKay, 1985; Kailola et al., 1993; May and Maxwell[1]).

The adult and juvenile biology of each of the four species has previously been documented by several authors (Scott, 1954; Gilmour, 1969; Lennanton, 1969; Robertson, 1977; Weng, 1983, 1986; Burchmore et al., 1988; Jones[2]; Jones et al.[3]), but very little is known of their early life history and neither the eggs nor the larvae of any of the four species have previously been described.

In 1986, the South Australian Department of Fisheries began an ichthyoplankton program to inves-

[1] May, J. L., and J. G. H. Maxwell. 1986. Field guide to trawl fish from temperate waters of Australia. CSIRO Division of Fisheries Res., Hobart, Tasmania, 492 p.

[2] Jones, G. K. 1979. Biological investigations on the marine scale fishery in South Australia. South Australian Dep. Agric. and Fisheries Rep., 72 p.

[3] Jones, G. K., D. A. Hall, K. L. Hill, and A. J. Staniford. 1989. The South Australian marine scale fishery: stock assessment, economics, management. South Australian Dep. Fisheries Green Paper, 186 p.

tigate the larval ecology of commercially important fishes of South Australian waters. An important prerequisite of any such program is the ability to make an accurate identification of larvae to species. This paper details the development of *Sillaginodes punctata*, *Sillago schomburgkii*, and *S. bassensis* larvae collected during this study.

Materials and methods

Specimens were obtained from plankton and beach seine samples collected between March 1986 and March 1991 aboard the research vessel MRV *Ngerin* in coastal waters and at various inshore nursery areas off South Australia. Details of sampling locations and procedures are described in Bruce (1989). Briefly, larvae were obtained from stepped oblique tows with 70-cm-diameter bongo nets fitted with 500-micron mesh. Postsettlement (refer to definition below) larvae and juveniles were captured with a fine mesh beach seine (7 m × 1.8 m, 2-mm mesh) as well as by dipnetting and diving. The field-collected series of *Sillaginodes punctata* was supplemented with larvae reared in the laboratory at West Beach, Adelaide.

All field-collected specimens used for description were fixed in a 10% formalin-seawater solution buffered with sodium tetraborate (borax) and were later transferred to a 5% solution buffered with sodium B-glycerophosphate (0.5 g per 1,000 mL). Reared larvae were fixed immediately in the 5% solution. Reared *S. punctata* were used for illustration when possible because of their superior condition. Some pigment differences were apparent between reared and field-collected larvae largely as a result of expansion or contraction of melanophores. Melanophores of field-collected larvae were generally less expanded than reared specimens. Reared larvae were typically greater in length than similarly developed field-collected material owing to increased shrinkage in the latter. Similar shrinkage effects have been previously reported for a variety of species (Theilacker, 1980; Hay, 1981; Bruce, 1988). Unless specified, development at length refers to field-collected material.

Representative series of *S. punctata* and *Sillago bassensis* are deposited with the I.S.R. Munro Fish Collection, CSIRO, Hobart Tasmania. Too few *S. schomburgkii* larvae were collected to allow a complete analysis and all are currently held in a collection maintained by the author at CSIRO Division of Fisheries, Hobart, Tasmania.

Developmental terminology and body measurements follow Leis and Trnski (1989). The term "postsettlement" is used to describe newly settled individuals prior to the acquisition of scales and juvenile colour patterns, after which they are referred to as juveniles. Body length measurements (BL) are measured as notochord length, NL (i.e. from the snout tip to the end of the notochord), in preflexion and flexion larvae, and standard length, SL (i.e. from the snout tip to the posterior margin of the superior hypural elements), in postflexion larvae and juveniles. Body depth is taken at two points. Body depth at pectoral (BDp) is equivalent to "body depth" as defined by Leis and Trnski (1989), that is, as "the vertical distance between body margins (exclusive of fins) through the anterior margin of the pectoral fin base." Body depth at anus (BDa) is defined as the vertical distance between body margins (exclusive of fins and, initially, the gut) through the midpoint of the anal opening. BDa includes the gut only after overlying musculature has developed. *Sillaginodes punctata* eggs were measured with a Zeiss photomicroscope III fitted with an ITC 510 video camera and linked to an Apple Macintosh SE computer via an HEI 582A video coordinate digitizer. Egg dimensions are reported to the nearest micron. Larvae were measured to the nearest 0.1 mm with a dissecting microscope fitted with an ocular micrometer. Postsettlement larvae and juveniles were measured to the nearest 0.1 mm with vernier calipers.

Meristic counts were made on *S. punctata* and *Sillago bassensis* specimens cleared and stained with alcian blue and alizarin red-S following Potthoff (1984). Insufficient specimens of *S. schomburgkii* were available for clearing and staining and therefore all meristics were taken from unstained material.

Descriptions are based primarily on the detailed examination of a representative series of specimens; however, comments on pigment and meristic variability stem from the routine examination of all larvae collected. The number of specimens examined in detail, the size range covered, and the museum reference numbers (for lodged material) are provided under each species account.

Results

Identification

Larvae were identified to family level from larval sillaginid characters reported in the literature. Sillaginid larvae are elongate and have 30–44 myomeres (Johnson, 1984; Miskiewicz, 1987; Leis and Trnski, 1989). The gut typically reaches to greater than 55% body length in preflexion larvae. The anus is reported to migrate anteriorly during development (often during flexion) as a result of coiling of the anterior section of the gut, thus shortening the preanal length

(Leis and Trnski, 1989). Sillaginids have a characteristic series of melanophores along the dorsal and ventral midlines (particularly prominent in small larvae) and generally have pigment located on the angle of the lower jaw.

Three types of sillaginid larvae were found during this study. Specific identity of two of the types (*S. schomburgkii* and *Sillaginodes punctata*) was established by comparing vertebral counts and fin meristics of postflexion larvae to those of adult and juvenile specimens. Smaller larvae were linked by establishing a developmental series based on the extent and appearance of dorsal midline pigment, lateral pigment on the tail, presence or absence of pigment above the notochord tip, myomere number, extent and timing of gut coiling, and size at flexion. The identity of *S. punctata* was also confirmed by comparison to reared larvae.

Though clearly separating *Sillaginodes punctata* from *Sillago schomburgkii*, fin meristics and vertebral counts overlap in the other two South Australian sillaginid species (*S. bassensis* and *S. flindersi*), thus making the specific separation of their larvae difficult. Sillaginid larvae from southern Tasmania (where only *S. flindersi* are found) and larvae believed to be *S. flindersi* from New South Wales (NSW) coastal waters were compared to the third sillaginid larval type collected in South Australia in order to ascertain its identity. The NSW and Tasmanian (referred to herein as eastern) specimens were highly similar but differed from the South Australian type with respect to two pigment characters. First, eastern specimens had a single prominent, elongate melanophore located below the level of the pectoral fin base and overlying the cleithrum that was absent in South Australian material (Fig. 1). Second, eastern specimens developed external lateral midline pigment on the tail at an earlier size (7.2 mm) than did South Australian material (14.8 mm). Two sillaginids are known from Tasmanian waters: *Sillaginodes punctata* and *Sillago flindersi* (Last et al., 1983). Only *S. flindersi* is known to spawn in Tasmanian waters. The eastern form was thus identified as *S. flindersi* and the South Australian specimens as *S. bassensis*. Insufficient material was available across the full size range to render an adequate description of the larval development of *S. flindersii,* and thus this species is not treated in further detail here.

The most useful meristic character separating the three South Australian larval types was number of myomeres. *Sillaginodes punctata* with 42–45 myomeres are easily distinguished from *Sillago schomburgkii* with 36–38 and *S. bassensis* with 32–35. Meristic details for these three species and *S. flindersi* are listed in Table 1.

Descriptions

King George whiting (*Sillaginodes punctata* Cuvier 1829), Figure 2

Material examined—75 specimens, 2.0–30.5 mm BL (CSIRO L587-01, L587-02, L587-03, L587-04, L587-05, L587-06; L588-01; L589-01).

Larval development—The pelagic eggs of *S. punctata* are spherical and have an unsegmented yolk and smooth chorion. Late stage eggs are 839–935 microns in diameter (mean 880, n=25) and have a single oil droplet 246–263 microns in diameter (mean 255, n=25). Reared larvae hatched at 2.00–2.15 mm (mean 2.07, n=24) at 16.5–18.7°C. The timing of fertilization was not recorded as spawning occurred in brood stock tanks overnight. Estimates for incubation period are 48–60 hours. The temperature of the spawning tank was 16.5°C and fertilized eggs were transferred to a 90-liter tank held at 18.0–18.7°C for subsequent incubation, 24 hours prior to hatching.

Newly hatched larvae have a posteriorly located oil droplet and adopt a head-down position in rearing containers. Yolk absorption was complete in reared larvae by 3.5 mm (8 days), although the small-

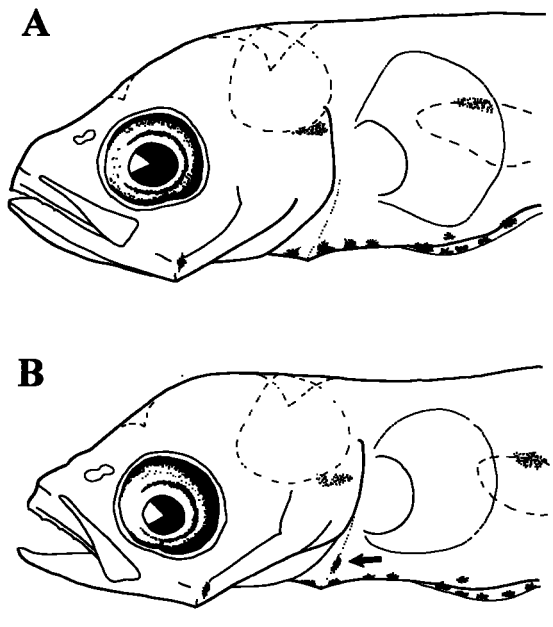

Figure 1

Detail of head and trunk pigment of (**A**) *Sillago bassensis* and (**B**) *Sillago flindersi*. Myomeres have been omitted for clarity. Position of cleithrum is indicated by a dotted line. Arrow indicates characteristic melanophore overlying cleithrum in *S. flindersi*.

Table 1

Selected early life history features useful for identifying sillaginid larvae (sizes are in mm).

Species	Size at gut coiling	Size at flexion	Size at first lat. midline pigment	Size at first dorsal banding	Size at settlement	Completion of fin formation[6]	Number of myomeres	Dorsal fin	Anal fin	Pectoral fin
Sillaginodes punctata[1]	21.0–24.0	5.7–7.0	8.0	6.5–7.0	15.0–18.0	C,P1,A,D2+D1,P2	42–45	XII–XIII+I,25–27	II,21–24	13–15
Sillago bassensis[1]	4.1–7.5	4.8–6.5	14.0	12.0–13.0	12.0–13.0	C,P1,A,D1+D2,P2	32–35	X–XII+I,16–19	II,18–20	15–16
Sillago schomburgkii[1]	>5.1<10.1[7]	4.8–?	2.7	<10.1	12.0–13.0	[8]	36–38	X–XII+I,19–22	II,17–20	15–16
Sillago ciliata[2,3]	<5.0	4.0–5.6	5.3	6.5	15.5	C,A,D2,D1,P1,P2	30–34	XI+I,16–18	II,15–17	15–17
Sillago maculata[2]	[8]	4.6–6.5	3.3	10.6	[8]	C,P1,A,D2,D1,P2	33–36	XI–XII+I,19–21	II,19–20	15–17
Sillago sihama[4]	5.9	5.9	5.9	9.0	[8]	[8]	33–34	XI+I,20–23	II,21–23	15–17
Sillago japonica[5]	<7.6	<7.6	7.6	7.6	11.5	[8]	35–37	XI+I,21–23	II,22–24	15–17

[1] This study.
[2] Miskiewicz, 1987.
[3] Munro, 1945.
[4] Uchida et al., 1958.
[5] Mito, 1966 (as *Sillago japonicus*); Kinoshita, 1988.
[6] Based on all elements present and ossified, C = caudal, P1 = pectoral, P2 = pelvic, A = anal, D1 = first dorsal, D2 = second dorsal.
[7] No specimens between 5.1 and 10.1 mm were available. Coiling of the gut had not commenced in the 5.1-mm specimen but had been completed in the 10.1-mm specimen.
[8] Data not available.

est field-collected larvae (2.9 mm) had already completed yolk absorption.

Larvae are elongate (BDp=11–16% BL) and have 42–45 myomeres (17–21 abdominal + 23 – 27 candal). Body depth at anus increases slightly from 7% to 9% BL during development. Other body proportions remain relatively constant (Table 2). The gut is initially straight and differentiates into defined fore, mid and hind gut sections by 3.7 mm. The gut exhibits some convolution but does not coil during the larval phase. The midgut becomes rugose by approximately 5.0 mm and remains so, although overlying musculature obscures this feature in postsettlement larvae larger than 21.0 mm. The gut begins to coil in postsettlement larvae of 21.0 –24.0 mm and is complete by 26.0 mm. Coiling of the gut proceeds without migration of the anus and is achieved by elongation and anterior looping of the midgut. Consequently, body proportions do not show a significant change in preanal length which remains at 50–52% BL. The gas bladder is first visible in reared larvae by 3.5 mm (5 days) and is prominent and inflated in 86% of field-collected larvae (random subsample, n=50; all larvae collected at night) and all postsettlement larvae collected (all postsettlement larvae collected during day). The gas bladder has its origin at myomeres 2–5 in preflexion larvae but migrates posteriorly during development to myomeres 13–18 by 18.7 mm.

The snout is initially slightly concave in profile, but after flexion, this gradually changes to straight or slightly convex. The eye is round. The mouth initially reaches to below the eye, but is short of the eye in postflexion larvae. Six to eight small villiform teeth are present on the premaxilla by 5.8 mm. The number of teeth increases to 10–12 by late flexion (6.5–7.0 mm). There are no head spines.

Scales are first present around the gut and lateral midline by approximately 27.5 mm.

The development of fins in larval and juvenile *S. punctata* is summarized in Table 1. Completion of fin development occurs in the following sequence: caudal; pectoral; anal and second dorsal (almost simultaneously); first dorsal; and pelvic.

The rays of the caudal fin are present just prior to flexion in larvae of 5.6 mm. Flexion commences by 5.7–6.0 mm and is usually complete by 7.0 mm. Pectoral fin buds are present in reared larvae as slight swellings on the body above the anterior margin of the oil droplet by 3.1 mm (2 days post hatch). Incipient rays are first visible by 7.5 mm and commence ossification by 8.5 mm. A full complement of 13–15 pectoral rays is present by 11.5 mm. Anal and second dorsal fin anlagen appear during flexion (5.8 mm). Distinct bases are present by 7.0 mm, incipient rays by 7.2 mm, and ossification commences by 8.0 mm. The anal and second dorsal fins complete development by 13.0 mm. The

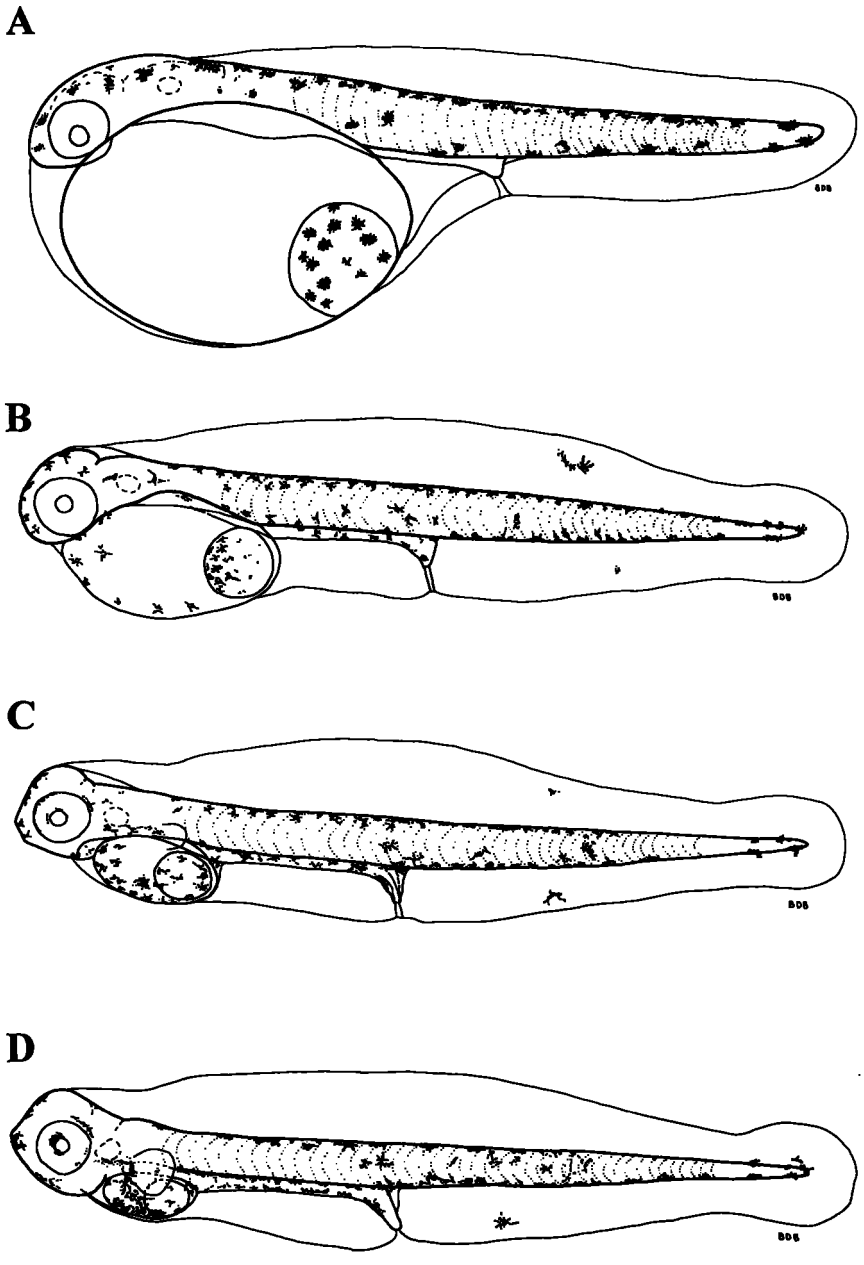

Figure 2

Development of *Sillaginodes punctata*. (**A**) 2.1 mm; (**B**) 2.9 mm; (**C**) 3.1 mm; (**D**) 3.5 mm; (**E**) 3.6 mm; (**F**) 4.2 mm; (**G**) 5.8 mm; (**H**) 6.5 mm; (**I**) 8.5 mm; (**J**) 12.0 mm; (**K**) 18.7 mm postsettlement; (**L**) 22.4 mm (postsettlement: myomeres omitted for clarity). A–I are reared specimens, J–L are field-collected specimens.

first dorsal fin anlage is present by 6.2 mm. Distinct bases are present by 7.6–8.6 mm and ossification of spines has commenced by 8.5–8.9 mm. The first dorsal fin completes development by 13.1 mm. Pelvic fins first appear as slight swellings on either side of the gut in 9.2-mm larvae. Well-developed buds are present by 13.0 mm, incipient rays form shortly thereafter. The pelvic fin does not complete development until 20.0–21.5 mm.

Larval pigment—The oil droplet is well pigmented with large stellate melanophores from at least 24

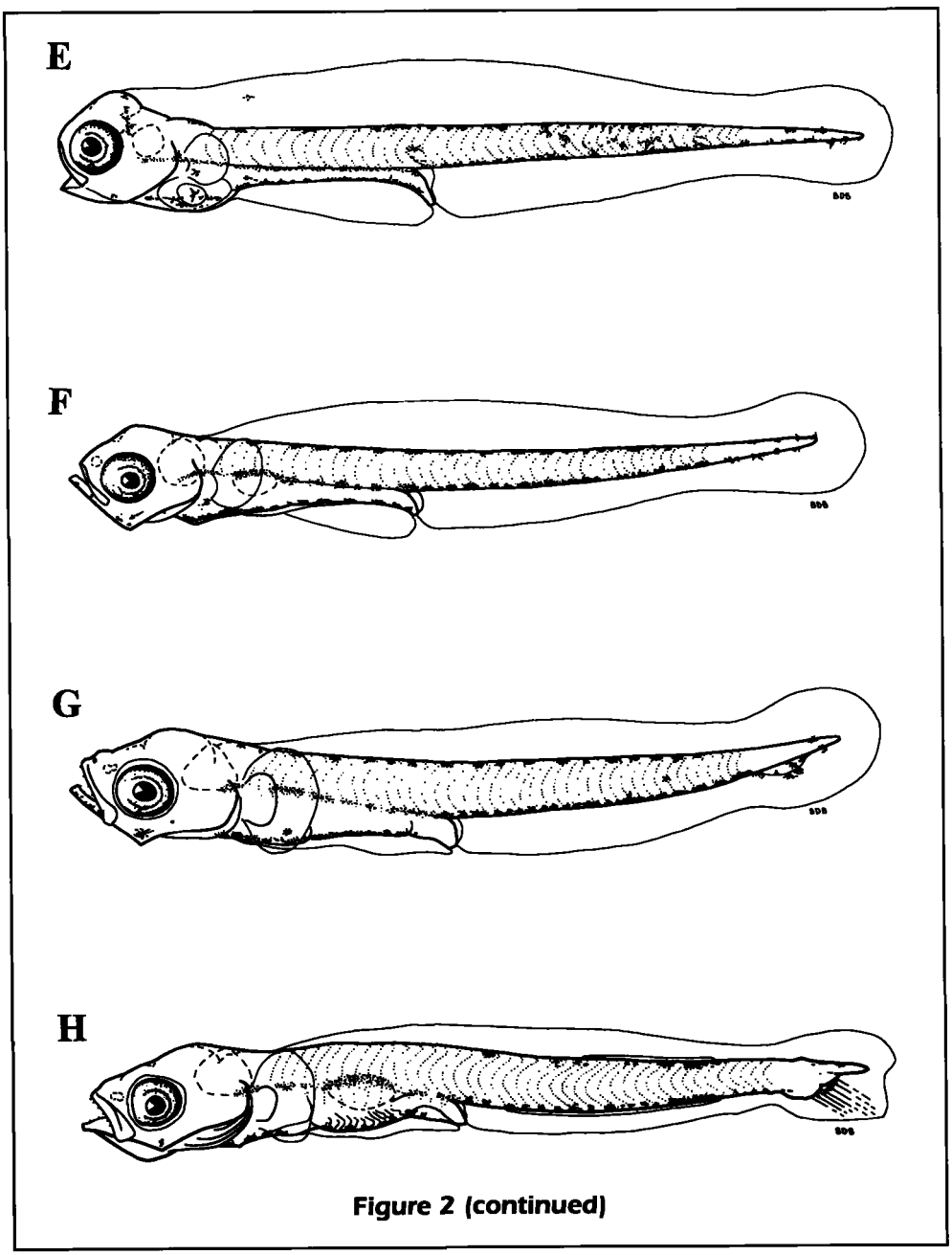

Figure 2 (continued)

hours prior to hatching until yolk exhaustion. Newly hatched larvae have melanophores scattered over the body. Melanophores appear on the ventral and anterior regions of the yolk sac by 2.8 mm and pigment also appears within the finfold (both dorsal and anal) between myomeres 25–32 in reared larvae (not apparent in field-collected larvae — probably owing to finfold damage). Finfold pigment disappears by 3.5 mm.

Initially, melanophores are scattered over the snout but they disappear by 3.5 mm. Pigment appears at the angle of the lower jaw and is retained throughout the larval period. Melanophores are typically present on the lower jaw, ventrally on the gular membrane, and internally below the otic capsule. Further pigment does not form on the head until after settlement.

The dorsal surface of both the gut and the gas bladder are covered with melanophores during development. A linear series of discrete melanophores is present on the ventral midline of the gut in preflexion and flexion larvae. Ventral melanophores disappear from the hindgut by 10.0 mm and this region then remains unpigmented. Concurrently, the remaining 5–8 melanophores between the cleithral symphysis and the hindgut become elongate and are retained in postsettlement larvae.

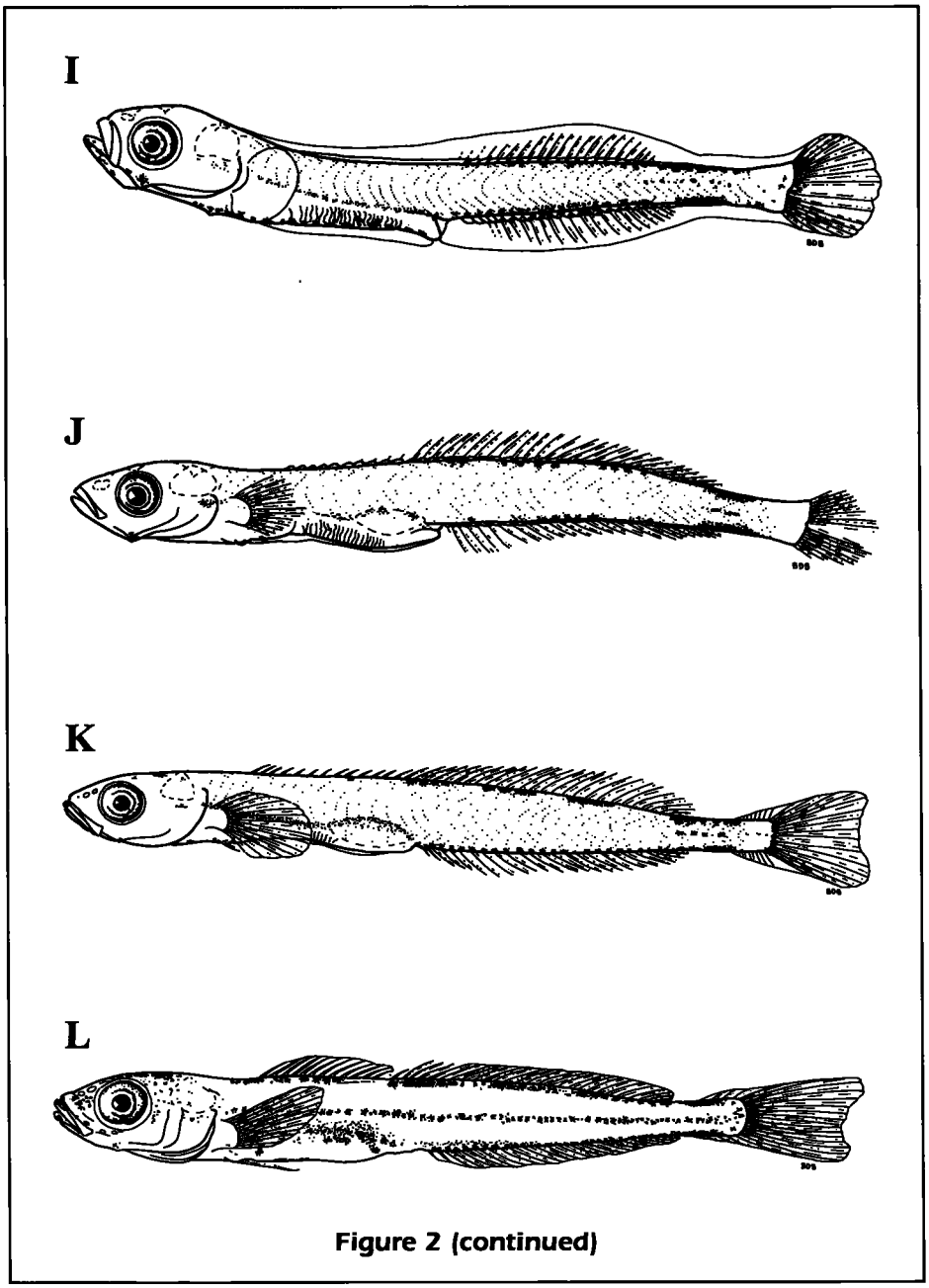

Figure 2 (continued)

By 4.0 mm, pigment on the dorsal surface of the trunk and tail coalesce to form 11–18 discrete, evenly placed melanophores that extend in a linear series posteriorly from the nape to within about 4 or 5 myomeres from the notochord tip. The dorsal surface of the notochord tip has 0–3 melanophores (most commonly 1 or 2) and when present they are useful in separating preflexion *Sillaginodes punctata* from *Sillago bassensis* and *S. schomburgkii*, both of which lack pigment dorsally on the notochord tip. The dorsal series of melanophores on the trunk and tail gradually disappears by the end of flexion (6.5–7.0 mm), excepting those between myomeres 31–40, which become prominent and may extend laterally over the body surface when expanded. Lateral midline pigment develops in this area during late flexion and is retained throughout the postflexion stage. Dorsal pigment gradually redevelops in postflexion larvae as a series of discrete bands, each comprising 3 or 4 pairs of stellate melanophores. Postsettlement larvae have 4–6 such bands which subsequently increase in number to 8–10 as juvenile pigmentation develops.

Ventral pigment on the tail in newly hatched larvae is initially scattered but coalesces to form a se-

Table 2

Body proportions of larvae of *Sillaginodes punctata* (expressed as a percentage of body length). d = damaged; g = gas bladder not visible; — = character not yet formed. Specimens between dotted lines were undergoing flexion.

Body length (mm)	Pre-anal length	Pre-dorsal fin length	Pre-gas-bladder length	Head length	Snout length	Eye diameter	Vent to anal fin length	Body depth at pectoral	Body depth at anus
3.1	51.6	—	37.1	22.5	6.4	9.7	—	12.9	8.1
3.2	53.1	—	23.4	18.7	3.1	6.2	—	10.9	6.2
3.3	51.5	—	28.8	24.2	6.1	9.1	—	15.1	9.1
3.6	51.3	—	22.2	19.4	4.1	8.3	—	11.1	5.5
3.7	51.3	—	24.3	21.6	4.1	8.1	—	12.2	6.8
4.1	47.5	—	24.4	19.5	3.7	7.3	—	12.2	6.1
4.2	50.0	—	23.8	19.0	2.3	7.1	—	11.9	7.1
4.3	55.8	—	32.5	23.2	4.6	9.3	—	16.2	9.3
4.7	51.1	—	34.0	23.4	4.2	8.5	—	14.9	8.5
5.0	50.0	—	30.0	24.0	5.0	8.0	—	13.0	8.0
5.3	52.8	—	32.1	22.6	3.7	7.5	—	13.2	8.5
5.4	50.0	—	29.6	20.4	1.8	7.4	—	13.0	7.4
5.7	47.3	—	31.6	22.8	5.3	7.0	—	12.3	7.9
5.9	45.8	—	28.8	18.6	5.1	6.8	—	11.9	6.8
6.0	48.3	60.0	31.6	23.3	6.7	6.7	—	13.3	8.3
6.2	50.0	—	31.4	21.0	4.0	6.4	6.4	12.1	8.1
6.3	47.6	50.8	33.3	23.8	6.3	6.3	4.2	11.1	7.9
6.4	51.6	46.9	32.0	20.3	6.2	6.2	—	12.5	7.8
6.5	47.7	49.2	33.1	23.8	6.1	d	6.9	12.3	7.7
6.6	47.0	—	30.3	22.7	5.3	6.1	6.6	10.6	7.5
6.8	50.0	48.5	30.9	20.6	5.9	6.6	—	12.5	8.1
7.0	51.4	52.3	34.3	21.4	d	d	—	11.4	10.0
7.2	54.1	50.0	37.5	23.6	5.7	7.6	0.7	11.1	8.3
7.6	52.6	53.9	34.2	22.3	5.3	7.2	2.6	11.8	7.9
8.4	52.3	40.4	40.4	21.4	5.9	7.1	0.0	12.5	10.7
9.3	52.3	30.1	39.7	21.5	6.4	6.4	1.6	10.7	9.1
10.3	52.4	31.1	40.8	21.3	5.8	6.8	0.5	11.1	9.7
12.0	50.0	27.5	39.2	21.7	6.7	5.0	0.6	10.0	9.2
13.1	49.6	27.5	40.4	19.8	5.3	5.3	0.7	9.2	8.4
15.7	50.9	27.4	40.8	19.1	5.7	d	0.0	10.2	11.5
16.1	50.9	26.7	41.0	19.2	5.0	5.6	0.0	9.9	9.9
18.2	51.1	27.5	40.6	20.3	6.0	6.0	0.5	9.9	10.4
18.7	49.2	25.7	38.0	19.8	5.3	5.9	1.1	9.6	9.1

ries of closely spaced melanophores extending to the notochord tip by 3.6 mm. Preflexion larvae have 2–4 melanophores ventrally on the notochord tip. During flexion, melanophores between myomeres 23–38 become more prominent (similar to the dorsal series). The ventral series of melanophores on the tail becomes gradually obscured by overlying musculature (excepting the prominent region between myomeres 32–38) in postflexion larvae. Paired external melanophores develop ventrally on the tail in larvae greater than 8.5 mm and by settlement stage, approximately one pair per myomere is present. This ventral series forms a regular pattern of expanded and contracted melanophores in postsettlement specimens, matching the banding pattern of the dorsal series.

School whiting (*Sillago bassensis* Cuvier, 1829), Figure 3

Materials examined—40 specimens, 2.3–17.2 mm BL (CSIRO L586-01—10 specimens).

Larval development—The smallest *S. bassensis* larva examined was 2.3 mm BL. At this size the mouth and gut are functional, the eyes are pigmented, a gas bladder is present, and yolk absorption is complete.

Larvae are elongate (BDp=13–20% BL) and have 32–35 myomeres (11–15+19–23). Body depth at anus increases slightly from 8–12% BL during development. Other body proportions remain relatively constant (Table 3). The gut forms a convoluted tube in the smallest specimen and is already differentiated

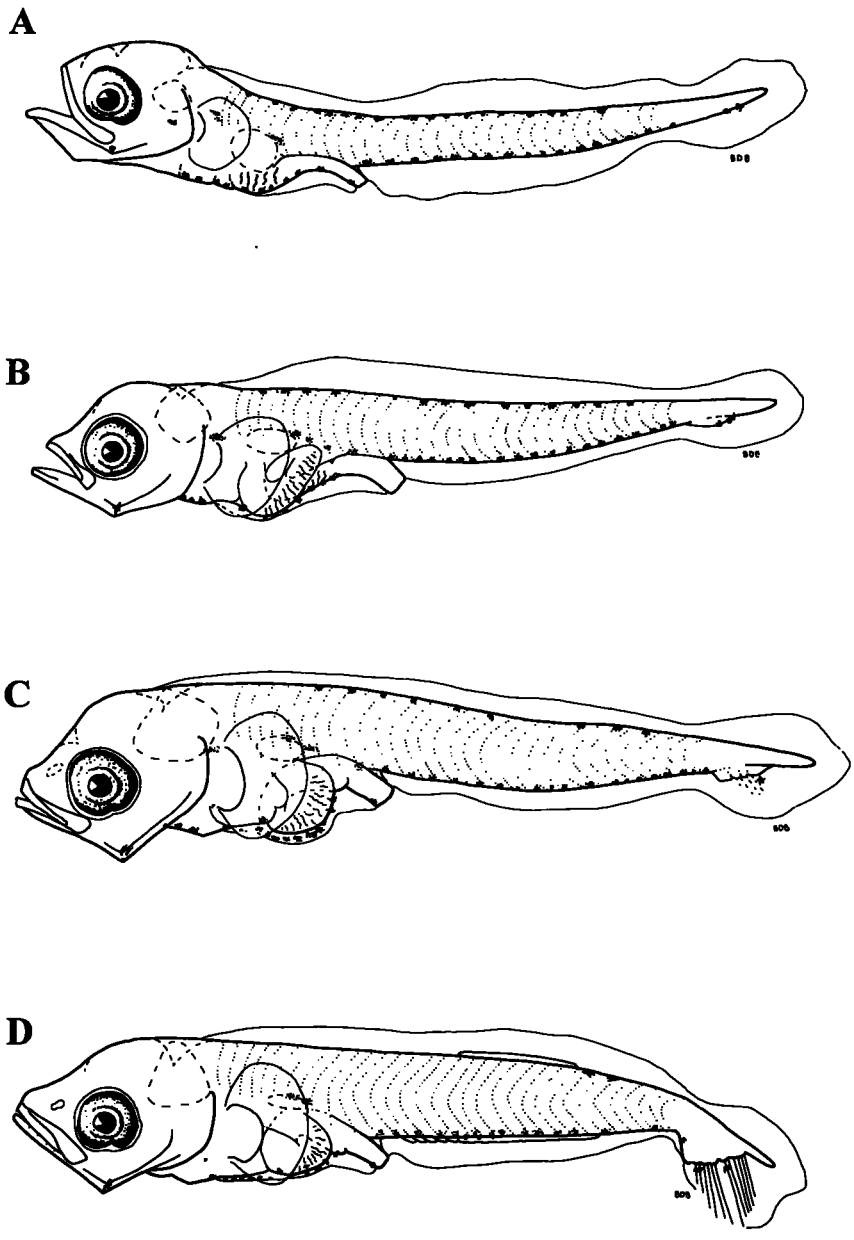

Figure 3

Development of *Sillago bassensis*. (**A**) 3.2 mm; (**B**) 4.4 mm; (**C**) 4.8 mm; (**D**) 5.9 mm; (**E**) 7.2 mm; (**F**) 11.2 mm; (**G**) 12.7 mm (postsettlement).

into fore, mid, and hindgut regions. The midgut becomes rugose by 3.0 mm and remains so, although overlying musculature obscures this feature prior to settlement. The gut begins to coil in preflexion larvae by 4.1 mm. Coiling proceeds without migration of the anus and is achieved by elongation and anterior looping of the midgut (Fig. 4). Consequently, body proportions do not show a significant change in preanal length which remains at 47–48% BL. Coiling of the gut is completed in postflexion larvae (7.0–7.5 mm). The gas bladder has its origin at myomeres 2–8 in preflexion larvae but migrates posteriorly during development to myomeres 5–10 in postflexion larvae. The gas bladder is inflated and prominent in 90% of field-collected larvae (random subsample n=40; all larvae were collected at night).

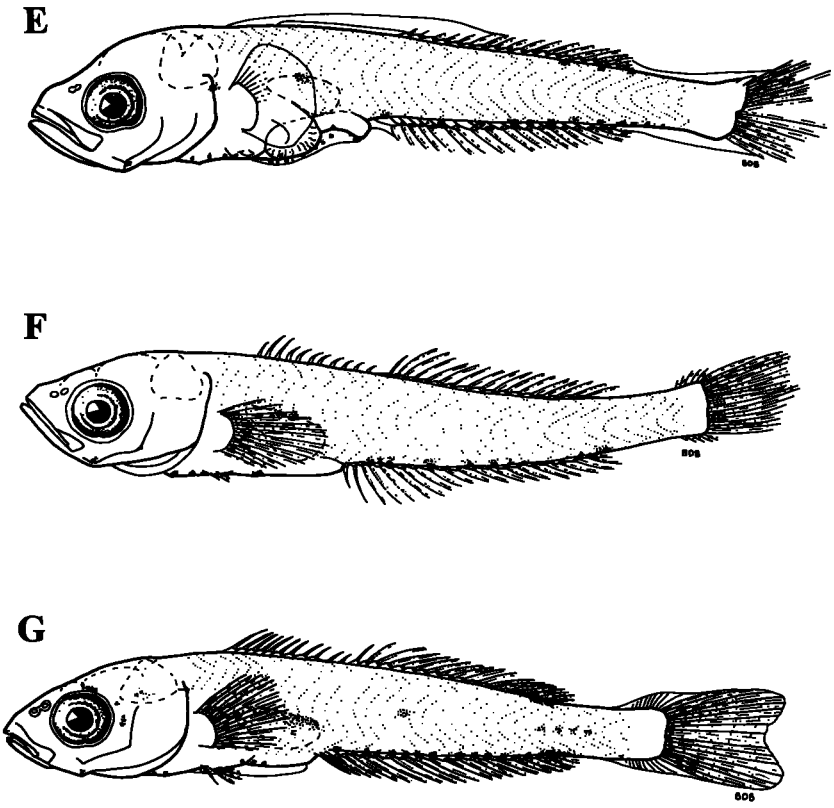

Figure 3 (continued)

The snout is initially slightly concave in profile, but after flexion, this gradually changes to straight or slightly convex. The eye is round. The mouth initially reaches to below the center of the eye but extends only to the anterior margin of the eye in postflexion larvae. Four to six small villiform teeth are present on the premaxilla by 4.7 mm. The number of teeth increases to 7 or 8 during flexion (4.8–6.5 mm). Head spination is only weakly developed. A single minute preopercular spine is present by 7.8 mm but is not visible after settlement (12.5 mm). A weak posttemporal ridge is present by 7.2 mm and is retained; however, no posttemporal spines develop. The single opercular spine is first visible by 12.7 mm and is retained in juveniles.

Scales develop after settlement and are first visible around the gut and lateral midline of the tail by approximately 16.0 mm.

The development of fins in larval and juvenile *S. bassensis* is summarized in Table 1. Completion of fin development occurs in the following sequence: caudal; pectoral; anal, first dorsal and second dorsal fins (almost simultaneously); and pelvic.

The rays of the caudal fin are present just prior to flexion in larvae of 4.4 mm. Flexion commences by 4.8–5.0 mm and is complete by 6.8 mm. Pectoral fin buds are present in the smallest specimen (2.3 mm), incipient rays form during flexion (5.8–6.0 mm), and a full complement of 15 or 16 rays is present by 10.0 mm. Anal-fin and second-dorsal-fin anlagen appear during flexion. Distinct bases are present by 6.5–7.0 mm, incipient rays by 6.8–7.1 mm, and ossification of posterior rays has regularly commenced by 7.2 mm. Ossification of dorsal and anal elements proceeds anteriorly and both fins complete development by 10.0–10.5 mm. The first dorsal fin anlage is present by 7.0 mm. Distinct bases are present by 7.5–8.0 mm and ossification of spines has commenced by 8.0–8.5 mm. Development of the first dorsal fin is complete by 10.0–10.5 mm. Pelvic fin buds are present in 7.0–7.2 mm larvae below the pectoral fin bases. Development of the pelvic fin is complete by 12.5 mm.

Larval pigment—*S. bassensis* larvae were the least pigmented of the three sillaginid species examined.

Pigment on the head in preflexion larvae is limited to the angle of the lower jaw and internally to

Table 3

Body proportions of larvae of *Sillago bassensis* (expressed as a percentage of body length). d = damaged; g = gas bladder not visible; — = character not yet formed. Specimens between dotted lines were undergoing flexion.

Body-length (mm)	Pre-anal length	Pre-dorsal fin length	Pre-gas-bladder length	Head length	Snout length	Eye diameter	Vent to anal fin length	Body depth at pectoral	Body depth at anus
2.3	56.5	—	g	23.9	4.3	8.6	—	17.4	6.5
3.1	48.4	—	27.4	24.2	d	d	—	16.1	8.1
3.4	44.1	—	23.5	19.1	5.9	7.3	—	14.7	5.9
3.7	51.3	—	28.4	d	4.1	8.1	—	16.2	8.1
3.8	47.4	—	25.0	22.4	3.9	9.2	—	17.1	6.6
4.1	51.2	—	29.3	26.8	6.1	8.5	—	18.3	8.5
4.2	52.4	—	29.8	26.2	7.1	8.3	—	19.0	10.7
4.3	46.5	—	g	23.2	5.8	7.0	—	13.9	6.9
4.4	52.3	—	34.1	28.4	6.8	9.1	—	20.4	11.4
4.5	50.0	—	g	24.4	4.4	7.7	—	15.5	8.9
4.6	44.6	—	28.2	23.9	6.5	8.7	—	14.1	7.6
4.7	44.7	—	29.8	22.3	6.4	7.4	—	12.8	6.4
4.8	54.2	—	36.4	29.2	6.2	8.3	2.1	18.7	12.5
4.9	44.9	—	29.6	22.4	5.1	8.2	—	13.3	8.2
5.3	47.2	—	33.0	26.4	7.5	7.5	—	15.1	8.5
5.5	50.9	38.1	g	30.9	9.1	9.1	0.0	20.9	12.7
5.7	50.9	—	31.6	29.8	8.8	8.8	0.0	17.5	10.5
5.8	44.8	56.9	56.9	25.9	6.9	7.7	0.6	13.8	7.7
5.9	49.1	55.9	g	27.1	8.5	8.5	2.5	18.6	11.0
6.3	46.0	47.6	33.3	26.2	6.3	7.9	0.8	14.	8.7
7.7	49.3	54.5	32.5	25.3	7.8	7.8	0.0	18.8	13.6
7.9	45.6	53.2	32.9	25.3	6.3	7.6	2.5	13.9	8.9
8.9	51.7	38.2	34.3	28.6	7.8	7.8	0.0	18.5	16.3
9.6	47.9	33.3	37.5	25.0	7.3	8.3	0.0	14.6	12.5
10.1	44.5	30.7	g	22.8	4.9	7.9	0.9	14.8	10.9
10.2	45.1	31.3	g	24.5	5.9	8.3	1.0	14.7	10.8
11.3	46.9	33.6	33.6	28.3	7.1	8.0	0.0	16.8	13.3

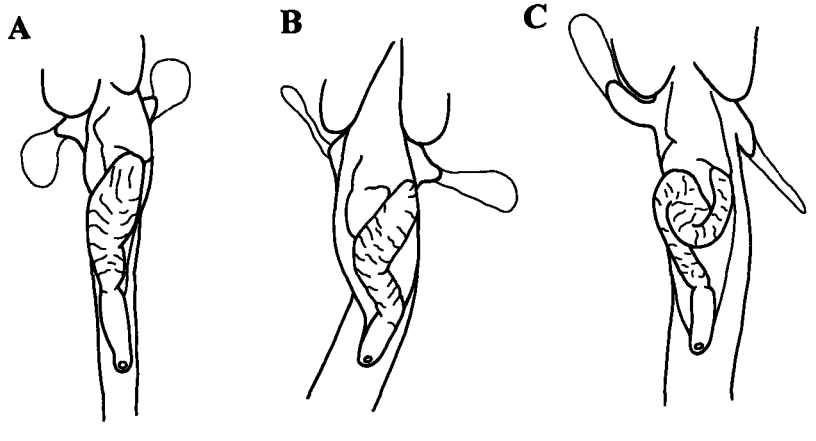

Figure 4

Morphology of the gut in *Sillago bassensis* (ventral view of pigment omitted). (**A**) 2.9 mm; (**B**) 4.2 mm; (**C**) 5.5 mm.

below the otic capsule. Melanophores are irregularly present ventrally on the gular membrane. Additional pigment on the head does not develop until after settlement. Melanophores then develop immediately anterior to and above the eye as well as on the snout and lower jaw. Larger specimens quickly develop a cap of melanophores over the mid and hindbrain.

Pigment on the dorsal surface of the gut consists of 2–7 approximately evenly spaced melanophores in preflexion larvae. This reduces to 2 or 3 just prior to flexion. In postflexion larvae, internal pigment over the gut is restricted to above the gas bladder. Ventral pigment on the gut consists of a midline series of 8–14 melanophores extending from just anterior to the cleithral symphysis to the anus in both preflexion and flexion larvae. One to two additional melanophores are usually present either side of this series below the level of the pectoral fin base (76% of larvae, random subsample n=25), forming a diamond pattern when viewed ventrally (Fig. 5).

Preflexion larvae have 10–18 discrete, evenly placed melanophores that extend in a dorsal linear series on the trunk and tail to within 1–3 myomeres of the notochord tip. The dorsal surface of the notochord tip remains unpigmented throughout development. The dorsal series of melanophores gradually disappears during flexion (4.9–6.5 mm). Postflexion larvae have 0–3 melanophores (most commonly 0) below the bases of the second dorsal fin. Dorsal pigment redevelops after settlement as a series of discrete bands each comprising 3–6 pairs of stellate melanophores. The first of these bands develops immediately below the posterior-most second dorsal fin rays, 5 or 6 additional bands subsequently develop anteriorly, and a single band developes posteriorly on the caudal peduncle by 20.0 mm. Lateral midline pigment on the tail does not form until after settlement, although some internal pigment may be present over vertebrae between myomeres 25–30 after 11.0 mm.

A single row of 14–19 melanophores is present along the ventral midline of the tail in preflexion larvae. This ventral row is gradually obscured by overlying musculature during flexion. Paired external melanophores subsequently develop ventrally on the tail in postflexion larvae, approximately one pair per myomere. After settlement, this ventral series forms a regular pattern of expanded and contracted melanophores producing a similar banding pattern to the dorsal series. One to two (most commonly 2) melanophores are present ventrally on the notochord tip in preflexion larvae. These are retained in postflexion larvae and, with additional melanophores, form a band of pigment over the caudal-fin ray bases.

Yellow fin whiting (*Sillago schomburgkii* Peters 1865), Figure 6

Material examined—16 specimens, 2.7–18.7 mm BL.

Larval development—The smallest *S. schomburgkii* examined was 2.7 mm. At this size the mouth and gut are functional, the eyes are pigmented, a gas bladder is present, and yolk absorption is complete.

Larvae are elongate (BDp=14–18% BL) and have 36–38 myomeres (15–17+20–22). Body depth at anus increases from 8 to 16% BL during development. Other body proportions remain relatively constant (Table 4). The gut forms a convoluted tube in the smallest specimen and is already differentiated into fore, mid and hindgut regions. The midgut becomes rugose by 4.4 mm and remains so, although overlying musculature obscures this feature prior to settlement. The gut has not begun coiling in the largest flexion-stage larva available (5.1 mm). Coiling of the midgut has begun in the 10.1-mm larva and is well developed in all postsettlement larvae. Insufficient specimens were available to further document the timing of gut coiling. Coiling of the gut proceeds without migration of the anus and is achieved by elongation and anterior looping of the midgut. Consequently, body proportions do not show a significant change in preanal length which remains at 51–53% BL. The gas bladder has its origin at myomeres 1–8 in preflexion larvae and is inflated and prominent in all larvae collected during night tows. The gas bladder is inconspicuous in larvae caught during the day.

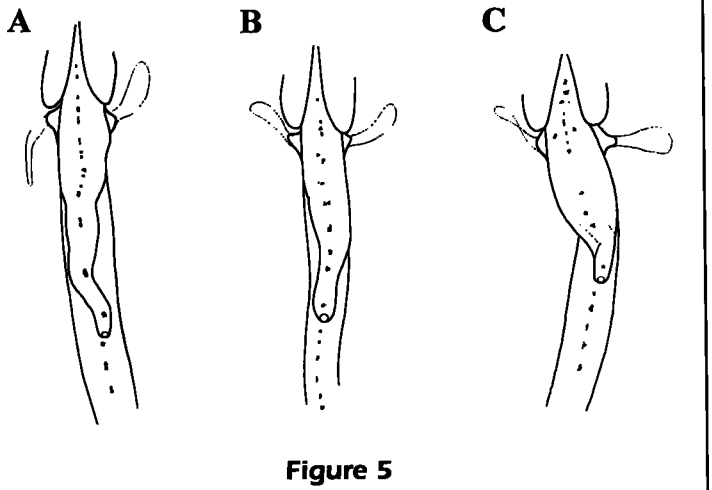

Figure 5

Ventral pigment on the gut: (**A**) *Sillaginodes punctata*, 4.7 mm; (**B**) *Sillago schomburgkii*, 4.4 mm; (**C**) *Sillago bassensis*, 4.1 mm.

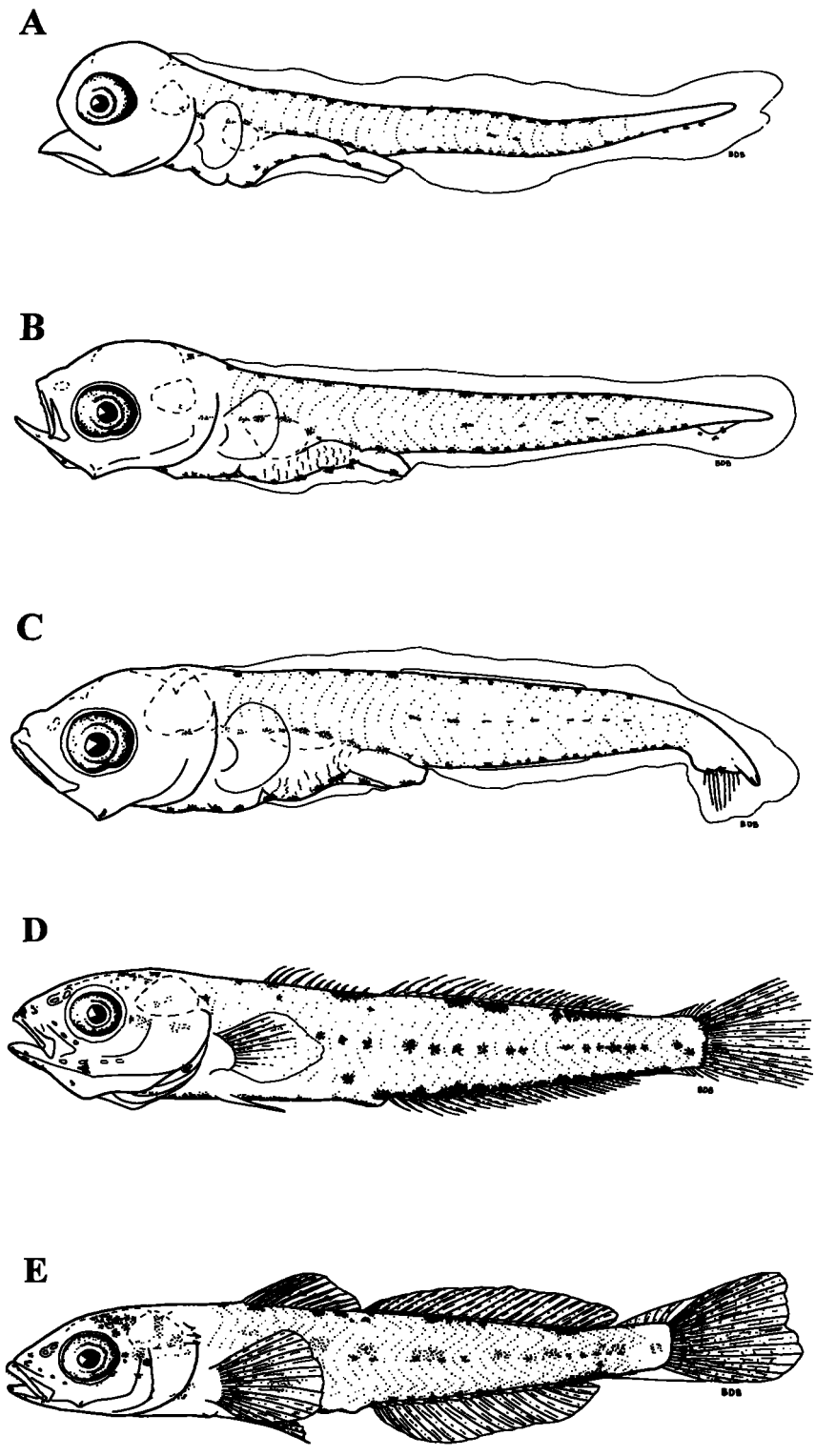

Figure 6

Development of *Sillago schomburgkii*. (**A**) 2.7 mm; (**B**) 4.4 mm; (**C**) 5.0 mm; (**D**) 10.1 mm; (**E**) 13.0 mm (postsettlement).

The snout is initially slightly concave in profile, but after flexion this gradually changes to straight or slightly convex. The eye is round. The mouth initially reaches below the eye but is short of the eye in postflexion larvae. Four to six small villiform teeth are present on the premaxilla by 4.4 mm. The number of teeth increases from 10 to 12 during flexion (from 4.8 to greater than 5.1 mm). Head spination is only weakly developed. One to two preopercular spines are discernible in postsettlement larvae. A weak posttemporal ridge with 1 or 2 small spines is developed in the 10.1-mm postflexion larva and is present in all postsettlement larvae examined. The single opercular spine is not visible in the 10.1-mm larva but is present in postsettlement larvae and is retained in juveniles.

Scales develop after settlement and are first visible around the gut and lateral midline by 17.2 mm.

Insufficient numbers of specimens were available to document the full sequence of fin development or the completion of flexion in *S. schomburgkii*.

The rays of the caudal fin are present in flexion larvae of 4.8 mm. Flexion commences by 4.8 mm. Pectoral fin buds are present in the smallest specimen (2.7 mm) and incipient rays form during flexion. Rays of the pectoral fin have commenced ossification in the 10.1-mm postflexion larva. A full complement of 15 or 16 pectoral fin rays is present in the smallest postsettlement larva (12.7 mm). Anal-fin and second-dorsal-fin anlagen appear during flexion. Full complements (spines and rays) of the anal fin and both dorsal fins are present in the 10.1-mm specimen. The pelvic fin has commenced development in the 10.1-mm larva and has completed development by 12.7 mm.

Larval pigmentation—Pigment on the head in preflexion *S. schomburgkii* larvae is limited to the angle of the lower jaw and internally to the base of the otic capsule. One or two melanophores are also present ventrally on the gular membrane, increasing to three during flexion. Additional melanophores develop on the snout tip, scattered over the lateral surface of the head, and a cap of pigment forms over the mid and hindbrain in postflexion larvae.

Pigment on the dorsal surface of the gut and gas bladder consists of 8–10 approximately evenly spaced melanophores. Scattered internal melanophores gradually spread over the lateral walls of the gut in postflexion larvae. Ventral pigment on the gut consists of a midline series of 8–14 melanophores extending from just anterior of the cleithral symphysis to the anus (Fig. 5).

Preflexion larvae have 15–22 discrete, evenly spaced melanophores that extend in a dorsal linear series from the nape to within 2–5 myomeres of the notochord tip. The number of dorsal melanophores decreases to 13 by 5.0 mm. A series of three discrete dorsal bands consisting of 3–5 paired stellate melanophores has replaced this dorsal series in the 10.1 mm postflexion larva. Lateral midline pigment in *S. schomburgkii* larvae is the most pronounced of all three species examined and is present on the tail in the smallest larva (2.7 mm) as 2 or 3 elongated mel-

Table 4

Body proportions of larvae of *Sillago schomburgkii* (expressed as a percentage of body length). d = damaged; g = gas bladder not visible; — = character not yet formed. Specimens between dotted lines were undergoing flexion.

Body length (mm)	Pre-anal length	Pre-dorsal fin length	Pre-gas-bladder length	Head length	Snout length	Eye diameter	Vent to anal fin length	Body depth at pectoral	Body depth at anus
2.7	53.7	—	24.1	20.4	3.7	9.2	—	14.8	6.3
3.3	51.5	—	25.7	21.2	5.1	9.1	—	15.1	7.6
3.6	48.6	—	g	25.0	6.1	8.3	—	13.9	8.3
3.7	50.0	—	g	24.3	5.4	8.1	—	16.2	9.4
3.8	51.3	—	25.0	22.4	2.6	7.9	—	14.5	7.9
3.9	52.3	—	28.2	22.3	6.4	7.7	—	15.4	7.7
4.0	51.2	—	g	25.0	7.5	7.5	—	17.5	9.0
4.3	52.3	—	g	22.1	5.8	8.1	—	15.1	9.3
4.4	53.4	—	28.4	22.7	5.7	8.4	—	14.8	7.9
4.8	53.1	—	31.2	25.0	6.2	8.3	—	15.6	10.4
5.0	53.0	—	34.0	25.0	7.0	9.0	8.0	18.0	11.0
10.1	52.5	34.6	g	27.7	8.9	6.9	2.0	17.8	15.8
13.6	49.3	32.3	g	27.2	7.3	8.1	3.6	16.9	14.7
17.2	53.5	36.0	g	30.2	9.3	8.1	2.9	17.4	14.5

anophores in the vicinity of myomeres 24–26. Lateral midline pigment spreads both anteriorly and posteriorly as a linear series of elongated myomeres during development. By 10.1 mm, lateral midline pigment consists of 18 stellate and approximately evenly spaced melanophores extending from the pectoral fin to the caudal peduncle. Internal pigment along the vertebrae is visible in the 10.1-mm postflexion larva but is most pronounced in postsettlement larvae as clusters of melanophores located over every 2–5 vertebrae.

A single row of 16–18 melanophores is present along the ventral midline of the tail in preflexion larvae. This ventral row is gradually obscured by overlying musculature during flexion. Paired external melanophores (approximately one pair per myomere) subsequently develop ventrally on the tail in postflexion larvae, approximately one per myomere. Two to three (most commonly three) melanophores are present ventrally on the notochord tip in preflexion larvae. These are retained in postflexion larvae and form a band of pigment over the caudal-fin ray bases.

Discussion

Egg or larval development, or both, have been described for only four other species of sillaginid larvae: *Sillago japonica* (Kamiya, 1925; Ueno and Fujita, 1954; Ueno et al., 1958; Mito, 1966 — as *Sillago japonicus*; Ikeda and Mito, 1988; Kinoshita, 1988; Oozeki et al., 1992); *Sillago sihama* (Gopinath, 1946; Uchida et al., 1958; Ikeda and Mito, 1988; Kinoshita, 1988); *Sillago maculata* (Miskiewicz, 1987; Kinoshita, 1988); and *Sillago ciliata* (Munro, 1945; Miskiewicz 1987; Tosh[4]). In addition, Miskiewicz (1987, p. 62) reported a series of unidentified sillaginid larvae which, based on pigment on the lateral wall of the gut below the pectoral fin base, were almost certainly *Sillago flindersi*.

Characters useful for the identification of tropical sillaginid larvae at the family level and similarity of sillaginid larvae to those from other families have been considered in detail by Leis and Trnski (1989) and Miskiewicz (1987). Although most of the characters discussed by these authors also apply to the temperate species considered here, an exception was the timing of gut coiling. Leis and Trnski (1989) reported that the gut of tropical sillaginid larvae commenced coiling during notochord flexion and was accompanied by the anterior migration of the anus. In the South Australian species, coiling of the gut commenced prior to flexion in *S. bassensis*, after settlement in *Sillaginodes punctata,* and had not yet commenced in the largest flexion larva available for *Sillago schomburgkii* (although coiling of the gut was present in a 10.1-mm postflexion larva). In all cases, coiling of the gut proceeded without migration of the anus and was achieved by anterior looping of the midgut. The implications of these variations are unclear but suggest that, although useful on a specific level, the timing of gut coiling and migration of the anus are not useful characters for the identification of temperate sillaginids at the family level.

The significance of gut coiling may relate to shifts in diet. Robertson (1977) reported a dietary shift in postsettlement *Sillaginodes punctatus* (= *punctata*) in Westernport Bay (Victoria) between November and December, a shift from harpacticoid copepods, gammarid amphipods, and mysids to larvae of the ghost prawn *Callianassa australiensis*, polychaetes, and juvenile crabs. Robertson correlated this dietary shift with increasing body size and mouth gape as well as with the availability of *C. australiensis* larvae. However, from his length-frequency data, this period also corresponds to the size range during which postsettlement *S. punctata* undergo gut coiling. Alternatively, because evacuation rates are believed to decrease after gut coiling (Arthur, 1976, and references within; Young[5]), perceived changes in diet may be confounded by increased food retention times. Stomach contents were not analyzed during this study; they provide a valuable topic for further research.

Despite seasonal sampling over five years, larvae of only three of the four sillaginid species with adult distributions extending to South Australia were located during this study. The lack of *Sillago flindersi* larvae suggests either that this species does not spawn in South Australian waters, that sampling frequency was too course to detect the presence of larvae of this species, or that *S. flindersi* larvae behave differently from other sillaginid species and are less prone to capture (e.g. epibenthic and neustonic).

Sillago flindersi larvae are frequently encountered in similar sampling regimes in coastal waters of eastern Australia[6] and in Tasmanian waters (author's pers. observ.) and thus it seems unlikely that a lack of their larvae in South Australian samples represents an artifact of sampling or that their behavior is fundamentally different from other sillaginid larvae.

[4] Tosh, J. R. 1903. Notes on the habits, development etc. of the common food fishes of Moreton Bay. Queensland Marine Dep.: Marine Biologist's Report.

[5] Young, J. W. CSIRO Div. Fisheries, GPO Box 1538 Hobart, Tasmania, Australia 7001. Personal commun., 1993.

[6] Miskiewicz, A. G. Sydney Water Board, PO Box A53, Sydney South, NSW, Australia 2000. Personal commun., 1993.

South Australian waters represent the western distributional limit of *S. flindersi* in southern Australia (McKay, 1992; Gomon et al., 1994; Kailola et al., 1993). Spawning times for *S. flindersi* vary throughout its range; a summer spawning is recorded for Victorian populations (Hobday and Wankowski[7]). No data are available on either the reproductive condition of *S. flindersi* or on the presence or absence of juveniles in South Australian waters. However, on the basis of a lack of larvae, I suggest that spawning does not occur in South Australia and that the western limit of *S. flindersi* comprises fish recruited from eastern populations.

Acknowlegments

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Responses of Tanner crabs, *Chionoecetes bairdi*, exposed to cold air

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Abstract.—Female and sublegal-size male Tanner crabs, *Chionoecetes bairdi*, are often caught incidentally in the males-only fishery for this species. Effects of low air temperature during the winter fishery on juvenile and female adult crabs and on the developing eggs brooded by the females were simulated in the laboratory by exposing crabs to cold air (–20 to +5°C) up to 32 minutes; controls were not exposed. Exposure was expressed as degree-hours (°h), the product of temperature (°C) and time (hours). Severe exposure caused death: median lethal exposure stabilized at –3.3 ± 0.8°h for juveniles and –4.3 ± 0.5°h for adults after 16 days. Exposure also reduced vigor (measured by righting ability), caused pereiopod autotomy, and depressed adult feeding rates and juvenile growth. Exposures causing one-half the crabs to cease righting were –1.2 ± 0.3°h for juveniles and –2.1 ± 0.3°h for adults (measured immediately after exposure). Mean pereiopod autotomy ranged up to 44% for juveniles exposed to –2°h, and up to 10% for adults exposed to –10.6°h. Ecdysis of juveniles was not affected, but exposed juveniles frequently shed additional pereiopods with the molt. Prompt return of incidentally caught Tanner crabs to the sea when temperatures are below freezing should reduce adverse effects of cold aerial exposure.

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Tanner crabs, *Chionoecetes bairdi* Rathbun, 1893, are the target of a large commercial pot fishery and are an important commercial species in Alaskan waters (Otto, 1989). Landings of *C. bairdi* rose to a peak of 57,923 metric tons (t) in 1978, then declined to 5,390 t in 1987; landings increased to 23,507 t in 1990.[1]

Current Alaska fishing regulations require release of small (<139-mm carapace width) male and all female *C. bairdi*. Commercial fishery openings in recent years have generally ranged from November through April,[2] when minimum daily air temperatures can drop to –21°C.[3] The amount of time incidentally captured crabs remain on deck varies, ranging from a few minutes during pot fishing to hours in some trawling operations (Stevens, 1990). Exposure to cold air during fishing operations may be detrimental to individual crabs (Carls and O'Clair, 1990), exposed egg clutches, and possibly—with sufficient fishing pressure—to the population. Regulations also require that Tanner crabs caught incidentally by multispecies trawling operations in the eastern Bering Sea be returned to the sea, but these regulations may be ineffective because of poor survival (22 ± 3.6% for *C. bairdi*) of the culled crabs (Stevens, 1990).

Here we report the responses of juvenile and adult female Tanner crabs and their offspring exposed to cold air. Our objectives were to determine the effects (immediate

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1989e. Synopsis of the Montague Strait experimental harvest area 1985–1988. ADF&G Regional Information Rep. No. 2C89-04. ADF&G, Div. Commercial Fisheries, Central Region, 333 Raspberry Rd., Anchorage, AK 99581, 21 p.
1989f. Report to the Board of Fisheries Norton Sound red king crab fishery (summer fishery only). ADF&G Regional Information Rep. No. 3N89-05. ADF&G, Div. Commercial Fisheries, Central Region, Juneau, AK, 14 p.

[3] NOAA. 1987. Local climatological data, monthly and annual summaries with comparative data. U.S. Dep. Commer., National Climatic Data Center, Asheville, NC 28801.

and long-term) of exposure to cold air on 1) survival; 2) sublethal responses, including righting response, limb autotomy, feeding rate, ecdysis (juveniles), and growth; and 3) reproductive responses including egg survival, zoeal production, zoeal viability, and subsequent egg extrusion and viability of the extruded clutch.

Methods

Experimental crabs were collected with crab pots. Juvenile crabs (both sexes) were collected in Auke Bay, Alaska (lat. 58°21'N, long. 134°41'W) on 14 and 19 January 1988. Ovigerous females were captured near Eagle River (lat. 58°31'N, long. 134°48'W) and Lena Point (lat. 58°24'N, long. 134°47'W) in Favorite Channel, Alaska, on 11 February 1988.

In the laboratory, carapace length (distance from the posterior margin of the right ocular orbit to the midpoint of the posterior margin of the carapace) was measured to the nearest millimeter. Carapace width was subsequently estimated by regressing carapace widths and lengths of Tanner crabs measured at a later date.[4] Live weight was measured to the nearest 0.1 g. Juvenile crab weights ranged from 26 to 229 g ($\bar{x}$=109 ±14 g), and carapace lengths ranged from 35 to 64 mm ($\bar{x}$=49 ±2.3 mm) (Fig. 1). Estimated juvenile carapace widths (for both sexes) ranged from 46 to 74 mm (width=–0.237 + 1.318 × length, r^2=0.994, n=145). The immature condition of males was determined solely by body size. Adult female crab weights ranged from 182 to 553 g ($\bar{x}$ = 329 ± 8 g), and carapace lengths ranged from 65 to 96 mm ($\bar{x}$=80 ±1.0 mm) (Fig. 1). Estimated female carapace widths ranged from 85 to 124 mm (width=1.746 × 1.274 × length, r^2=0.995, n=70).

Crabs were maintained in 500-L tanks at ambient seawater temperatures (6.0–6.9°C for juveniles, 5.3–6.0°C for adults) until exposure to test air temperatures; after exposure they were returned to the same tanks for 32–35 days of observation (4.7–6.7°C for juveniles, 4.7–5.2°C for adults). A subset of 40 female crabs was retained for an additional three months of observation.

Crabs were exposed in a modified chest freezer divided by a vertical baffle into two compartments of unequal size (Carls and O'Clair, 1990). Infrared heat lamps were placed in the smaller compartment for temperature control. To ensure uniform temperatures, a small fan (in the center bottom of the baffle) drew air from the exposure chamber into the small chamber at 45 ± 5 cm/sec. Return air circulated over the baffle into the exposure chamber. Temperatures were measured with a thermistor located in the exposure area near the fan and were regulated manually by switching the heat lamps on or off. Temperatures were controlled to ±0.1°C after the chamber had cooled to the desired temperature. Crabs were exposed to cold air on the plywood bottom of the exposure chamber.

Juvenile crabs were randomly placed in six groups with 10 crabs per group and were exposed to cold air on 21 and 25 January (about one week after capture). Exposure temperatures ranged from –5.0 to –20.0°C; exposure durations were 0, 12, 16, or 24 minutes to yield 0, –1.0, –1.5, –2.1, –4.0, and –8.0°h exposures (Table 1). The lengths ($F_{5,54}$=0.06, P>0.99) and

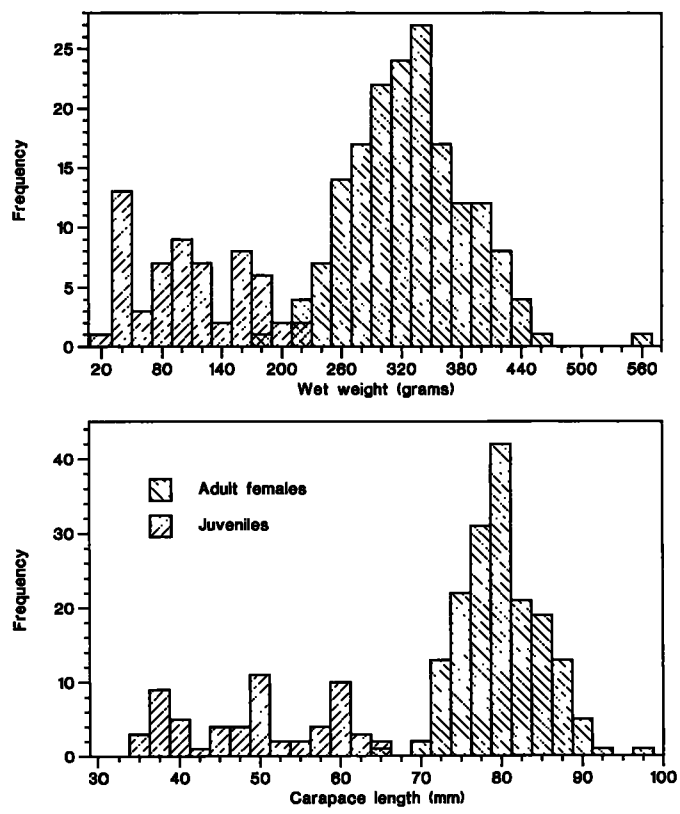

Figure 1

Chionoecetes bairdi length and weight frequencies. Adult female frequencies may not be directly comparable to juvenile frequencies because they were taken from a different locality.

[4] r^2>0.99. Stone, R. NMFS Auke Bay Lab., Juneau, AK 99801–8626. Unpubl. data, May 1992.

Table 1

Temperature and duration of exposure of *Chionoecetes bairdi* to cold air. The number of crabs exposed (*n*) is also indicated. Controls were not exposed to air. SE = standard error.

Air temperature (Celcius) mean	SE	Exposure time (minutes)	Degree-hours	*n*
Juveniles				
—	—	0	0.00	10
–5.0	0.02	12	–0.99	10
–7.5	0.05	12	–1.50	10
–10.2	0.24	12	–2.05	10
–15.0	0.03	16	–4.00	10
–20.0	0.07	24	–8.02	10
Adults				
5.1	0.12	8	0.683	7
5.0	0.01	32	2.672	7
—	—	0	0.000	31
–3.2	0.21	4	–0.211	8
–3.1	0.04	8	–0.411	8
–3.1	0.06	16	–0.813	8
–3.0	0.03	32	–1.621	8
–8.2	0.19	4	–0.544	8
–8.1	0.11	8	–1.075	8
–8.1	0.06	16	–2.149	8
–8.1	0.03	32	–4.299	7
–13.1	0.18	4	–0.875	8
–12.9	0.08	8	–1.720	8
–13.0	0.03	16	–3.472	7
–13.0	0.02	32	–6.933	8
–20.3	0.34	4	–1.353	8
–20.1	0.15	8	–2.676	8
–18.4	0.08	16	–4.899	8
–19.9	0.04	32	–10.597	8

weights ($F_{5,54}$=0.02, P>0.99) of the crabs did not differ significantly between treatments. Change in juvenile crab body weight was estimated from initial and final measurements (32 d).

Female crabs were randomly placed in 20 groups (including controls) in a complete 4 (temperature) by 5 (length of exposure) design, with 7 to 8 crabs per group. Treatment temperatures ranged from –3.1 to –20.3°C and exposure duration ranged from 0 (controls) to 32 minutes (Table 1). Two additional groups were tested at 5°C for 8 and 32 minutes (Table 1). The crabs did not differ significantly in length ($F_{21,149}$=1.13, P=0.324) or weight ($F_{21,149}$=1.36, P=0.149) between treatments. Exposure took place 16 and 17 February (about six days after capture). Observation continued through 22 June.

Mortality and limb autotomy were monitored daily. Crabs were judged dead when scaphognathite movement stopped. Generally, dead crabs were rechecked the following day before they were removed from test tanks. The number of legs missing on each crab was counted and autotomized legs were removed from the tanks.

Righting response (the time it took a crab to right itself when placed on its back underwater), which we considered to be a measure of vigor, was timed to the nearest 0.01 second immediately after aerial exposure and 1, 2, 4, 8, 16, 24, and 32 days thereafter. Crabs that could not right themselves after 2 minutes were recorded as "not righting" and were placed upright in the tank.

A subset of 40 female crabs randomly selected from the entire exposure range was used for reproductive observations. The crabs were isolated 32 days after exposure in covered 70-L tanks that overflowed into 19-L buckets containing conical 363-μ mesh nets designed to trap zoeae. Flow rates were approximately 1.5 L/minute; 95% turnover time was 2.3 hours and water temperatures ranged from 5.2 to 5.9°C during this period (23 March–11 May).

Feeding rates were measured before and after the zoeal hatch while the 40 ovigerous females were individually isolated. Mussels, *Mytilus trossulus*, were fed ad libitum to crabs during each feeding period. Live mussels were cut in half and drained tissue-side down on paper towels for five minutes, weighed, then placed in the tanks. Twenty-four hours later the remaining food was removed, drained, and weighed as before. At each feeding, four food portions were placed as controls in tanks without crabs. Consumption was corrected for the mean weight changes in the control portions. Feeding observations were repeated every 1 to 3 days, from 41 to 60 and from 85 to 98 days after exposure.

Zoeae were collected daily, rinsed from the nets, concentrated in a known volume, and subsampled with a 5- or 10-mL Hensen-Stemple pipette (Carls and O'Clair, 1990). Subsamples, which contained a minimum of 200 zoeae, were preserved in 5% formalin and counted later; the occasional large subsample was divided with a Folsom plankton splitter before being counted. After zoeal hatching, all debris from each tank bottom was preserved to determine the number of dead eggs and zoeae.

Responses of the crabs were related to aerial exposure, expressed as the product of air temperature (°C) and length of time in air (hours), i.e. degree-hours (°h). In a similar experiment, Carls and O'Clair (1990) demonstrated the usefulness of this technique for interpreting responses to aerial exposure in adult king crabs, *Paralithodes camtschaticus*. Because the responses of the Tanner crabs to exposure (in °h) were similar in form to those of the king crabs over identi-

cal treatment ranges (0–32 minutes, –20 to +5°C; see Results section) and could be described by the same types of simple linear or nonlinear models, we used the same technique here.

Regression techniques and logit analysis were used to relate response variables to exposure (Berkson, 1957; BMDP, 1983). We compared median lethal responses with log-likelihood ratio tests (Fujioka, 1986). Multiple regression was used to test for differences in the slopes of regression lines and to adjust for covariates (Kleinbaum and Kupper, 1983). The relation of selected response variables to one another was tested with parametric correlation. After one-way analysis of variance, comparisons of treatment means were made with Tukey's or Dunnett's a posteriori multiple comparison tests and judged significantly different if $P \leq 0.05$. Proportional data were arcsine transformed. Reported error ranges are ±95% confidence limits.

Results

Mortality

Below –1 to –3 degree hours, exposure to cold air killed crabs. Almost all mortality occurred 1–2 days after exposure; in groups where more than half the crabs died, mortality always reached 50% within 2 days. Mortality was inversely related to exposure and increased rapidly below –1°h for juveniles and below –3°h for adults (logistic regressions [large *P*-values indicate good fits], $P_{juvenile}=0.959$, $P_{adult}=0.882$; Fig. 2). Nearly all deaths occurred within 8 days after exposure; no crabs died after day 16. For juveniles, calculated median lethal exposures rose from –7.7 ± 3.4°h 1 day after exposure to –3.3 ± 0.8°h 16 days after exposure, and for adults from –7.2 ± 1.6°h to –4.3 ± 0.5°h over the same time period (Table 2).

Righting response

The speed with which crabs righted themselves when placed on their backs was inversely related to exposure (Fig. 3A). The response was most clearly described by the percentage of crabs not righting within two minutes (logistic regressions, $P=0.799$ [$n=6$] for juveniles; $P=0.978$ [$n=22$] for adults; Fig. 3B). Percentages of crabs not righting increased sharply below –1.0°h for juveniles and below –2.2°h for adults, and crabs ceased righting entirely after exposure to ≤–4.0°h for juveniles and ≤–6.9°h for adults (Fig. 3B). Median exposures causing one-half the crabs to cease righting (EC50) were –1.2 ± 0.3°h for juveniles and –2.1 ± 0.3°h for adults, measured immediately after exposure; values declined to –1.6 ± 0.3°h for juveniles and –3.8 ± 0.5°h for adults measured 32 days after exposure (Table 3). The percentage of crabs unable to right themselves immediately after exposure was significantly correlated with cumulative mortality ($P_{juvenile}=0.003$, $r^2_{juvenile}=0.91$, $n=6$; $P_{adult}<0.001$, $r^2_{adult}=0.67$, $n=22$) and, therefore, could serve as a predictor of death.

Righting times tended to improve (decrease) during the first eight days after exposure, but this recovery was generally not statistically significant.

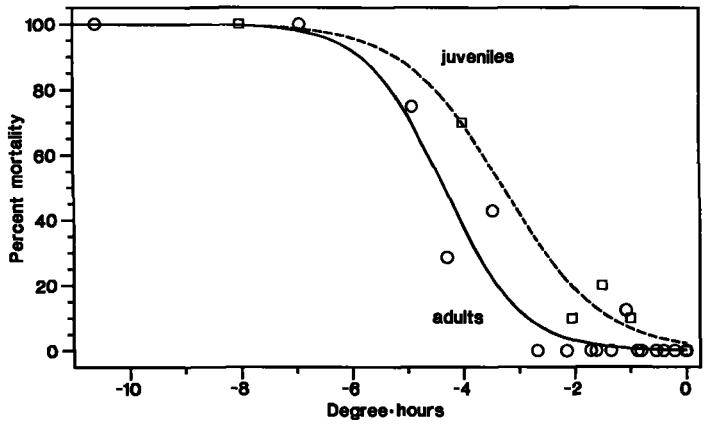

Figure 2

Cumulative percent mortality (*P*) of juvenile and adult female *Chionoecetes bairdi*, observed 32 days after emersion, as a function of exposure (°h): $P_{juveniles}=100 / (1 + e^{(3.74 + 1.14x^{\circ}h)})$, $P_{adult}=100 / (1 + e^{(6.42 + 1.48x^{\circ}h)})$.

Righting times of juvenile crabs from all exposures tended to decrease over time (Fig. 4). The righting times of adult crabs exposed to ≤–2.2°h generally showed little evidence of recovery. Median exposures causing one-half the crabs to cease righting also generally declined, but 95% confidence bars overlapped.

Pereiopod autotomy

Exposure to cold air caused pereiopod autotomy. Juvenile pereiopod losses increased from 0 to –2°h but declined towards the most severe exposure (–8°h), possibly because early mortality precluded autotomy (Fig. 5A). Juvenile crabs often dropped legs or chela during aerial exposure, but losses also continued after exposure (Fig. 5B), often during ecdysis (Fig. 6).

Adult crabs autotomized fewer pereiopods than juveniles; as with juveniles, loss was most frequent immediately after exposure. Loss of pereiopods in adults was directly related to severity of exposure ($P<0.001$, $r^2=0.85$, $n=19$; Fig. 5A). Autotomy was correlated with mortality in adult crabs ($P<0.001$, $r^2=0.81$, $n=19$) but not in juveniles ($P=0.621$, $r^2=0.07$, $n=6$). Autotomy was also correlated with the percentage of adult crabs not righting as measured immediately after exposure ($P<0.001$, $r^2=0.81$, $n=22$).

Ecdysis

Juvenile crabs began molting 22 January and continued through 21 February. Molt timing was not correlated with exposure ($r^2=0.09$). Juveniles exposed

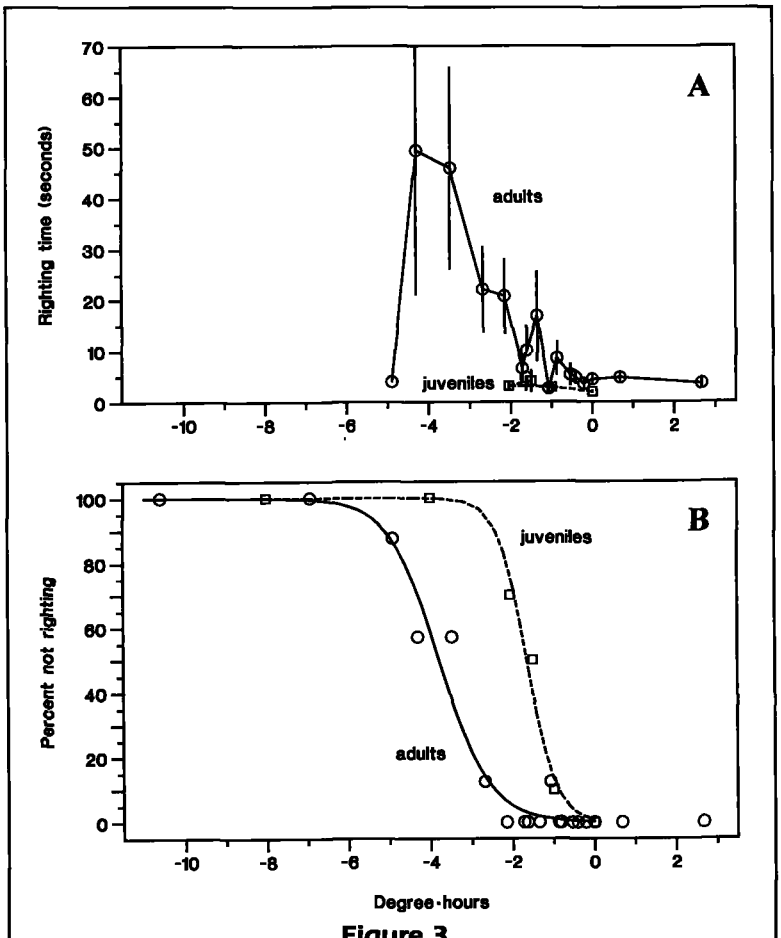

Figure 3

Righting times of juvenile and adult female *Chionoecetes bairdi* capable of righting (A), and percentage not righting (B) observed 32 days after emersion as functions of exposure (°h). Percentages not righting were $100/(1 + e^{(6.235 + 1.651 \times °h)})$ for adults and $100 / (1 + e^{(4.701 + 2.858 \times °h)})$ for juveniles. Error bars are ±1 standard error. The ability of the single surviving –4.9°h adult crab improved over time; its righting time 32 days after exposure was similar to that of controls.

Table 2

Degree-hours causing death (LC) in *Chionoecetes bairdi* exposed to cold air, estimated with logit analysis. The LC number indicates the percentage of crabs affected; e.g. LC50 is the median lethal degree-hours. The error term (CI) is the estimated 95% confidence interval.

Day	LC10	LC30	LC50	LC70	LC90	CI
Juveniles						
1	−0.9	−5.1	−7.7	−10.4	−14.6	3.4
2	−1.0	−4.6	−6.8	−9.0	−12.6	2.6
4	−1.3	−3.9	−5.5	−7.1	−9.7	1.7
8	−1.3	−2.9	−3.9	−4.8	−6.4	1.1
16	−1.3	−2.5	−3.3	−4.0	−5.2	0.8
32	−1.3	−2.5	−3.3	−4.0	−5.2	0.8
Adults						
1	−3.1	−5.6	−7.2	−8.8	−11.3	1.6
2	−2.8	−5.2	−6.7	−8.2	−10.6	1.5
4	−2.6	−4.8	−6.2	−7.5	−9.7	1.3
8	−3.0	−4.0	−4.6	−5.1	−6.1	0.6
16	−3.2	−3.9	−4.3	−4.8	−5.5	0.5
32	−2.8	−3.8	−4.3	−4.9	−5.8	0.6

Table 3

Effective degree-hours causing cessation of righting (EC) in *Chionoecetes bairdi* exposed to cold air, estimated with logit analysis. The EC number indicates the percentage of crabs affected; EC50 is the median effective degree-hours. The error term (CI) is the estimated 95% confidence interval.

Day	EC10	EC30	EC50	EC70	EC90	CI
Juveniles						
0	−0.2	−0.8	−1.2	−1.6	−2.2	0.3
1	−0.7	−1.2	−1.5	−1.7	−2.2	0.3
2	−0.6	−1.1	−1.5	−1.8	−2.3	0.3
4	−0.5	−1.1	−1.4	−1.7	−2.2	0.3
8	−1.1	−1.4	−1.7	−1.9	−2.3	0.3
16	−0.9	−1.3	−1.6	−1.9	−2.4	0.3
24	−0.8	−1.4	−1.7	−2.1	−2.6	0.3
32	−0.9	−1.3	−1.6	−1.9	−2.4	0.3
Adults						
0	−1.3	−1.8	−2.1	−2.5	−3.0	0.3
1	−2.0	−2.7	−3.1	−3.5	−4.1	0.4
2	−1.8	−2.4	−2.8	−3.2	−3.8	0.4
4	−2.3	−2.8	−3.1	−3.4	−3.9	0.4
8	−2.1	−2.7	−3.0	−3.4	−4.0	0.4
16	−2.2	−2.7	−3.1	−3.5	−4.0	0.4
24	−2.2	−2.9	−3.4	−3.8	−4.6	0.5
32	−2.4	−3.3	−3.8	−4.3	−5.1	0.5

to cold air frequently lost pereiopods during ecdysis; losses increased from 0 to −4°h. The only crab exposed to −8°h that attempted to molt lost no limbs, but died during ecdysis (Fig. 6).

Feeding rates

Feeding rates of adult female Tanner crabs were significantly depressed by exposure to cold air ($P_{ANOVA} \leq 0.001$). In general, adult females exposed to <−2.7°h (62% of the median lethal exposure) ate significantly less than did controls (Tukey test). Feeding rates measured shortly before zoeal hatching (41 to 60 days after exposure) were significantly less ($P \leq 0.05$) for all crabs than feeding rates after zoeal hatching (85–98 days after exposure), but the slopes (feeding rate/exposure) before and after hatching did not differ (multivariate regression, $P > 0.50$; Fig. 7). The frequency of feeding also increased significantly after zoeal hatching ($P < 0.001$) and was significantly related to aerial exposure before and after larval hatching ($P_{linear} < 0.001$). The most severely treated crabs (−4.9°h) did not eat before zoeal release but ate 57% of the time after release.

Weight change

Change in weight of juvenile crabs was reduced by exposure to cold air. Wet weights of juvenile crabs that did not molt declined with increasing exposure severity ($P=0.002$, $r^2=0.42$, $n=20$; Fig. 8). The weight increment of juvenile crabs that molted also declined with decreasing exposure (Fig. 8). This trend was not significant until an outlier at −2.0°h was removed ($P=0.021$, $r^2=0.56$, $n=9$). Pereiopod autotomy probably influenced these weight outcomes. The weight changes of juvenile crabs that did not molt were correlated with righting response measured immediately after exposure ($P=0.018$, $r^2=0.88$, $n=5$, $Y=a+bx^3$). Changes in weight of adult crabs were not correlated with exposure ($P \geq 0.07$, $r^2=0.08$, $n=44$).

Reproduction

Exposure of ovigerous female crabs to cold air generally did not affect the eggs or subsequently released zoeae unless the female died; all eggs died if the female died. Timing of initial zoeal release (20 April ± 1 day), duration of release (11 ± 1 day), and median release date (26 April ± 1 day) did not vary with exposure ($r^2=0.04$, $n=44$; Fig. 9). Zoeae placed in separate containers for two days were not significantly affected by exposure prior to hatching ($P=0.425$, $r^2=0.02$, $n=43$), and 87 ±3% continued swimming through the test period. Larval mortality, measured as the percentage of zoeae that sank to tank bottoms and died (0.4 ±0.2%), did not vary with exposure ($r^2=0.03$, $n=44$). Zoeal mortality (2 ±2%) during swimming tests was not correlated with exposure ($r^2=0.09$).

The percentage of eggs that hatched may have been slightly affected by exposure, but our results were inconclusive ($P_{regression:arcsin}$=0.036, but $P_{lack\ of\ fit}$<0.019, and r^2=0.10). The percentage of eggs hatching in the –5.3°h treatment differed significantly from the control (Dunnett's test), but the difference was minor (99.1% versus 99.8% hatching).

Egg extrusion may have been influenced by exposure, but the data were inconsistent. Elapsed time between larval hatching and subsequent egg extrusion tended to be prolonged by exposure, but the response was variable (P_{linear}=0.005, $P_{lack\ of\ fit}$=0.719, r^2=0.19, n=41). Egg extrusion generally occurred two days (median) after zoeal release but ranged from 0 to 18 days; only crabs in the two most severe treatments (≤–4.3°h) exceeded nine days. The date of extrusion (4 May ±7 days) may also have been changed by exposure, but again the statistical results were inconclusive (P_{linear}=0.011, $P_{lack\ of\ fit}$=0.700, r^2=0.16, n=41). Exposure did not affect the percentage of Tanner crabs extruding eggs (93%, P_{linear}=0.730, r^2=0.03, n=6).

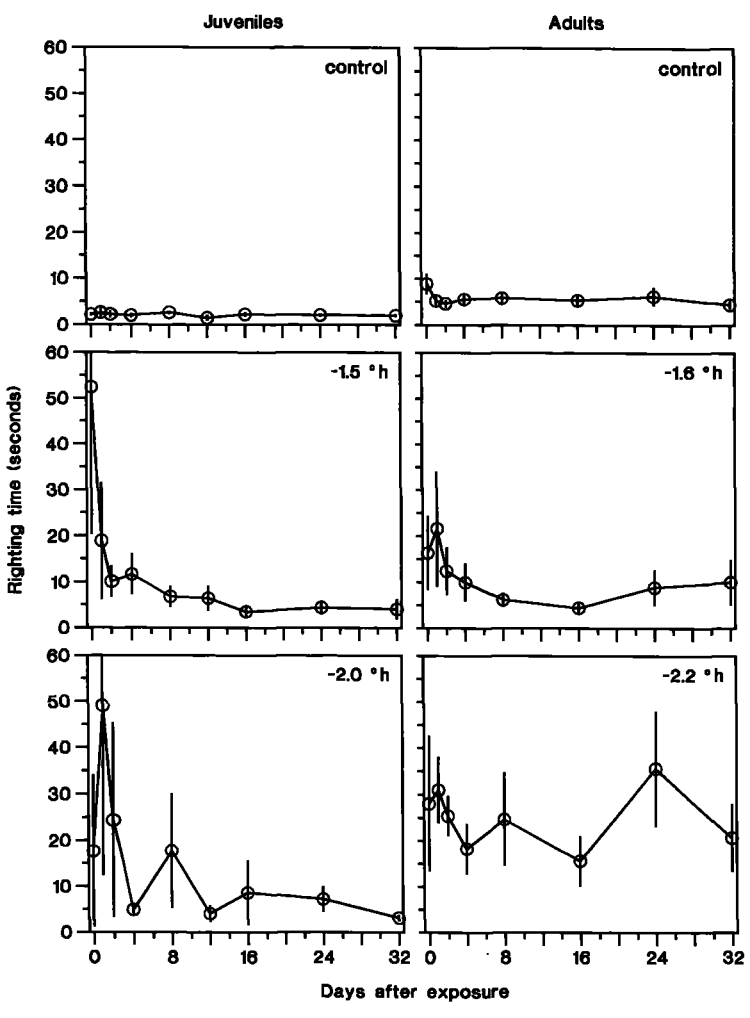

Figure 4

Righting times of juvenile and adult *Chionoecetes bairdi* as a function of time in days after emersion. Error bars are ±1 standard error.

Discussion

Extreme exposure to cold air was lethal to Tanner crabs. It is also possible that thermal shock caused when the crabs were returned to water following exposure was also damaging. Following sublethal exposure, crabs exhibited a slowed righting response, autotomy of pereiopods, depressed feeding rates (adults), and weight loss or reduced weight gain (juveniles).

Temperature and duration of treatment were both critical factors in determining how aerial exposure affected Tanner crabs. In a similar experiment with king crabs, the response of crabs to exposure was clearly observed when exposure was defined as the product of temperature and the length of exposure time (Carls and O'Clair, 1990). The use of this composite variable worked well with the current data set. However, our approach may not be generally applicable (for discussion see Carls and O'Clair, [1990]).

Design of this experiment precluded independent analysis of temperature and time factors. However, either factor may be predicted as a function of the other. For example, at –10°C, 10% of juvenile crabs may be killed by an 8-minute exposure, and 50% may be killed by a 20-minute exposure. Similarly, a 10-minute exposure would impair righting in 50% of juvenile crab at –7°C. Predicted times and temperatures were calculated from degree-hours causing death (LC) or from effective degree-hours causing cessation of righting (EC) estimates (Tables 2 and 3); temperature multiplied by time (units are Celcius and hours) matched the LC or EC estimates. Predictions of adult and juvenile Tanner crab response are summarized in Figure 10 and Appendices. In our example (Fig. 10), short-term effects are predicted by ability to right immediately after exposure; impaired crabs may be subject to increased predation at this time. Long-term effects are pre-

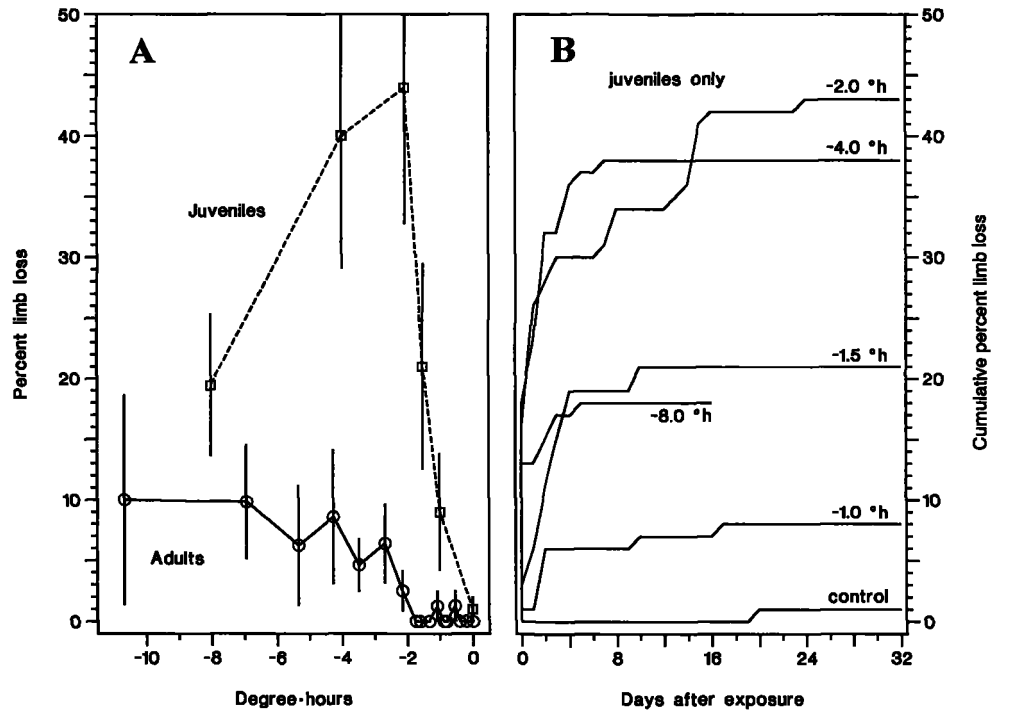

Figure 5

Percent of total pereiopod loss by juvenile and adult female Tanner crabs as a function of exposure (**A**) and as a function of time for juveniles (**B**). Error bars are ±1 standard error.

dicted by mortality after exposure-induced death ceased.

Mortality of adult Tanner crabs was significantly greater below –3°h and vigor was reduced below –2°h compared with control crabs. Exposures that are this severe probably occur infrequently on the fishing grounds except during winter in the northern Gulf of Alaska and the Bering Sea. Data are lacking on the time incidentally captured crabs remain on deck before being released, but duration probably varies widely. Larger vessels employing assembly-line techniques may process crabs more rapidly than do smaller vessels. Poor handling of culls combined with prolonged exposure may further reduce survival of incidentally caught crabs.

Crabs captured incidentally during trawling are probably stressed more than those caught in pots. Stevens (1990) reported trawl tows ranging up to 6.4 hours and retention times of Tanner crabs up to 17 hours; the median lethal holding time for Tanner crabs was 8.3 hours. Net type influenced survival, and injuries were present in a greater proportion of dead than of live crabs (Stevens, 1990).

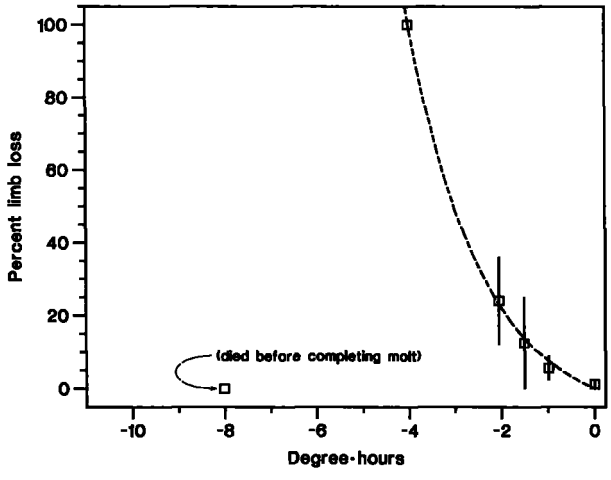

Figure 6

Limb loss by juvenile *Chionoecetes bairdi* at ecdysis as a function of exposure: percent loss=–8.856 + 4,756.960 $e^{-0.629 \times (°h + 10)}$. Error bars are ±1 standard error. Numbers molting in each group were 4, 4, 2, 6, 1, and 1 for controls through –8°h, respectively.

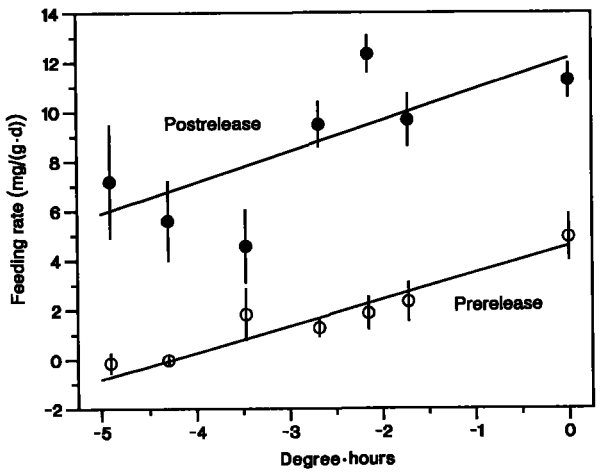

Figure 7

Feeding rates (milligram food/gram crab weight/day) of adult female *Chionoecetes bairdi* before (F_{pre}=4.556 + 1.071 × °h) and after (F_{post}=12.161 + 1.255 × °h) zoeal hatching as a functions of exposure (°h). Error bars indicate 95% CI.

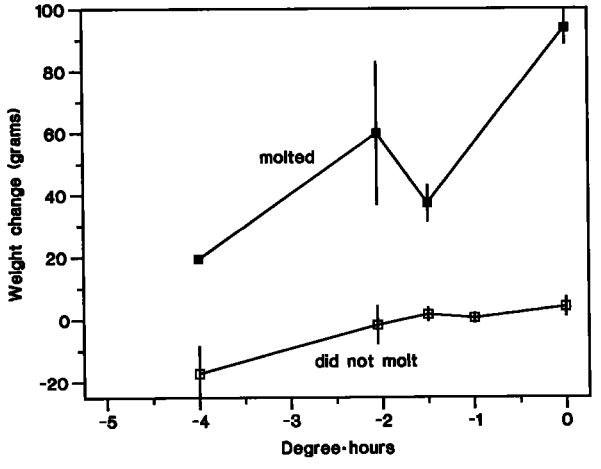

Figure 8

Changes in wet weight of juvenile *Chionoecetes bairdi* as a function of exposure. Weights of crabs that molted versus those that did not were treated separately. Error bars are ±1 standard error.

Mortality and injury due to aerial exposure have been reported for other commercially harvested decapod crustaceans. For example, king crabs were affected by exposure to cold air, but were less sensitive than Tanner crabs (Carls and O'Clair, 1990). The western rock lobster, *Panulirus cygnus*, was significantly affected by ≥15 minutes exposure to warm air (27–35°C); recapture rates were lower than for unexposed controls, and the probability of mortality due to predation rose (Brown and Caputi, 1983).

We do not know what physiological mechanism(s) caused the abnormal events during ecdysis that often resulted in death. O'Brien et al. (1986) induced apolysis (the separation of integumentary tissues from the exoskeleton during proecdysis) in several species of brachyurans by packing crabs in ice. Apolysis occurred within one hour in most cases and was not caused by death (O'Brien et al., 1986). O'Brien et al. (1986) did not observe ecdysis in their experimental crabs; therefore, the effect of apolysis on the timing, duration, and success of ecdysis in crabs is not known. In the present experiment, although mortality occurred during ecdysis in juvenile crabs, the timing of ecdysis was not affected.

Evaporative water loss during exposure probably did not contribute significantly to the effects we observed. The fact that warmer exposures, such as the 32-minute exposure at +5°C, caused little or no effect supports this supposition. Similar observations were made for king crab (Carls and O'Clair, 1990). In a study by Taylor and Whiteley (1989), the lobster *Homarus gammarus vulgaris*, which rarely comes in contact with air in its natural environment, was exposed to air at 15°C for up to 14 hours. Water loss, inferred from the constancy of most hemolymph ion concentrations, was minimal (Taylor and Whiteley, 1989). Oxygen delivered to *H. gammarus* tissues was substantially reduced, and CO_2 accumulated, but levels returned rapidly to normal after a 14-hour exposure. Lactate levels increased, but elevation of bicarbonate ions increased the buffering capacity of the hemolymph. Because exposures did not exceed 32 minutes, it is unlikely that reduced oxygen directly caused Tanner crab mortality in our experiment. However, at low air temperatures, gills may have been damaged by frost, thus impairing respiratory gas, metabolite, and ion exchange after the crabs were returned to the water.

The ability of crabs to right themselves proved to be a sensitive measure of crab viability. Righting response data collected immediately after exposure correlated strongly with less-immediate responses such as mortality and growth. Pereiopod loss also impaired righting.

Pereiopod autotomy in adult crabs was a function of exposure. Mortality may have influenced the autotomy response curve for juvenile crabs: during severe exposure, crabs apparently died before autotomy could take place.

Aerial exposure reduced weight gain in juvenile crabs and caused weight loss in juveniles that did not molt. However, wet weights of the adult crabs (all anecdysial) did not vary with exposure. This ab-

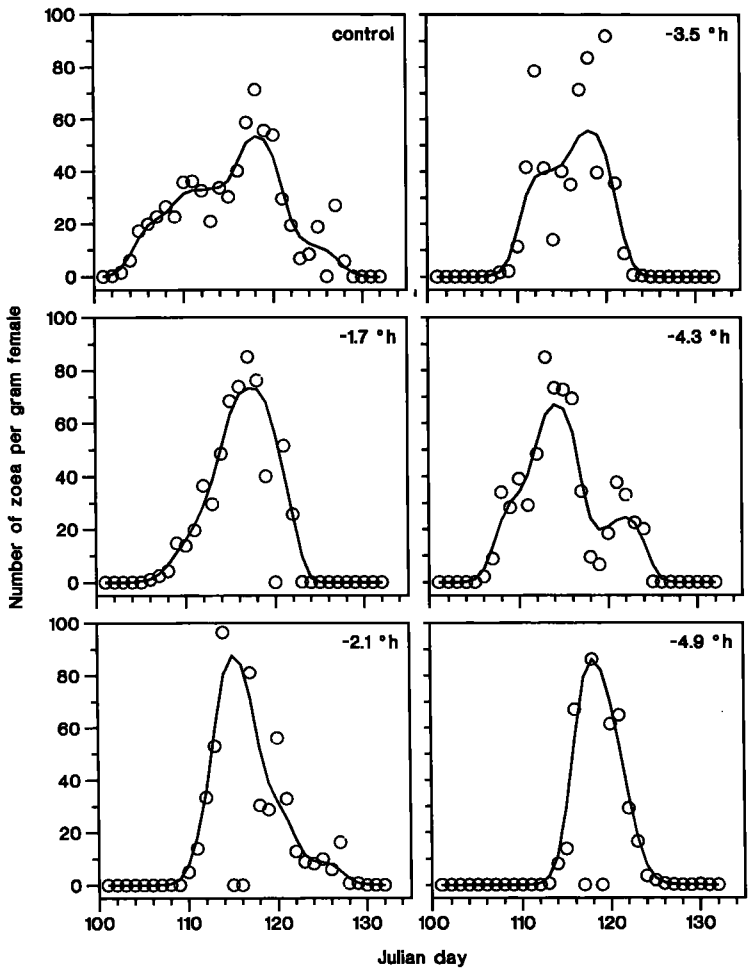

Figure 9

Zoeal production (number of zoeae per gram female *Chionoecetes bairdi*) as a function of time. Curves were fit with smoothing techniques (4253H) (Velleman and Hoaglin, 1981). Units are in °h.

sence of weight changes in the adults is puzzling because feeding rates were significantly depressed by exposure. Growth of adult western rock lobsters was reduced by exposure (Brown and Caputi, 1985).

Body size, shape, and volume may be important factors in predicting crab response to cold-air exposure. Results of the present experiment support this hypothesis: smaller crabs (juveniles) were more sensitive to exposure than were larger crabs (adults). Additionally, adult Tanner crabs were more sensitive to exposure than were larger king crabs (Carls and O'Clair, 1990), but unknown interspecific factors may have influenced this difference. An experiment involving a broad size range of conspecific individuals is needed to test whether sensitivity to exposure is size-dependent in crabs.

Surprisingly, aerial exposure did not measurably affect the developing larvae of exposed females unless the female died. Surviving crabs produced normal zoeae. Moreover, the timing of larval release, larval swimming ability, and viability were not affected by exposure. Longer-term larval responses, such as survival past the first molt and zoeal growth, were not examined. Exposure may have reduced hatching success (by <1%) of the Tanner crab larvae and possibly may have affected the timing of egg extrusion, but these responses did not vary strongly. Schlieder (1980) reported a 13% reduction in hatching success in the stone crab, *Menippe mercenaria*, compared with controls when the crabs were exposed to air at 27–33°C for two hours. Hatching success was reduced further by a five-hour exposure and by autospasy (Schlieder, 1980).

In summary, although environmental conditions as severe as those tested are uncommon on the fishing grounds during fishing operations (except in the central and northern Bering Sea), low-temperature aerial exposure during fishing operations can adversely affect incidentally captured crabs. Exposure to cold air reduced crab vigor and feeding rates, caused limb autotomy, and killed the crabs in severe situations. Progeny died if exposure to cold air killed females brooding them, otherwise larvae were not measurably affected. Prompt return of incidentally caught Tanner crabs to the sea, especially during extremely cold weather, should reduce adverse effects of exposure to cold air.

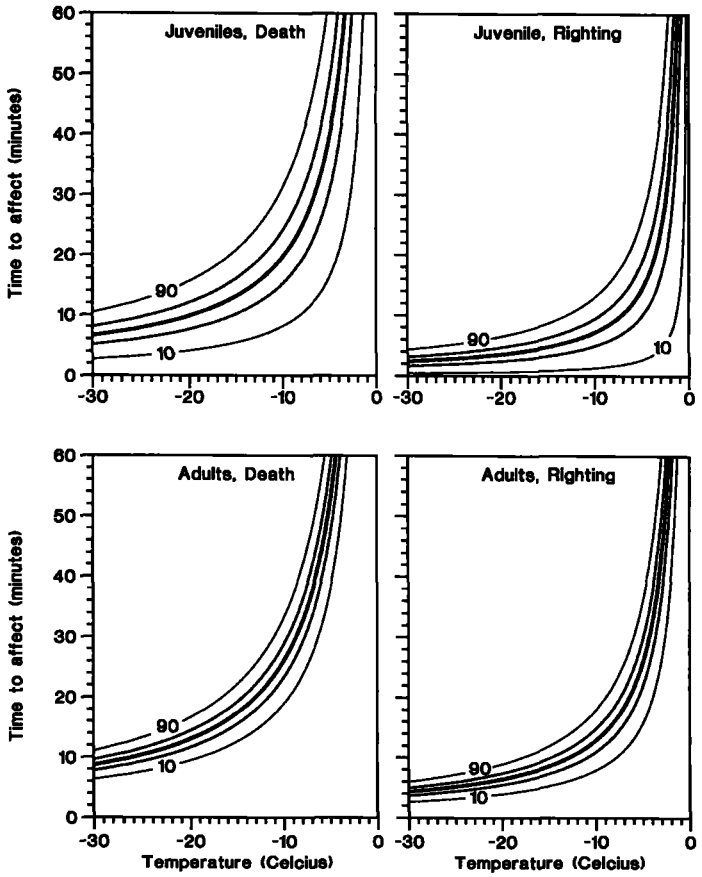

Figure 10

Predicted time in minutes required to cause death or impair righting of juvenile and ovigerous female *Chionoecetes bairdi* following exposure to cold air. Mortality predictions are based on cumulative mortality through day 16; no deaths were observed in the ensuing 16 days. Righting predictions are based on responses immediately after exposure; there was a tendancy for righting times to improve after exposure, but improvements were generally not statistically significant.

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We thank Tyrus Brouillette for his technical assistance during this experiment and the reviewers who improved this manuscript with their helpful suggestions.

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Appendix Table 1

Predicted time in minutes required to cause death of the listed percentage of adult *Chionoecetes bairdi* at indicated temperatures (°C). Calculations are based lethal responses (LC10, LC30, . . . LC90) estimated on day 16.

Temperature	10%	30%	50%	70%	90%	Temperature	10%	30%	50%	70%	90%
−1.0	189	233	260	288	332	−16.0	12	15	16	18	21
−2.0	95	116	130	144	166	−17.0	11.1	13.7	15.3	16.9	19.5
−3.0	63	78	87	96	111	−18.0	10.5	12.9	14.5	16.0	18.4
−4.0	47	58	65	72	83	−19.0	9.9	12.3	13.7	15.2	17.5
−5.0	38	47	52	58	66	−20.0	9.5	11.6	13.0	14.4	16.6
−6.0	32	39	43	48	55	−21.0	9.0	11.1	12.4	13.7	15.8
−7.0	27	33	37	41	47	−22.0	8.6	10.6	11.8	13.1	15.1
−8.0	24	29	33	36	41	−23.0	8.2	10.1	11.3	12.5	14.4
−9.0	21	26	29	32	37	−24.0	7.9	9.7	10.9	12.0	13.8
−10.0	19	23	26	29	33	−25.0	7.6	9.3	10.4	11.5	13.3
−11.0	17	21	24	26	30	−26.0	7.3	9.0	10.0	11.1	12.8
−12.0	16	19	22	24	28	−27.0	7.0	8.6	9.6	10.7	12.3
−13.0	15	18	20	22	26	−28.0	6.8	8.3	9.3	10.3	11.9
−14.0	14	17	19	21	24	−29.0	6.5	8.0	9.0	9.9	11.4
−15.0	13	16	17	19	22	−30.0	6.3	7.8	8.7	9.6	11.1

Appendix Table 2

Predicted time in minutes required to cause death of the listed percentage of juvenile *Chionoecetes bairdi* at indicated temperatures (°C). Calculations are based lethal responses (LC10, LC30, . . . LC90) estimated on day 16.

Temperature	10%	30%	50%	70%	90%	Temperature	10%	30%	50%	70%	90%
−1.0	81	152	196	241	311	−16.0	5.1	9.5	12.3	15.0	19.5
−2.0	41	76	98	120	156	−17.0	4.8	8.9	11.5	14.2	18.3
−3.0	27	51	65	80	104	−18.0	4.5	8.4	10.9	13.4	17.3
−4.0	20	38	49	60	78	−19.0	4.3	8.0	10.3	12.7	16.4
−5.0	16	30	39	48	62	−20.0	4.1	7.6	9.8	12.0	15.6
−6.0	14	25	33	40	52	−21.0	3.9	7.2	9.3	11.5	14.8
−7.0	12	22	28	34	44	−22.0	3.7	6.9	8.9	10.9	14.2
−8.0	10	19	25	30	39	−23.0	3.5	6.6	8.5	10.5	13.5
−9.0	9	17	22	27	35	−24.0	3.4	6.3	8.2	10.0	13.0
−10.0	8	15	20	24	31	−25.0	3.2	6.1	7.8	9.6	12.5
−11.0	7.4	13.8	17.8	21.9	28.3	−26.0	3.1	5.8	7.5	9.3	12.0
−12.0	6.8	12.7	16.4	20.1	26.0	−27.0	3.0	5.6	7.3	8.9	11.5
−13.0	6.2	11.7	15.1	18.5	24.0	−28.0	2.9	5.4	7.0	8.6	11.1
−14.0	5.8	10.8	14.0	17.2	22.2	−29.0	2.8	5.2	6.8	8.3	10.7
−15.0	5.4	10.1	13.1	16.0	20.8	−30.0	2.7	5.1	6.5	8.0	10.4

Appendix Table 3

Predicted time in minutes required to impair righting response of the listed percentage of adult *Chionoecetes bairdi* at indicated temperatures (°C). Calculations are based on righting responses (EC10, EC30, . . . EC90) estimated immediately after exposure.

Temperature	10%	30%	50%	70%	90%
−1.0	79	109	129	148	179
−2.0	39	55	64	74	89
−3.0	26	36	43	49	60
−4.0	20	27	32	37	45
−5.0	16	22	26	30	36
−6.0	13	18	21	25	30
−7.0	11	16	18	21	26
−8.0	10	14	16	19	22
−9.0	9	12	14	16	20
−10.0	8	11	13	15	18
−11.0	7.1	9.9	11.7	13.5	16.3
−12.0	6.5	9.1	10.7	12.3	14.9
−13.0	6.0	8.4	9.9	11.4	13.8
−14.0	5.6	7.8	9.2	10.6	12.8
−15.0	5.2	7.3	8.6	9.9	11.9
−16.0	4.9	6.8	8.0	9.3	11.2
−17.0	4.6	6.4	7.6	8.7	10.5
−18.0	4.4	6.1	7.2	8.2	9.9
−19.0	4.1	5.8	6.8	7.8	9.4
−20.0	3.9	5.5	6.4	7.4	8.9
−21.0	3.7	5.2	6.1	7.0	8.5
−22.0	3.6	5.0	5.9	6.7	8.1
−23.0	3.4	4.8	5.6	6.4	7.8
−24.0	3.3	4.6	5.4	6.2	7.5
−25.0	3.1	4.4	5.1	5.9	7.2
−26.0	3.0	4.2	5.0	5.7	6.9
−27.0	2.9	4.0	4.8	5.5	6.6
−28.0	2.8	3.9	4.6	5.3	6.4
−29.0	2.7	3.8	4.4	5.1	6.2
−30.0	2.6	3.6	4.3	4.9	6.0

Appendix Table 4

Predicted time in minutes required to impair righting response of the listed percentage of juvenile *Chionoecetes bairdi* at indicated temperatures (°C). Calculations are based on righting responses (EC10, EC30, . . . EC90) estimated immediately after exposure.

Temperature	10%	30%	50%	70%	90%
−1.0	13	49	71	93	129
−2.0	7	24	36	47	65
−3.0	4	16	24	31	43
−4.0	3.3	12.2	17.8	23.4	32.3
−5.0	2.7	9.8	14.2	18.7	25.8
−6.0	2.2	8.1	11.9	15.6	21.5
−7.0	1.9	7.0	10.2	13.4	18.4
−8.0	1.7	6.1	8.9	11.7	16.1
−9.0	1.5	5.4	7.9	10.4	14.3
−10.0	1.3	4.9	7.1	9.3	12.9
−11.0	1.2	4.4	6.5	8.5	11.7
−12.0	1.1	4.1	5.9	7.8	10.8
−13.0	1.0	3.8	5.5	7.2	9.9
−14.0	0.9	3.5	5.1	6.7	9.2
−15.0	0.88	3.26	4.74	6.23	8.60
−16.0	0.83	3.05	4.45	5.84	8.07
−17.0	0.78	2.87	4.19	5.50	7.59
−18.0	0.74	2.71	3.95	5.19	7.17
−19.0	0.70	2.57	3.75	4.92	6.79
−20.0	0.66	2.44	3.56	4.67	6.45
−21.0	0.63	2.33	3.39	4.45	6.15
−22.0	0.60	2.22	3.23	4.25	5.87
−23.0	0.58	2.12	3.09	4.06	5.61
−24.0	0.55	2.04	2.97	3.90	5.38
−25.0	0.53	1.95	2.85	3.74	5.16
−26.0	0.51	1.88	2.74	3.60	4.96
−27.0	0.49	1.81	2.64	3.46	4.78
−28.0	0.47	1.74	2.54	3.34	4.61
−29.0	0.46	1.68	2.45	3.22	4.45
−30.0	0.44	1.63	2.37	3.12	4.30

Demographic analysis of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, in the Gulf of Mexico

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Abstract.—The Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, is a small coastal species caught in recreational fisheries and as bycatch in the shrimp trawl and longline fisheries in the Gulf of Mexico. Demographic analyses incorporating the best available information on validated age and growth, age at maturity (t_{mat}), maximum age (t_{max}), reproductive habits, and age-specific natural mortality and fecundity were performed. An initial set of three life history tables based on input parameters t_{mat}=4, t_{max}=10, constant age 1+ survivorship (S=0.657), and varying first year survivorship (S_0=0.432, scenario 1; S_0=0.512, scenario 2; S_0=0.657, scenario 3 or best case scenario) yielded net reproductive rates (R_0) ranging from 0.844 to 1.284, a generation length (G) of 5.8 years, and instantaneous rates of population change (r) ranging from –0.029 to 0.044. Further simulations were performed to test the sensitivity of the computed demographic parameter values to modifications in various input biological parameter values (scenarios 4 through 14). Overall, manipulations of biological parameters m_x, t_{mat}, and t_{max} caused large variations in demographic parameters r, $t_{\times 2}$, and R_0, while G remained relatively stable. All the demographic parameters proved more sensitive to changes in S than to changes in S_0. The initial set of analyses (scenarios 1 through 3) was then rerun with the estimated mean fishing mortality from 1986 to 1989 (F=0.428) added to natural mortality. Age 6+ sharks can enter the fishery under the best case scenario only to allow the population to replace itself. Ages at first capture (A_{rep}) with F=0.428 that would allow full population replacement were also calculated for scenarios 4 through 14. This study indicates that management of *R. terraenovae* under the Federal Management Plan (FMP) for sharks of the Atlantic Ocean is based on unrealistic biological characteristics for this species.

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The Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, is an abundant coastal carcharhinid species found in shelf waters of the western North Atlantic and Gulf of Mexico (Compagno, 1984), reported to reach a maximum size of approximately 110 cm total length (Compagno, 1984). Although not targeted by any U.S. commercial fisheries, in the Gulf of Mexico it is caught in recreational fisheries and discarded as bycatch in the shrimp trawl fishery (NMFS, 1993) and shark and reef fish longline fisheries (person. obs.). However, age at first entry in the various fisheries is unknown. *R. terraenovae* is grouped under the "small coastal" species category in the Federal Management Plan (FMP) for sharks of the Atlantic Ocean, which determined that this species group was not overfished, based on a stock assessment resulting in an estimate of finite rate of population increase (e^r) of 1.91. Thus, no quotas or size limits exist for this species despite its importance in several fisheries.

Biological and life history characteristics of *R. terraenovae* in the Gulf of Mexico are now well documented (Parsons, 1983, 1985; Branstetter, 1986, 1987). However, this information has not yet been applied to analyses of the population dynamics of this species, nor have the results of such analyses been published. Furthermore, as is the case with most shark species, sufficient information necessary for stock assessment is lacking (Hoff, 1990). Because long-term records of catch and effort or the age composition by species are not available, traditional surplus production models or more elaborate age-structured methods of stock assessment have seldom been used for sharks. Owing to the paucity of fisheries data, several investigators have used demographic analysis to gain insight into the population dynamics and exploitation rates of shark resources. This type of analysis has been utilized to construct life history tables or Leslie matrices (Caughley, 1977; Krebs, 1985), which are summaries of age-specific mortality and fertility rates operating on a population with the assumption of a stable age distribution. This technique allows estimation of parameters important to the dynamics of any given population. Thus, Hoenig and Gruber (1990), Cailliet (1992), and Cailliet et al. (1992) produced estimates of population dynamics by applying a demographic analysis of the lemon shark, *Negaprion brevirostris*, the leopard shark, *Triakis semifasciata*, and the angel shark, *Squatina californica*, respectively. Hoff (1990), in addition, estimated maximum sustainable yield for the sandbar shark, *Carcharhinus plumbeus*, in a modified stock production model incorporating life history information.

This study was prompted by the existence of validated age and growth data (Branstetter and McEachran, 1986) and reproductive information (Parsons, 1983) on *R. terraenovae*, which provided several important parameters needed for construction of a life history table, i.e. lifespan, fecundity, and age at maturity.

The purpose of this study was 1) to produce, using the life history table approach and the best biological information available, reliable estimates of demographic parameters for *R. terraenovae* in the Gulf of Mexico, 2) to assess the sensitivity of the computed demographic parameters of the population to a variety of biological (input) parameter manipulations and harvest scenarios, and 3) to compare the resultant rates of population increase with that calculated for the "small coastal" shark group in the FMP for sharks of the Atlantic Ocean and to evaluate the biological basis of the stock assessment on which present management measures are based.

Materials and methods

Life history tables incorporating the best biological information available on *R. terraenovae* in the Gulf of Mexico were constructed. Maximum age (lifespan or longevity; t_{max}) has been estimated to be 8 to 10 years (Branstetter, 1987), and age at maturity (t_{mat}) for females has been estimated at 4 years (Branstetter, 1987), and from 2.4 to 3.9 years (Parsons, 1985). For this study, it was assumed that all females reproduced after reaching maturity. Parsons (1983) reported that parturition was annual, gestation period was 10 to 11 months, and sex ratios at birth were 1:1. He also found a significant relationship between total length of gravid females and number of offspring produced. Fecundity at size was calculated from the regression equation $Y = -8.4109 + 0.1396X$ (r=0.50, P<0.001, n=78; Parsons[1]), where X is female total length and Y is number of offspring. Female length at age was obtained from the von Bertalanffy growth function for both sexes combined derived by Branstetter (1987): $L_t = L_\infty(1-e^{-K(t-t_0)})$, where K=0.359, L_∞=108, and t_0=–0.985. Number of offspring was further divided by two, because the natality function (m_x) at age represents the number of female offspring per female parent and sex ratios at birth are 1:1 and parturition is annual (Parsons, 1983). Reports of unusually large litter sizes in tropical populations of *R. terraenovae* were also incorporated in some of the analyses that follow by doubling fecundity at age (m_x).

[1] Parsons, G. Univ. Mississippi, MI 38677. Personal commun., 1993.

The instantaneous natural mortality rate (M) was calculated from Hoenig's (1983) equation relating maximum age to total mortality rate, derived from data pertaining to unexploited or lightly exploited stocks. A value of 0.42 for Z (instantaneous total mortality rate) was derived from the regression equation $\ln(Z) = 1.46 - 1.01 \ln(t_{max})$, where t_{max} is longevity in years. Assuming that maximum age was determined from a time when there was no fishing directed at this species, Z can be approximated to M. The proportion of survivors at the start of each age interval (x) was $l_x = N_0(e^{-Mx})$, where N_0 is the number of individuals at time 0.

Demographic parameters were computed following methodology by Krebs (1985) and included R_0 (net reproductive rate per generation), G (generation length in years), and r (intrinsic rate of population change). All the values of r reported in this study were refined by using the Euler equation (Wilson and Bossert, 1971; Krebs, 1985):

$$\sum_{x=0}^{\infty} l_x m_x e^{-rx} = 1.$$

The finite or annual rate of change (e^r) was then calculated from the refined values of r. In addition, the theoretical population doubling or halving time in years ($t_{\times 2}$) assuming a stable age distribution was computed as (ln 2)/r or (ln 0.5)/r, respectively (Krebs, 1985).

The initial set of analyses, consisting of three different scenarios, was run by using the most reliable input biological parameters: t_{max}=10, t_{mat}=4, m_x=baseline age-specific natality, and S=0.657. In scenario 1, first year natural mortality was arbitrarily doubled (M=0.42 × 2=0.84) or S_0=0.432. In scenario 2, a value of S_0=0.512 was obtained from the Leslie matrix algorithm by assuming an equilibrium (or stationary) population (Vaughan and Saila, 1976). Thus, the following equation was solved for S_0 after assuming r=0:

$$S_o = \frac{e^r}{m_1 + \sum_{i=1}^{I-1}\left[\left(m_{i+1}e^{-ir}\right)\left(\prod_{j=1}^{i} S_j\right)\right]},$$

where m_i is fecundity at age, I is the oldest age group in the population (10 years), and S_j is survival from age j to j+1. In scenario 3, (referred to as the best case scenario), S_0 was assumed to be equal to survivorship in the following years (S_0=S=0.657=$e^{-0.42}$). For this best case scenario, the stable age distribution (C_x) was calculated according to Krebs (1985) and plotted.

In a second set of analyses, the input biological or life history parameters (t_{mat}, t_{max}, m_x, S, S_0) were varied to test the sensitivity of the resultant demographic parameters (R_0, G, r, and $t_{\times 2}$). These sensitivity analyses measured the percentage change of the output de-

mographic parameter of interest relative to the best case scenario. In the case of $t_{\times 2}$, sensitivity was assessed by calculating a multiplication factor that measures the number of times the population doubling time changes relative to the best case scenario (example: if $t_{\times 2}$=15.7 in the best case scenario and 4.1 in the altered state, then the multiplication factor [mf]=15.7/4.1=3.8, i.e. $t_{\times 2}$ has been shortened 3.8 times in the altered state).

Based on the results from the initial set of analyses (scenarios 1 through 3), the existing knowledge of life history traits in *R. terraenovae*, and the results from the FMP (e^r=1.91), input parameter values were manipulated in the direction that would be favorable to population increase and should thus be regarded as optimistic scenarios. The following variations, relative to the best case scenario, were applied: doubling m_x (m_x=2; scenario 4); reducing t_{mat} by 1 year (t_{mat}=3; scenario 5) and by 2 years (t_{mat}=2; scenario 6); reducing t_{mat} by 1 year and doubling m_x (t_{mat}=3, m_x=2; scenario 7); reducing t_{mat} by 2 years and doubling m_x (t_{mat}=2, m_x=2; scenario 8); increasing S_0 by 10% (S_0=0.723; scenario 9) and by up to 50% (S_0=0.985; scenario 10); increasing S by 10% (S=0.723; scenario 11) and by up to 50% (S=0.985; scenario 12); doubling t_{max} (t_{max}=20 [note that S and S_0 will also vary, since they depend on t_{max}]; scenario 13); and an extreme manipulation that was undertaken to approximate the FMP value of e^r=1.91 (equivalent to an r of 0.647), where t_{mat} was reduced by 1 year, m_x was doubled, and S and S_0 set at 95% (t_{mat}=3, m_x=2, S=S_0=0.95; scenario 14).

A third set of simulations was run incorporating the estimated mean instantaneous fishing mortality rate from 1986 to 1989 (F=0.428), as used in the stock assessment of small coastal species (Parrack[2]) on which the FMP for sharks of the Atlantic Ocean is based, to demonstrate the effect of exploitation and various age-at-first-entry scenarios. Fishing mortality (F) was added to natural mortality (M) in the survivorship function $l_x = N_0(e^{-[M+F]x})$, with F initially starting at age 0, then sequentially up to age 9. A_{rep}, the minimum age at which individuals can first enter the fishery and still allow the population to replace itself ($r \geq 0$) was calculated by noting the age at which the intrinsic rate of increase (r) becomes zero or positive. These simulations were run first under scenarios 1 through 3, and then under scenarios 4 through 14.

Results

The initial set of life history tables yielded net reproductive rates per generation (R_0), ranging from 0.844 to 1.284, a generation length (G) of 5.8 years, and intrinsic rates of population change (r), ranging from –0.029 to 0.044 (Table 1) depending on the value of first year survivorship (S_0) used. In scenario 1 (S_0=0.432), the results indicated that the population would decrease at a rate of 2.9% per year and would halve about every 24 years. Halving times are indicated by negative values in the $t_{\times 2}$ column. In scenario 2 (S_0=0.512), r is equal to 0 by definition. Under the best case scenario (scenario 3; S_0=0.657), the

[2] Parrack, M. L. 1990. A preliminary study of shark exploitation during 1986–1989 in the U.S. FCZ. Contrib. MIA-90-493, NOAA, NMFS, SEFC, Miami, FL 33149, 23 p.

Table 1

Simulations of the Gulf of Mexico population of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, under three scenarios that use input parameter values representing the best biological information available. Only natural mortality is included in these analyses. First year survival rates (S_0) were obtained as follows: S_0=0.432 (scenario 1) was obtained by doubling the natural mortality value computed from Hoenig's (1983) relationship between mortality rate and maximum age; S_0=0.512 (scenario 2) was computed from the Leslie matrix algorithm (see text) assuming an equilibrium population (Vaughan and Saila, 1976). The third line (in italics) represents the best case scenario (scenario 3; S_0=S=0.657).

	Input parameter values[1]					Computed parameter values[2]				
Scenario	t_{mat}	t_{max}	m_x	S	S_0	R_0	G	r	e^r	$t_{\times 2}$
1	4	10	1[3]	0.657	0.432	0.844	5.762	–0.029	0.971	–23.9
2	4	10	1	0.657	0.512	1.000	5.762	0.	1.000	—
3	*4*	*10*	*1*	*0.657*	*0.657*	*1.284*	*5.762*	*0.044*	*1.045*	*15.7*

[1] t_{mat}=age at maturity; t_{max}=maximum age; m_x=age-specific natality; S=survivorship after the first year of life; S_0=survivorship for the first year of life.

[2] R_0=net reproductive rate per generation; G=generation length, in years; r=intrinsic rate of population change refined through the Euler equation (see text); e^r=finite rate of population change; $t_{\times 2}$=theoretical doubling (positive values) or halving (negative values) time in years assuming a stable age distribution.

[3] "1" indicates baseline age-specific natality.

population increased at 4.5% per year and doubled about every 16 years.

The predicted stable age distribution (C_x) for the best case scenario (Fig. 1) suggested that about 80% of the population was composed of immature individuals. Because of the lack of data on sizes and ages at first capture in the recreational and commercial fisheries, the actual proportion of the population subject to fishing is unknown. Likewise, no size or age composition of this population is available from surveys, precluding any comparisons with the theoretical C_x.

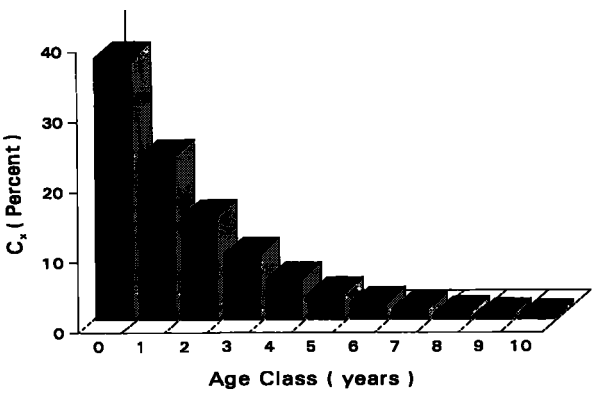

Figure 1

Predicted stable age distribution of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, under the best case scenario presented in Table 1, assuming geometric growth (with r=0.044) and constant age-specific mortality and fertility rates.

Results of the sensitivity analyses indicated that doubling age-specific natality, m_x, had a distinct effect (a 286% increase) on the population's rate of increase, r (scenario 4), and would allow the population to double in only 4.1 years or 3.8 times faster than in the best case scenario (Table 2). Generation length, G, remained the same, while net reproductive rate per generation, R_0, increased 100% (Table 3).

Decreasing age at maturity, t_{mat}, by one year (scenario 5) produced a smaller change in r, $t_{\times 2}$, and R_0 (Tables 2 and 3) than doubling m_x, but decreased G by 12% (Table 3). Further decreasing t_{mat} by another year (scenario 6) produced almost the same values of r and $t_{\times 2}$ as those obtained in scenario 4 (Table 2), although R_0 increased only 5% and G decreased by 20%. The combined effect of decreasing t_{mat} and doubling m_x together (scenarios 7 and 8) produced increases in r up to near 700% and $t_{\times 2}$ values up to 8 times shorter than in the best case scenario (Table 2). Under scenarios 7 and 8, R_0 also increased by up to more than 200%, while G decreased by up to 20%.

Increasing first year survivorship, S_0, by 10% (scenario 9) yielded a value of r 39% higher and a value of $t_{\times 2}$ 1.4 times shorter than in the best case scenario (Table 2), affected R_0 very little (a 10% increase only), and had no effect on G (Table 3). A further increase

Table 2

Simulations of the Gulf of Mexico population of *Rhizoprionodon terraenovae* to test the sensitivity of computed population rate of increase and doubling time to input biological parameter values. Input values were manipulated in scenarios 4 through 14; the best case scenario (BC; top row) is shown in italics to facilitate comparison. All other symbols are as defined in Table 1.

	Input parameter values					Computed parameter values			
Scenario	t_{mat}	t_{max}	m_x	S	S_0	r	% change of r[1]	$t_{\times 2}$	mf[2]
BC	*4*	*10*	*1*	*0.657*	*0.657*	*0.044*	—	*15.7*	—
4	4	10	2[3]	0.657	0.657	0.170	286	4.1	3.8
5	3	10	1	0.657	0.657	0.111	152	6.2	2.5
6	2	10	1	0.657	0.657	0.168	282	4.1	3.8
7	3	10	2	0.657	0.657	0.265	502	2.6	6.0
8	2	10	2	0.657	0.657	0.356	709	1.9	8.3
9	4	10	1	0.657	0.723	0.061	39	11.4	1.4
10	4	10	1	0.657	0.985	0.117	166	5.9	2.7
11	4	10	1	0.723	0.657	0.123	179	5.6	2.8
12	4	10	1	0.985	0.657	0.378	759	1.8	8.7
13	4	20	1	0.811	0.658	0.228	418	3.0	5.2
14	3	10	2	0.950	0.950	0.634	1,341	1.1	14.3

[1] % change of r relative to the best case scenario.

[2] Multiplication factor indicating the number of times $t_{\times 2}$ has been shortened relative to the best case scenario.

[3] "2" indicates baseline age-specific natality values have been doubled.

Table 3

Simulations of the Gulf of Mexico population of *Rhizoprionodon terraenovae* to test the sensitivity of computed net reproductive rate per generation and generation length to input biological parameter values. Input values were manipulated in scenarios 4 through 14; the best case scenario (BC; top row) is shown in italics to facilitate comparison. All other symbols are as defined in Table 1.

	Input parameter values					Computed parameter values			
Scenario	t_{mat}	t_{max}	m_x	S	S_0	R_0	% change of R_0[1]	G	% change of G[1]
BC	*4*	*10*	*1*	*0.657*	*0.657*	*1.28*	—	*5.76*	—
4	4	10	2[2]	0.657	0.657	2.57	100	5.76	0
5	3	10	1	0.657	0.657	1.72	34	5.06	−12
6	2	10	1	0.657	0.657	1.34	5	4.58	−20
7	3	10	2	0.657	0.657	3.43	168	5.06	−12
8	2	10	2	0.657	0.657	4.08	219	4.58	−20
9	4	10	1	0.657	0.723	1.41	10	5.76	0
10	4	10	1	0.657	0.985	1.92	50	5.76	0
11	4	10	1	0.723	0.657	2.05	60	6.06	5
12	4	10	1	0.985	0.657	11.66	809	7.20	25
13	4	20	1	0.811	0.658	4.99	290	8.30	44
14	3	10	2	0.950	0.950	29.6	2,212	6.7	16.3

[1] % change of R_0 and G relative to the best case scenario.

[2] "2" indicates baseline age-specific natality values have been doubled.

in S_0 up to 50% (scenario 10) had a more distinct effect on r (166% increase), t_{x2} (2.7 times shorter), and R_0 (50% increase), but did not affect G (Tables 2 and 3). Increasing age 1+ survivorship (S) by 10% (scenario 11) had a similar effect on all the demographic parameters to increasing S_0 by 50% (scenario 10; Tables 2 and 3), whereas increasing S by 50% (scenario 12) had a very profound effect on all the demographic parameters, increasing r by 759%, shortening t_{x2} by almost 9 times (similar to scenario 8), increasing R_0 by over 800% and lengthening G by 25% (Tables 2 and 3).

Doubling longevity (t_{max}) to 20 years (scenario 13) also markedly affected r (418% increase), t_{x2} (5 times shorter), and R_0 (290% increase), and produced the largest value of G (8.3 or a 44% increase) in all scenarios (Tables 2 and 3).

Finally, the extreme manipulations of scenario 14 (reducing t_{mat} to 3 years, doubling m_x, increasing S and S_0 to 95%, with a t_{max} of 10 years) produced a 13-fold increase in r, a value of t_{x2} more than 14 times shorter, a 22-fold increase in R_0 and only a 16.3% increase in G (Tables 2 and 3).

For all simulations, population doubling time (t_{x2}) was lessened and generation length (G) was the demographic parameter less sensitive to changes in input biological parameter values.

With the estimated mean fishing mortality from 1986 to 1989 (F=0.428) added to natural mortality starting at each age interval from 9 to 0, R_0 and r were progressively reduced as F was progressively started closer to age-0 (Table 4). In scenarios 1 (S_0=0.432) and 2 (S_0=0.512), r was always negative and became increasingly so as simulated fishing started earlier in the life of *R. terraenovae*. Only by using best case scenario (scenario 3) values could the population be made to replace itself or grow by manipulating age at first capture. When fishing pressure was applied between 6 and 5 years of age or about 97 cm total length (TL) the population was able to replace itself. Generation length remained the same under the three scenarios but progressively decreased as fishing mortality included progressively earlier ages. Theoretical halving time also progressively shortened as fishing started at younger ages, whereas in the best case scenario doubling time increased as age at first capture dropped from 9 to 6 years.

The effect of added fishing mortality on survivorship can be identified as a progressive decrease in percentage survival as fishing starts progressively earlier in the lifespan of the shark (Fig. 2). Age-specific reproduction also decreases significantly as fishing mortality is applied at progressively earlier ages (Fig. 3).

When the estimated mean fishing mortality from 1986 to 1989 (F=0.428) was added to natural mortality in scenarios 4 through 14 (Table 5), A_{rep}, the earliest age at which sharks can first be captured to

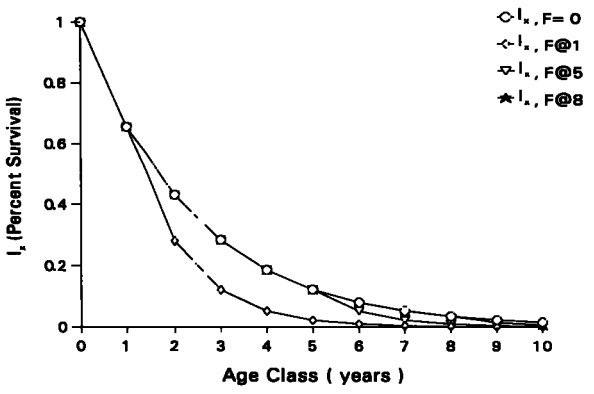

Figure 2

Survivorship curves for *Rhizoprionodon terraenovae* under the survival conditions presented in Table 1 for the best case scenario (S=S_0=0.657) and fishing mortality as in Table 4 (F=0.428), starting at three different ages (1, 5, and 8 years).

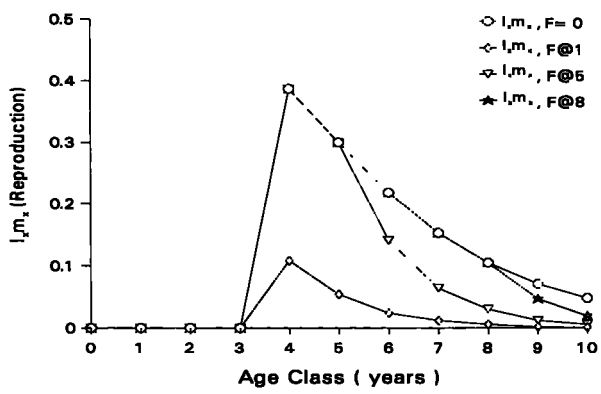

Figure 3

Age-specific reproduction for *Rhizoprionodon terraenovae* under the survival conditions presented in Table 1 for the best case scenario (S=S_0=0.657) and fishing mortality as in Table 4 (F=0.428), starting at three different ages (1, 5, and 8 years).

Table 4

Simulations of the Gulf of Mexico population of *Rhizoprionodon terraenovae* under the three same scenarios as in Table 1 but with estimated mean fishing mortality from 1986 to 1989 (F=0.428 [Parrack[2]]) added to natural mortality starting at different ages. All symbols are as defined in Table 1. Computations based on the following first year survival rates: scenario 1 (S_0=0.432); scenario 2 (S_0=0.512); and scenario 3 (best case, S_0=0.657).

Demographic parameter	Age at first capture									
	9	8	7	6	5	4	3	2	1	0
Scenario 1										
R_0	0.83	0.81	0.77	0.71	0.62	0.49	0.32	0.21	0.14	0.09
G	5.70	5.60	5.45	5.27	5.06	4.86	4.86	4.86	4.86	4.86
r	–0.03	–0.04	–0.05	–0.07	–0.09	–0.14	–0.23	–0.31	–0.38	–0.46
e^r	0.97	0.96	0.95	0.94	0.91	0.87	0.80	0.74	0.68	0.63
$t_{\times 2}$	–21.7	–18.2	–14.4	–10.7	–7.4	–4.9	–3.1	–2.3	–1.8	–1.5
Scenario 2										
R_0	0.99	0.96	0.91	0.84	0.73	0.58	0.38	0.25	0.16	0.10
G	5.71	5.60	5.45	5.27	5.06	4.86	4.86	4.86	4.86	4.86
r	–0.00	–0.01	–0.02	–0.03	–0.06	–0.11	–0.19	–0.27	–0.35	–0.43
e^r	1.00	0.99	0.98	0.97	0.94	0.90	0.82	0.76	0.70	0.65
$t_{\times 2}$	–346.6	–99.0	–40.8	–21.0	–11.4	–6.3	–3.6	–2.5	–2.0	–1.6
Scenario 3 (best case)										
R_0	1.27	1.23	1.17	1.08	0.94	0.75	0.49	0.32	0.21	0.13
G	5.71	5.60	5.45	5.27	5.06	4.86	4.86	4.86	4.86	4.86
r	0.04	0.04	0.03	0.01	–0.01	–0.06	–0.14	–0.22	–0.31	–0.38
e^r	1.04	1.04	1.03	1.01	0.99	0.94	0.86	0.80	0.73	0.68
$t_{\times 2}$	16.5	18.7	23.9	49.5	–57.8	–11.7	–4.8	–3.0	–2.2	–1.8
size[1]	105	103.7	101.9	99.2	95.4	90	82.2	71.0	55.0	32.3

[1] Total length, in cm, obtained from the von Bertalanffy growth equation relating age to length (see text).

Table 5

Simulations of the Gulf of Mexico population of *Rhizoprionodon terraenovae* under several scenarios (4 through 14) using different input biological parameter values and with fishing mortality (F=0.428) as in Table 4. The best case scenario (BC; top row) is included in italics to facilitate comparison. All other symbols are as defined in Table 1; A_{rep} is the age at which sharks can first enter the fishery and still allow the population to replace itself.

	Input parameter values					Computed parameter values					
Scenario	t_{mat}	t_{max}	m_x	S	S_0	A_{rep}	R_0	G	r	e^r	$t_{\times 2}$
BC	*4*	*10*	*1*	*0.657*	*0.657*	*6*[1]	*1.08*	*5.27*	*0.010*	*1.010*	*49.5*
4	4	10	2[2]	0.657	0.657	4	1.50	4.87	0.084	1.088	8.2
5	3	10	1	0.657	0.657	4	1.18	4.18	0.040	1.041	17.3
6	2	10	1	0.657	0.657	3	1.25	3.47	0.064	1.066	10.8
7	3	10	2	0.657	0.657	2	1.20	3.99	0.046	1.047	15.1
8	2	10	2	0.657	0.657	1	1.20	3.29	0.057	1.059	12.2
9	4	10	1	0.657	0.723	5	1.04	5.06	0.007	1.007	99.0
10	4	10	1	0.657	0.985	4	1.12	4.86	0.024	1.024	28.9
11	4	10	1	0.723	0.657	4	1.09	5.01	0.017	1.017	40.8
12	4	10	1	0.985	0.657	1	1.15	5.70	0.025	1.025	27.7
13	4	20	1	0.811	0.658	3	1.16	5.33	0.028	1.028	24.7
14	3	10	2	0.950	0.950	0	2.56	4.86	0.206	1.229	3.4

[1] Under this scenario, sharks can enter the fishery at age 6 and above with a fishing mortality rate of F=0.428 (F=0 for all sharks ages 5 and below) added to the natural mortality rate and still allow the population to replace itself ($r \geq 0$).

[2] "2" indicates baseline age-specific natality values have been doubled.

allow for full population replacement ($r \geq 0$) given the fishing mortality, became progressively smaller as the value of r increased (see Table 2 for reference). Increasing S_0 by 10% (scenario 9) allowed for an age at first capture of 5 years, while doubling m_x (scenario 4), reducing t_{mat} to 3 years of age (scenario 5), increasing S_0 by 50% (scenario 10), or increasing S by 10% (scenario 11) all had the same effect of allowing for an age at first capture of 4 years (90 cm TL) compared with 6 years (99 cm TL) under the best case scenario. Reducing t_{mat} by 2 years (scenario 6) or increasing t_{max} to 20 years (scenario 13) both allowed for an A_{rep} of 3 years (82 cm TL), while reducing t_{mat} by 1 year and doubling m_x (scenario 7) allowed an A_{rep} of 2 years. Under the most extreme manipulations, which included reducing t_{mat} by 2 years and doubling m_x (scenario 8), increasing S by 50% (scenario 12), and reducing t_{mat} to 3 years, doubling m_x, and setting S and S_0 at 95% (scenario 14), an age at first capture of 1 year (55 cm TL; scenarios 8 and 12) and of 0 years (32 cm TL) could be applied in a given year.

Discussion

These demographic analyses using the best available information indicate that the Gulf of Mexico population of *R. terraenovae* may be very vulnerable to fishing pressure. Results showed that, based on known life history parameters, the population's intrinsic rate of increase was, at best, only r=0.044, equating to a finite rate of e^r=1.045, which is much lower than the rate estimated for "small coastal" species in the stock assessment used to develop the FMP for sharks of the Atlantic Ocean (e^r=1.91). Furthermore, comparable rates to the FMP values were only obtained after extreme manipulations of the input life history parameters, which diverged too widely from observed life history parameters to be realistic. For example, one of the possible scenarios that would yield an estimate of e^r of 1.91 implies that age at maturity has to be decreased from 4 to 3 years, fertility doubled, and survivorship increased by almost 50% relative to the most optimistic initial scenario, i.e. the best case scenario, resulting in estimates of 29.6 for R_0, 6.7 for G, and 1.1 for $t_{\times 2}$. This means that, in the absence of fishing, the population would almost double every year.

Rhizoprionodon terraenovae is the main species caught in the Texas recreational shark fishery and is also caught by the headboat and other recreational fisheries in the Gulf of Mexico. More importantly, it represents a significant bycatch in the shrimp trawl fishery operating in the Gulf of Mexico and to a lesser extent in the longline reef fish and shark fisheries, and in the gillnet fishery in the same area. The lack of data on the age and size at which individuals of *R.*

terraenovae first enter these fisheries, as well as the relative proportions of each age and size group represented, preclude a more detailed analysis at this time. However, the demographic analysis representing the best case scenario indicated that under the present fishing level *R. terraenovae* should not enter the fishery until individuals reach about 97 cm TL or almost 6 years of age if the population was managed to just replace itself. There is evidence that smaller animals are being caught in the various fisheries, but the proportions of each age class are unknown.

The biological parameters incorporated in scenarios 1 through 3 represent the best, most reliable information available. Data on age and growth were taken from a tetracycline-validated laboratory study (Branstetter, 1987) which indicated that females mature entering their fifth year of life (age-4) and that maximum age is between 8 and 10 years. In another study (Parsons, 1985), female maturity was estimated at between 2.4 to 3.9 years. However, this study used only males and mean lengths for age classes, which, as pointed out by Branstetter (1987), affected the von Bertalanffy parameters. The possibility of earlier female age at maturity and even longer lifespan was incorporated in several of the demographic analyses (scenarios 5, 6, 7, 8, 13, and 14), which evidently yielded more liberal results on which more risk-prone management decisions could be based.

The unpublished information on fertility at age was derived from a study on the reproductive biology of *R. terraenovae* (Parsons, 1983) and relates female total length to number of uterine eggs or embryos for 78 specimens. Parsons (1983) also noted that tropical populations of *R. terraenovae* had been reported to have as many as 12 embryos. This possibility was taken into account by doubling fertility at age in several analyses (scenarios 4, 7, 8, and 14), which again produced more optimistic estimates of population parameters.

The age, growth, and reproduction information used in this study was based on animals collected in the northern central and western Gulf of Mexico. The extent to which this information is applicable to the entire population or whether there are different stocks in the Gulf with different age, growth, and reproductive capabilities is not known. For example, I recently examined an 82-cm-TL pregnant female with 3 embryos, measurements which fit nicely the regression equation of Parsons (1983), but which would result in a back-calculated age of 3 years with the von Bertalanffy growth function, although the female could have been older, e.g. age 4, owing to variability in size at age, which is not uncommon in sharks (Kusher et al., 1992, and references therein).

The most important and also the most difficult parameter to estimate is natural mortality (M). The value of M used in this study was taken from Hoenig's (1983) relationship between longevity and total mortality for virgin or lightly exploited stocks. The assumption that Z could be approximated to M, or that no fishing mortality occurred during the period for which growth parameters for this species were derived, may have been violated. However, the possibility of lower natural mortality values was incorporated in several analyses (scenarios 9 through 14). While Hoenig's equation represents a shortcut and obvious simplification of reality, the lack of catch and effort data, or age or size composition for stocks of this species precludes calculation of any other estimates of M at this time. Lack or inappropriateness of both fishery and biological data may explain why several other researchers have used the same approach to estimate natural mortality in shark population studies. Except for age-0 *Negaprion brevirostris* (Manire and Gruber, 1993), no actual age-specific estimates of natural mortality are available for any shark species.

The value derived for M (0.42) in this study is equivalent to an annual survivorship of 0.66, which is low when compared with survival estimates for other species of sharks. Values derived from Hoenig's (1983) regression equation include 0.82 for the angel shark, *Squatina californica*, (Cailliet et al., 1992); 0.85 for *N. brevirostris* (Hoenig and Gruber, 1990); 0.87 for *Triakis semifasciata* (Smith and Abramson, 1990; Cailliet, 1992); and 0.90 for *Carcharhinus plumbeus* (Hoff, 1990). Grant et al. (1979) derived a value of 0.90 for the Australian school shark, *Galeorhinus australis*, using cohort analysis, and Walker (1992) used a value of 0.82 in a dynamic pool fishery simulation model of the gummy shark, *Mustelus antarcticus*, which was also obtained through cohort analysis. The lower survivorship value for *R. terraenovae* may be due to the smaller size of this species which would make it more susceptible to predation by other sharks, especially at early ages, since pups are born at about only 30 cm TL in coastal waters about 10 m deep (Castro, 1993).

The very high estimate of F (0.428) used in this study was derived from a shark stock assessment that is the basis for the recently implemented (26 April 1993) FMP for sharks of the Atlantic Ocean. However, the accuracy of this estimate, based on a 4-year catch-and-effort time series, is uncertain, and the demographic analyses undertaken in this study indicate that *R. terraenovae* is vulnerable to high removal levels in the early years of life.

It is also possible that the age, growth, and reproductive data used in this study are only representative of the population at a time when fishing pressure was not as high as it is at present. Potential

Table 6

Life history parameters for several species of sharks compared to the best case scenario for *Rhizoprionodon terraenovae* in the Gulf of Mexico.

Species	R_0	G	r	e^r	t_{x2}	Study
Triakis semifasciata	4.47	22.35	0.067	1.069	10.3	Cailliet, 1992
Negaprion brevirostris	1.27	16.23	0.015	1.015	46.7	Hoenig and Gruber, 1990
Squalus acanthias	3.05	49.63	0.023	1.023	30.1	Jones and Geen, 1977[1]
Carcharhinus plumbeus	1.48	21.5	0.018	1.018	38.5	Hoff, 1990
Squatina californica	2.25	14.5	0.056	1.057	12.4	Cailliet et al., 1992
Rhizoprionodon terraenovae	1.28	5.78	0.044	1.045	15.7	This study

[1] Modified by Eguchi and Cailliet (Gregor Cailliet, Moss Landing Marine Laboratories, Moss Landing, CA 95039-0450. Personal commun., 1994).

compensatory mechanisms countering stock depletion may include increased growth with corresponding earlier age at maturity, earlier size at maturity, higher fecundity, immigration of stocks from other areas, and increased survival rates through density-dependent regulation (Walker, 1992).

The estimates of demographic parameters derived under the best case scenario in this study are within the range of values derived for other species of sharks (Table 6). The estimate of R_0 (1.28) for *R. terraenovae* is almost identical to that derived by Hoenig and Gruber (1990) for *N. brevirostris* (1.27), probably owing to the similar fecundity in the two species. Generation length (G) is considerably shorter in *R. terraenovae* than in any other species because of its shorter lifespan. The estimates of r and e^r fall between those for other species. These relatively low values in a fast-growing, short-lived species such as *R. terraenovae* can be explained mainly by low fecundity and high mortality levels as the demographic analyses showed. Theoretical doubling time (t_{x2}) also lies between estimates for other species of sharks.

In the light of the incomplete yet reasonable biological information available, it seems sound to conclude that *R. terraenovae*, as perhaps some of the other small coastal species included in the FMP, is a species vulnerable to fishing. This becomes especially relevant with the recent implementation of the shark FMP which has set quotas and trip limits and has provided for fisheries closures for larger coastal species while allowing the unrestricted capture of small coastal sharks, of which *R. terraenovae* is the most representative species. Increased fishing pressure on *R. terraenovae*, especially on younger animals, would certainly deplete the stocks of this species.

The present study raises some serious concerns about the use of surplus production models utilizing very short series of catch and effort data and not taking into account the biological characteristics of a species. In the particular case of *R. terraenovae*, it can lead to policies that in turn lead to overfishing and stock depletion. It is advised that bycatch of *R. terraenovae* in the shrimp fishery and other fisheries in the Gulf of Mexico, as well as in the eventual development of a directed fishery for this species, be closely monitored in the near future. Development of stock identification techniques are also needed to determine stock structure and the degree of mixing and immigration of this species into fishing areas. Updated, more complete fisheries statistics combined with improved biological information should be used to re-assess the status of *R. terraenovae* in the small coastal species group of the shark FMP for future sound management actions.

Acknowledgments

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Abstract.—Bottom longline and baited video camera operations were conducted at 39 stations off the Hawaiian Islands of Oahu, Maui, and Kauai during 1992. Objectives of the 1992 cruise were to assess the precision, accuracy, and efficiency of a video camera system versus a traditional abundance index (longline catch per unit of effort [CPUE]) for juvenile pink snapper ("opakapaka"), *Pristipomoides filamentosus*, a commercially important eteline snapper in Hawaii. Precision of the video samples was reevaluated with data from 18 stations sampled during 1993 off Kaneohe Bay. The video index of the maximum number of opakapaka observed (MAXNO, the natural log-transformed mean of three camera drops) was best correlated with the log of longline CPUE (r=0.79, P<0.001, n=15). Variation in the data for video MAXNO was nominally less than that of the longline CPUE. No monotone trend over stations was noted in samples from 1993. Sample sizes of 33 stations for longline and 18 stations for video would be necessary to detect twofold changes in abundance of opakapaka at a site, based on our analysis of the two end positions of the 10 windward Oahu stations that had three quantitative deployments. Reanalysis of power with data from the 1993 cruise indicates that a sample size of approximately 22 stations (α_2=0.05) or approximately 17 stations (α_2=0.1) would be necessary to detect twofold changes.

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Evaluation of a video camera technique for indexing abundances of juvenile pink snapper, *Pristipomoides filamentosus*, and other Hawaiian insular shelf fishes

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Deep-water snappers (family: Lutjanidae) support an important commercial fishery around the main Hawaiian Islands (MHI) and the Northwestern Hawaiian Islands (NWHI). Pink snapper (or "opakapaka"), *Pristipomoides filamentosus*, has been one of the most important species in terms of landings (20–30% of total weight) and revenue for many years[1] (Ralston and Polovina, 1982; WPRFMC[2]). Research on adult *P. filamentosus* has included studies on sexual maturity and growth (Ralston and Miyamoto, 1983; Kikkawa, 1984; Okamoto[3]), trophic ecology (Parrish, 1987; Haight et al., 1993); distribution (Kami, 1973; Moffitt, 1980); habitat (Ralston et al., 1986; Moffitt et al., 1989); and mortality (Ralston, 1987). Relatively few larval and pelagic juvenile specimens of opakapaka have been collected; therefore, little is known of their early life history (Leis, 1987).

Exploratory research on recruited, epibenthic juvenile *P. filamentosus* has been conducted by the Honolulu Laboratory of the National Marine Fisheries Service (NMFS) since 1988. This has included initial habitat description[4] and work on age and growth of juveniles at Kaneohe Bay, Oahu (Parrish, 1989; DeMartini et al., 1994). Recent work has focused on evaluating techniques for assessing the distribution and abundance of juvenile opakapaka in Hawaiian waters. Characterizations of juvenile opakapaka abundance based on rod and reel, handlines, and bottom trawls, however, are either biased, imprecise, or destructive of habitat.[5]

[1] Kawamoto, K. E. 1992. Northwestern Hawaiian Islands bottomfish fishery, 1991. Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822–2396. Southwest Fish. Sci. Cent. Admin. Rep. H-92-12, 20 p.

[2] WPRFMC (Western Pacific Regional Fisheries Management Council). 1992. Bottomfish and seamount groundfish fisheries of the Western Pacific region, p. 57–71. 1991 Annual Report for the WPRFMC, Honolulu, HI 96813.

[3] Okamoto, H. Y. 1993. Project to develop opakapaka (pink snapper) tagging techniques to assess movement behavior. Sept. 1, 1990 to Aug. 31, 1992. Final Rep. of HI. Dep. Land and Nat. Res. (HDLNR) to NOAA., Award no. NA90AA-D-IJ466. HDLNR, DAR, Honolulu, HI 96814, 18 p.

[4] Moffitt, R. B., and F. A. Parrish. In review. Habitat use and life history of juvenile Hawaiian pink snappers, *Pristipomoides filamentosus*. Bull. Mar. Sci.

[5] Ellis, D. M., E. E. DeMartini, and R. B. Moffitt. 1992. Bottom trawl catches of juvenile opakapaka, *Pristipomoides filamentosus* (F. Lutjanidae), and associated fishes, *Townsend Cromwell* cruise TC-90-10, 1990. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Sci. Cent. Admin. Rep H-92-03, 33 p.

Still and video cameras (baited and unbaited) have been used to sample other marine habitats, e.g. to compare data collected with other methods and to reduce biases associated with remote collection techniques (Uzmann et al., 1978; Grimes et al., 1982; Matlock et al., 1991; Moffitt and Parrish, 1992), and to study the natural history and estimate the abundance indices of different species (Miller, 1975; Priede et al., 1990; Auster et al., 1991; Armstrong et al., 1992; Michalopoulos et al., 1992). Baited video systems have some inherent biases (such as loss of odor attractant (or bait; Isaacs and Schwartzlose, 1975), and intra- or inter-specific competition for bait (Armstrong et al., 1992). Towed video systems and remotely operated vehicles (ROV's) have been used to collect analogous data without the use of bait. A towed system or ROV can sample a known area and assess organismal densities directly within that area. Although a towed and unbaited video system might be preferable if the objective is to estimate absolute fish density, we chose a stationary, baited system both in order to minimize the disturbance of bottom habitat and to provide an index of relative abundance similar to catch per unit of effort (CPUE) that would be sufficient for temporal comparisons.

In this paper, we assess the precision, accuracy, and efficiency of a baited video camera system for producing indices of fish abundance based on a visual record, and we compare these video data with a more traditional abundance index of longline CPUE. We first compared the two methods by pair-sampling during an initial cruise in 1992. Preliminary estimates of video precision were made with these data. Power and sample sizes for video sampling were again estimated with data obtained during 1993. Effects of station and depth for the 1993 cruise were also examined. We emphasize data for the target species, opakapaka, but include complementary data for Bleeker's balloonfish ("puffers"), *Torquigener florealis*, because of its numerical dominance in both types of samples.

Materials and methods

Sampling

Simultaneous longline and video camera operations were conducted for four days offshore of windward Oahu embayments (Fig. 1) and three days offshore of embayments at each of two other islands (Maui and Kauai) during a May 1992 cruise of the NOAA ship *Townsend Cromwell*. Additional video camera operations were conducted from small craft during May 1993 outside Kaneohe Bay, Oahu (Fig. 1). Sampling was conducted on flat, unconsolidated bottoms (Parrish, 1989; Moffitt and Parrish[4]) between 0800 and 1530 hours. Longline depths ranged from 54 m to 107 m and video camera depths ranged from 52 m to 87 m for the 1992 cruise, the approximate depth range for juvenile opakapaka (Parrish 1989; Ellis et al.[5]). Paired video-longline samples were collected in 1992 over a longshore spatial scale of 10 nmi (18.5 km) off Oahu (Fig. 1). The longshore spatial scales for Kahului Bay, Maui, and Hanalei Bay, Kauai, were 9.1 nmi (16.9 km) and 9.5 nmi (17.6 km), respectively. From one to three video deployments were made per station at shallow, mid-, and deep depths along the longline set. A total of 39 longline and video stations were completed (15 at Oahu, and 24 combined for Maui and Kauai). A complete set of three (shallow, mid-, and deep) video camera deployments were completed per station for 10 of the 15 stations off Oahu. In 1993, video sampling was refocused on a finer spatial scale (2.4 nmi or 4.4 km) off Kaneohe Bay, Oahu, over known bottom topography to increase the probability of sampling more homogeneous habitat. Two video deployments per station were made at shallow (73 m to 77 m) and deep (83 m to 85 m) positions in 1993. A total of 18 stations were completed in 1993.

Video camera and longline stations were parallel within 50 to 75 m of each other. The spacing between video-longline stations during any particular day was approximately 1 km (0.5 nmi) longshore during 1992. Spacing between video deployments was approximately 100 to 300 m. Longshore distance between video stations in 1993 was about 200 m (0.1 nmi). At distances of ≥100 m separating adjacent stations, successive video deployments were likely independent, because the greatest distance of fish attraction to the bait was only 48 to 90 m. This estimate was based on average maximum bottom current speeds of 0.1 to 0.2 m/s respectively (Bathen, 1978), a soak time of 10 minutes, and a swimming speed for opakapaka of 0.6 m/s (or approximately 3 body lengths (BL) per second, where one BL=20 cm; Videler, 1993). Depths of all video and longline sets were determined by depth sounders aboard the research vessels, and positions were determined by GPS (Global Positioning System) or sighting compass, as Loran-C capabilities were unavailable.

Longlines were deployed approximately perpendicular to depth contours. Bottom longline operations used modified Kali longlines,[6] each with 30 individu-

[6] Shiota, P. M. 1987. A comparison of bottom longline and deep-sea handline for sampling bottom fishes in the Hawaiian Archipelago. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-87-5, 18 p.

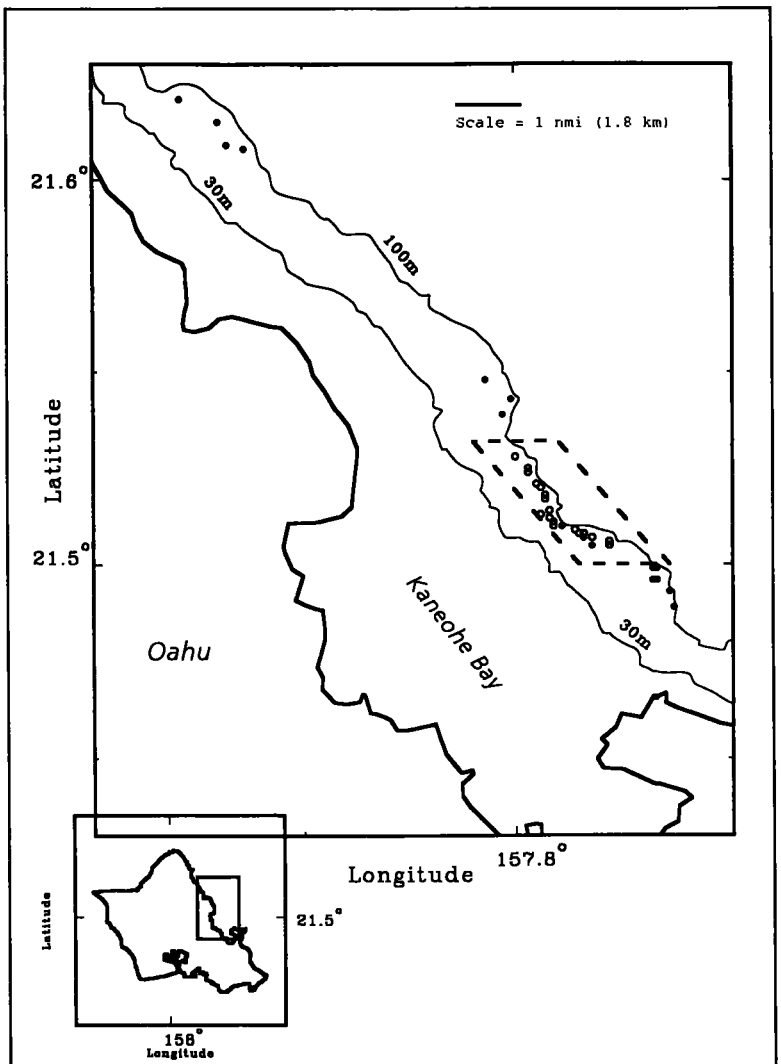

Figure 1

Area of operations off Kaneohe Bay, Oahu, for video and longline surveys for opakapaka, *Pristipomoides filamentosus*. Stations for video and longline in 1992 are midpoints identified by solid circles. Area of video coverage in 1993 is enclosed within the dotted lines and stations are midpoints identified by hollow circles.

ally weighted and buoyed 3-m PVC droppers. Droppers were attached along the main line about 18 m apart. A 9.07-kg test, hard monofilament branch leader and a 3.63-kg test, hard monofilament hook leader were used. Each dropper had five leaders with size–12 Izuo circle hooks (AH style), for a total of 150 hooks per longline set. Stripped squid was used as bait. The standard soak time was 30 minutes, and three to four sets were completed each day.

Two separate, 8-mm video camera assemblies were used for the video operations. Each video camera was equipped with a No. 1 diopter magnification lens and a wide angle zoom lens with a red filter for underwater correction. Camera focus, sensitivity, and white balance were manually adjusted, but an automatic aperture setting was used. The focus distance for both video cameras was fixed at 2.13 m, and the focal length of the lens was set at 11 mm. Each video camera was enclosed in an underwater housing and secured in a weighted frame (Fig. 2). A single, 15-cm long bait container was positioned 60 cm in front of the camera lens and mounted on a PVC rod. The bait container held a single (≈0.5-kg) mackerel (*Scomber* sp.) and one whole squid (*Loligo* sp.) tie-wrapped to the outside, both of which were changed after each deployment. The camera assemblies were manually

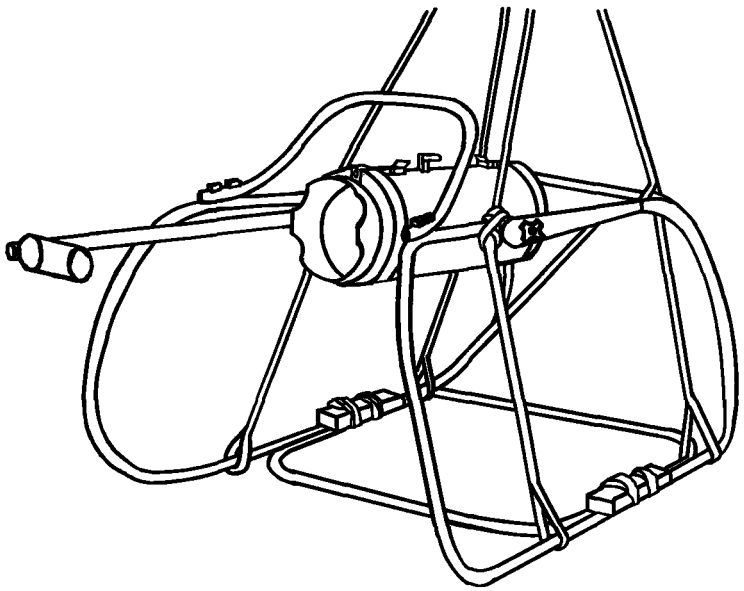

Figure 2
Baited video camera assembly with bait container positioned 60 cm in front of the camera lens.

lowered to the bottom and marked by a buoy; later they were raised to the surface by outboard engine power. Cameras were allowed to rest on the bottom for a standard interval of 10 minutes before retrieval.

The duration and number of video camera deployments to be used on the ship cruise were estimated on the basis of three earlier pilot deployments of the video assembly from small craft. These prior tests indicated that about 10 minutes were required to deploy and retrieve the camera assembly. The time to first appearance (TFAP) of opakapaka from the three pilot stations was 227 ± 300 sec (mean ± 1 standard deviation of the data [SD]) after bottom contact. A bottom time of 10 minutes was chosen to accommodate likely extremes and also to allow 6 deployments per 2-h tape (20 min per deployment × 6 deployments). With two cameras, 12 deployments per day could be made without changing tapes. The maximum number of longline sets was limited to four per day, based on three camera deployments per longline set.

Types of data

Species presence, total number of individuals per species, and the number of hooks lost were recorded for each longline set. Species presence and duration of squid bait attachment to the bait container (BTM) were recorded for each video sequence. In addition, for each video sequence, three indices of abundance were scored for each species taped: maximum number (MAXNO); time to first appearance (TFAP); and total duration in sequence (TOTTM). The MAXNO index was determined as the peak number of a species visible at any one time (maximum interval one second) during a deployment. Fork length (FL) to the nearest 0.1 centimeter (cm) was recorded for fish caught on the longline. The FL of opakapaka observed on video was estimated and rounded to the nearest 5 cm by comparing fish swimming in the plane of the bait container with the known size of the container.

Statistics

An average maximum number of fish recorded for data collected in 1992 was calculated for each of nine sequences (three video stations) by using a mean weighted by the duration of each occurrence:

$$\overline{X}_W = \frac{\sum_{h=1}^{n} X_h \cdot N_h}{N}, \quad (1)$$

where $\overline{X}_W$=the weighted average maximum number of fish, n=total number of occurrences, X_h= maximum number of fish seen in the hth occurrence, N_h=duration (s) of the hth occurrence, and $N=\Sigma N_h$= 600 s.

Video indexes were calculated as means (of up to 3 deployments) to standardize for multiple deployments per station. Video indices were derived in two logarithmic forms—mean of logs (ML),

$$ML = \frac{\sum_{i=1}^{n} \ln(x_i + 1)}{n}, \quad (2)$$

and log of means (LM),

$$LM = \ln\left[\left(\frac{\sum_{i=1}^{n} x_i}{n}\right) + 1\right], \quad (3)$$

where x_i = individual datum for a variable (i.e., the value for the variable MAXNO, TFAP, or TOTTM for each deployment at a station) and n=number of deployments per station. The longline index consisted of log-transformed individual set data [ln (catch +

1)]. The number of stations where each species was caught or seen was also tallied for each gear type. For nonzero mean data collected in 1993, the best form of the video index (*LM'*, see Results section), was calculated as follows:

$$LM' = \ln\left[\left(\frac{\sum_{i=1}^{n} x_i}{n}\right)\right], \quad (4)$$

where x_i = individual datum for MAXNO and n=number of deployments per station.

A matrix of Pearson's correlation coefficients was calculated for 1992 data (SAS, 1987) with the log-transformed variables to detect interrelationships among all the video and longline indices. Spearman's rank correlations were also calculated and compared. Multiple linear regression (SAS, 1987) was used to estimate the effect of competition between opakapaka and puffers for longline hooks on the basis of the following model:

$$Y = \beta_1 X_1 + \beta_2 X_2 + \varepsilon, \quad (5)$$

where Y=ln (opakapaka video MAXNO), X_1=ln (no. hooks lost + no. puffers caught), and X_2=ln (number of opakapaka caught). The model was run as a forward regression without an intercept and with an entry level for significance equal to $P \leq 0.10$. The precision (repeatability) of video and longline was described by the coefficient of variation (V, Sokal and Rohlf, 1981; Zar, 1984):

$$V = \left(\frac{SD}{\text{mean}}\right) \times 100(\%), \quad (6)$$

where SD is the standard deviation.

Longshore station and relative depth effects for 1993 data were analyzed by using standard parametric and nonparametric procedures (SAS, 1987).

Sample size and power analysis

We evaluated video and longline data in a power analysis for the t-test of means. Specifically, we estimated the sample sizes required to detect a twofold change in abundance by using either sampling method. Skalski and McKenzie (1982) set a precedent for use of the criterion of twofold change in environmental monitoring studies; annual variations much larger than this are typical for marine fishes (Hennemuth et al., 1980; Francis, 1993). The effect size (ES) was calculated as follows:

$$ES = \frac{0.693}{SD}, \quad (7)$$

where 0.693= $|\pm$ twofold difference in $\bar{x}|$ for the natural log ($\bar{x}$) and SD is the standard deviation. Cohen (Tables 2.3.4 and 2.4.1, 1988) was consulted for the requisite sample sizes. The ES for each gear was evaluated at ß=0.20, power (1–ß)=0.8, and α_2=0.05. For the 1993 data, ES was also evaluated at α_2=0.1.

Results and discussion

Sample composition

The mean time to first appearance (TFAP) of opakapaka for 1992 video tapes with opakapaka present (all islands included) was 203 ±165 (SD) seconds. The total time (TOTTM) of opakapaka during a deployment averaged 122 ± 133 seconds. The maximum number (MAXNO) of opakapaka appeared on tape at approximately 354 (±153) s, based on the nine video sequences for which the weighted average MAXNO ($\bar{X}_W$) was calculated. These data confirm our initial choice of a 10-min bottom time.

In 1992, only windward Oahu data were used for comparisons and statistical analyses, because the opakapaka measures from Maui and Kauai included large percentages (92% and 67%) of "double-zeros" (zero longline catch, zero fish recorded). Catches of *P. filamentosus* also were greatest for the windward Oahu site; 54 of the 58 juvenile opakapaka were longlined off windward Oahu. Puffers were prevalent at windward Oahu and at Maui. Both longlined and video-recorded opakapaka were juvenile size (13 to 21 cm FL, and 15 to 25 cm FL, respectively; Kikkawa, 1984; Moffitt and Parrish[4]).

Frequency of occurrence data and total number of species differed between longline catches and video records (Fig. 3). Puffers ranked first in abundance and opakapaka second in both the longline and video data. Video cameras recorded the presence of opakapaka and puffers more often than did the longlines (Fig. 3). Video tapes also recorded a greater diversity of species (Table 1), suggesting greater accuracy of the video system. Fish that were not caught by the longline but were seen on video included reef-associated species (e.g. pennant butterflyfish, *Heniochus diphreutes*, and whitesaddle goatfish, *Parupeneus porphyreus*, sharks (*Carcharhinus* sp.), and rays (*Dasyatis* sp.). Longlines also undersampled the lizardfish, *Trachinocephalus myops* (Fig. 3), a major component of this deep-water, soft-bottom fish assemblage.[5] No major differences in species composition occurred in video surveys from 1992 and 1993.

1992 video-longline relations

The MAXNO index for opakapaka and puffers was highly correlated with the total duration on film

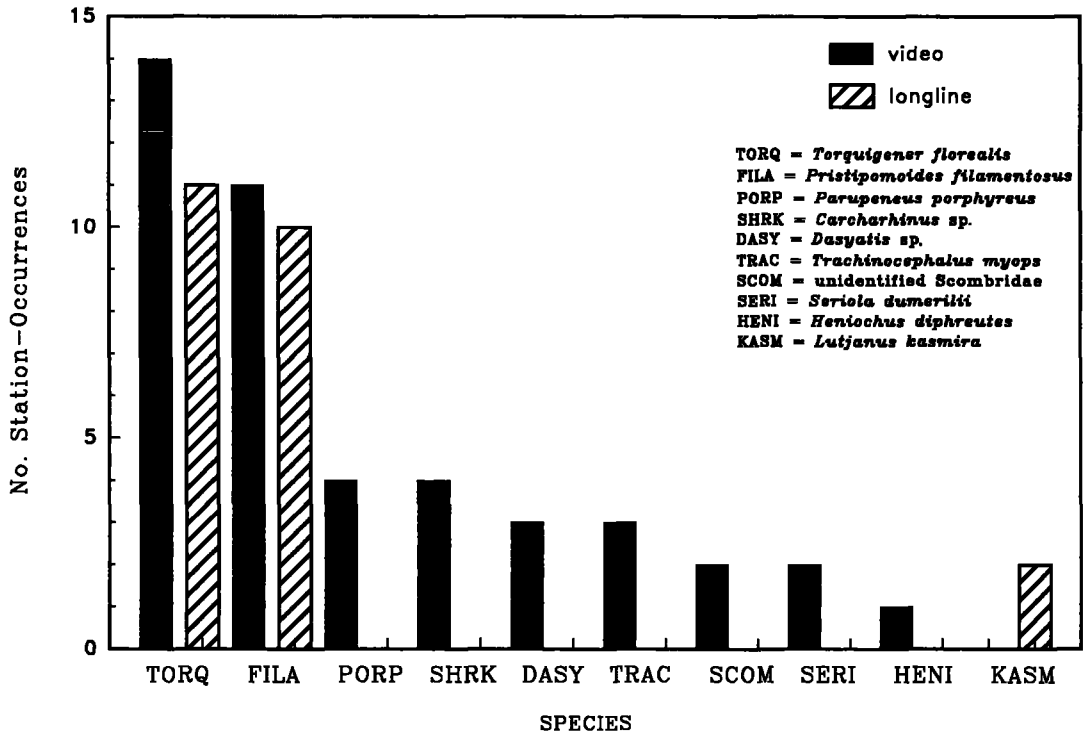

Figure 3

Frequency of occurrence of ten common species on video camera deployments and longline sets conducted during 1992 off windward Oahu (n=15 stations). Refer to Table 1 for common names.

Table 1

Total numbers of fish seen and caught at 15 video and longline stations located off windward Oahu during 1992. Total number for a fish taxon for video stations is the sum of the maximum numbers seen on 38 films. Total number for longline stations is the number of fish caught.

Species	Common names	Video	Longline
Torquigener florealis	Bleeker's balloonfish	221	80
Pristipomoides filamentosus	Pink snapper (opakapaka)	94	54
Heniochus diphreutes	Pennant butterflyfish	25	—
Parupeneus porphyreus	Whitesaddle goatfish	10	—
unidentified Scombridae	Tuna or mackeral	6	—
Trachinocephalus myops	Lizardfish	5	—
Carcharhinus sp.	Shark	4	—
Sphyrna sp.	Hammerhead shark	4	—
Seriola dumerilii	Amberjack	3	—
Dasyatis sp.	Stingray	3	—
Chaetodon miliaris	Milletseed butterflyfish	3	—
unidentified teleosts	Bony fish	2	—
Parupeneus pleurostigma	Sidespot goatfish	1	—
Sufflamen fraenatus	Bridle triggerfish	1	—
Canthigaster rivulata	Maze toby	1	—
Parupeneus sp.	Goatfish	1	—
Lutjanus kasmira	Bluestripe snapper	—	3

(TOTTM) and time to first appearance (TFAP) of the respective species (Table 2, LM form). The duration of squid bait (BTM index) was significantly correlated with the MAXNO index and the other video indices for opakapaka but was more strongly correlated with the MAXNO index for puffers (Table 2). Videos indicated that puffers were usually responsible for the removal of the squid bait; a direct relationship between puffer numbers and the rate of bait disappearance was evident. Spearman's rank correlations mirrored the parametric correlations.

After log-transformation, the data pairs were approximately bivariate normal. Among all the video indices, MAXNO was best correlated with lnCPUE (LLNO) for opakapaka (Table 2). The ML and LM forms of the MAXNO video index were compared separately with the longline CPUE, and the LM form provided a slight but consistently better Pearson's correlation than did the ML form for both opakapaka and puffers. Therefore, the LM form of the MAXNO index was used for all further parametric comparisons and analyses.

The MAXNO-CPUE relationship was approximately linear (Fig. 4A), and its residual plot showed neither discernible pattern nor slope (P=1.0, Fig. 4B). If all double-zero data are deleted, the correlation between video MAXNO and longline CPUE loses significance (r=0.55, P=0.08, n=11). However, the double-zero data were retained in subsequent analyses because there was no a priori reason to believe they did not represent real absences.

The observed magnitude of hook loss ($\bar{x}$=32%) indicates that longline CPUE is fundamentally inaccurate and biased for sampling this habitat and species assemblage. Apparently, most hook loss occurred when puffers bit through the leader above the hook. Hook competition is often a problem with longlines when hooked fish begin to saturate available hooks (Rothschild, 1967). Removal of hooks has a similar effect. A multiple linear regression with two descriptive variables, a puffer factor (X_1) equal to the number of hooks lost plus puffer catch and opakapaka catch (X_2), was run to determine the effect of puffers on the relation between longline CPUE and the video MAXNO index for opakapaka. X_1 and X_2 were first determined to be uncorrelated (r^2=0.02, P=0.62). The model (Eqn. 5) for the multiple regression was forced through the origin, because neither sampling device could record the presence of fish in its absence. The total variation in the opakapaka video index explained by the model was 87% (R^2=0.87, P<0.001). Opakapaka longline CPUE explained 83% of the variation (r^2=0.83, P<0.001), and the puffer factor explained an additional 4% of the variation (r^2=0.04, P=0.07). The latter observation suggests that the puffer factor might strongly influence video-longline relations for opakapaka at times of relatively high puffer abundance.

Precision for longline and video cameras was separately examined. For both opakapaka and puffers, cameras had nominally but consistently better precision (V=81% and 48%) than did longline CPUE (V=91% and 71%).

Table 2

Correlation between log-transformed mean video indices (LM) and log-transformed longline catch per unit of effort (lnCPUE) from the 1992 windward Oahu site (n=15 stations). Pearson correlation coefficients (r) are displayed above their respective P-values (Prob> $|R|$, H_0: Rho=0) for *Pristipomoides filamentosus* and *Torquigener florealis*. MAXNO = maximum number seen on tape; TOTTM=total duration of a species on tape; TFAP=time to first appearance of a species; BTM=duration of external squid bait; and LLNO=longline CPUE.

	TOTTM	TFAP	BTM	LLNO
Pristipomoides filamentosus				
MAXNO	0.9665	−0.9143	−0.5748	0.7855
	0.0001	0.0001	0.0250	0.0005
TOTTM		−0.8500	−0.5681	0.7285
		0.0001	0.0271	0.0021
TFAP			0.5729	−0.6467
			0.0256	0.0092
BTM				−0.2982
				0.2803
Torquigener florealis				
MAXNO	0.9465	−0.5770	−0.6654	0.5365
	0.0001	0.0243	0.0068	0.0392
TOTTM		−0.6030	−0.5902	0.5932
		0.0173	0.0205	0.0198
TFAP			0.5141	−0.1143
			0.0499	0.6851
BTM				−0.5193
				0.0473

1993 video statistics

The MAXNO video index did not differ between shallow and deep positions (Student's t=0.27, P=0.79; Kruskal-Wallis χ^2=0.09, P=0.76) in May 1993 (Fig. 5). The mean MAXNO data lack a monotone trend over stations (P=0.5), even though raw MAXNO values were atypically large at several stations (χ^2=28.0, P=0.04; Fig. 5). Overall, however, dependence among stations was absent and neither precluded simple t-tests of the means nor power estimates for tests of the means.

Power analysis

Power was estimated for opakapaka abundance indices. Sample sizes for longline and video gear would

be limited in practice by the duration and availability of a large research vessel (a maximum of five days at one location) and by estimates of maximum effort attainable for each gear. The latter considered the time needed for deployment, retrieval, and processing of specimens for longlines and the time required for video camera battery and tape changes. The estimated upper limit for sample size was 30 stations (at 6 stations per day) for both the longline and the video cameras; a video station consisted of three camera deployments. All 1992 data from windward Oahu (n=15 stations) were analyzed first. Sample sizes of 26 stations for video and 33 stations for longlines were estimated as necessary to detect a twofold change in numbers of juvenile opakapaka.

Power was next estimated by using only those 1992 windward Oahu stations with the full complement of three deployments (n=10). The variability (V=81%) of the video MAXNO index at these 10 stations (3 deployments inclusive) did not differ from the total Oahu data set. A sample size of 17 stations (51 deployments) was estimated as necessary to detect a twofold change in the MAXNO index, within the practical limit of 30 stations. The estimated sample size for longline, based on data for these same 10 stations, was still 33 stations, slightly over the limit of 30 stations.

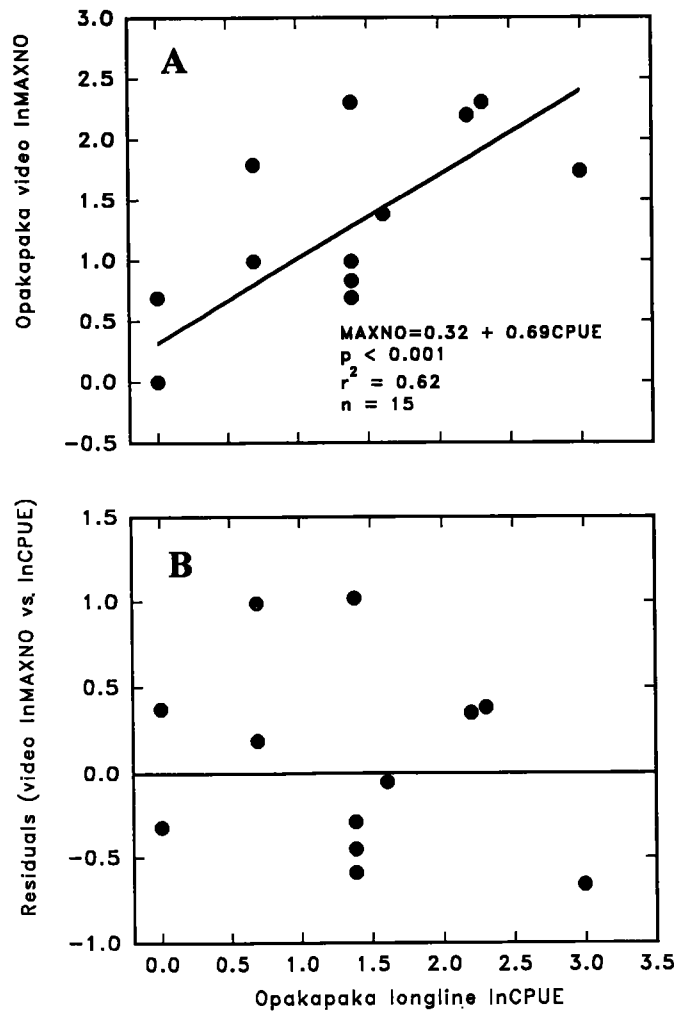

Figure 4

(A) Scatterplot and fitted regression line for the video index maximum number seen (lnMAXNO) and longline lnCPUE for *Pristipomoides filamentosus* (opakapaka) for 1992 data. Four double-zero observations were coincident. (B) Plot of residuals from the video versus longline regression of Fig. 4A versus longline lnCPUE for 1992 data; zero line is included. Four points were coincident as in 4A.

Power was next reexamined to determine the effect of reducing effort to two video deployments per station, rather than to three. By using only the shallow and deep sets of the 10 1992 stations with three complete deployments, variability improved slightly (V=76%), and only 18 stations (36 deployments) were estimated as necessary to detect a twofold change for opakapaka. Video MAXNO remained significantly correlated with longline CPUE for opakapaka by using two deployments per station (r=0.66, P=0.04, n=10).

The 18 pairs of 1993 video data were used to reevaluate power and sample size for a smaller, more homogeneous study area. The LM' form of the video MAXNO index was used to avoid possible bias introduced by adding a constant to the data. The calculations used 17 pairs of deployments because the mean of one data pair was zero, the log of zero being undefined. Variability (V) for the 1993 data improved to 49% with these refinements. Twenty-two stations were estimated as necessary to detect a twofold change in abundance at α_2=0.05. If α_2 were relaxed to 0.1, 17 stations would be necessary to detect a twofold change. In practice, slightly greater numbers of samples would be necessary, because deleting the single zero-mean datum artificially inflated our power estimate. Nonetheless, the 1993 samples provide the best data for evaluating precision that are presently available.

Comparison with other baited camera studies

Previous baited camera studies of deep-sea species (Priede et al., 1990; Armstrong et al.,

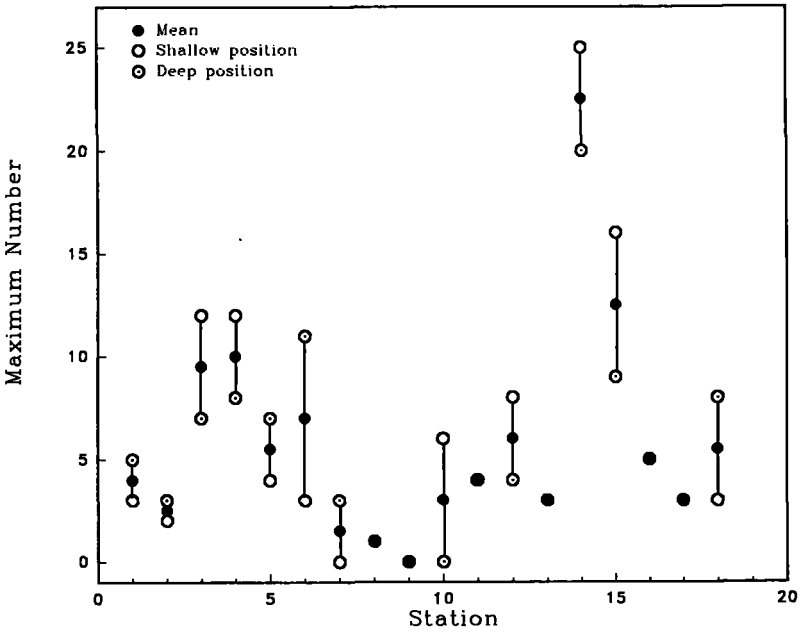

Figure 5

Scatterplot of maximum number of opakapaka observed (MAXNO) for shallow and deep positions and their mean by stations for data collected during May 1993. Stations are ordered in geographic sequence from farthest southeast (sta. 1) to farthest northwest (sta. 18). Means with component data hidden represent coincident shallow and deep values.

1992) observed that, although time of arrival of the first fish (TFAP) was strongly related to estimated fish densities, the maximum number of fish seen at a station (MAXNO) either was unrelated or inversely related to densities. Our observation that MAXNO was highly correlated with an abundance estimate (CPUE) may at first seem contradictory to these prior findings. However, there are important differences between our methods and those of previous studies: previous deep-sea work operated in unproductive depths >2,000 m and cameras recorded data for at least 11 hours per station, whereas our study was limited to productive depths ≤100 m for which a relatively short soak time (10 min) was sufficient. In the deep-sea studies, all bait was open to consumption. The partly internal bait of our system created a reservoir of odor that persisted for the soak duration in most cases; puffers removed all bait in only 3 out of 75 deployments. Differences in rates of bait consumption between the two deep-sea stations and resulting variations in bait attractiveness may have contributed to the disparity between MAXNO and fish density in the deep-sea studies.

The MAXNO and TFAP indices in our study were highly correlated (Table 2). This correlation suggests that the greater the density, the faster the fish arrive at the bait. These data agree with the observations of Priede et al. (1990), where fish arrived at the camera faster at the station with presumed higher densities. Since the MAXNO and TFAP indices were both significantly correlated with CPUE in our study (Table 2), the MAXNO index was chosen as the best index of abundance because it had the better correlation. A persistent bait source and short soak time may have contributed to this stronger correlation. In the future, the use of MAXNO as an index of abundance should be reevaluated separately for each species and application.

Conclusions

Video cameras provide an accurate tool for sampling juvenile opakapaka, and the video MAXNO variable provides a relatively precise and accurate index of abundance. Based on 1993 data for a series of two camera deployments per station, minima of 17 to 22 pairs of deployments (34–44 sets) per study area would be necessary to detect a twofold change in juvenile opakapaka numbers (at α_2=0.1, 0.05, respec-

tively). This could be accomplished within practical time limits (3–5 days) by using a large research vessel with two auxiliary small craft. If specimens are not needed—e.g. for age-growth studies—the video assembly described seems to be an ideal sampling technique for obtaining an index of abundance for comparisons between different areas or between different times, or between both. Additionally, video cameras can provide important, new information on habitat and behavior of juvenile opakapaka and associated species, an important aspect of our continuing research.

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Evolution of cytochrome *b* in the Scombroidei (Teleostei): molecular insights into billfish (Istiophoridae and Xiphiidae) relationships

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Abstract.—The suborder Scombroidei (Teleostei) has an extensive taxonomic history which traces its beginnings to at least 1832 (Cuvier and Valenciennes). However, a single well-corroborated phylogenetic hypothesis for the scombroid fishes does not exist. To date, efforts to define this suborder and determine the interrelationships of its constituent taxa have utilized morphological data almost exclusively. In this paper we present a molecular data set for addressing scombroid relationships: DNA sequences from the mitochondrial gene cytochrome *b*. These data provide valuable insights into scombroid relationships, especially regarding the long-standing debate over the placement of the billfishes (Istiophoridae and Xiphiidae). The cytochrome *b* data strongly refute a close relationship between Scombridae and billfishes and also support separation of the billfishes from the Scombroidei. In addition, these data suggest a new hypothesis on the evolutionary relationships among istiophorid billfishes.

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Fishery Bulletin 93:78–96 (1995).

The suborder Scombroidei is a well studied assemblage of more than 100 marine teleosts. A consensus on the taxonomic limits and intrarelationships of this group remains elusive despite more than 150 years of study (Cuvier and Valenciennes, 1832; Regan, 1909; Gregory, 1933; Berg, 1940; Fraser-Brunner, 1950; Collette et al., 1984; Johnson, 1986; Potthoff et al., 1986; Block et al., 1993). In 1832, Cuvier and Valenciennes proposed the Scombroidei as a natural group containing the oilfishes and snake mackerels (family: Gempylidae), the cutlassfishes (Trichiuridae), and the "tunnies" (Scombridae). Regan (1909) expanded the Scombroidei by adding three families: Istiophoridae (marlins, sailfish, and spearfishes); Xiphiidae (the swordfish); and Luvaridae (the louvar). Most subsequent classifications agree that the monotypic Luvaridae is not a scombroid but an acanthuroid (Leis and Richards, 1984; Tyler et al., 1989). However, there is substantial disagreement over the relationships of the families Istiophoridae and Xiphiidae, collectively known as billfishes.

In the last ten years three morphological studies have proposed three different hypotheses on the relationships of billfishes. In 1984, Collette et al. published a scombroid phylogeny based on 40 morphological characters (Fig. 1). They proposed that billfishes are the sister group of the Scombridae. Their cladogram suggested that several synapomorphies unite billfishes and scombrids, including a pharyngeal toothplate stay, a pair of lateral keels on the caudal peduncle, and the extension of the caudal-fin rays to cover the hypural plate. However, the position of billfishes was not strongly defined in the Collette et al. study because of homoplasious character evolution. Of the twelve character-state transitions that occurred within the billfish lineage on their cladogram, five were reversals to the primitive state, and six occurred independently in other lineages. Collette et al. (1984) considered the placement of billfishes within the suborder Scombroidei to be uncertain and conditional upon additional evidence. They cited larval evidence (Potthoff et al., 1986) which indicates that the scombroid families Scombridae, Gempylidae, and Trichiuridae are closely related to each other and are distantly related to billfishes. We will refer to the Collette et al. hypothesis as the scombrid sister group hypothesis.

In 1986, Johnson published a scombroid phylogeny using many of the characters from the Collette et

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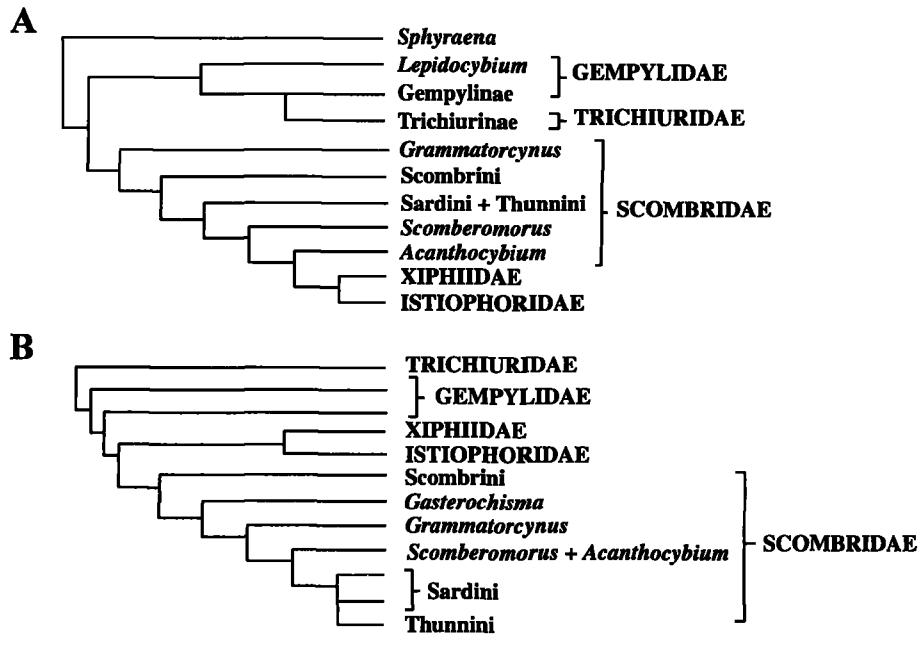

Figure 1

Two phylogenetic hypotheses for the scombroid fishes based on morphological evidence. The studies of (**A**) Johnson (1986) and (**B**) Collette et al. (1984) are examples of the scombrid-subgroup and the scombrid-sister group hypotheses of billfish (Istiophoridae and Xiphiidae) relationships. Johnson (1986) considered billfishes a subgroup of the family Scombridae most closely related to the wahoo, *Acanthocybium solandri*. Collette et al. (1984) placed the billfishes as a sister group to the Scombridae. Both hypotheses propose that billfishes and scombrids share a common ancestor to the exclusion of other scombroids. An alternative hypothesis for billfish relationships is that billfishes are not scombroids. This hypothesis has never been depicted explicitly in the form of a cladogram (Gosline, 1968; Nakamura, 1983; Potthoff et al., 1980; Potthoff et al., 1986).

al. (1984) study and several additional characters (Fig. 1). Like Collette et al., Johnson proposed that billfishes and scombrids compose a monophyletic group, but he regarded billfishes as a subgroup of the Scombridae. A critical piece of evidence supporting this hypothesis that billfishes are a derived group within scombrids is the presence of cartilaginous interconnections between gill filaments in billfishes and the scombrid *Acanthocybium solandri*. Based largely on this proposed synapomorphy, Johnson placed Istiophoridae and Xiphiidae as derived scombrids and *Acanthocybium* as their sister group. This association has been suggested by others (Lütken, 1880; Fraser-Brunner, 1950). However the position of billfishes in Johnson's study was only weakly supported because of homoplasy. For example, five of the ten character-state transitions that support billfish monophyly on Johnson's cladogram are reversals. We will refer to the Johnson hypothesis as the scombrid subgroup hypothesis.

Other workers have proposed that billfishes are not scombroids. In 1986, Potthoff et al. published a study of bone development in scombroids in which they discussed scombroid phylogeny. They concluded that billfishes are not scombroids because of their lack of resemblance to other scombroids in vertebral number and osteological development. They suggested that these characters indicate billfish affinities to the percoids. This hypothesis has been suggested in previous studies (Potthoff et al., 1980; Nakamura, 1983). We will refer to this hypothesis as the nonscombroid hypothesis.

It is evident from the morphological studies that there has been a great deal of homoplasious morphological evolution in billfishes. Therefore, it is difficult to reconstruct the evolutionary relationships of this group based on morphology alone. In an attempt to derive additional, independent data on scombroid intrarelationships and, in particular, to address the position of billfishes, we compiled a mo-

lecular data set that consists of DNA sequences from the mitochondrial gene cytochrome *b*. This gene codes for a functionally conserved protein that should facilitate sequence alignment over ancient divergences. Additionally, it has been used to examine both intraspecific genealogy (Finnerty and Block, 1992) and much deeper phylogenetic questions such as the origin of the mammalian orders (Irwin et al., 1991). The initial scombroid radiation probably occurred in the Paleocene epoch (Bannikov, 1985; Carroll, 1988). Therefore, cytochrome *b* sequence should be phylogenetically informative about divergences within the suborder.

The analysis presented in this paper builds on our earlier molecular study (Block et al., 1993). However, we have improved on the previous study in several ways which allow us to directly test the competing hypotheses of billfish relationships. First, we have obtained sequences from additional outgroups. The inclusion of presumably more distant outgroups permits us to address the question of scombroid monophyly. This is important because the nonscombroid hypothesis of billfish relationships argues that the Scombroidei is not a monophyletic group. Second, we include sequence information from the scombrid *Acanthocybium*, a taxon which is integral to the scombrid subgroup hypothesis. Third, we utilize statistical tests to directly compare different hypotheses of billfish relationships. Finally, we emphasize character-state changes that accrue relatively slowly in order to minimize the effects of phylogenetic noise.

Materials and methods

Samples

Partial cytochrome *b* sequences (590 base pairs) were obtained from 75 individuals representing 34 species of perciform fishes: 30 scombroid species and four putative outgroup taxa (*Sphyraena*, *Coryphaena*, *Mycteroperca*, and *Morone*; Table 1). We included *Sphyraena* based on the placement by Johnson (1986) of this taxon as the most primitive member of the Scombroidei. Several percoid taxa (*Coryphaena*, *Mycteroperca*, and *Morone*) were included because of the suggestion by some authors that billfishes are percoids (Gosline, 1968; Potthoff et al., 1980; Nakamura, 1983; Potthoff et al., 1986). Published cytochrome *b* sequences from two cypriniform fishes obtained from Genbank were used to root the phylogenetic analysis (*Crossostoma lacustre* [Tzeng et al., 1990] and *Cyprinus carpio* [Chang, 1994]). We verified the outgroup status of the cyprinids by first conducting a phylogenetic analysis using published sequence from the sturgeon *Acipenser transmontanus*, a holostean, to root a parsimony analysis. We attempted but were unable to obtain full length sequences (590 base pairs) from two fixed and preserved specimens of *Scombrolabrax heterolepis* possibly because of DNA degradation in these specimens.

DNA extraction

DNA was obtained from frozen tissue samples of the mitochondria-rich "heater tissue" (found in Istiophoridae, Xiphiidae, and *Gasterochisma melampus*; Block, 1986), red muscle, white muscle, or liver. Digestion of 0.1–0.6 g tissue was performed in ten volumes of extraction buffer containing 100 mM Tris Cl (pH 8.0), 10 mM EDTA, 100 mM NaCl, 0.1% SDS, 50 mM DTT, and 0.7 mg/mL proteinase K. Digestion proceeded for 2–4 hours at 41°C. The homogenate was extracted twice with equal volumes of phenol (pH 8.0), once with 1:1 phenol/chloroform, and once with chloroform. The final extract was precipitated with 1/9 volume of 3M sodium acetate (pH 5.2) and 2.5 volumes of 100% ethanol.

DNA amplification and sequencing

The polymerase chain reaction (PCR) was used to amplify a 700 base pair region of cytochrome *b*. A 305 base pair segment (not including primers) was generated by using published oligonucleotide sequences (Kocher et al., 1989). We amplified an overlapping, 425-bp region farther downstream with primers L15079 (5'-GAGGCCTCTACTATGGCTCTTACC-3') or L15080 (5'-CGAGGCCTTTACTACGGCTCTTACCT-3') and H15497 (5'-GCTAGGGTATAATT GTCTGGGTCGCC-3'). Double stranded amplification was performed in a 100-µL volume containing 50 mM KCl, 10 mM Tris-HCl (pH 8.3), 1.5–3.0 mM MgCl, 200 µM of each dNTP, each primer at 1 mM, 1 µg of template DNA, and 2 units of Amplitaq DNA polymerase (Perkin-Elmer/Cetus). Most templates were amplified through thirty cycles of PCR [1 minute denaturation (92–95°C), 1 minute annealing (40–50°C), and 3 minutes extension (72°C)] on an Ericomp thermal cycler. Alternatively, PCR was performed on a DNA Thermal Cycler 480 (Perkin-Elmer) with the following temperature cycling regime: 5 cycles of 1 minute denaturation at 95°C, 1 minute primer annealing at 40°C, 1:30 ramp to 72°C, and one minute extension at 72°C, followed by 25–35 cycles with an annealing temperature of 45°C. An 18-µL aliquot of the double stranded product was run by means of electrophoresis through a 1X TBE 1% agarose gel (Sea Plaque, FMC) at 5 V/cm for 45 minutes. A single stranded template was produced by asymmetric PCR (Gyl-

Table 1

Partial cytochrome b sequences (590 base pairs) were obtained from 34 perciform fishes, including 30 scombroid species. Published cytochrome *b* sequences were also obtained from Genbank for two cypriniform fishes.

Order and suborder[1]	Family and species	Common name	*n*	Locales[2]
Perciformes:Scombroidei	Istiophoridae			
	Istiophorus platypterus	sailfish	2	A, P
	Makaira indica	black marlin	2	I
	Makaira nigricans	blue marlin	8	A, P
	Tetrapturus albidus	white marlin	2	A
	Tetrapturus angustirostris	shortbill spearfish	2	P
	Tetrapturus audax	striped marlin	3	P
	Tetrapturus belone	Mediterranean spearfish	2	M
	Tetrapturus pfluegeri	longbill spearfish	1	A
	Xiphiidae			
	Xiphias gladius	broadbill swordfish	6	A, P
	Scombridae			
	Acanthocybium solandri	wahoo	3	A
	Scomberomorus cavalla	king mackerel	1	A
	Scomberomorus maculata	Spanish mackerel	2	A
	Gasterochisma melampus	butterfly mackerel	3	T
	Auxis thazard	frigate mackerel	2	P
	Euthynnus affinis	kawakawa	2	P
	Euthynnus alletteratus	little tunny	2	A
	Katsuwonus pelamis	skipjack tuna	2	P
	Thunnus alalunga	albacore tuna	2	P
	Thunnus albacares	yellowfin tuna	2	P
	Thunnus maccoyii	southern bluefin tuna	2	T
	Thunnus obesus	bigeye tuna	2	P
	Thunnus thynnus	northern bluefin tuna	2	A
	Sarda chiliensis	eastern Pacific bonito	1	P
	Sarda sarda	Atlantic bonito	2	A
	Scomber scombrus	Boston mackerel	2	A
	Scomber japonicus	chub mackerel	2	P
	Gempylidae			
	Gempylus serpens	snake mackerel	2	P
	Lepidocybium flavobrunneum	escolar	2	P
	Ruvettus pretiosus	oilfish	2	A
	Trichiuridae			
	Trichiurus lepturus	scabbard fish	3	A
Perciformes:Percoidei	Coryphaenidae			
	Coryphaena equiselis	pompano dolphin	2	P
	Serranidae			
	Mycteroperca interstitialis	yellowmouth grouper	1	A
	Percichthyidae			
	Morone saxatilis	striped bass	1	P
Perciformes:Sphyraenoidei	Sphyraenidae			
	Sphyraena sphyraena	Atlantic barracuda	1	A
Cypriniformes	Balitoridae			
	Crossostoma lacustre	hillstream loach	Tzeng et al., 1992	
	Cyprinidae			
	Cyprinus carpio	carp	Chang et al., 1994	

[1] Eschmeyer, 1990.

[2] A=Atlantic ocean; P=Pacific ocean; I=Indian ocean; T= Tasman sea; M=Mediterranean Sea.

lensten and Erlich, 1988) carried out in a 100-μL volume containing the same reactants as the initial PCR but using 10 μL of the dissolved gel band and reducing one primer concentration 100-fold. The product was washed by centrifugal dialysis with sterile water in Centricon microconcentrators (Amicon) to remove excess dNTP's. Sequencing was performed with the Sequenase kit (United States Biochemical, Cleveland, Ohio) by using the limiting primer from the asymmetric PCR reaction. Data from eight species were obtained by directly sequencing double-stranded PCR products. The template was purified prior to sequencing (either directly from the PCR reaction mix or following excision of the appropriate band from low-melt agarose) with Magic PCR Preps (Promega). Sequencing was performed with the Sequenase kit according to the specifications of Casanova et al. (1991). Sequences from *Mycteroperca* and *Morone* was obtained after first cloning the PCR products in pGEM t-vector (Promega) according to the manufacturer's instructions. Transformation was carried out by using XL–1 blue cells. Two positive clones were selected for each PCR product. Double-stranded sequencing (Sequenase 2.0) was performed following alkaline denaturation as recommended by the manufacturer. Sequence was obtained from both strands of the amplified fragment for all individuals.

Analysis

Sequences were aligned by using the MacVector program (IBI Biotechnologies). Maximum parsimony analysis was performed with PAUP 3.1. (Swofford, 1991). Neighbor-joining (Saitou and Nei, 1987) and UPGMA dendograms were constructed with Phylip 3.5 (Felsenstein, 1993). The strength of support for various nodes was assessed by using the bootstrap analysis (Felsenstein, 1985). Specific conditions for each analysis are contained in the figure legends.

Competing phylogenetic hypotheses were compared by using the "enforce topological constraints" option of PAUP 3.1. This option allowed us to determine the length difference between the most parsimonious trees that support each hypothesis. The cladistic permutation test for monophyly and nonmonophyly (Faith, 1991) was then used to ascertain whether the more parsimonious hypothesis is significantly better than the competing hypothesis according to the criterion of parsimony. The test was performed as follows. The actual length difference between trees supporting the two opposing hypotheses was obtained. Then 99 permuted data sets were constructed from the original data set by randomly shuffling the character states for each character. We then obtained the length difference between trees supporting the two opposing hypotheses for each permuted data set. If the actual length difference was matched or exceeded fewer than 5 times in all 100 data sets (the original data set plus 99 permuted data sets), then the more parsimonious hypothesis was considered to be significantly better than the less parsimonious hypothesis. This corresponds to a topology-dependent permutation tail probability, or T-PTP, of less than or equal to 0.05.

The effects of character weighting on parsimony analysis were assessed by EOR weighting (Thomas and Beckenbach, 1989; Knight and Mindell, 1993): each type of nucleotide substitution was weighted according to the ratio of its expected number of occurrences divided by its observed number of occurrences, or EOR. There are six types of nucleotide substitutions if we disregard the direction of change: A⇔G, C⇔T, G⇔T, G⇔C, A⇔T, and A⇔C. The observed number of each substitution type was obtained through pairwise sequence comparisons. Pairwise comparisons were performed between sets of sister species (sister species were identified through an initial unweighted phylogenetic analysis; see Fig. 2). Sister-species comparisons were used for two reasons. First, within a clade, sister species will tend to represent relatively recent speciation events. This recency lessens the chance that multiple substitutions have occurred at the same site and that more recent substitutions obscure older ones. Second, all comparisons between pairs of sister species are mutually independent. Therefore, if we restrict our comparisons to sister species, we cannot count the same base substitution twice.

We modified the method of Knight and Mindell (1993) to derive the expected number of substitutions in each class. This method accounts for differences in the frequencies of the four nucleotides that greatly influence the expected frequency of each substitution type. For instance, if guanine residues are very rare, then substitutions of other nucleotides for guanine will also be rare. The L-strand base composition of cytochrome *b* in scombroid fishes is strongly skewed (Table 2), as it is in other groups examined (for example, Irwin et al., 1991). Cytosines and thymidines each compose nearly 30% of the total nucleotide population whereas guanines compose less than 16%. In order to incorporate knowledge of the base composition into our derivation of the expected number of each substitution type, we proceeded as follows. First, the average frequency of each nucleotide (f) was obtained for all species used in the pairwise sequence comparisons. Second, the observed number of each substitution type ($S_{O[i \Leftrightarrow j]}$), where i and j represent two different nucleotides, was obtained by summing the results from all pairwise comparisons of

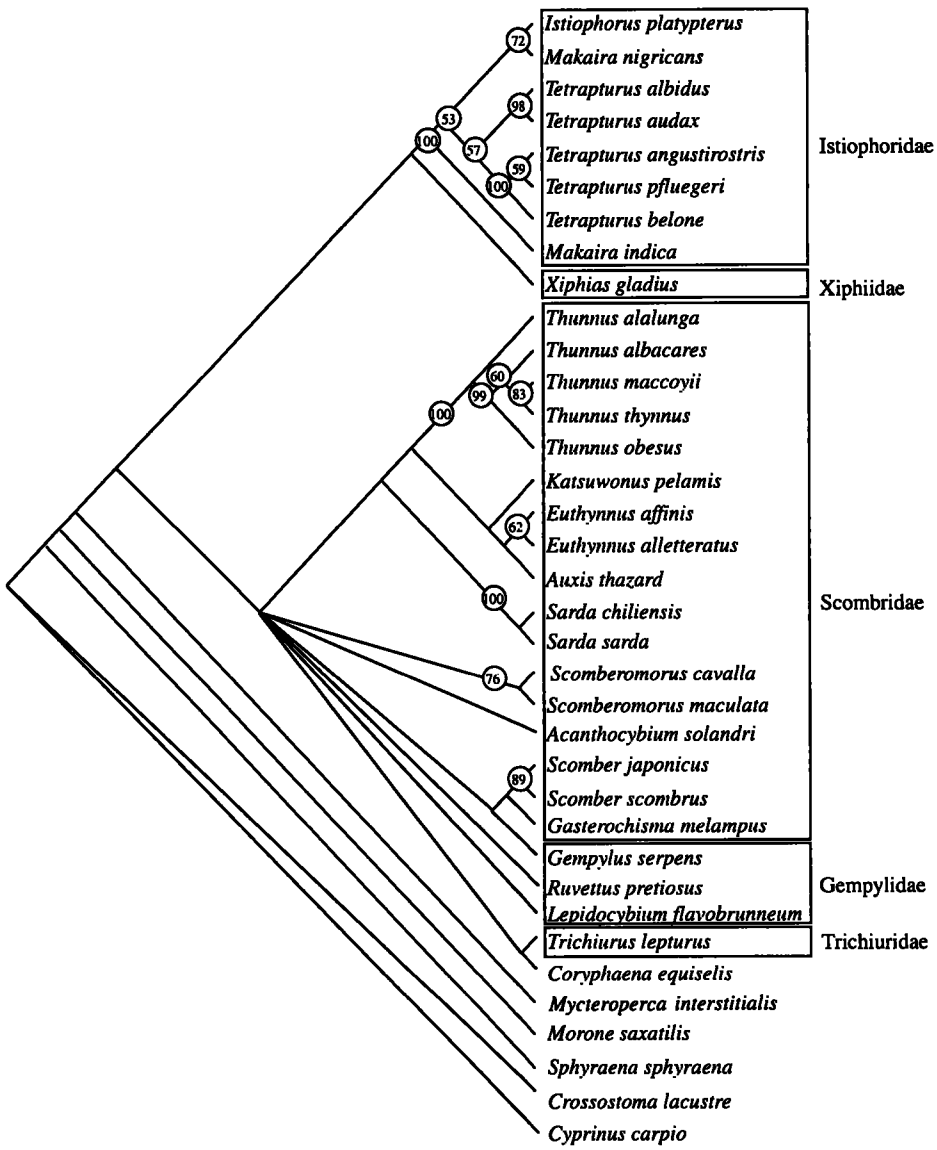

Figure 2

Phylogeny of the Scombroidei based on an unweighted analysis of 248 phylogenetically informative nucleotide sites. The cladogram depicted is a strict consensus of four equally parsimonious trees identified by using a heuristic search procedure on the program PAUP 3.1. (Swofford, 1991): TBR (tree bissection and reconnection) branch swapping was performed on 10 starting trees generated through random stepwise addition of taxa. *Crossostoma* and *Carpio* were specified as the outgroup. Length, consistency index, and retention index are the following: L=1595, CI=0.317, RI=0.539. Circled numbers at nodes indicated the percentage of trials in which a given partition between taxa is supported in 1,000 replications of the bootstrap analysis (Felsenstein, 1985). Only nodes supported in >50% of bootstrap replications are indicated.

sister species. The expected number of each of the six substitution types ($S_{E[i\Leftrightarrow j]}$)was then derived as follows:

$$S_{E[i\Leftrightarrow j]} = \left(f_i + f_j\right)\left(S_{0[total]}\right)/3.$$

We divide by three because three types of base substitutions are possible for each base, and we are interested in obtaining an expectation for one of them. For example, the expected number of A⇔T substitutions equals the average frequency of A's (0.23) plus

Table 2

Nucleotide substitutions by type determined through pairwise alignments. The observed substitutions for each type, $S_{O[total]}$, where i and j represent two different nucleotides, were calculated by summing the results from 8 pairwise comparisons of sister taxa. The expected substitutions for each type, $S_{E[total]}$, were calculated according to the formula $S_{E[total]}=(f_i+f_j)(S_{O[total]})/3$, where f_i and f_j are the frequency of nucleotides i and j. Average base frequencies for the 16 species are as follows: G=0.16, A=0.23, T=0.29, C=0.32.

	Substitution Types						
	TRANSITIONS			TRANSVERSIONS			
Pairwise comparison	A⇔G	C⇔T	G⇔T	G⇔C	A⇔T	A⇔C	Total
Tetrapturus audax vs. *Tetrapturus albidus*	0	0	0	1	1	0	2
Tetrapturus angustirostris vs. *Tetrapturus pfluegeri*	7	1	0	0	0	0	8
Makaira nigricans vs. *Istiophorus platypterus*	1	21	0	0	1	0	23
Euthynnus affinis vs. *Euthynnus alletteratus*	5	27	0	0	3	3	38
Thunnus thynnus vs. *Thunnus maccoyii*	4	3	0	0	1	0	8
Scomberomorus maculata vs. *Scomberomorus cavalla*	13	38	1	1	8	11	72
Sarda sarda vs. *Sarda chiliensis*	6	15	0	3	0	2	26
Scomber japonicus vs. *Scomber scombrus*	25	35	2	5	6	6	79
Total observed substitutions	61	140	3	10	20	22	256
Expected substitutions (see Methods section)	33.28	52.05	38.40	40.96	44.37	46.92	256
Expected/observed ratio (EOR)	0.55	0.37	12.80	4.10	2.22	2.13	

the average frequency of T's (0.29) multiplied by the total number of substitutions (256) divided by three, or 44.37 (Table 2).

The weights used for each substitution type (Table 2) are the ratios of expected substitutions divided by observed substitutions for that substitution type, rounded to the nearest integer (expected divided by observed ratios, or EOR's). All EOR's less than one were rounded to one. Weights were entered into PAUP 3.1. (Swofford, 1991) in the form of a step matrix.

Results

Sequence evolution and interfamilial relationships

Molecular data sets, such as the cytochrome *b* sequences presented in this study, are known to encompass subsets of characters that evolve at different rates. Subsets of data that differ in their evolutionary rates will also differ in their phylogenetic utility. Character state changes that accrue very rapidly should permit resolution of very recent divergences. However, these rapid character state changes can provide false inferences about distant relationships because of homoplasy. The likelihood of reversals and independent acquisitions is high if a particular site is evolving rapidly because there are only four possible character states (G, A, T, and C) and only six possible types of character state change (A⇔G, C⇔T, G⇔T, G⇔C, A⇔T, and A⇔C). Therefore, in order to make an accurate reconstruction of the earliest branching events in scombroid history, we should emphasize slowly evolving character state changes.

In an effort to best utilize the phylogenetic information from both slowly and rapidly evolving character state changes, our phylogenetic analysis proceeds in several discrete steps. We begin with an unweighted analysis of all informative nucleotide sites. This analysis is strongly influenced by nucleotide substitutions that accrue rapidly and should be most informative concerning recent speciation events. We then attempt to improve our resolution of more ancient divergences by giving greater weight to less frequent types of nucleotide substitutions. We conclude with a phylogenetic analysis based on the inferred amino acid sequences. The amino acid sequences evolve very slowly and should provide our most reliable estimates of the earliest splits between lineages. In each instance, the phylogenetic analysis is preceded by a discussion of the evolutionary variation in the character subset under consideration.

Unweighted nucleotide analysis

A 590-base pair fragment of the cytochrome *b* gene, representing positions 134 through 723 of the human cytochrome *b* sequence, was aligned across all

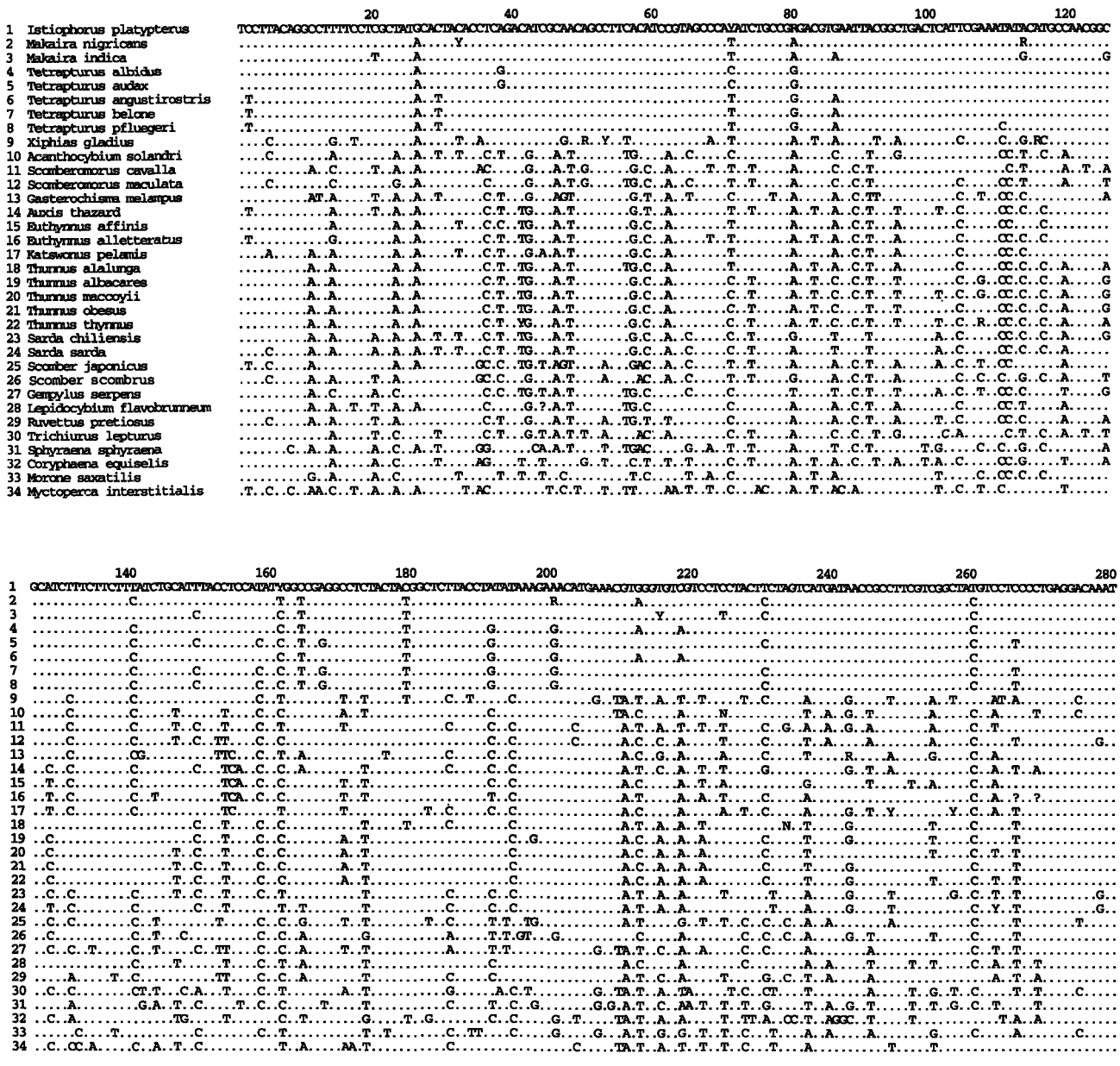

Figure 3

Alignment of partial cytochrome *b* sequence (590 base pairs) across 34 species of perciform fishes and two species of Cypriniformes. Nucleotide position 1 is equivalent to position 134 of the human cytochrome *b* gene. Intraspecific polymorphism is indicated as follows: R=A/G, Y=C/T, M=A/C, S=C/G, K=G/T, W=A/T, H=A/T/C, D=A/G/T. Ambiguities are indicated by '?'

thirty-six species included in the analysis (Fig. 3). No deletions or insertions were detected. Overall, 293 nucleotide positions are variable; 248 were potentially phylogenetically informative. As expected for a protein coding sequence, the degree of nucleotide variability differs according to codon position (Table 3). The third position is most variable and the second position is least variable. Differences in nucleotide variability at the three codon positions are due to the fact that many third position substitutions are silent, whereas many second position substitutions result in nonconservative amino acid replacements.

The differences in substitution rates between codon positions becomes more apparent when we compare

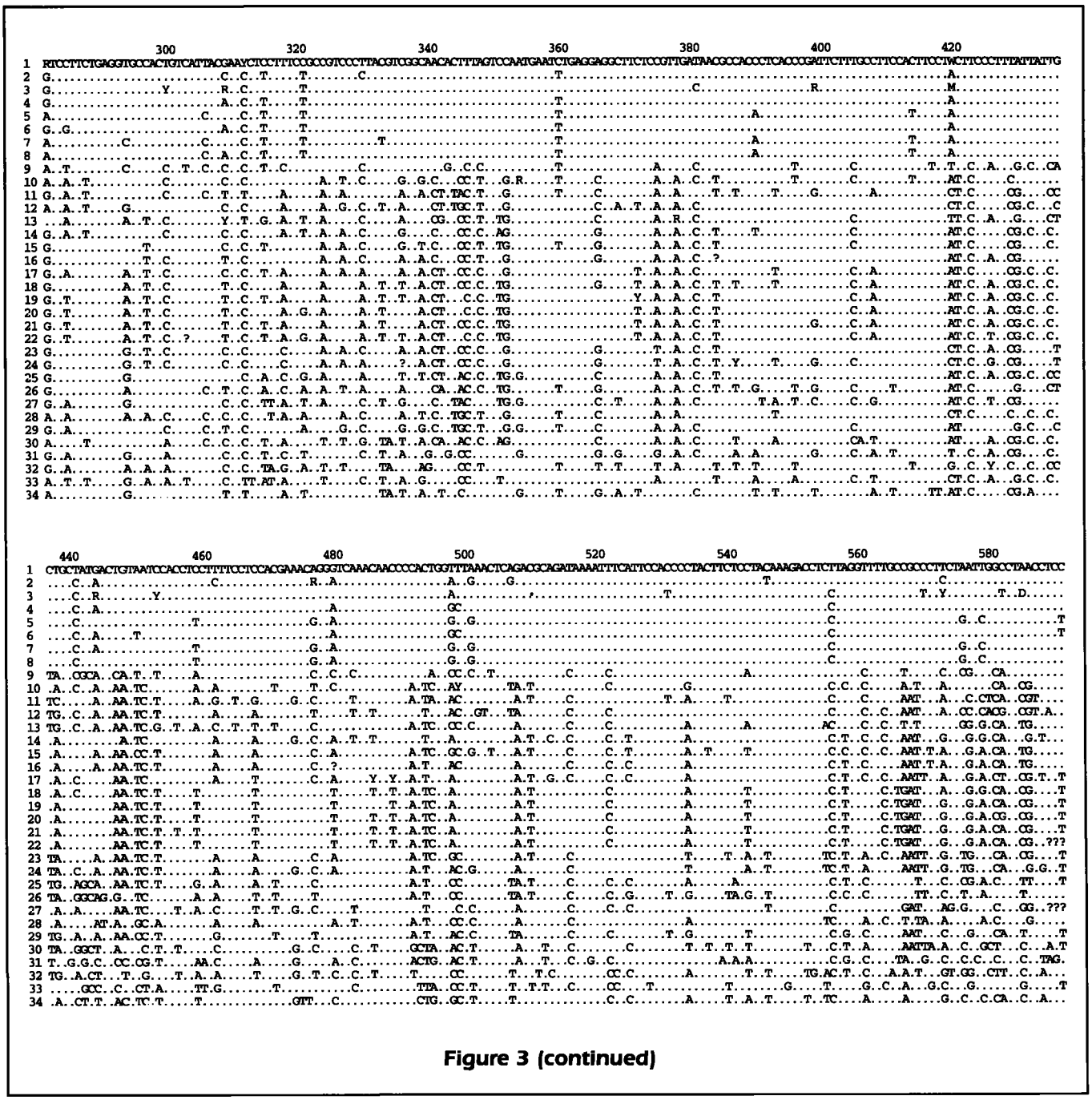

Figure 3 (continued)

the inferred number of substitutions (Table 3). For example, if a nucleotide site is twofold variable, i.e. if two bases occur at that position in an alignment of all species, then at least one base substitution has occurred at that position during the evolutionary history of the species concerned. Likewise, if a position is threefold variable, at least two substitutions have occurred, and so on. By this approximation, the 293 variable positions have experienced at least 521 substitutions, and substitutions at the third position outnumber substitutions at the first and second positions by nearly 4 to 1 and by more than 12 to 1, respectively.

Figure 2 presents a phylogeny of the Scombroidei based on an unweighted parsimony analysis of all informative nucleotide sites. In this cladogram, only the relationships among recently diverged taxa are strongly supported. There is support for the monophyly of genera within the family Scombridae (*Thunnus*, *Euthynnus*, *Sarda*, *Scomber*, and *Scom-*

Table 3

Variable sites in the cytochrome *b* nucleotide alignment (Fig. 2) according to codon position. Variable sites are further characterized according to how many nucleotide states are present: 2 states=twofold variable, 3 states=threefold variable, fourstates=fourfold variable.

	Codon position			
	1	2	3	Total
Total sites	196	197	197	590
Variable sites	72	29	192	293
A) twofold variable sites	50	27	69	146
B) threefold variable sites	15	2	49	66
C) fourfold variable sites	7	0	74	81
Minimum inferred substitutions = [(A) + 2(B) + 3(C)]	101	31	389	521
Phylogenetically informative variable sites	42	18	188	248

beromorus), and for the monophyly of the family Istiophoridae. Interrelationships within the family Istiophoridae and the genus *Thunnus* are well resolved. No other nodes are supported by more than fifty percent of bootstrap replicates (Felsenstein, 1985). Furthermore, there is a substantial polychotomy.

Weighted nucleotide analysis

The lack of resolution in the unweighted nucleotide analysis is not entirely unexpected. From Table 3, we can surmise that many nucleotide sites have incurred multiple substitutions and therefore the likelihood of convergent substitutions or reversals is high. In order to minimize the confounding effects of these homoplasious base substitutions, we have weighted infrequent substitution types more heavily using a modification of the method of Knight and Mindell (1993). If we disregard the direction of character change, we can place all nucleotide substitutions into six classes : A⇔G, C⇔T, G⇔T, G⇔C, A⇔T, and A⇔C. Through pairwise sequence comparisons we obtained observed counts for each of these substitution types (Table 2; also see Methods section). We observe a nearly 50-fold difference between the most common (C⇔T) and the least common (G⇔T) substitution types. Then, from the total number of observed substitutions and the observed frequency of each base, we derived the expected number of occurrences for each substitution type. The ratios of expected occurrences to observed occurrences for each substitution type (EOR's) were then used to weight the six types of base substitutions. The result of this weighting scheme is that substitution types that occur less frequently than expected are weighted more heavily.

A phylogeny based on EOR weighting of nucleotide substitutions is presented in Figure 4. It retains all of the strongly supported nodes that appear in the unweighted topology. In addition, the weighted topology contains three more basal nodes that are strongly supported by the bootstrap analysis (>50%): the node uniting Gempylidae, Scombridae, and Trichiuridae, the node uniting Xiphiidae and Istiophoridae, and the node uniting *Auxis* and *Euthynnus*. This suggests that the character weighting scheme has accomplished its goal to some extent: we have retained the phylogenetic signal from rapidly evolving substitutions while emphasizing the phylogenetic signal from slowly evolving substitutions.

According to the weighted cladogram (Fig. 4), all scombroids fall into two clades. The billfishes comprise one clade consisting of a monophyletic Istiophoridae and its sister group, Xiphiidae. All other scombroids (Gempylidae, Scombridae, and Trichiuridae) fall into a separate clade. This major split within the suborder Scombroidei is in agreement with our previous study (Block et al., 1993). However, in contrast with our previous study, the use of character weighting and the inclusion of more distant outgroups leads to the result that the suborder Scombroidei is not monophyletic. On the most parsimonious tree, *Sphyraena* and *Coryphaena* share a common ancestor with the gempylid-scombrid-trichiurid clade to the exclusion of billfishes, though this node does not receive particularly strong support from the bootstrap analysis. This result indicates some support for the hypothesis that billfishes are not scombroids. More importantly, the cladogram excludes the possibility that billfishes and scombrids comprise a monophyletic group within the Scombroidei, as required by the scombrid subgroup and scombrid sister group hypotheses. In summary, the weighted analysis agrees with the nonscombroid hypothesis and conflicts with the scombroid subgroup and scombroid sister group hypotheses.

Amino acid analysis

Amino acid substitutions occur far less frequently than nucleotide substitutions owing to the strong functional constraints on many regions of the molecule. Cytochrome *b* is a component of the electron transport chain and spans the inner mitochondrial membrane. The portion of the gene sequenced in this study encodes 195 amino acids corresponding to residues 46 through 240 of the human cytochrome *b* (Fig. 5).

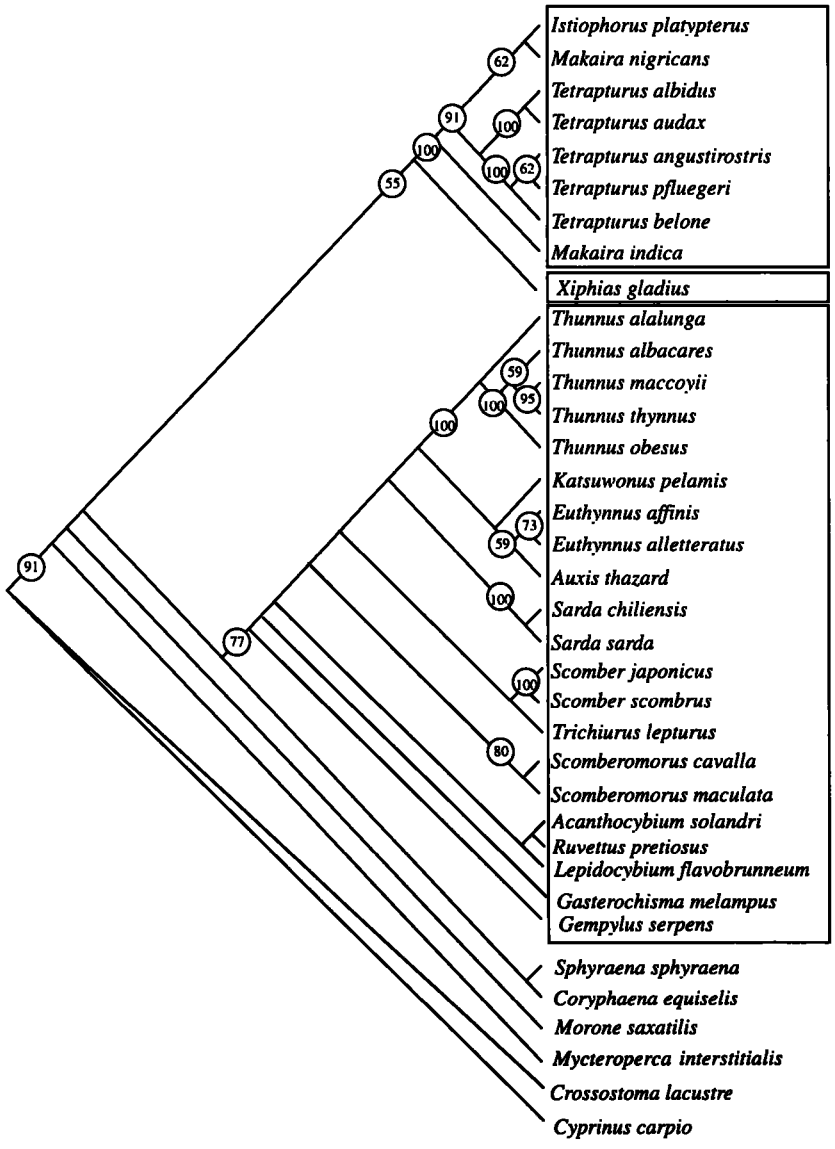

Figure 4

Phylogeny of the Scombroidei based on a weighted, maximum parsimony analysis of informative nucleotide sites. The six types of nucleotide substitutions are weighted according to the ratio of their expected occurrence to their observed occurrence (see Table 3). Weights used for each substitution type are the following: A⇔G=1, C⇔T=1, G⇔T=13, G⇔C=4, A⇔T=2, and A⇔C=2. *Crossostoma* and *Carpio* were specified as the outgroup. The tree depicted is the single most parsimonious topology identified in a heuristic search: TBR branch swapping was performed on 10 starting trees generated through random stepwise addition of taxa. Tree length is 2,348 steps. PAUP 3.1. was unable to derive consistency and retention indices for the cladogram that incorporated the weighting scheme. Circled numbers at nodes indicate the percentage of trials in which a given partition between taxa is supported in 1,000 replications of the bootstrap analysis (Felsenstein, 1985).

This fragment spans four transmembrane domains and includes part of the region implicated as the outer membrane redox reaction center (Howell and Gilbert, 1988; Howell, 1989; Fig. 6). In a comparison of the inferred peptide sequences across the 36 species included in this study, 134 (69%) of the 195 amino acid residues are invariant, 34 (17%) occur in 2 amino acid states, and 27 (14%) occur in 3 or more states.

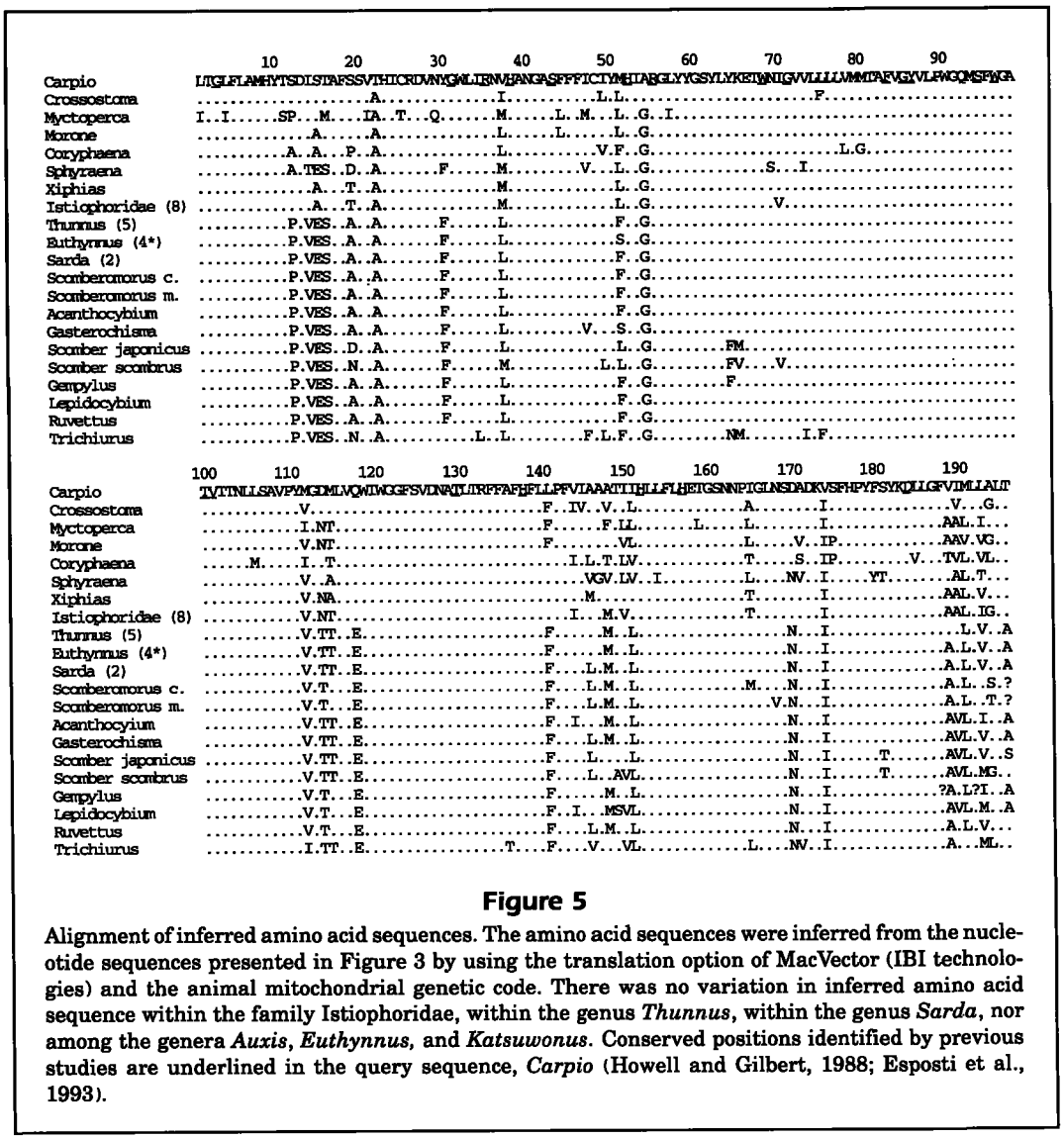

Figure 5

Alignment of inferred amino acid sequences. The amino acid sequences were inferred from the nucleotide sequences presented in Figure 3 by using the translation option of MacVector (IBI technologies) and the animal mitochondrial genetic code. There was no variation in inferred amino acid sequence within the family Istiophoridae, within the genus *Thunnus*, within the genus *Sarda*, nor among the genera *Auxis*, *Euthynnus*, and *Katsuwonus*. Conserved positions identified by previous studies are underlined in the query sequence, *Carpio* (Howell and Gilbert, 1988; Esposti et al., 1993).

This level of variability in amino acid sequence is very similar to that reported in a study of placental mammals, a group whose divergence times are probably comparable to scombroids (Irwin et al., 1991). Much of the variation in scombroid cytochrome *b* occurs in the transmembrane portion of the molecule and represents substitutions between hydrophobic residues (leucine, isoleucine, and valine). The largest stretches of invariant residues (21 and 17) occur in a region implicated as part of the Q_0 redox reaction center (Howell and Gilbert, 1988; Howell, 1989; Fig. 6). All of the functionally constrained sites identified by previous studies are conserved throughout the fishes included in this study (see Fig. 5; Howell and Gilbert, 1988; Esposti et al., 1993).

Figure 7 presents a parsimony analysis based on 38 informative amino acid sites. The amino acid sequences do not provide information about more recent speciation events because they evolve very slowly, but they contain important evidence about the relationship of billfishes to other scombroids. The amino acid analysis shares two important similarities with the weighted nucleotide analysis: first, Scombridae, Gempylidae, and Trichiuridae comprise a clade, and second, *Sphyraena* and *Coryphaena* share a common ancestry with this Scombridae-Gempylidae-Trichiuridae assemblage to the exclusion of the billfishes (Xiphiidae and Istiophoridae). The node uniting *Sphyraena* with the scombrid-gempylid-trichiurid clade is one of the more strongly supported nodes according to the bootstrap analysis. Therefore, cytochrome *b* amino acid substitutions support the non-scombroid hypothesis and conflict with the scombrid subgroup and scombrid sister group hypotheses.

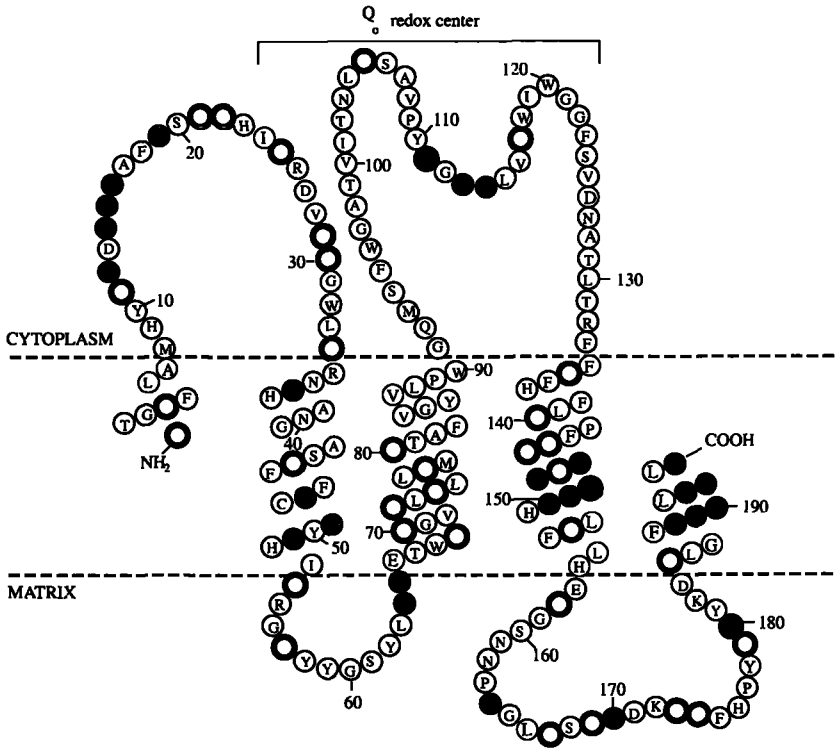

Figure 6

Variability in amino acid sequence superimposed over a structural model for cytochrome *b* (Howell, 1989). Hypervariable residues, present in three or more amino acid states, are indicated by solid circles. Variable residues, present in two states, are indicated by open circles. The amino acids present at invariant residues are specified on the diagram. Residue 1 of this fragment is equivalent to the forty-sixth residue from the amino terminal of the protein in humans.

The strength of the evidence that billfishes are not scombroids can be emphasized by directly examining the amino acid characters that are informative about this issue. Of the 38 informative amino acid sites, no sites unite billfishes and other scombroids to the exclusion of other perciforms, whereas eight sites unambiguously separate billfishes from all other scombroids, i.e. sites where all billfishes possess one character state and all other scombroids possess some other character state (characters 12, 14, 15, 16, 113, 117, 140, and 169; Fig. 5). At all of these sites, billfishes share the same character state as one or more of the percoid fishes. Furthermore, at three of these eight sites (15, 16, and 169), Gempylidae, Scombridae, and Trichiuridae share a common state with *Sphyraena* to the exclusion of all other species in the study. As this character analysis emphasizes, the amino acids are consistent with the hypothesis that billfishes are not scombroids and that *Sphyraena* is the sister group of a clade consisting of Gempylidae, Scombridae, and Trichiuridae.

Intrafamilial relationships

Within the family Istiophoridae (*Istiophorus*, *Makaira*, and *Tetrapturus*), cytochrome *b* nucleotide sequence provides a particularly well resolved and strongly supported phylogenetic signal. This is probably due to the recency of the istiophorid radiation. The maximum sequence divergence between any two species within this clade is less than five percent. We have performed a more in depth analysis of the interrelationships of istiophorids using the exhaustive search option of PAUP 3.1 (Swofford, 1991). Use of the exhaustive search option guarantees identification of the most parsimonious tree. The topology of this tree is identical to the topology of the istiophorid clade within the more inclusive scombroid phylogeny (Fig. 8, cf. Fig. 2). Neighbor-joining and UPGMA analyses produce an identical topology. Computer simulations suggest that agreement between these three methods should increase our confidence in a phylogenetic hypothesis (Kim, 1993).

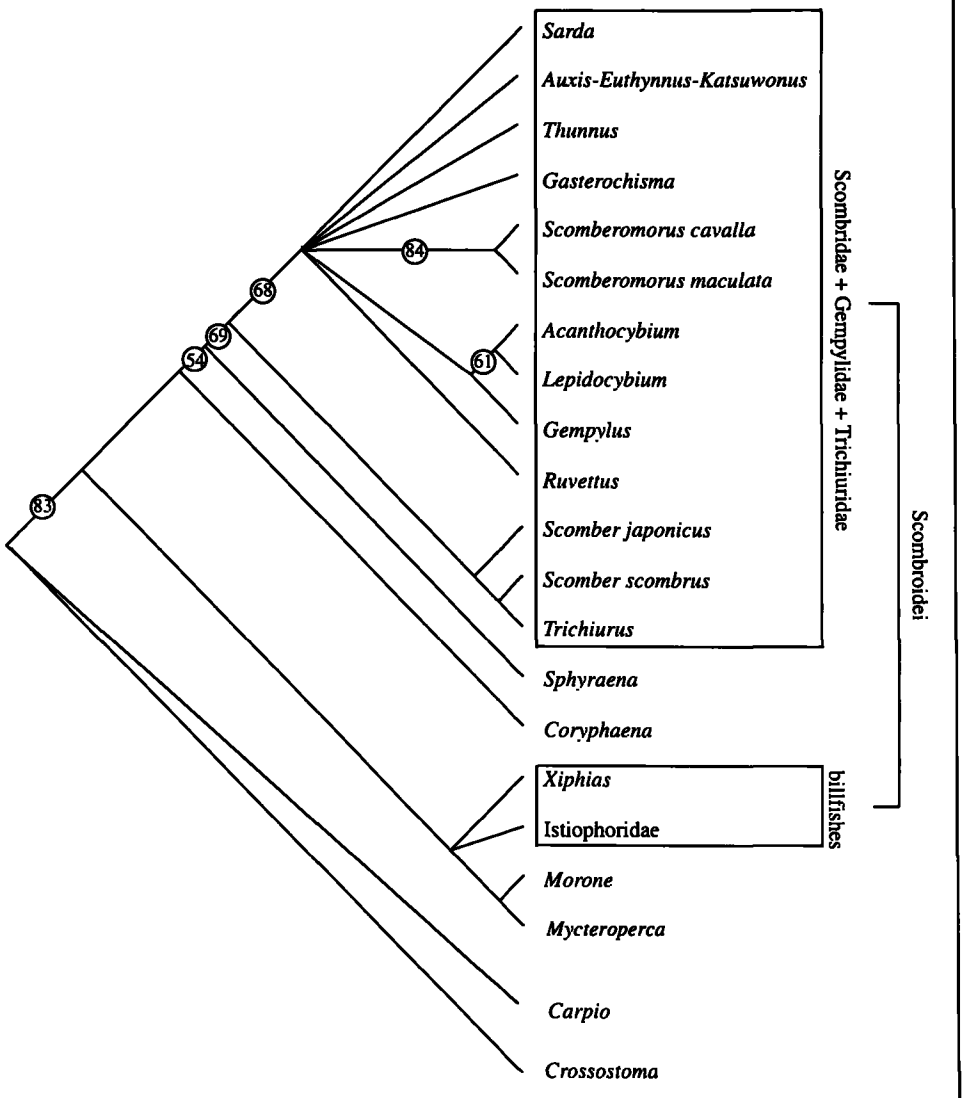

Figure 7

Phylogeny of the Scombroidei based on maximum parsimony analysis of inferred amino acid sequences. The cladogram depicted is a strict consensus of 68 equally parsimonious trees identified through a heuristic search procedure: TBR branch swapping was performed on 10 starting trees generated through random stepwise addition of taxa. *Crossostoma* and *Carpio* were specified as the outgroup. Length, consistency index, and retention index are the following: L=141, CI=0.567, RI=0.619. Circled numbers at nodes indicate the percentage of trials in which a given partition between taxa is supported in 1,000 replications of the bootstrap analysis (Felsenstein, 1985).

Cytochrome *b* sequence strongly supports the monophyly of the Istiophoridae. The extant members of this family have experienced a long period of common ancestry as indicated by numerous istiophorid synapomorphies (20 transitions and 35 transversions, Fig. 8). The monophyly of *Tetrapturus*, and within this genus, clades consisting of *audax* + *albidus* and *pfluegeri* + *angustirostris* + *belone*, are also supported. The number of substitutions separating *Tetrapturus audax* from *T. albidus*, and *T. angustirostris* from *T. belone* and *T. pfluegeri* indicates that these mitochondrial lineages share a recent common ancestry (Table 3). The sequence differences between these species (<0.5%) are small compared to the maximum intraspecific sequence difference (1.8%) detected among blue marlin, *M. nigricans*, over a similar region of cytochrome *b* (Finnerty and Block, 1992). These data call into question the status of *T. audax*

and *T. albidus* as separate species as well as *T. pfluegeri*, *T. angustirostris*, and *T. belone*.

Our data conflict with other aspects of current istiophorid taxonomy at the generic level. Analysis of cytochrome *b* does not support the monophyly of the genus *Makaira*. The black marlin, *Makaira indica*, appears to be the sister group of a clade containing all other istiophorids, while the blue marlin, *M. nigricans*, is sister group of the sailfish, *I. platypterus*. The most parsimonious tree that contains a monophyletic *Makaira* is six steps longer than the shortest tree overall (158 versus 152), and on the most parsimonious tree, the *M. nigricans-I. platypterus* node is strongly supported by bootstrap analysis (85%).

Cytochrome *b* provides good resolution of the relationships of the genera of the tribe Thunnini (*Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*). According to the nucleotide data the nine Thunnini species sequenced in this study comprise two clades, one consisting of the genus *Thunnus* and one containing the other genera: *Auxis*, *Euthynnus*, and *Katsuwonus*. This distinct split in the Thunnini was proposed by Kishinouye in 1923 and is consistent with the morphological hypothesis of Collette et al. (1984). Support for the monophyly of the *Thunnus* clade is particularly robust; however, the relationships within the genus cannot be resolved without the inclusion of both *Thunnus tonggol* and *Thunnus atlanticus* which were not sequenced in this study. The number of substitutions separating *T. thynnus* from *T. maccoyii* (<0.5% sequence divergence) are small considering their status as separate species.

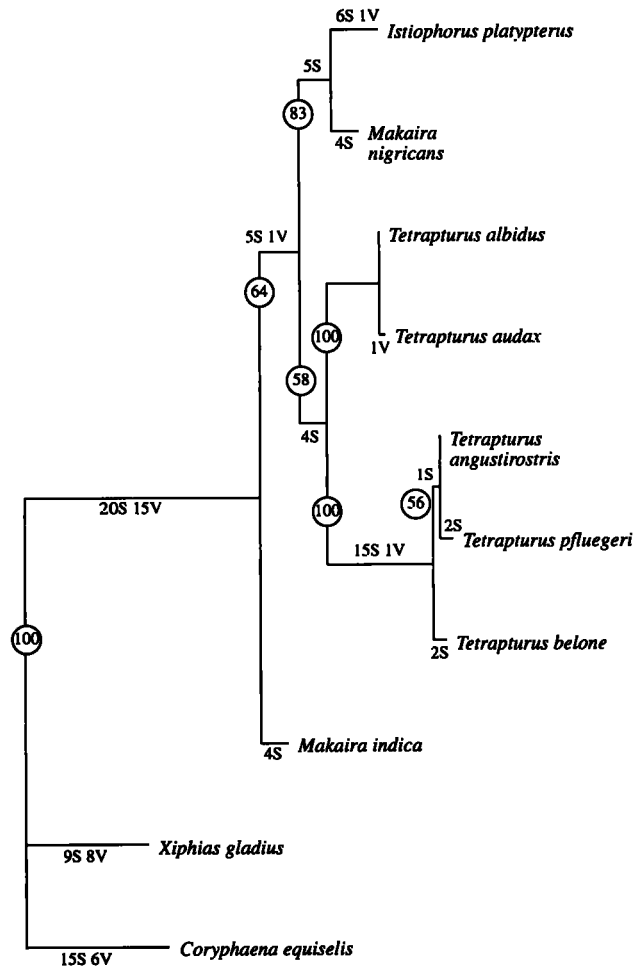

Figure 8

Phylogeny of the Istiophoridae based on 78 informative nucleotide sites. The phylogram depicted is the single most parsimonious tree identified by the exhaustive search option of PAUP 3.1 (Swofford, 1991). *Xiphias gladius* and *Coryphaena equiselis* were specified as the outgroup. Length, consistency index, and retention index are the following: L=152, CI=0.776, RI=0.721. Circled numbers at nodes indicate the percentage of trials in which a given partition between taxa is supported in 2,000 replications of the bootstrap analysis (Felsenstein, 1985). Character state transformations were inferred by using the accelerated transformation (ACCTRAN) option of PAUP: S=nucleotide transitions (A⇔G or C⇔T); V=nucleotide transversions (C/T⇔A/G). Within the Istiophoridae transitions outnumber transversions 54 to 6. Neighbor-joining (Saitou and Nei, 1987) and UPGMA dendrograms produced with Phylip 3.5 (Felsenstein, 1993) have the same topology. Distance trees were constructed by using Kimura's (1980) two parameter genetic distance, and by assuming a transition to transversion bias of 9:1.

Discussion

Interfamilial relationships and the limits of the Scombroidei

Throughout this analysis, we have focused on the long-standing controversy over the limits of the Scombroidei and, particularly, whether billfishes are scombroids. Cytochrome *b* appears to be informative on this issue. In the two phylogenetic analyses that emphasize the more slowly evolving characters (see Figs. 4 and 7), the most parsimonious tree topology is clearly most consistent with the hypothesis that billfish are not scombroids: in each case, one or more nonscombroids share a common ancestry with the scombrid-gempylid-trichiurid clade to the exclusion of billfishes (Table 4). Therefore, according to the criterion of parsimony, the nonscombroid hypothesis is superior to the scombrid subgroup and to the scombrid sister group hypotheses. However, in our opinion, the

most parsimonious trees alone do not constitute sufficient evidence to reject these unfavored hypotheses. The question we must ask is the following: How unparsimonious are these hypotheses?

In comparing the tree topologies that support each competing hypotheses (Table 4), it is clear that our data refute the notion that billfishes share a common ancestor with the Scombridae to the exclusion of other scombroids (Gregory and Conrad, 1937; Berg, 1940; Fraser-Brunner, 1950; Collette et al., 1984; Johnson, 1986). For example, the shortest trees supporting a billfish-scombrid clade are 13% longer than the minimum-length tree based on inferred amino acid sequence (Table 4). According to the cladistic permutation test for nonmonophyly (Faith, 1991), this length difference constitutes significant evidence against the monophyly of scombrids plus billfishes. The condition that billfishes and scombrids comprise a monophyletic group is a requirement of both the scombrid subgroup and scombrid sister group hypotheses. Therefore, according to the cytochrome *b* data, we reject these two hypotheses.

The cytochrome *b* data clearly support the third hypothesis, that billfishes are not scombroids, though not as strongly as they refute the first two hypotheses. According to the inferred amino acid sequences, the shortest tree that supports scombroid monophyly places billfishes as sister group to all other scombroids and is nearly 3% longer than the most parsimonious tree overall (145 versus 141 steps). This length difference alone does not constitute significant evidence against the monophyly of the Scombroidei according to a cladistic permutation test for nonmonophyly (see Methods section; Faith, 1991). However, as previously mentioned, there are three amino acid characters that unite scombrids, gempylids, and trichiurids with *Sphyraena* to the exclusion of billfishes (amino acids 15, 16, and 169). There are no characters that unite scombrids, gempylids, and trichiurids with billfishes to the exclusion of the putative outgroups. Our study is consistent with the hypothesis that billfishes are most closely related to some percoid lineage (Nakamura, 1983; Potthoff et al., 1986). The question of which taxon is most closely related to billfishes remains unanswered. On the basis of this evidence, we support a conservative definition of the Scombroidei, including only the families Scombridae, Gempylidae,

Table 4

Comparison of three competing hypotheses of billfish (Istiophoridae and Xiphiidae) relationships based on inferred amino acid sequences from cytochrome *b*. 'na' = not applicable.

	Hypothesis		
	I: Scombrid subgroup	II: Scombrid sister group	III: Nonscombroid
Characteristics of tree which would support hypothesis	Scombridae + billfishes are a monophyletic group *Acanthocybium* is the sister group of billfishes	Billfishes are sister group of a monophyletic Scombridae	Billfishes do not compose part of a monophyletic group with any other scombroid taxon or taxa
Does the most parsimonious tree support the hypothesis?	No	No	Yes
If the answer to B is no, how much longer is the shortest tree which does support the hypothesis?	13.5% (160 steps vs. 141 steps)	13.0% (159 steps vs. 141 steps)	na
Based on the increase in tree length, can we reject the underlying hypothesis with statistical significance?	Yes (*T-PTP* = 0.01)	Yes (*T-PTP* = 0.01)	na

[1] The topology dependent permutation tail probability (*T-PTP;* Faith, 1991) was used to determine the significance of the length difference. Values of *T-PTP*≤0.05 were considered significant. See Methods section.

and Trichiuridae (Cuvier and Valenciennes, 1832; Gosline, 1968; Potthoff et al., 1986).

How can these inferences from molecular data be reconciled with the morphological data? We believe that this is an instance where molecular data complement morphological data well. Cytochrome *b* provides an unambiguous phylogenetic signal that billfishes are genetically distant from other scombroids. In contrast, the existing morphological data does not clearly discriminate between a number of hypotheses. The number of character reversals in morphological phylogenies that classify billfishes as scombroids indicates that there have been many homoplastic changes in the billfish lineage. According to the morphological evidence, either billfishes are scombroids and have undergone several reversals to the primitive state, such as their low number of vertebrae, or billfishes are not scombroids but have evolved many convergent similarities to scombroids, such as their paired lateral caudal keels.

Many of the morphological characters that unite billfishes to other scombroids, particularly to Scombridae, may be adaptations for continuous swimming, and are therefore of questionable phylogenetic value. These include hypurostegy, the projection of the caudal fin-ray bases anteriorly to cover the hypurals (Collette et al., 1984; Johnson, 1986), fusion of the hypurals (Collette et al., 1984; Johnson, 1986), and interfilamentar gill fusion (Johnson, 1986). Hypurostegy and interfilamentary gill fusion are known to have evolved convergently in nonscombroid taxa (*Luvarus imperialis* [Leis and Richards, 1984]; and *Amia calva* [Bevelander, 1934]). The molecular data presented here provide a phylogenetic signal that is independent of convergent morphological adaptations that might confound phylogenetic analysis. There has been convergent evolution in the molecular characters, but unlike many of the morphological characters mentioned, this convergent evolution does not appear to be the result of strong selection: most amino acid substitutions exchange amino acids with similar size, charge, and degree of polarity. Therefore, when compared with the existing morphological data, the phylogenetic signal in the molecular data is less likely to have been obscured by similar selective pressures acting upon distantly related lineages.

Istiophorid phylogeny

Historically, there have been numerous disagreements over the number of species within the Istiophoridae and their interrelationships (Goode, 1882; Jordan and Evermann, 1926; LaMonte and Marcy, 1941; Nakamura, 1983). This is evidenced by the synonymies for many istiophorids, e.g. the Mediterranean spearfish, *Tetrapturus belone*, has also been assigned to *Istiophorus* (Ben-Tuvia, 1953) and *Makaira* (Tortonese, 1958). The most thorough treatment of billfish systematics to date is a phenetic analysis conducted by Nakamura (1983). Nakamura recognized 11 species of istiophorid billfishes in three genera, including the designation of separate Atlantic and Indo-Pacific species for blue marlin (*Makaira nigricans* and *M. mazara*) and sailfish (*Istiophorus albicans* and *I. platypterus*).

The molecular evidence presented here agrees with Nakamura (1983) in supporting the monophyly of the genus *Tetrapturus*, and within this genus, clades consisting of *audax* + *albidus* and *pfluegeri* + *angustirostris* + *belone*. Cytochrome *b* does not support the recognition of separate Atlantic and Pacific species of blue marlin and sailfish. Previous results (Finnerty and Block, 1992) identified substantial overlap in the cytochrome *b* haplotypes found among Atlantic and Pacific populations of blue marlin. The sailfish sample in this study includes one Atlantic specimen and one Pacific specimen that differ at only two sites among 590 (0.3%). We infer from the cytochrome *b* data (Block et al., 1993; and this study) a nonmonophyletic *Makaira* and support for a clade consisting of the blue marlin (*Makaira nigricans*) and the sailfish (*Istiophorus platypterus*).

Based on the cytochrome *b* data, istiophorid taxonomy at the generic level is not concordant with phylogeny. It is premature to suggest taxonomic revision of istiophorid genera, but we believe it is imperative to obtain more molecular data, particularly from nuclear genes, to determine whether the inferences presented here can be corroborated. Furthermore, we recognize the need for an extensive cladistic analysis of istiophorid relationships based on additional morphological data. Another taxonomic issue raised by this study concerns the number of valid *Tetrapturus* species. An extensive genetic survey of several populations from each species is required to determine the number of evolutionarily independent or reproductively isolated lineages within this genus.

Relationships within the genus *Thunnus*

The systematics of the genus *Thunnus* have been well studied owing to the commercial importance of tunas and interest in physiological specializations associated with the evolution of endothermy. Collette (1978) suggested a taxonomic subdivision of the genus reflecting a split between tropical species (subgenus *Neothunnus*: blackfin tuna, *Thunnus atlanticus*, longtail tuna, *Thunnus tonggol*, and yellowfin tuna, *Thunnus albacares*) and species that inhabit cooler waters (subgenus *Thunnus*: bluefin tuna,

Thunnus thynnus, southern bluefin tuna, *Thunnus maccoyii*, albacore, *Thunnus alalunga*, and bigeye tuna, *Thunnus obesus*). According to this hypothesis, the primitive condition for the genus *Thunnus* is a tropical distribution, and the cold water tunas compose a monophyletic group united by specializations that allowed them to exploit cooler temperate or deep waters. The nucleotide analyses presented in Figures 2 and 4 are not consistent with this hypothesis. The cytochrome *b* phylogeny groups a tropical species, the yellowfin tuna, *Thunnus albacares*, with two species adapted for extremely cold water, the bluefin tuna and southern bluefin tuna (*Thunnus thynnus* and *Thunnus maccoyii*). However, it is premature to draw conclusions about relationships within the genus *Thunnus* until data are obtained from two tropical species not included in this study, *Thunnus atlanticus* and *Thunnus tonggol*.

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Assignment of *Homarus capensis* (Herbst, 1792), the Cape lobster of South Africa, to the new genus *Homarinus* (Decapoda: Nephropidae)

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Abstract.—Three species of nephropid lobsters have been recognized in the genus *Homarus*: the American and European lobsters, *H. americanus* and *H. gammarus* of the northwestern and northeastern Atlantic, respectively, and the Cape lobster of South Africa, *H. capensis*, few specimens of which have been studied until recently. Analysis of new specimens allows reconsideration of the systematic status of this species and a subsequent transfer to a monotypic new genus *Homarinus*. Far smaller than its northern relatives, with a maximum observed carapace length of 47 mm, the Cape lobster has first chelae adorned with a thick mat of plumose setae and less abundant setae on the carapace, tail fan, and abdominal pleura, whereas these setae are absent in *Homarus*. Relative length and shape of the carpus on pereopod 1, tooth pattern on cutting edges of first chelae, shape of the linguiform rostrum, large size of oviducal openings, and structure of male pleopods differ from corresponding features in *Homarus*. Comparative analysis of DNA from the mitochondrial 16s rRNA gene demonstrated considerable sequence divergence of the Cape lobster (9.7%) from its putative congeners. The magnitude of this estimate relative to that between the two North Atlantic species (1.3%) further suggests that taxonomic revision is warranted.

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Until now, three species of nephropid lobsters have been recognized in the genus *Homarus* Weber, 1795 (see Holthuis, 1991): *H. americanus* H. Milne-Edwards, 1837, the northwestern Atlantic American lobster; *H. gammarus* (Linnaeus, 1758), the northeastern Atlantic-Mediterranean European lobster; and *H. capensis* (Herbst, 1792), the South African Cape lobster. All are found in cool or cold temperate waters, and the North Atlantic species range into subarctic waters. The northern *H. americanus* and *H. gammarus* are well-known, abundant, and economically valuable species, but the southern *H. capensis* has long been problematic because only a few specimens (13 males, 1 female) were known to exist in collections (Barnard, 1950; Wolff, 1978; Holthuis, 1991). Gilchrist (1918) had seen only three specimens and remarked (p. 46) that "it is a very rare species, and is not even known to Cape Fishermen." Kensley (1981) recorded its distribution in the Cape Province as Table Bay to East London, and recent new collections extend the range to Transkei (Kado et al., 1994).

Regardless of its rarity, sufficient specimens of the Cape lobster, living and preserved, are now available for analysis of its distribution, morphological, and genetic attributes, and systematic status. Results of our studies indicate that this species should be removed from *Homarus* and placed in a genus of its own; this paper provides supporting evidence for this action and offers supplementary descriptive information on the species.

Homarinus, new genus Figs. 1–4

Type species—*Homarus capensis* (Herbst, 1792) by present designation and monotypy.

Description—Carapace moderately compressed, narrower than deep, sparsely setose, middorsal carina barely evident on gastric region, obsolescent on thoracic region posterior to deep cervical groove. Rostrum

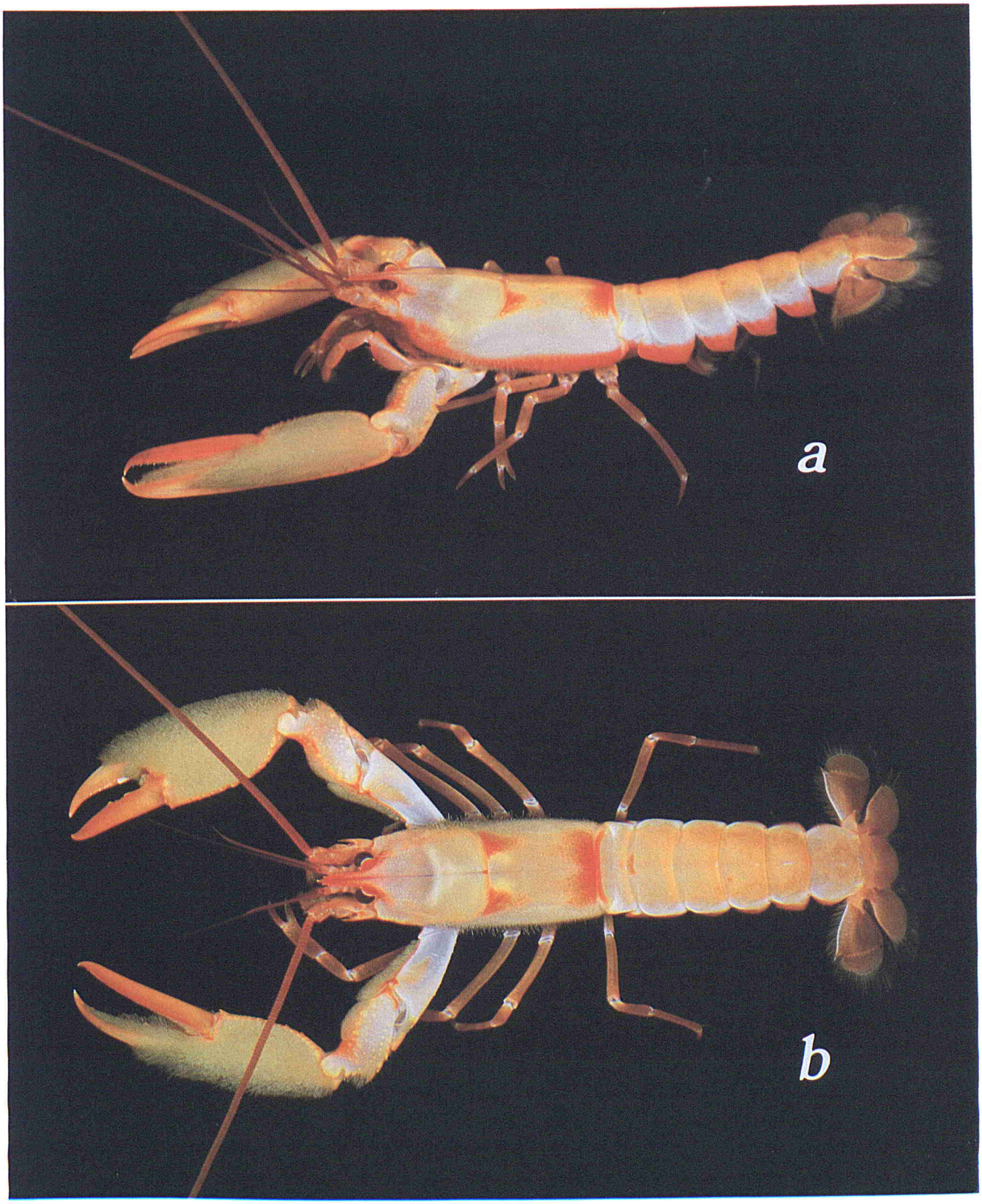

Figure 1

Homarinus capensis (Herbst). Living male, carapace length 3.41 cm, photographed in an aquarium in Sea Fisheries Research Institute, Cape Town, South Africa, by Robert Tarr. (***a***) Left lateral; (***b***) dorsal.

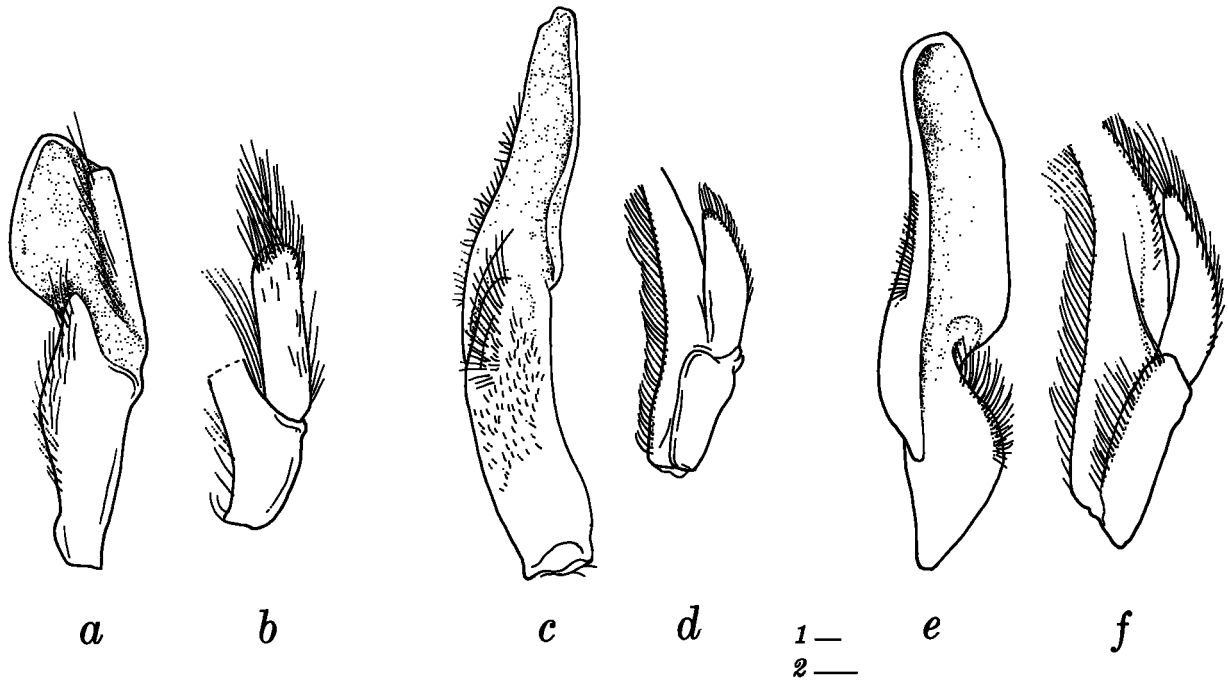

Figure 2

Male pleopods (pl); mesial views of pl 1 (slight lateral folds on tips not shown in these views), and mesial views of appendix masculina on mesial ramus of pl 2: (***a* and *b***) *Homarinus capensis*, left (USNM 251452); (***c* and *d***) *Homarus americanus*, right (USNM 13952); (***e* and *f***) *H. gammarus*, right (USNM 2085). Scale is 1 mm: bar 1 applies to *c* through *f*; bar 2 applies to *a* and *b*.

linguiform in dorsal view, broad at base where margins coalesce with orbits, margins bearing 4–6 small spines and gradually tapering anteriorly to rather abruptly pointed or narrowly rounded tip, reaching distal 1/3 of penultimate article of antennular peduncle, shallow dorsal concavity running its entire length.

Telson and uropods with thick fringe of plumose setae on distal margin and with scattered nonplumose long setae dorsally on these appendages and sixth abdominal segment. Telson as wide at base as long, with lateral margins slightly sinuous and subparallel bearing obsolescent spines and rugae, each side ending in fixed posterolateral spine; terminal margin beyond spine broadly convex; distal 1/3 of surface bearing obsolescent transverse rugae. Uropods broadly subovate, sparsely setose on dorsal surface; mesial ramus broadest near posterior margin with width about 0.73 length, row of obsolescent lateral marginal spines ending in fixed posterolateral spine; lateral ramus with width about 0.72 length, diaresis well behind midlength bearing row of fixed but irregularly worn spines ending in strongest spine at posterolateral angle.

Chelae of first pereopods with thick coat of long plumose setae on upper surface of palm, overhanging extensor margin and distributed a distance along fixed finger; similar setae on mesial surface of carpus and ventral surface of merus. Fingers not gaping; those of major chela with crushing teeth (often worn) opposed from near base to about midlength

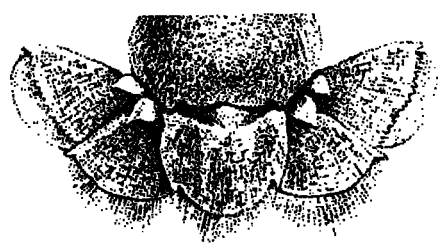

Figure 3

Homarinus capensis (Herbst), tail fan (from figure in H. Milne-Edwards, 1851).

```
Ha   ggtcgcaaacttttttgtcgatatgaactctcaaaataaataacgctgtt   50
Hg   ..................................................
Hc   ..................n...............................

Ha   atccctaaagtaacttaaatttttaatcaacaancaanggatcanttaca  100
Hg   ..................................................
Hc   ..........................ca.c.a.t........c..a.

Ha   cacnnnnnnaaatatctctgtattttaaatttaaacagttacnnaaatta  150
Hg   ........................g.....................
Hc   t..........c....t..a....a..t.....................

Ha   tatcatcgtcgccccaacgaaataattntagtatataaataatattaaac  200
Hg   ..........................c.....................
Hc   ...t.........................ac..c.....g......t..

Ha   tttcaactcatctaattatatactaaattattaagctttatagggtctta  250
Hg   ...t..............................................
Hc   ..a...t.............g.a...........................

Ha   tcgtccctttaaaatatttaagccttttcacttaaaagtcaaattcaatt  300
Hg   ..................................................
Hc   ........................................c..tg.a.

Ha   tttgtgtttgagacagtttgcttcttgtccaaccattcatacaagcctcc  350
Hg   a....a............................................
Hc   ac.t.t..c.........................................

Ha   aattaagagactaatgactatgctaccttc                     380
Hg   ............................
Hc   ......g.nn..................
```

Figure 4

Partial sequence for the mitochondrial 16s rRNA gene. Sequences for *Homarus americanus* (Ha), *H. gammarus* (Hg), and *Homarinus capensis* (Hc) have been deposited with GenBank Accession Numbers U11238, U11246, and U11247 respectively. Dots indicate nucleotides identical with Ha; letters indicate nucleotide substitutions at the homologous sites. Sites marked 'n' have unresolved nucleotides.

followed by row of intermittent noncrushing moderate conical teeth with 4–6 smaller ones in intervals between them; minor chela with latter pattern of noncrushing teeth on cutting edge of each finger; tips of fingers on each chela curved toward each other and crossing.

Carpus of major chela elongate; anterior margin with two prominent spines and smaller ones between, palmar condyle subcircular and flattened, with suggestion of spines or tubercles on its anteromesial margin; dorsomesial margin strongly tuberculate and partly obscured by setae; shorter dorsolateral margin also tuberculate but less prominently so; strong low spines on mesioventral margin. Merus bearing subdistal anterolateral spine, well-separated sharp tubercles on mesiodorsal margin, and mesioventral row of fairly uniform small tubercles.

Minor chela with similar but less developed ornamentation; merus with acute spines and spiniform tubercles.

Etymology—The name *Homarinus* is derived from French *homard*, lobster, and the adjectival combining form *-inus*, resembling. The gender is masculine.

Homarinus capensis (Herbst, 1792), new combination

Synonymy—Holthuis (1986:243, fig. 1) gave an exhaustive synonymy for *Homarus capensis*, and a later (1991:59) less inclusive account. These treatments are so recent and readily available that reiteration here would be unnecessarily redundant. Succeeding reference to the species follows.

Homarus capensis.—Kado, Kittaka, Hayakawa and Pollock, 1994:72, figs. 2, 3, 4.

Material—Cape Province, South Africa. USNM 251451. 1♂, East London?, R. Melville-Smith, 92-RMS–0, Nov 1992, regurg., dismembered, carapace length (cl) 26.5 mm, short carapace length (scl) 21 mm, abdomen length (abdl) 33.0 mm. USNM 251452. 1♂, southwest Dassen Island [33°26'S, 18°05'E], regurgitated from *Sebastichthys capensis*, badly crushed and partly dismembered, R.S. Steneck, 92-D–2, 1 Dec 1992, cl 32 mm, scl 25.5 mm. USNM 251453. 1♀, Still Bay [34°23'S, 21°27'E], dismembered, R. Melville-Smith, RMS7, abdl 45 mm. USNM 251454. 1♀, Still Bay, regurg., R. Melville-Smith, RMS8, 5 mm, abdl 47 mm.

Additional specimens reported to us by R. Melville-Smith, Sea Fisheries Institute, Cape Town: 1♂, North Dassen Island, tide pool, RSS, 92-D–1, 3 Feb 1992; 1♀. Port Alfred, RMS 1; 1♂, Houghham Park, Algoa Bay; 1♂, Dassen Island, west side, RMS 3; 1♂, Cape St. Francis, RMS 4; 1♂, Cintsa Reef, East London, RMS 5; 1♂, Sunday's River mouth, RMS 6; 2♂, Cape St. Francis, RMS 9 and 10; 1♀, Haga Haga, Transkei coast, RMS 11.

Description—As for genus with addition of the following details.

Abdominal pleura well developed, with rounded angles; pleuron of segment 1 small; pleuron of segment 2 broad, overlapping first and third pleura; pleura 3–4–5 with anteroventral angle rounded, posterolateral angle subrectangular; pleuron of segment 6 rounded ventrally, posterolateral angle rounded and confluent with anterolateral angle of telson.

Telson with dorsal setae distributed in 3 longitudinal tracts, central and submarginal on either side; central tuft proximally in midline and another near each anterolateral corner; sparse similar setae on abdominal pleura; lateral ramus of uropod with ventral submarginal row of setae laterally.

Eyes with distal edge of cornea slightly exceeding level of basicerite tip; this tip reaching to midlength of narrowly rounded antennal scale exceeded by its very strong anterolateral spine (rarely doubled) reaching distal edge of penultimate article in antennular peduncle; latter falling short of distal margin of terminal article in antennal peduncle.

Epistome with median anterior spine closely flanked at either side by shorter rounded spine.

Cheliped of pereopod 1 having fixed finger with narrowed extensor margin set off by shallow submarginal groove. Palm with compound row of low forward pointing spines and tubercles on flexor surface, similar development on extensor edge originating at carpal condyle and running along proximal margin of palm, across its basal end, and distally for a distance along palm.

Oviducal opening on coxa of pereopod 3 oval; its axes 1.3 × 1.8 mm on measured female noted below.

Pleopod 1 with distal article broader than shaft and hollowed mesially, forming flattened tubular opening when appressed to opposite member, tip irregularly rounded. Pleopod 2 with appendix masculina on mesial aspect of endopod bearing tuft of strong setae at apex.

Uropods with protopodite bearing 2 strong spines overhanging proximal end of mesial and lateral ramus respectively.

Variation—There is minor variation in development of spines, tubercles, etc., among the two females and two males examined. According to Stebbing (1900), sides of the rostrum may have 5, 6, or 7 spines on the margin. Density of setae on exoskeletal parts is subject to considerable variation, owing perhaps to recency of molting, age, or abrasion after preservation.

Color—Color of a living animal is shown in Figure 1. Published records summarized by Holthuis (1986) indicate that color may depart considerably from that shown here: coral-red to tawny or reddish yellow, which may have resulted from postmortem changes; or, in the fresh state, "of a rather dark olive colour, not dissimilar to that of the Northern lobster" Gilchrist (1918:45).

Molecular characterization—Comparative analysis of a portion of the 16s ribosomal RNA gene from mitochondrial DNA (mtDNA) was conducted by using standard protocols (Kocher et al., 1989). Mitochondrial DNA's purified by CsCl ultracentrifugation (Lansman et al., 1981) were amplified by PCR with the conserved primers 16sar and 16sbr of Palumbi et al. (1991). Following asymmetric amplification (*Homarus americanus* and *H. gammarus*) or cycle-sequencing (*Homarinus capensis*), DNA's were manually sequenced by the dideoxy chain-termination method of Sanger et al. (1977). Aligned sequences are presented in Figure 4. Sequence divergence between taxa was estimated by using the two-parameter method of Kimura (1980). Sequence divergence between *Homarus americanus* and *H. gammarus* was 1.3%, whereas average divergence between these two species and *Homarinus capensis* was 9.7%. The 16s rRNA gene is one of the most slowly evolving regions of the mtDNA molecule (Xiong and Kocher, 1994); this conservative property makes it particularly useful for comparative studies among distantly related taxa. Though there is no formal recognition of equivalence between levels of sequence divergence and taxonomic rank (Hillis and Moritz, 1990), it is clear that the relative magnitude of divergence can be a useful taxonomic indicator (Avise, 1994). The magnitude of sequence differentiation that we observed between *H. capensis* and the two North Atlantic taxa strongly suggested the existence of two discrete clades. Molecular divergence reinforced our conclusions from the reexamination of the morphology of these species.

Remarks—Morphological differences between *Homarinus capensis* and the two species of *Homarus* are clear cut. Perhaps the most obvious differences are that *Homarinus capensis* has a dense coat of setae on the outer surface of the palms and on other articles of the chelipeds (P1), and scattered setae distributed over the carapace, tail fan, sixth abdominal segment, and pleurae of the remaining abdominal segments; *Homarus americanus* and *H. gammarus* are smooth and glabrous. The telson of *Homarinus* has subparallel sides and its exposed surface bears many obsolescent transverse rugae (Fig. 3); the telson of *Homarus* species has sides converging toward the tip, giving a subtriangular shape. First pleopods are more elongate and slender in *Homarus* species than in *Homarinus* (Fig. 2).

The two species of *Homarus* attain large size (Wolff, 1978), whereas *Homarinus capensis* appears to be much smaller at maturity. No ovigerous females of *H. capensis* have been found, but openings of the oviducts are at least twice the size of those on comparably sized specimens of the species of *Homarus* (see Kado et al., 1994). This suggests that there are fewer eggs with accelerated larval development in *Homarinus capensis* relative to slower larval devel-

opment from smaller more numerous eggs in *Homarus* species (Kado et al., 1994).

Acknowledgments

Our conclusions converged independently from two viewpoints. A. B. W. and other carcinologists have long understood grounds for generic separation of the Cape lobster from *Homarus* on the basis of morphology. I. K. and R. S. S. concluded this on the basis of genetic divergence and were well into their analysis before forces were joined. A. B. W. drafted the systematic section and assembled the jointly produced text. Keiko Hiratsuka Moore rendered drawings of the pleopods. G. C. Steyskal provided advice on the choice of a new generic name. The manuscript was critically reviewed by W. Glanz, R. B. Manning, and T. A. Munroe. We are indebted especially to colleagues at the Sea Fisheries Institute, Cape Town, South Africa, who helped us in this study; Roy Melville-Smith provided materials and information, and Robert Tarr photographed the living specimen of Cape lobster. George M. Branch, University of Cape Town, provided logistic support and aided in specimen acquisition. Yan Kit Tam and Alex Parker provided sequence data. R. S. S. was supported by grants from the South African Foundation of Research Development, the Visiting Scholar Fund, and the Student Fund for Visiting Scholars of the University of Cape Town. Molecular work was supported by NOAA Sea Grant (NA90AAD-SG499) and NSF (EHR-9108766 and OCE-9203342).

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Ageing of three species of tropical snapper (Lutjanidae) from the Gulf of Carpentaria, Australia, using radiometry and otolith ring counts

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Abstract.—A radiometric ageing method was used to resolve conflicting results from ageing tropical lutjanids based on annual ring counts in whole and sectioned otoliths. The number of rings detected in sectioned otoliths of *Lutjanus erythropterus*, *L. malabaricus*, and *L. sebae* from unexploited populations in the Gulf of Carpentaria, Australia, were 1.6 to 2.4 times the number found in whole otoliths. To obtain an independent estimate of age, we measured $^{210}Pb/^{226}Ra$ radioactive disequilibria of both whole and cored otoliths. As all species had high levels of ^{226}Ra, they could be aged with relative accuracy by this method. Samples of whole otoliths and cores with a similar ring count had similar radiometric ages. In samples whose sectioned and whole-otolith ages differed by more than 4 years, the whole otolith ring count agreed better with the radiometric age (for an uptake activity ratio R=0.0). This result stands in marked contrast to the radiometric age validation of section counts for slow-growing, long-lived fish inhabiting temperate to subtemperate waters. In this region, all species lived less than 10 years and grew to a maximum size of up to 600 mm SL. They reached a similar length in one year, but *L. erythropterus* grew faster than the other two species thereafter. The sexes had the same growth rates. Our results were similar to those found for these species elsewhere and suggest that in tropical fishes, such as lutjanids, rings observed in sectioned otoliths and other hard parts may not be formed annually. Where possible, ages derived from counts in these structures should be verified by independent methods.

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Tropical fishes can be difficult to age because many species do not deposit annual rings in their hard parts (Longhurst and Pauly, 1987). Lutjanids, which are highly valued commercial fishes in the tropical Indo-Pacific region, often have ring patterns in their hard parts that are difficult to interprete (e.g. Davis and West, 1992). The age and growth of many lutjanid species have been well studied and the results of these studies have formed the basis of age-structured stock assessments upon which the management of these fisheries is based (e.g. Sainsbury, 1988).

In the western Pacific, *Lutjanus malabaricus* has been the most widely studied lutjanid, as it is the main catch of trawl and line fisheries in northern Australia, adjacent Indonesian waters, and in the South China Sea. The reported maximum age (up to 10 yr) and growth parameters differ both between regions (Lai and Lui, 1974, 1979) and within one area (northern Australia: Lai and Lui, 1979; Chen et al., 1984; Edwards, 1985; McPherson and Squire, 1992). These studies estimated age from growth rings in vertebrae (Lai and Lui, 1979; Chen et al., 1984; Edwards, 1985) or in whole otoliths (McPherson and Squire, 1992). The latter method may underestimate the age of longer-lived species because of the difficulty of distinguishing all the growth rings (Casselman, 1974).

The timing of formation of annual growth rings in *Lutjanus* from northern Australia has not been fully verified. Several authors (Lai and Lui, 1974, 1979; Chen et al., 1984; Yeh et al., 1986; Davis and West, 1992) have concluded that the outer ring is probably deposited

annually, but the season when this ring is formed varies between studies and species. Such ambiguities cast doubt on the validity of the conclusions and suggest that differences in the estimated growth rate and age of *Lutjanus* populations may be related to problems of interpretation rather than to biological differences.

A radiometric method has recently been used successfully to estimate the age of long-lived fishes (Bennett et al., 1982; Fenton et al., 1991). This method uses the known decay rates of isotopes of Radium–226 (^{226}Ra) and Lead–210 (^{210}Pb) in bony parts to estimate the age of fish. It does not rely on operator interpretation to estimate age and therefore is particularly useful for ageing long-lived species where the growth rings are often not clearly defined (Casselman, 1974).

The objectives of the present study were 1) to estimate the age and growth of *Lutjanus malabaricus*, *L. erythropterus*, and *L. sebae* from the Gulf of Carpentaria by counting rings in whole and sectioned otoliths; and 2) to use the ^{210}Pb/^{226}Ra radiometric ageing method to make an independent age estimation of the same fish.

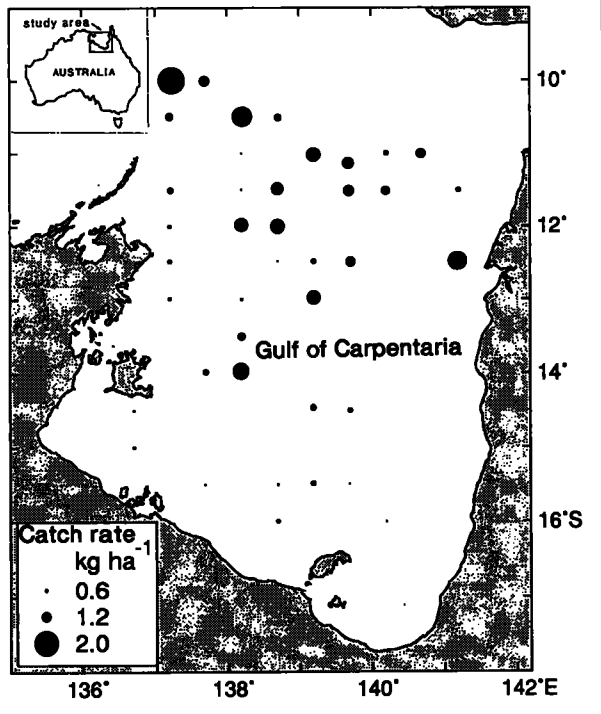

Figure 1

Map of the Gulf of Carpentaria showing the distribution and relative abundance of *Lutjanus erythropterus*, *L. malabaricus*, and *L. sebae* during a systematic survey in November 1990.

Materials and methods

Sampling

Most samples of *Lutjanus erythropterus*, *L. malabaricus*, and *L. sebae* were collected during a systematic survey of the Gulf of Carpentaria between long. 136° and 142°E in November 1990. Two similar random-sampling surveys were made across the northern Gulf of Carpentaria (north of lat. 14°30'S) in November 1991 and January 1993. Samples of *Lutjanus malabaricus* were also collected during a survey of eight areas in the Gulf of Carpen-taria by the commercial trawler *Clipper Bird* in June 1990 (Fig. 1). Details of survey design, trawl gears, and trawl durations are given in Blaber et al.(1994).

Commercial-sized *Lutjanus malabaricus* (1–3 kg) were obtained from fish retained for sale after the June 1990 survey. During the systematic survey in November 1990, all specimens of the three target species of lutjanids were retained for ageing studies. In November 1991 and January 1993, only fish from length classes underrepresented in previous samples were processed. All fish were measured (standard length [SL] in mm), weighed (±1 g), and sexed, and both sagittae were removed, dried, and stored in labelled bags for future analysis.

Radiometry

Radioanalysis requires about 1 g of sample material; therefore, fish were pooled to obtain the necessary sample weight. For juveniles, up to four otoliths were required to obtain this weight. Otoliths used for radioanalysis were chosen in two ways. First, for each species, otoliths from juvenile, maturing, and mature fish that had the same sectioned-otolith ages, similar otolith weights, and similar sizes, and came from the same region of the Gulf of Carpentaria were pooled for radioanalysis. Second, otoliths of the same whole-otolith age and from fish of similar size were abraded with a mechanical sander to a central core approximating the weight (see Table 2), length, and shape of the otolith of a fish whose whole-otolith age was 3 (otolith length=11.6 ± 0.7 for *L. erythropterus*; 12.7 ± 0.4 for *L. malabaricus*; and 11.4 ± 0.4 for *L. sebae*). The exception was sample 2490 for which otoliths were ground to a core age of 2 (weight 0.156 ± 0.005 g; otolith length 9.2 ± 0.16 mm; n=92). The otolith nucleus at the center of the cores was located by examining intact otolith morphology and by sectioning other samples (Campana et al., 1990). This age is less than the age at sexual maturity for all species.

The method of radioanalysis of the otoliths is detailed in Fenton et al. (1990, 1991). It involves measuring the specific activity of ^{226}Ra:^{210}Pb by alpha-spectrometry. Because of the extremely small specific activities measured (0.01–0.1 dpm·g^{-1} for Polonium–210 [^{210}Po]), cleanliness is of the utmost importance in the analytical procedure. Every item of laboratory ware that contacted the otolith solutions and otoliths was chemically decontaminated in alkaline 0.05M Na_4EDTA (pH 10.5). The otoliths were washed and rinsed several times in this solution, then washed several times in 0.1M HCl (<10 s) and finally washed twice in water.

Our analyses of ^{210}Pb, via its short-lived daughter-proxy ^{210}Po, and ^{226}Ra were made with high-resolution alpha-spectrometers according to the methods of Fenton et al. (1990). The mean ^{210}Po reagent blank was 0.0071 ± 0.0012 dpm. Recovery of ^{210}Po was always at least 90% and instrument background counts (for ^{208}Po and ^{210}Po) were less than one count·d^{-1}. ^{226}Ra was analyzed by a direct alpha-spectrometry method and chemical yield was measured by gamma spectrometry of a Barium–133 (^{133}Ba) tracer (Fenton et al., 1990, 1991). Mean activity of the ^{226}Ra blanks was 0.0174 ± 0.0026 dpm, which was lower than in previous studies (e.g. Bennett et al., 1982; Fenton et al., 1991) owing to careful control of reagents. Recovery of ^{226}Ra (as estimated by the recovery of ^{133}Ba tracer) was greater than 85% for all samples.

Data analysis

The ages of whole otoliths were calculated on the basis of a single constant (linear) growth rate by the equation originally derived by Bennett et al. (1982):

$$A = 1-(1-R)\frac{1-e^{-\lambda t}}{\lambda t}, \qquad (1)$$

where A=the ratio of the activity of ^{210}Pb to ^{226}Ra activity at time t (^{210}Pb/^{226}Ra)$_t$; R=ratio of ^{210}Pb to ^{226}Ra at the time of deposition [(^{210}Pb/^{226}Ra)$_0$]; and λ=decay constant for ^{210}Pb (0.03114 yr^{-1}). Assumption of a single linear mass growth rate produces radiometric ages that are greater than those that would result from assumption of an exponential (non-linear) rate, the bias always favoring a higher value (Campana et al., 1993). It should be understood that using this assumption (linear mass growth of the otolith) will produce age estimates that always overestimate the real age.

For otolith cores, ages were calculated from Smith et al.'s (1991) equation:

$$A = \left(1-e^{-\lambda(t-T)}\right)+\left(1-(1-R)\frac{\left(1-e^{-\lambda T}\right)}{\lambda T}\right)e^{-\lambda(t-T)}, \qquad (2)$$

where all parameters are the same as in the previous model, except T, which is the estimated age of the otolith core. A linear mass growth model was assumed only up to the age of the core. The initial uptake ^{210}Pb/^{226}Ra activity ratio was generally assumed to be R=0.0. This is the most conservative value, and so radiometric age estimates derived with this value must overestimate the maximum possible age of the sample. The above equations were solved numerically by a Newton-Raphson iteration method (Fenton et al., 1991).

Stable element analysis

The levels of lead and barium in otoliths are presumed to act as stable equivalents of ^{210}Pb and ^{226}Ra and so can be used to assess the uptake of the radioactive isotopes and to normalize the radiometric data (Fenton and Short, 1992). Therefore, the concentrations of stable lead, barium, strontium (Sr), and calcium (Ca) in each otolith sample were measured for an aliquot of each dissolved otolith solution used in the radiometric analysis. Each solution was analyzed by inductively coupled plasma mass spectrometry for lead and barium and by inductively coupled plasma atomic emission spectrometry for strontium and calcium.

Otolith ageing

Pairs of otoliths from each fish were cleaned of excess tissue, dried at 60°C for 24 h, weighed (± 0.1 mg) and measured along the longitudinal axis with dial calipers (± 0.05 mm). One otolith of each pair was embedded in polyester resin and cross-sectioned with a diamond saw (Augustine and Kenchington, 1987). Thin sections (approximately 200 μm) of each otolith were bonded to microscope slides with thermoplastic cement. Each section was polished on both faces with 800-grit wet-and-dry carborundum paper before being examined with a video-enhanced light microscope attached to a microcomputer with precise distance-measuring software. The rings (presumed annuli) were counted and the distance between them measured along the dorsal axis adjacent to the sulcus, where they were most clearly distinguishable. In whole otoliths, the rings were counted against a strong background point light source.

Counts of rings in all whole and sectioned otoliths were made independently by two readers. When the ring counts differed, the otoliths were reexamined by both readers. If the counts still differed by more

than one, the data were discarded (<5% of all otoliths). If counts differed by one, the higher value was chosen (10% of otoliths). The relative frequency of these discrepancies was similar for all species.

Data analysis

The length-at-age data were fitted to the reparameterized von Bertalanffy growth curve of Francis (1988). This method has the advantage that the parameters estimated are independent and can be compared directly between species and populations.

Most previous studies of lutjanid age and growth have fitted the von Bertalanffy growth equation to data on length at age (e.g. Lai and Lui, 1979; Manooch, 1987; Davis and West, 1992). However, the estimated parameters L_∞, K, and t_0 either do not have direct biological meaning (e.g. Knight, 1968; Schnute and Fournier, 1980; Ratkowsky, 1986) or are extrapolations from the data (Ratkowsky, 1986). Francis (1988) extended the equation of Schnute and Fournier (1980) to derive a new set of parameters L_1, L_2, and L_3 (his l_ϕ, l_χ, and l_w), which correspond to the length at the lower, middle, and upper limits of any arbitrarily defined age range, such that:

$$L_t = L_1 + (L_3 - L_1)\left(1 - r^{2(t-\phi)/(w-\phi)}\right)\Big/(1-r^2), \quad (3)$$

where $r = (L_3-L_2)/(L_2-L_1)$; L_t is the mean length of a fish at age t; and L_1, L_2 and L_3 are the length at the lower, middle, and upper limits of two arbitrary ages ϕ and w. By fitting a curve of this form, extrapolations beyond the data are avoided, as the three fitted parameters are chosen from within the range of the data and hence can be directly compared with the results of previous studies.

In this study, we set $\phi = 1$ ring and $w = 6$ rings for each species. This equation has the advantage that the age range to be examined can be chosen by the investigator, rather than having to be the largest and smallest age classes found, as required by the Schnute and Fournier (1980) equation. These parameters (L_1, L_2, and L_3) can also be expected to have similar properties to those of Schnute and Fournier (1980) and not to show the high negative correlation between L_∞ and K (Francis, 1988).

All parameters were estimated by an iterative least-squares method (SAS NLIN procedure with the Marquardt option; SAS, 1989). Vaughan and Kanciruk (1982) found that this procedure consistently showed the least bias in parameter estimates, converged rapidly, and provided more precise estimates than did standard linear techniques. A measure of goodness-of-fit was obtained by calculating an r^2 value from the residual and the explained sums of squares derived from the least-squares regression.

Relationship of ring counts in whole and sectioned otoliths with radiometric ages

The estimated age from ring counts in whole and sectioned otoliths used in the radiometry were compared for all species by two methods. First, the relationship between radiometric age and whole and sectioned otolith ages of the same fish were plotted. If the slope of the relationship was not significantly different from 1, the results of the two methods were considered to be in close agreement. Second, the two ageing methods were compared with the radiometric ages with a Wilcoxon matched-pairs ranks test (Conover, 1980). The two hypotheses tested were 1) that whole otolith ring counts underestimated true age (radiometric age) or 2) that sectioned otolith ring counts overestimated true age.

Results

Radiometry

Lutjanus erythropterus—The specific activity of ^{226}Ra and the ^{210}Pb/^{226}Ra activity ratio differed among the three samples of *L. erythropterus* (Tables 1 and 2). The activity ratio was highest in the cored sample (0.118 ± 0.031; Table 2). Ring counts in whole otoliths were linearly related to otolith mass (Fig. 2A) and ring count in sectioned otoliths, though the relationship was significantly weaker ($P<0.05$). Radiometric age estimates were calculated on the basis of a single constant (linear) growth rate for otolith mass, which removes the need to include the mass growth relation in the radiometric age calculation (Eq. 1). Under the assumption of a constant growth model, radiometric age estimates were most similar to those obtained from the ring counts in whole otoliths (Table 2). The match was best for the cored otolith sample where model assumptions are less stringent (sample 2673).

Lutjanus malabaricus—The specific activity of ^{226}Ra in *L. malabaricus* otoliths differed among samples and among size classes (Tables 1 and 2). The ^{210}Pb/^{226}Ra activity ratios ranged from less than 0.027 to 0.212 and varied to a similar degree in cored and whole-otolith samples (Table 2). Otolith weight was linearly related to the number of rings in whole otoliths (Fig. 2B), and this relationship was stronger than that for counts from sectioned otoliths

Table 1

Elemental composition of otoliths of three species of *Lutjanus* used in the radiometric analysis. Whole = whole otoliths used; cored = otoliths cored to age 3+ (*L. erythropterus*) or 2+(*L. malabaricus* and *L. sebae*). Numbers in parentheses represent repeated analyses of a sample in which several otoliths of similar whole and sectioned age had been combined.

Species	Sample	Whole/or cored	^{226}Radium dpm·g^{-1} (± 1σ)	^{210}Lead dpm·g^{-1} (± 1σ)	Lead (Pb) (ppm)	Barium (Ba) (ppm)	Pb/Ba mass ratio	Strontium (Sr) (ppm)	Calcium (Ca) (ppm)	Sr/Ca mass ratio
L. erythropterus	2065	Whole	0.2277 ± 0.0132	0.0174 ± 0.0047	0.08	18.7	0.004	2,800	395,000	0.0071
	2066	Whole	0.1623 ± 0.0087	0.0070 ± 0.0035	0.19	11.5	0.016	2,720	398,000	0.0068
	2673	Cored	0.1331 ± 0.0087	0.0157 ± 0.0040	0.66	9.2	0.071	—	—	—
L. malabaricus	2062(2)	Whole	0.2390 ± 0.0111	−0.0025 ± 0.0045	0.27	8.2	0.033	2,915	462,000	0.0063
	2063	Whole	0.0728 ± 0.0066	0.0067 ± 0.0042	3.49	6.5	0.537	3,330	470,000	0.0071
	2063(2)	Whole	0.0582 ± 0.0049	−0.0010 ± 0.0025	0.22	13.4	0.016	1,990	321,000	0.0062
	2063(3)	Whole	0.0916 ± 0.0053	0.0072 ± 0.0017	0.55	4.8	0.114	2,240	399,000	0.0056
	2064	Whole	0.2118 ± 0.0164	0.0173 ± 0.0024	2.28	5.8	0.390	3,000	395,000	0.0076
	2438	Whole	0.1014 ± 0.0064	0.0068 ± 0.0036	0.41	5.3	0.080	2,005	426,000	0.0047
	2439	Whole	0.2942 ± 0.0141	0.0133 ± 0.0043	0.06	7.5	0.008	2,250	415,000	0.0054
	2440	Whole	0.1080 ± 0.0068	0.0135 ± 0.0029	0.18	6.2	0.029	2,910	438,000	0.0067
	2489	Cored	0.1678 ± 0.0088	0.0356 ± 0.0055	<0.09	6.7	<0.014	2,160	407,000	0.0053
	2490	Cored	0.1219 ± 0.0078	0.0180 ± 0.0037	<0.09	6.2	<0.014	2,040	416,000	0.0049
L. sebae	2068	Whole	0.1036 ± 0.0064	0.0139 ± 0.0034	3.13	8.7	0.360	2,360	396,000	0.0060
	2069	Whole	0.1046 ± 0.0058	0.0312 ± 0.0037	1.38	8.1	0.170	2,510	398,000	0.0063
	2070	Whole	0.0460 ± 0.0042	0.0100 ± 0.0023	0.46	5.0	0.092	—	—	—
	2647	Cored	0.2143 ± 0.0114	0.0373 ± 0.0049	0.50	11.5	0.043	—	—	—
	2648	Cored	0.1756 ± 0.0099	0.0458 ± 0.0052	0.66	9.4	0.071	—	—	—

Table 2

Results of radiometric and direct ageing otoliths of *Lutjanus malabaricus*, *L. erythropterus* and *L. sebae* from the Gulf of Carpentaria. Radiometric ages were calculated by using a constant growth rate model and by using R = 0.0 (where R = initial ^{210}Pb:^{226}Ra activity ratio at time of deposition). All errors in radiometric age estimates expressed at 1σ level (n = number of otoliths in sample). SE = Standard error. Numbers in parentheses represent repeated analyses of a sample in which several otoliths of similar whole and sectioned age had been combined.

Species	Sample	n	Mean length (mm) ± SE	Mean otolith mass (g) ± SE	Whole otolith age	Sectioned otolith age	^{210}Pb:^{226}Ra activity ratio	Radiometric age
L. erythropterus	2065	3	316 ± 2	0.3315 ± 0.0186	3	3	0.076 ± 0.021	5.1 ± 1.5
	2066	2	364 ± –	0.3875 ± –	3.3	6	0.043 ± 0.022	2.8 ± 1.5
	2673	3	368 ± 7	0.4750 ± 0.0507	4	9	0.118 ± 0.031	5.5 ± 1.1
L. malabaricus	2062(2)	2	310 ± –	0.4852 ± –	3	3	<0.027 (95% CL)	<1.8 (95% CL)
	2063	2	350 ± –	0.5775 ± –	4	6	0.092 ± 0.058	5.7 +4.3,–4.0
	2063(2)	2	348 ± –	0.6170 ± –	4	6	<0.069 (95% CL)	<4.6 (95% CL)
	2063(3)	3	346 ± 7	0.6118 ± 0.0133	4	6	0.079 ± 0.019	0.8 ± 0.8
	2064	3	443 ± 7	1.5591 ± 0.0493	6.7	14	0.082 ± 0.013	5.6 ± 0.9
	2438	4	250 ± 2	0.2517 ± 0.0063	3	3.5	0.067 ± 0.036	4.5 +2.6,–2.5
	2439	1	650	2.1155	9	13	0.045 ± 0.015	3.0 ± 1.0
	2440	1	560	2.1111	7	19	0.125 ± 0.028	8.8 + 2.2,–2.1
	2489	4	455 ± 10	1.6185 ± 0.1349	9	13	0.212 ± 0.035	8.7 +1.5,–1.4
	2490	5	422 ± 7	1.1055 ± 0.0501	8	8	0.148 ± 0.032	6.1 ± 1.2
L. sebae	2068	4	222 ± 5	0.2429 ± 0.0261	2	3	0.134 ± 0.034	9.5 + 2.7,–2.6
	2069	2	304 ± –	0.6152 ± –	3.5	7	0.298 ± 0.039	24.2 +4.2,–3.9
	2070	2	399 ± –	1.5658 ± –	5.5	15	0.217 ± 0.054	16.4 +5.1,–4.6
	2647	3	400 ± 15	1.4462 ± 0.0184	5	12.3	0.174 ± 0.023	7.1 ± 1.0
	2648	2	462 ± –	2.1000 ± –	7	15.5	0.261 ± 0.033	11.2 +1.5,–1.4

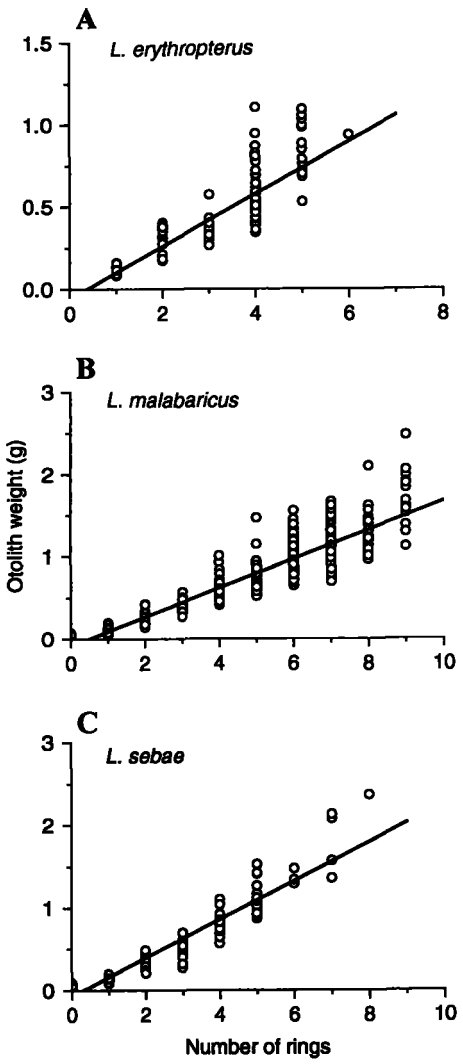

Figure 2

The relationship between otolith weight and the number of rings counted in whole otoliths of (**A**) *L. erythropterus*, (**B**) *L. malabaricus*, and (**C**) *L. sebae*.

(P<0.05). Under the assumption of a constant mass growth model, radiometric age estimates were again most similar to those found for whole otolith ring counts. The match was best for samples of cored otoliths (2489, 2490) where assumption of a mass growth model is almost absent (Table 2).

Lutjanus sebae —The specific activity of ^{226}Ra and the $^{210}Pb/^{226}Ra$ activity ratio varied less between samples in *L. sebae* than in the other species (Tables 1 and 2). As with the other species, otolith weight was linearly related to the ring counts of whole otoliths; therefore, a single constant growth rate was assumed in interpretation of the radiometric data (Fig. 2C). The radiometric age estimates of intact otolith samples of juveniles (2068, 2069, 2070), based on the assumption of no allogenic ^{210}Pb uptake in the otoliths (R=0.0), were higher than the ring counts for both sectioned and whole otoliths (Table 2). Samples 2068 and 2069 were probably subject to high rates of allogenic ^{210}Pb uptake, as indicated by the high stable Pb/Ba mass ratios (Table 1). Radiometric ages of both sets of cored otoliths were most similar to the age estimates based on whole otolith counts. However, both these samples (2647 and 2648) had very low stable Pb/Ba mass ratios (Table 1). Modelled radiometric ages of *L. sebae* samples (both whole and cored) for different values of R indicate that $R = 0.10$ best matches the ring count of whole otoliths (Table 3).

Lead:Barium ratios

The stable lead:barium ratios of all samples were plotted against radiometric age assuming an initial activity ratio $R = 0.0$ (Fig. 3). Neither *L. malabaricus* nor *L. erythropterus* showed an increase in the ratio with increasing age. However, in four of the five *L. sebae* samples radiometric age increased rapidly with increasing stable lead (Fig. 3).

Otolith ageing

Lutjanus erythropterus—The growth curves of *L. erythropterus* based on ring counts in whole otoliths

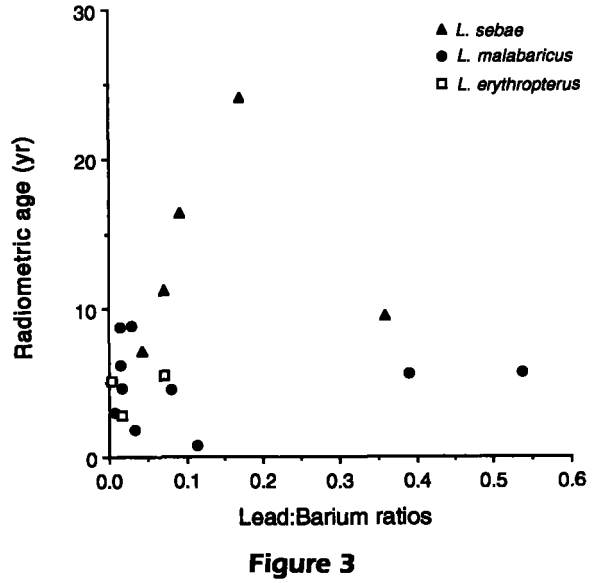

Figure 3

Plot of the relationship between radiometric age and lead:barium ratios for the three species of *Lutjanus*.

Table 3

Radiometric age estimates of samples of both whole and cored(*) *Lutjanus sebae* otoliths for a range of initial uptake $^{210}Pb/^{226}Ra$ activity ratios (R). [ ] denotes best match of radiometric age to whole age. Standard errors of samples 2069 and 2070 were unavoidably large, resulting in a poor agreement with either whole or sectioned ages. For whole otoliths, radiometric age estimates assumed linear mass growth for otoliths throughout. For cored otoliths, radiometric age estimates assumed linear mass growth for otoliths only to age 2+, thereafter they were irrelevant.

Sample number	Mean whole otolith age	Mean sectioned otolith age	Radiometric age (yr) for various R values			
			$R_{0.0}$	$R_{0.05}$	$R_{0.1}$	$R_{0.15}$
2068	2	3	9.5+2.7,–2.6	6.0+2.7,–2.5	[2.5+2.5,–1.9]	0.3±0.4,–0.3
2069	3.5	7	24.2+4.2,–3.9	20.4+4.1,–3.8	16.6+4.0,–3.7	12.5+4.1,–3.5
2070	5.5	15	16.4+5.1,–4.6	12.8+4.9,–4.5	9.1+4.9,–4.4	[5.4+4.7,–3.8]
2647*	5	12.3	7.1±1.0	6.0±0.9	[4.3±0.9]	1.9±0.9
2648*	7	15.5	11.2+1.5,–1.4	9.6+1.5,–1.4	[7.8+1.5,–1.4]	5.5±1.4

differed from those obtained from sectioned otoliths (Figs. 4A and 5). Fewer rings were counted in whole than in sectioned otoliths but they were linearly related (Fig. 6A; whole otolith count=0.40 × (sectioned otolith count) + 1.02; r^2=0.69, $F_{1,170}$=368.7, P<0.0001). However, the length-at-age data overlapped for all the size classes detected in whole otoliths (Fig. 4A). Both sexes had similar growth parameters based on whole otlith ring counts (P>0.3) (Table 4) and lived to a similar age.

Lutjanus malabaricus—The growth curves expressing the best fit of length-at-age data from both sectioned otoliths and whole otoliths show significant differences (P<0.05) in the estimated growth rates (Fig. 4B). More rings were counted in sectioned otoliths than in whole otoliths from the same fish (Fig. 6B), but were linearly related (whole otolith count=0.64 × (sectioned otolith count) + 0.79; r^2=0.81, $F_{1,869}$=3614.7, P<0.001).

Growth parameters of the reparameterized von Bertalanffy equation of male and female *L. malabaricus* did not differ except for L_3; this parameter was larger in males (P<0.05). Not all fish collected were sexed, but the growth parameters of the combined equation differed from that obtained from the subsets that were sexed (Table 4).

Lutjanus sebae—Ages based on counts of sectioned and whole otoliths differed significantly in *L. sebae* over 350 mm SL (P<0.05; Fig. 4C). More rings were detected in the otoliths of these fish when they were sectioned than when examined intact, although the number of rings detected by the two methods were linearly related (Fig. 6C; whole otolith count=0.50 × (sectioned otolith count) + 0.19; r^2=0.80, $F_{1,140}$=546.0, P<0.0001).

The growth parameters of the reparameterized von Bertalanffy equation were similar for both sexes (Table 4). *Lutjanus sebae* were larger at one year (L_1)

Table 4

Growth parameters (SL ± SE) of the reparameterized von Bertalanffy growth equations for *Lutjanus malabaricus, L. erythropterus,* and *L. sebae* (1–6 rings) from the Gulf of Carpentaria (r^2 = nonlinear estimate of goodness-of-fit).

Species	Sex	n	L_1 ± SE	L_2 ± SE	L_3 ± SE	r^2
L. erythropterus	both	172	75.40 ± 11.67	335.21 ± 2.73	457.12 ± 10.01	0.93
	females	61	75.03 ± 17.57	346.66 ± 5.07	477.29 ± 15.64	0.95
	males	30	86.06 ± 22.0	337.47 ± 4.50	468.66 ± 18.55	0.94
L. malabaricus	both	878	78.09 ± 2.99	298.94 ± 1.72	424.92 ± 1.37	0.95
	females	159	195.37 ± 27.37	329.09 ± 4.31	423.19 ± 2.70	0.70
	males	73	100.63 ± 15.50	313.62 ± 6.91	442.67 ± 4.54	0.92
L. sebae	both	144	122.27 ± 3.22	287.28 ± 2.18	451.50 ± 3.27	0.97
	females	14	99.92 ± 17.84	277.43 ± 8.58	443.96 ± 7.54	0.99
	males	9	113.50 ± 3.98	284.83 ± 5.30	461.10 ± 4.41	0.99

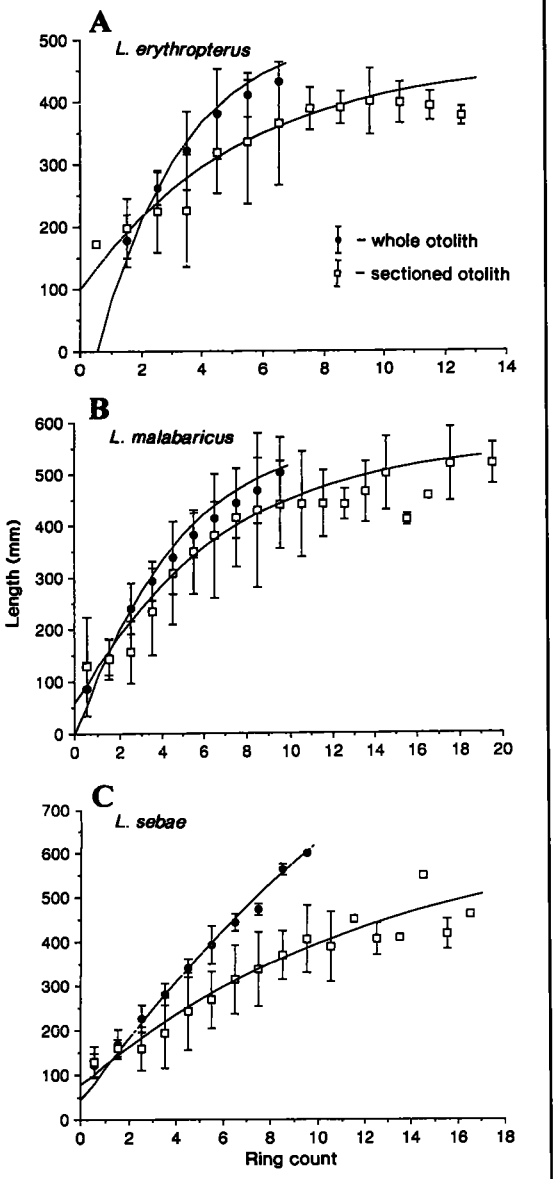

Figure 4

Plot of the mean length-at-age (±) range and the growth curves of the three species of *Lutjanus* based on ring counts in whole and sectioned otoliths.

than were other species ($P<0.05$). However, at six years of age (L_3) they were about the same size as *L. erythropterus* but were larger than *L. malabaricus* ($P<0.05$).

Relationship of ring counts in whole and sectioned otoliths with radiometric ages

There was a significant linear relationship between both whole and sectioned otolith ring counts and radiometric age (Fig. 7; $P<0.001$ in both cases). The slopes of the lines of best fit differed ($\beta=1.04 \pm 0.11$; $r^2=0.84$ for whole otolith ring counts and $\beta=1.83 \pm 0.06$; $r^2=0.87$ for sectioned otolith ring counts). Because the initial activity ratios of the *L. sebae* samples (R) were obviously greater than 0.0 in at least the whole otolith samples, these were not included in the analyses.

There was no significant difference between whole otolith ring counts and radiometric ages for all species combined ($T=53.5$; $P>0.30$, $n=15$) or for *L. malabaricus* ($T=17.5$; $P>0.15$, $n=10$). However, for all species combined we found that the sectioned ring counts were significantly greater than the radiometric age of the same fish ($T=6.5$; $P<0.001$, $n=15$). The sectioned ring counts of *L. malabaricus* were also greater than the radiometric ages ($T=2$; $P<0.005$, $n=10$).

Discussion

This is the first study to use $^{210}Pb/^{226}Ra$ activity ratios to verify the age of relatively short-lived tropical fishes. Previous studies that have used these ratios to estimate age have focussed on species that live to at least 70 years (Bennett et al., 1982; Campana et al., 1990; Fenton et al., 1991). In the Lutjanidae, natural levels of ^{226}Ra in the otoliths were high, which helped to minimize the variances in the $^{210}Pb/^{226}Ra$ activity ratio and hence the errors in the age estimates. Radiometry provided strong evidence that the rings counted in whole otoliths were the best estimate of the true age of the three lutjanids studied.

The radiometric methods we used tend to overestimate age because the assumptions concerning the otolith mass growth model and rate of incorporation of allogenic ^{210}Pb were conservative. The only conceivable mechanism that would lead to underestimation of ages radiometrically would be a significant loss of radon (^{222}Rn) from otoliths during growth (West and Gauldie, in press).

Radon is the daughter of ^{226}Ra and the only gaseous precursor of ^{210}Pb in the decay chain. Its mean lifetime is only 4.8×10^5 seconds, and its effective (physical) diffusivity in otoliths would be about 0.5×10^{-12} $m^2 \cdot s^{-1}$. Radon diffusion out of otoliths would be further retarded by adsorption to organic matter (Wong et al., 1992). Simple calculations based on the known microstructure of otoliths (Campana and Neilson, 1985) and on the existing data on radon emanation (Morawska and Phillips, 1993) show that significant loss of radon from otoliths is extremely unlikely, as previously suggested from empirical studies (Fenton and Short, 1992).

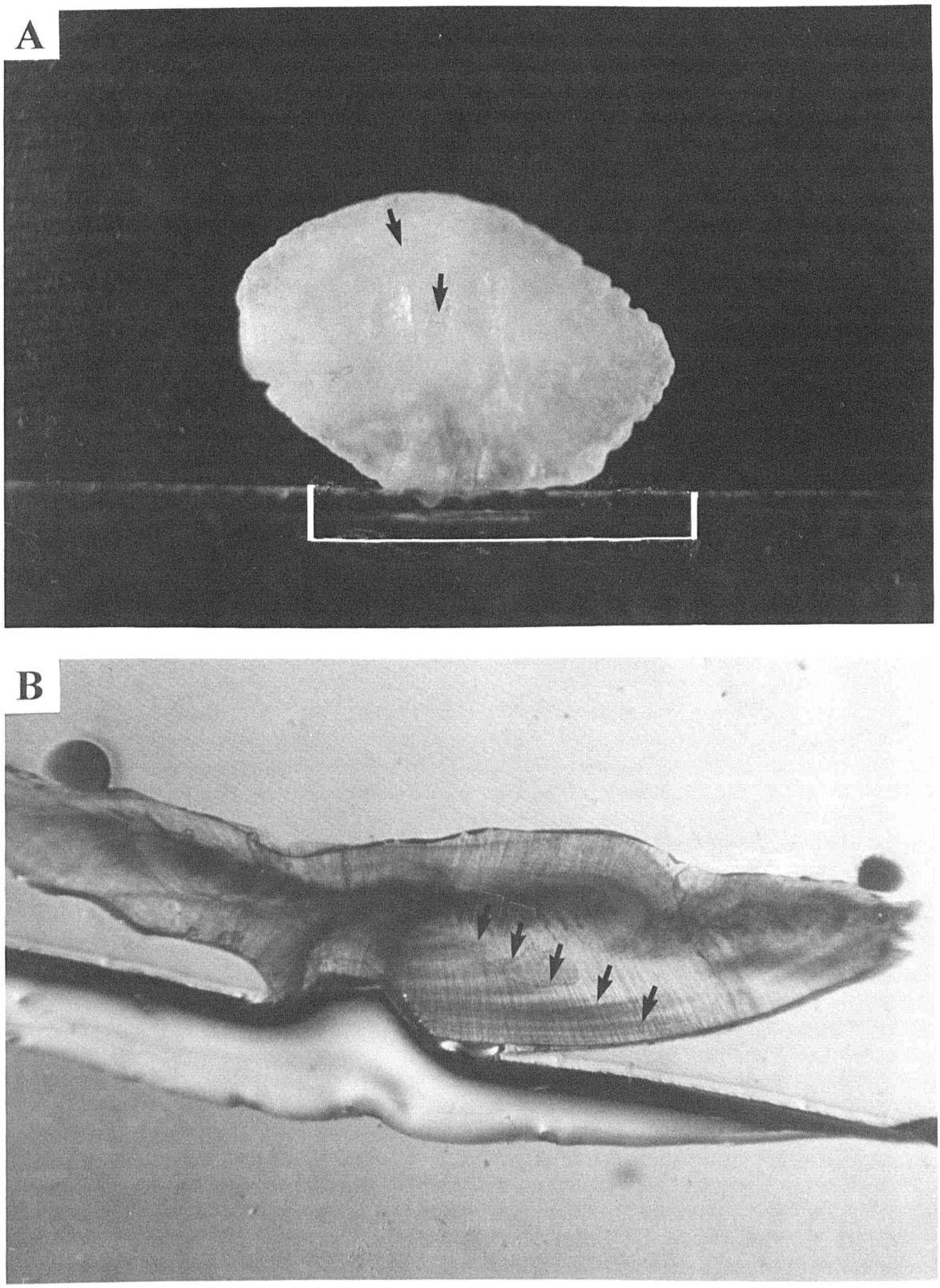

Figure 5

Photographs of an otolith of a 270-mm *L. erythropterus* showing the discrepancy between the number of rings seen by examining (**A**) the intact otolith (2 rings) and (**B**) after sectioning (5 rings). Scale=1 cm.

Why ages derived from whole and sectioned otoliths were significantly different remains unclear. The differences in ring counts increased with the size of the fish, and the slope of the regression (whole vs. sectioned ring count) was steepest for the fastest-growing species, *L. erythropterus*. The otoliths were large (up to 30 mm long, and weighing 3 g), so the daily rings during periods of reduced or variable growth of younger fish were still relatively widely spaced. Thus, what would appear as a diffuse, single hyaline zone in a whole otolith examined against reflected light may have appeared in section as a group of hyaline and opaque zones. These problems in otolith interpretation were most marked in *L. erythropterus* and led to the greatest discrepancy in ring counts.

Studies of the age and growth of *Lutjanus malabaricus* from northern Australia and the South China Sea used ring counts in vertebrae (Lai and Liu, 1974, 1979; Edwards, 1985), sectioned otoliths (Chen et al., 1984), and whole otoliths (McPherson and Squire, 1992). Their estimates were similar to the estimates we obtained from whole-otolith ageing, although *L. malabaricus* from the Great Barrier Reef appear to grow much faster and live at least one year less than those found in other areas (McPherson and Squire, 1992). However, the previous studies and our study provide different estimates of the von Bertalanffy growth parameters L_∞ and K (Table 5). These differences may have major impacts on age-structured fishery models (e.g. yield per recruit) that use these parameters to estimate optimal yield.

Lutjanus erythropterus and *L. sebae* from the Gulf of Carpentaria grew at similar rates to those reported from other parts of northern Australia (Ju et al., 1988; McPherson and Squire, 1992) and elsewhere within their range (Druzhinin and Filatova 1980; Yeh et al., 1986; McPherson and Squire, 1992). However, the growth of *L. sebae* in the Gulf of Carpentaria did not decline as they approached the maximum age observed. This may have been caused by an error in the ring count in otoliths of older fish or because the older age classes were not caught in the trawls. The maximum size of L. sebae in Australian waters has been reported to be between 1.0 and 1.4 m (Allen,

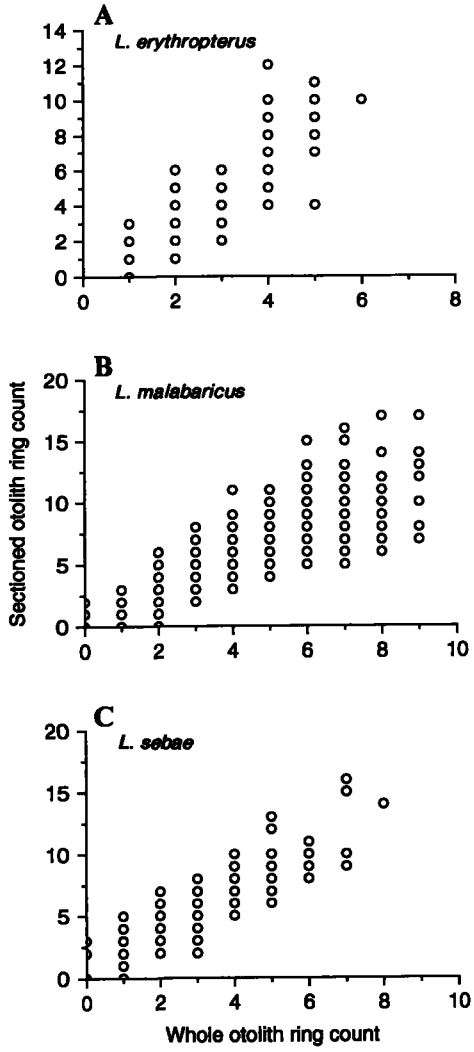

Figure 6

Plot of the relationship between whole and sectioned otolith ring counts of the three species of *Lutjanus*.

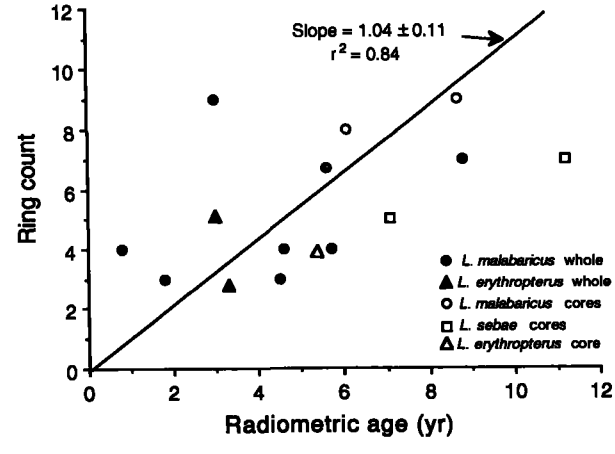

Figure 7

The relationship between radiometric age (yr) and whole otolith ring counts of all samples (except *L. sebae* whole otolith samples).

Table 5

Von Bertalanffy growth parameters of tropical *Lutjanus* from northern Australia and elsewhere within their range (W=whole otoliths; S=sectioned otoliths; V=vertebrae; U=urohyal; Sc=scales).

Species	Locality	Sex	Method	K	L_∞	Maximum age	Reference
L. erythropterus	Gulf of Carpentaria	Both	W	0.30	565	6	Present study
	Great Barrier Reef	F	W	0.44	500	7	McPherson and Squire (1992)
		M	W	0.41	500	7	McPherson and Squire (1992)
	Northwest Shelf	Both	V	0.21	603	7	Ju et al. (1988)
L. malabaricus	Arafura Sea	Both	V	0.17	707	10	Edwards (1985)
		Both	V	0.12	790	8	Lai and Lui (1979)
	Gulf of Carpentaria	Both	W	0.22	592	9	Present study
	N.W. Australia	Both	V	0.13	768	8	Lai and Lui (1979)
		Both	V	0.25	715	10	Chen et al. (1984)
	S. China Sea	Both	V	0.14	790	11	Lai and Lui (1974)
	Great Barrier Reef	F	W	0.23	696	7	McPherson and Squire (1992)
		M	W	0.18	820	7	McPherson and Squire (1992)
	Vanuatu	Both	S	0.31	600	—	Brouard and Grandperrin (1984)
L. sebae	Gulf of Aden	Both	Sc	0.16	660	11	Druzhinin and Filatova (1980)
	Gulf of Carpentaria	Both	W	0.06	1483	9	Present study
	N.W. Australia	Both	V	0.13	678	10	Yeh et al. (1986)
	Great Barrier Reef	F	W	0.18	851	8	McPherson and Squire (1992)
		M	W	0.15	736	8	McPherson and Squire (1992)
L. vittus	N.W. Australia	F	U	0.37	267	7	Davis and West (1992)
		M	U	0.22	346	8	Davis and West (1992)

1985; Grant, 1985) or 16 to 22 kg (Grant, 1985; Allen and Swainston, 1988), which is much greater than we recorded (5 kg). This species may, therefore, live more than 10 years. Indeed, large *L. sebae* (over 800 mm) from the Great Barrier Reef are known to live on deep coral reefs at depths greater than 60 m[1]; the deepest part of the Gulf of Carpentaria is only 55 m. This suggests that fish may move from this region as they grow.

Our radiometric ageing results have several important implications beyond the verification of the age structure of each species. First, they demonstrated that for species that have a high otolith ^{226}Ra specific activity, $^{210}Pb/^{226}Ra$ activity ratios can be used to age fish as young as 3 years with accuracy. Previously these radioisotopes have only been used to age long-lived species (>10 yr; Bennett et al., 1982; Campana et al., 1990; Fenton et al., 1991). Other radioisotope pairs (^{228}Th:^{228}Ra) have been used to age short-lived tropical species (Campana et al., 1993), but these are only useful for fish up to 5 years old because of the short half-life of Th–228.

Second, for relatively short-lived species, radiometric ageing of whole otoliths and cores using a single-phase linear model of otolith mass growth rate gave similar results. Campana et al. (1990) and Smith et al. (1991) argued that new material accreting to the outer surface of the otolith may not accrete ^{226}Ra in similar specific activities to the juvenile ($t \approx 0$). This would invalidate the use of a simple otolith mass growth model to interpret the radiometric data for otoliths of postjuvenile fish. However, even with a single-phase linear mass growth model (a two-phase model would have reduced the age estimates), we were able to verify that the ring counts in whole otoliths were a more accurate measure of the true age than counts from sectioned otoliths (in accord with core radiometric ages). However, we agree with Smith et al. (1991) that otoliths should be cored for radiometric ageing, if possible, which would avoid the use of an otolith mass growth model.

The third point that arises from our analyses relates to the ratio of allogenic to radiogenic lead in *Lutjanus* otoliths. We set the uptake activity ratio value at zero (R=0.0) because higher values would have lowered the age estimates (e.g. Smith et al., 1991). However, from the stable lead/barium ratios and the high age estimates of two of the *L. sebae* samples (2068 and 2069) it appears that, at least for this species, the juveniles may be taking up more allogenic ^{210}Pb than the adults (Fenton and Short, 1992). There was no systematic increase in the Pb/Ba mass ratios of *L. malabaricus* and there is insufficient data for *L. erythropterus* to be conclusive (Fig.

[1] Williams, D. Australian Institute of Marine Science, PMB No. 3, Townsville 4810, Queensland, Australia. Personal commun., 1993.

3). However, for lutjanids it appears that a Pb/Ba mass ratio <0.2 probably indicates that the assumption of a low initial activity ratio (R) is valid, whereas the three samples where the Pb/Ba mass ratio is 0.3–0.6 indicate that the assumption of low R may be invalid. The Pb/Ba ratios are, therefore, a useful test of the validity of the low R assumption.

Finally, this appears to be the first instance where radiometric methods are more consistent with whole-otolith ages rather than sectioned-otolith ages. All previous radiometric studies of fish from temperate and subtemperate waters have verified section counts (Bennett et al., 1982; Campana et al., 1990; Fenton et al., 1990, 1991; Smith et al., 1991). The metabolic effects of the annual cycle of inorganic and organic deposition in otoliths may be more pronounced in these environments resulting in clear annuli in otoliths of fish from more temperate regions.

Conclusions

This study has shown that radiometry using $^{210}Pb/^{226}Ra$ activity ratios in both whole and cored otoliths can accurately estimate the ages of fish as young as 3 years. Stable lead:barium mass ratios were used to identify samples that may invalidate the assumption of constant uptake of allogenic lead (R=0). For the lutjanids examined, ring counts in sectioned otoliths were shown to overestimate fish ages. Methods such as marginal increment analysis do not verify that the ageing method used is accurate unless the pattern is demonstrated to be consistent for all age classes. This indicates that tropical fish should be aged by two independent methods where possible to help minimize possible ageing errors.

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Abstract.—Age and growth of the dusky shark, *Carcharhinus obscurus*, was estimated from bands in the vertebral centra of 122 individuals and from length-frequency data from 341 individuals. The von Bertalanffy growth function parameters from the vertebral analysis were considered more robust (L_∞=373, K=0.038, t_0=–6.28, male; L_∞=349, K=0.039, t_0=–7.04, female). Comparison of male and female growth curves generated from vertebral data indicate a statistically significant difference; however, these differences are due primarily to larger sizes attained by adult females. Estimates of age at maturity indicate that dusky sharks follow the typical carcharhinid pattern of slow growth and late age at maturity. The size at maturity is reported at 231 cm FL and 235 cm FL for males and females, respectively. These lengths correspond to approximately 19 years for males and 21 years for females. The oldest fish aged from vertebrae was a 33+ year-old female.

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Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean

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Sharks have become increasingly important in U.S. commercial fisheries in the western North Atlantic Ocean in recent years. U.S. landings of large coastal sharks, represented primarily by several species in the family Carcharhinidae, increased from 135 to 7,122 metric tons (t) from 1979 to 1989 (Anon., 1993). Musick et al. (1993) reported that annual recreational catches are estimated to be 35,000 U.S. tons and related annual mortality is over 10,000 U.S. tons (9,074 t). As a group, sharks tend to exhibit slow growth, late age at maturity, and low fecundity (Holden, 1973). As a consequence of these life history characteristics, recruitment in sharks is directly dependent on stock size (Holden, 1973). This direct relationship means that elasmobranchs may not be able to recover readily from overexploitation (Holden, 1973).

The dusky shark, *Carcharhinus obscurus*, is part of the species complex presently managed under the Secretarial Shark Fisheries Management Plan (FMP) for the Atlantic Ocean (Anon. 1993). Currently, dusky sharks are harvested in commercial fisheries off the southeastern United States and in the Gulf of Mexico. Recreational fishermen off the northeastern United States also catch dusky sharks (Casey and Hoey, 1985; Musick et al., 1993). The shark FMP (Anon. 1993) details the need for accurate life history information on individual species taken in the shark fishery. Proper management at the species level requires specific information on age and growth.

The dusky shark is a common coastal pelagic species with a worldwide distribution in temperate and tropical waters (Compagno, 1984). In the western North Atlantic, it ranges from as far as Banquereau Bank off Nova Scotia, Canada, to southern Brazil, including the Gulf of Mexico and Caribbean Sea (Hoey, 1983; Compagno, 1984). Tagging studies show dusky shark movements from southern New England to Yucatan, Mexico (Casey et al.[1]; Hoey, 1983).

Age and growth studies of large sharks are difficult because many species are highly migratory, making them available for only short seasonal periods, and different elements of the population segregate spatially by size and sex (Hoenig and Gruber, 1990). In addition, the large size attained by adults makes them difficult to sample. Recent literature has discussed the benefits of growth and longevity estimates attained from tag and recapture

[1] Casey, J. G., H. L. Pratt Jr., and C. E. Stillwell. 1980. The shark tagger summary. Newsletter of the Coop. Shark Tagging Program. U.S. Dep. Commer., Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., 28 Tarzwell Rd., Narragansett, RI, 02882-1199.

studies (Casey and Natanson, 1992). These data are not available for the dusky shark nor is validation of vertebral band periodicity. Previous attempts to age the dusky shark were based on limited data and were inconclusive (Lawler, 1976; Hoenig, 1979; Schwartz, 1983). We have attempted to strengthen age estimates of *C. obscurus* by using vertebral band counts together with marginal increment analysis and by using comparisons with length-frequency data. With the von Bertalanffy growth function thus derived, we estimate age at maturity and longevity for this species.

Materials and methods

Data and vertebral samples from dusky sharks were obtained between 1963 and 1993 from research cruises, sport fishing tournaments, and commercial shark fishermen from Cape Cod, Massachusetts, to off the east coast of Florida. Vertebral samples were taken in all months except January, March, and November.

Length measurements

Total and fork lengths were measured to the nearest centimeter (cm) for each specimen. Fork length (FL) was measured from the tip of the snout to the fork of the tail. Total length (TL) is defined as the distance from the snout to a point on the horizontal axis intersecting a perpendicular line extending downward from the tip of the upper caudal lobe to form a right angle (Kohler et al.[2]). All lengths used are fork lengths unless otherwise noted. FL can be converted to TL by using the regression equation:

$$FL = 0.8352\,(TL) - 2.2973.\ [r^2 = 0.99,\ n = 167]$$

Vertebral samples

Vertebral samples were taken from above the branchial chamber. Sections of vertebral columns were trimmed of excess tissue and then frozen or preserved in 70% ethanol (Casey et al., 1985).

Two vertebrae from each specimen were processed histologically following Casey et al. (1985), with the exception of the use of RDO (DuPage Kinetics) for decalcification. All vertebral sections were cut sagittally through the focus to a thickness of 80–100 microns, stained with Harris hematoxylin, and mounted in glycerin jelly (Humason, 1972).

Bands in the vertebra were counted from an image projected on a Summagraphics MM-1812 digitizing tablet (Skomal, 1990). Measurements from the focus to growth bands at points along the internal corpus calcareum were digitized directly into an IBM PC-XT computer. The radius of each centrum was measured from the focus to the distal margin of the intermedialia along the same diagonal as the band measurements. Annual growth marks were defined following Casey et al. (1985) for the sandbar shark, *Carcharhinus plumbeus*, where the annual mark is defined by a wide translucent zone that traverses the intermedialia and continues into the corpus calcareum as an opaque band.

Vertebral sections from 171 dusky sharks were prepared. Bands in the same centrum section were counted at least once by each of four investigators to verify that the band counts were repeatable. Sections were considered unreadable if bands could not be discerned in accordance with the above definition. If two readers considered the section unreadable, the sample was eliminated from the final analysis.

Counts were accepted if two or more readers agreed. The individual ring measurements for all readers in agreement were then averaged. If two readers agreed on one count and two on another for the same specimen, the higher count was accepted. Specimens where there was no initial agreement were recounted until two of the investigators reached a consensus or the sections were discarded.

The relationship between vertebral radius (VR) and FL was calculated to determine the most appropriate method for back calculation of the size-at-age data (Ricker, 1969). The FL to VR relationship was linear but did not pass through the origin. Therefore, the Lee method was considered more appropriate (Ricker, 1969):

$$l = a + (b \times s),$$

where l = the length of fish when the vertebra was obtained;
a = the intercept on the length axis;
b = the slope of the line; and
s = the total vertebral radius.

A von Bertalanffy growth function (VBGF) was fitted to the data by using the following equation (von Bertalanffy, 1938):

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

where L_t = predicted length at time t;
L_∞ = mean asymptotic fork length (of the fish);
K = a growth rate constant (yr^{-1}); and
t_0 = the theoretical age at which the fish would have been zero length.

[2] Kohler, N. E., J. G. Casey, and P. A. Turner. Length-weight relationships for 13 Atlantic sharks. Unpubl. manuscr.

Growth in length data were analyzed by using FISHPARM, an IBM PC compatible program (Prager et al., 1987), which implements Marquardt's algorithm for nonlinear least squares parameter estimation (Marquardt, 1963).

Bernard's (1981) multivariate analysis for comparing growth curves was employed to test the hypothesis that male and female vertebral growth curves were the same. This method also determines which of the von Bertalanffy parameters are the most statistically significant cause of any differences in growth.

Marginal increment analysis

Validation, the confirmation of the temporal meaning of the growth increment (Brothers, 1983), is difficult to attain for large pelagic species and was attempted by using marginal increment analysis. The marginal increment ratio (MIR) (Skomal, 1990) was calculated by using the following equation:

$$MIR = (VR - R_n)/(R_n - R_{n-1}),$$

where VR = the vertebral radius;
R_n = the last complete band; and
R_{n-1} = the next to last complete band.

Mean MIR was plotted against month to locate periodic trends in band formation. The MIR relates the edge formation to the width of the previous completed band, which corrects for differences in band width between small and large fish.

Length frequency

Length-frequency distributions were analyzed by using Shepherd's (1987) model. The sample was separated by sex and calculations were made at 3-cm intervals. Initial values of L_∞ and K, based on biological parameters obtained from the literature (Springer, 1960; Compagno, 1984) were entered into the program which was then rerun until the highest score function was attained. The L_∞ and K associated with this score function were used to calculate t_0 by using the following equation:

$$t_0 = t + (1/K)\,(\ln[L_\infty - L_t]/L_\infty),$$

where t_0 = 0 (birth);
L_t = mean size at birth;
K = the von Bertalanffy growth constant; and
L_∞ = the mean asymptotic fork length.

Longevity

Estimates of longevity were obtained by using tag and recapture data. Data on eight recaptured dusky sharks at liberty for greater than 10 years were examined. Age at tagging was assigned from the size estimate provided at the time of release. This estimated age was based on growth curves derived from vertebrae. The number of years at liberty were then added to estimate age at recapture.

Results

Vertebral samples

Of the 171 processed vertebra, 36 (21.0%) were considered unreadable. Initial agreement by two or more readers was reached on 89 specimens. The remaining 50 sections were recounted by two of the investigators. A consensus was reached on 37 of those recounted and the rest were discarded as unreadable. Six were then eliminated for having no information on sex. The remaining 120 (70.2%) consisted of 53 male and 67 female specimens ranging in size from a 73 cm FL neonate to a 296 cm FL adult female. The FL-VR regression showed a linear relationship:

$$FL = 12.82(VR) + 24.99\ [n = 114;\ r^2 = 0.99]\ .$$

The FL to VR relationship was significantly different between the sexes for all fish combined (ANCOVA, $P<0.05$). However, this was due to three large females whose removal from the analysis altered the curves and showed the males and females to be statistically indistinguishable ($P<0.05$) (Fig. 1). We chose to use the combined relationship without those three samples.

Back-calculated as compared with empirical length-at-age data show a smaller estimated size for fish of younger ages, when calculated from the vertebrae of the older fish, indicating the presence of a slight Lee's phenomenon for both sexes (Table 1). Lee's phenomenon was more pronounced in females and increased with age.

The MIR data showed a distinct, periodic trend of increasing increment growth from April through June (female) or July (male); after this peak there was a slight decrease and apparent leveling (Fig. 2). The decrease in incremental growth is not large enough to indicate a double band formation. The graph suggests that an annual winter band is formed between September and April. This band can be visible by February in males; no data were available for females. The time of annulus formation cannot

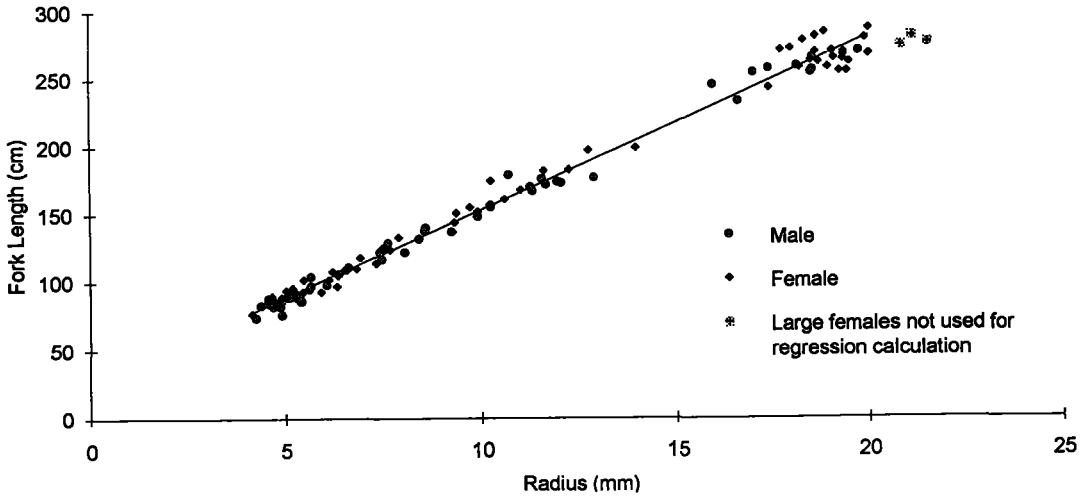

Figure 1

Relationship between vertebral radius (cm) and fork length (cm) for male and female dusky sharks, *Carcharhinus obscurus*.

be further established owing to a lack of winter samples. January was used as the month of band formation for the assignment of age classes (Casey et al., 1985).

Back-calculated length at first band (80.2 cm FL male; 85.8 cm FL female) corresponded closely to the known size at birth of 85–100 cm TL (Castro, 1983; Compagno, 1984). The first winter band would have formed after approximately six months growth (assuming January deposition and spring parturition), and the following bands represented annual growth (Branstetter, 1987). The oldest female in the sample was 33+ years and the oldest male, 25+ years.

The parameters of the VBGF determined from the back-calculated data were similar to known life history characteristics except that the predicted L_∞ for males was higher than that for females (Table 2). Those samples that were neonates with no visible birthmark were excluded from the VBGF analysis. Therefore, only 114 samples (47 male and 67 female) were included in the final calculations. The t_0 and K values appear similar between the sexes (Table 2). However, the male and female growth curves are significantly different ($P<0.05$) based on Bernard's (1981) multivariate analysis (Table 3). The results indicated that the differences were caused by the t_0 and L_∞ values (in order of significance).

The reported size at maturity for the dusky shark is 231 cm FL and 235 cm FL for males and females, respectively. These lengths correspond to 19 years for males and 21 years for females based on the vertebral growth curves (Table 4).

Length frequency

Length observations from a total of 208 female and 133 male dusky sharks were used to calculate von Bertalanffy parameters by using length-frequency analysis. Samples were obtained from 1961 to 1987 for the months May through November. Because of small yearly sample sizes, data for all years were combined by month.

A comparison of the VBGF parameters from the length-frequency analysis [LF] with those derived from vertebral analysis (Table 2) shows that the L_∞ and t_0 values from the vertebral analysis for females were lower than those derived from the length-frequency analysis, and that the K value for females was basically the same for both data sets. The length-frequency analysis for males results in a lower L_∞ than that from the vertebral analysis and in higher t_0 and K values. The VBGF differences in both sexes are not large and both curves indicate late age at maturity (males: 25 yr [LF], 19 yr [vertebral]; females: 16 yr [LF], 21 yr [vertebral]) and slow growth (males: K=0.049 [LF], 0.038 [vertebral]; females: K=0.040 [LF], 0.039 [vertebral]) (Fig. 3). The von Bertalanffy parameters for the sexes combined are shown for comparison (Table 2).

Longevity

Tagging records from NMFS Cooperative Shark Tagging Program show that 6,067 dusky sharks were tagged and 131 recaptured between 1962 and 1992.

Table 1

Back-calculated and observed size-at-age data for male and female dusky shark, *Carcharhinus obscurus*.

	Male Ring (age in years)										
	Birth	6 months	0	1	2	3	4	5	6	7	8
Back-calculated											
$\bar{X}$	80.2	87.3	94.1	103	113.9	124.4	132	140.5	149.7	157.7	163.8
SD	5.6	5.5	6.2	7	9.2	10.6	10.7	11.7	12.7	12.6	10.5
n	47	34	30	28	25	21	20	20	19	17	
Observed											
$\bar{X}$	87.7	100.5	123.5	116.7	124.5	138		148	173.5	164	
SD	5.1	53.		2.1	5.5	4.9	0		0	0.7	7.9
n	13	4		2	3	4	1		1	2	3

	Male Ring (age in years)										
	9	10	11	12	13	14	15	16	17	18	19
Back-calculated											
$\bar{X}$	161.7	179.2	188.6	196.1	202.4	209.8	216.1	220.5	226.5	232.3	237.9
SD	11.6	12.3	10.4	11.8	11.7	13.5	13	11.4	11.7	12.4	12.5
n	14	13	11	10	10	10	10	9	9	8	8
Observed											
$\bar{X}$	172	177.5	177				233		245		260.5
SD	0	2.1	0				0		0		9.2
n	1	2	1				1		1		2

	Male Ring (age in years)										
	20	21	22	23	24	25	26	27	28	29	30
Back-calculated											
$\bar{X}$	246.4	252.6	254.9	256.6	252.6	255.2					
SD	14.5	13.2	15.1	16.1	0	0					
n	6	6	4	3	1	1					
Observed											
$\bar{X}$		256.5	256	263.5		265					
SD		3.5	0	9.2		0					
n		2	1	2	1						

	Female Ring (age in years)										
	Birth	6 months	0	1	2	3	4	5	6	7	8
Back-calculated											
$\bar{X}$	85.8	92.3	99.3	107.4	118.8	128.6	136.2	143.7	150.5	157.8	164.8
SD	5.1	4.5	5	6.3	8.4	9.4	9.5	8.5	8.8	9.4	9.9
n	67	55	52	50	48	45	41	38	35	33	33
Observed											
$\bar{X}$	91.8	104.3	106.5	107	122.3	134.8	138.3	161	154.5		
SD	4.5	7.2	6.4	2.8	3.8	16.8	26	12.5	3.5		
n	12	3	2	2	3	4	3	3	2		

Table 1 (continued)

	Female Ring (age in years)										
	9	10	11	12	13	14	15	16	17	18	19
Back-calculated											
$\bar{X}$	171.5	178.8	186.3	192.9	199.8	206.2	212.4	216.7	222.6	228.4	233.4
SD	10.2	9.6	10.8	10.9	12.4	12.9	13.3	10.5	11.6	12.3	12.6
n	33	30	28	28	28	28	28	27	27	27	27
Observed											
$\bar{X}$	183	190					262				281
SD	15.5	9.9					0				0
n	3	2					1				1

	Female Ring (age in years)										
	20	21	22	23	24	25	26	27	28	29	30
Back-calculated											
$\bar{X}$	237.9	242.1	246	149.8	252.9	256.4	258.6	262.9	265.4	266.2	265.1
SD	12.3	12.1	12.5	12.2	12.6	13.5	11.9	13.3	11.8	15.2	12.7
n	26	24	23	22	20	16	15	13	9	5	4
Observed											
$\bar{X}$	253.4	263	284	156.5	161.5	274	266.5	272	270.8	281	262
SD	14.8	0	0	2.1	9	0	16.3	10.5	6.5	0	0
n	2	1	1	2	4	1	2	4	4	1	1

	Female Ring (age in years)										
	31	32	33	34	35	36	37	38	39	40	41
Back-calculated											
$\bar{X}$	267.9	277.1	291.4								
SD	15.2	16.6	0								
n	3	2	1								
Observed											
$\bar{X}$	269	269	276								
SD	0	0	0								
n	1	1	1								

Eight of these fish were at liberty from 10.1 to 15.8 years. Estimated ages at tagging were based on the vertebral growth curve and ranged from birth to 27 years. The best example of longevity came from a dusky shark that was tagged at an estimated 27 years (260 cm FL) and was recaptured 12 years later at an estimated age of 39 years (Table 5).

Discussion

In the present study, vertebral data and length-frequency data were independently analyzed to derive estimates of von Bertalanffy growth parameters for the dusky shark. Because of the differences between the methods and their sensitivity to the data used to calculate the VBGF parameters, each method produced slightly different growth curves and, therefore, different estimates of age at maturity and longevity (calculated based on maximum reported size). The length-frequency estimates obtained from the dusky shark data are probably somewhat biased owing to limitations of the data and properties of the length-frequency model (Majkowski et al., 1987; Shepherd

et al., 1987; Natanson, 1990). As a slow-growing, long-lived species, the dusky shark may have overlapping lengths at age which may obscure length modes and bias the estimates of model parameters (Rosenberg and Beddington, 1987; Shepherd et al., 1987). The vertebral method is therefore considered the more robust method and the length-frequency parameters are used for comparison only.

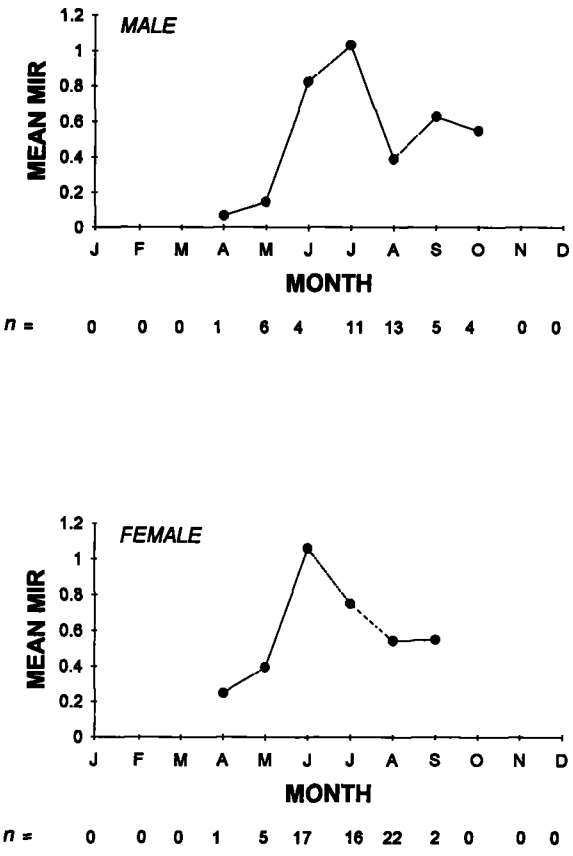

Figure 2

Mean vertebral marginal increment ratios (MIR) by month for each of four readers for the dusky shark, *Carcharhinus obscurus*. Number of samples used to calculate the means for each month are located below the figure.

Yoccoz (1991) has brought up questions as to the validity of judging biological significance based on statistical tests. He suggests that statistical significance is not necessarily indicative of biological significance; this appears to be the case with the dusky shark. The statistically significant differences shown between male and female dusky shark vertebral growth curves may not reflect biological differences. Examination of the length-at-age data suggests that biologically the differences between male and female vertebral curves are small. The age and size at maturity differ by only two years and five centimeters for males and females (Table 4). Females are presumed to grow ultimately to a larger size than males. This means that either growth slows in males after maturity or that males do not live as long as females.

The vertebral VBGF derived in this study is very similar to the curve attained by Hoenig (1979) for combined sexes for the ages under consideration (birth to 33 years) but is different from data presented by Lawler (1976) and Schwartz (1983). Hoenig's (1979) parameter values for the VBGF have a slightly higher L_∞ and t_0 and lower K than parameters derived from vertebral analysis in the present study (Table 2). Lawler (1976), using vertebral analysis to determine the age of female dusky sharks, obtained VBGF-parameter values markedly different from the present study (Table 2). The L_∞ in his study is more than twice as large as the L_∞ reported here and his K value suggests a much slower growth rate. These two factors combine to make Lawler's (1976) curve appear as a straight line from birth to 34 years.

Table 2

The von Bertalanffy parameters derived in this study compared to those derived in Hoenig's (1979) study of male and female dusky sharks and Lawler's (1976) study of female dusky sharks, *Carcharhinus obscurus*.

	Male				Female				Combined			
Parameters	L_∞	K	t_0	n	L_∞	K	t_0	n	L_∞	K	t_0	n
This study:												
Vertebrae	373	0.038	–6.28	47	349	0.039	–7.04	67	352	0.040	–6.43	120
Length-frequency	293	0.049	–5.99	133	392	0.040	–5.34	208	296	0.062	–4.68	350
Hoenig, 1979									385	0.034	–5.99	22
Lawler, 1976					732	0.014	–6.7	13				

Lawler's (1976) L_∞ is unrealistically high when compared with the maximum reported size from the literature (308 cm FL [Springer, 1960]) and with those derived in both Hoenig's (1979) study and the present one. Schwartz (1983) also used vertebral bands in an attempt to age the dusky shark. In general, his back-calculated size-at-age data (Schwartz, 1983; Table 4) are lower than those in the present study. His estimates of size at birth are much lower than reported sizes at birth, suggesting that prebirth bands may have been counted (Casey et al., 1985). Marginal increment data from the present study do not support Schwartz's (1983) hypothesis of a much faster growth rate with two bands per year based on his marginal increment data.

Tagging data combined with vertebral estimates indicate that the dusky shark can live for at least 40 years. The largest reported dusky shark in the literature was a 308 cm FL female (Springer, 1960) which corresponds to 51 years based on our vertebral VBGF. Tag and recapture data on the large dusky shark at liberty for 12 years add credence to the vertebral longevity estimate by verifying that these fish do live up to 40 years. Thus, the dusky shark appears to be a long-lived, late-maturing species, exhibiting a pattern typical of carcharhinids. The female bull shark, *C. leucas*, can live over 24 years and does not reach maturity until at least 18 years of age (Branstetter and Stiles, 1987). Tagging evidence has shown that the sandbar shark, *C. plumbeus*, can reach ages of at least 40 years and may not mature until 29 years of age (Casey and Natanson, 1992). The lemon shark, *Negaprion brevirostris*, which reaches at least 20 years of age and does not reproduce until 11 to 13 years, also follows this pattern (Brown and Gruber, 1988). Preliminary estimates on the age of the bronze whaler, *C. brachyurus*, indicate that males do not mature for 13 to 19 years and females for 19 to 20 years. Both may attain ages over 30 years (Walter and Ebert, 1991). The blue shark, *Prionace glauca*, appears to be atypical of most carcharhinids in having a relatively fast growth rate and a short life-span (13–16 years) (Skomal, 1990). A recent recapture from an Australian school shark, *Galeorhinus australis*, after 42 years at liberty indicates that the galeorhinids also follow this pattern.[3]

Casey and Natanson's (1992) study on the age of the sandbar shark (*C. plumbeus*) showed that in a

Table 3

Results of comparison of the vertebral von Bertalanffy growth equations for male and female dusky sharks, *Carcharhinus obscurus*, using Bernard's (1981) multivariate analysis. Shown is the estimated variance-covariance matrix (S).

	L_∞	K	t_0	
L_∞	131.9769	−0.02831	−3.16979	
K		0.0000065	0.00077	$= S$
t_0			0.115042	

[3] Olsen, A. H. Newton 5074, South Australia. Personal commun., Jan. 1994.

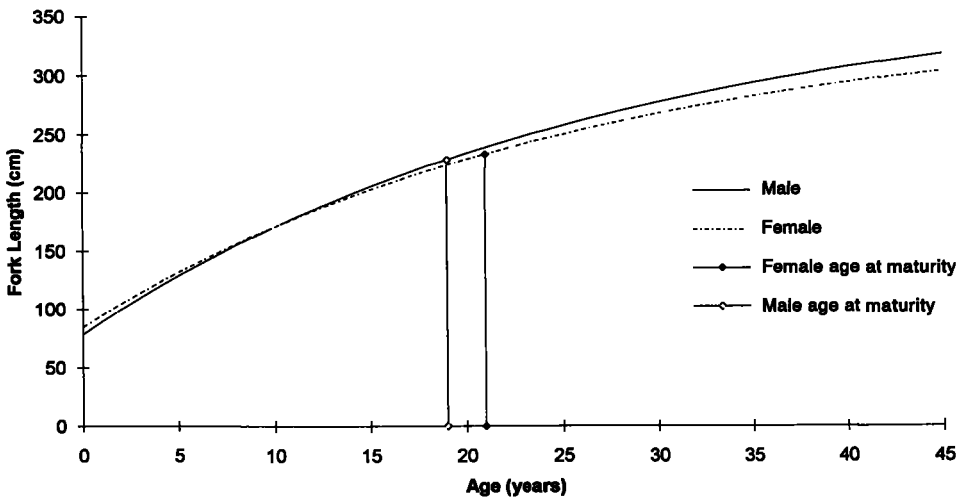

Figure 3

Von Bertalanffy growth curves generated from vertebral data for male and female dusky sharks, *Carcharhinus obscurus*.

species where good tag and recapture data are available (i.e. where specimens are measured at both tagging and recapture, properly identified, and there is sufficient sample size), a better estimate of longevity is produced than from hardpart analysis. They concluded that the initial growth curve based on vertebrae for the sandbar shark had severely underestimated the age at maturity and maximum age and had overestimated the growth rate (Casey et al., 1985). At the present time, the vertebral growth curve

Table 4

Size at age of the dusky shark, *Carcharhinus obscurus*, calculated from the von Bertalanffy growth equations. Size at age closest to maturity is in bold type.

Years	Length-frequency male	Length-frequency female	Length-frequency combined	Vertebral male	Vertebral female	Vertebral combined
Birth	75	75	75	78	84	81
1	95	100	100	89	95	92
2	104	111	112	100	105	102
3	113	122	123	110	114	112
4	122	133	134	119	123	121
5	130	143	143	129	132	131
6	138	153	153	138	140	139
7	145	162	161	146	148	148
8	152	171	169	155	156	156
9	159	180	177	163	163	164
10	166	188	184	170	171	171
11	172	196	191	178	177	178
12	177	204	197	185	184	185
13	183	211	203	192	190	192
14	188	218	209	199	197	198
15	193	225	214	205	202	204
16	198	**232**	219	211	208	210
17	203	238	223	217	214	216
18	207	244	228	223	219	221
19	211	250	**232**	**228**	224	226
20	215	255	**236**	234	229	**231**
21	219	261	239	239	**233**	236
22	222	266	243	244	238	241
23	226	271	246	249	242	245
24	229	276	249	253	246	250
25	**232**	280	252	258	250	254
26	235	294	254	262	254	257
27	238	289	257	266	258	261
28	240	293	259	270	261	265
29	243	297	262	274	264	268
30	245	300	264	277	268	272
31	247	304	266	281	271	275
32	250	307	267	284	274	278
33	252	311	269	287	277	281
34	254	314	271	291	280	284
35	256	317	272	294	282	286
36	257	320	274	297	285	289
37	259	323	275	299	287	292
38	261	325	276	302	290	294
39	262	328	277	305	292	296
40	264	331	279	307	294	298
41	265	333	280	310	296	301
42	266	335	281	312	298	303
43	268	338	282	314	300	305
44	269	340	282	316	302	307
45	270	342	283	318	304	308

Table 5

Tag and recapture data used to obtain longevity estimates for the dusky shark, *Carcharhinus obscurus*. N/A = not available.

		Tagging			
Tag number	Sex	Fork length (cm) (estimated)	Age (estimated)	Time at liberty (years)	Total age (years)
63647	N/A	260	27 yr	12	39
YR200X	N/A	84	6 months	15.8	16.3
42204	F	130	4+ yr	11.9	16+
21367	F	73	Birth	11.6	11.6
48478	N/A	116	3+ yr	10.9	13.9+
39360	F	111	2+ yr	10.1	12.1+
F66 8802	M	73	Birth	11.8	11.8
37913	F	122	4 yr	14.5	18.5

is the best estimate available for the dusky shark. However, it should be kept in mind that the vertebral growth curve generated for the dusky shark may also underestimate age at maturity and maximum age.

Acknowledgments

We are grateful to the many fishermen and tournament officials who voluntarily provided us with data and specimens for examination. We are particularly indebted to commercial fishermen Tris Colket and Eric Sander who dissected vertebrae and provided precise length measurements on dusky sharks. We appreciate the statistical expertise provided by Carolyn Belcher and the assistance in field dissections provided by our colleagues C. Stillwell and H. W. Pratt of the Apex Predator Investigation.

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Abstract.—Arrowtooth flounder, *Atheresthes stomias*, were sampled for macroscopic maturity stage, and females were subsampled for gonosomatic index (GSI) from commercial trawl landings from July 1991 to July 1992 and during the NMFS triennnial bottom trawl survey from September to November 1992. Arrowtooth flounder are batch spawners and spawn from fall to winter off Washington at depths of at least 366 m (200 fm). Hydrated oocytes were first seen in September 1991 when mean GSI for yolked oocyte-bearing females approximately doubled. Postovulatory follicles were present in all macroscopic stages of mature ovaries sampled for histology in late December 1991. By March 1992 all mature females were spent; females with hydrated oocytes were again seen in November 1992. Arrowtooth flounder show a group-synchronous pattern of oocyte development. Catch rates from trawl logbook data suggest that the mature population migrates seasonally, from depths of about 183 m (100 fm) in summer to depths exceeding 475 m (260 fm) in winter. Fork length at which 50% of fish were sexually mature ($L_{50\%}$) calculated from survey data was 28.0 cm for males and 36.8 cm for females, similar to estimates from Washington commercial trawl data but less than estimates from Oregon in the 1970's. Female $L_{50\%}$ varied seasonally. Problems of bias associated with sampling commercial trawl landings for size at maturity are discussed.

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Maturity, spawning, and seasonal movement of arrowtooth flounder, *Atheresthes stomias*, off Washington

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Arrowtooth flounder, *Atheresthes stomias*, is a large, predatory flatfish ranging from the Bering Sea to central California (Hart, 1973). It is estimated to be the single most abundant species in the Gulf of Alaska and has shown significant increases there in both population numbers and biomass.[1] Arrowtooth flounder is typically not considered a high-value species in the Washington trawl fishery, but recent landings have been substantial. In 1990–92 more arrowtooth flounder were landed from areas off Washington than any other groundfish species except Pacific whiting,[2] and management interest in arrowtooth flounder has intensified. Little detailed information is available on arrowtooth flounder in the eastern Pacific Ocean. Kabata and Forrester (1974) studied parasitic infection of arrowtooth flounder off British Columbia and noted the population length and age structure as well as diet, but did not examine maturity. Pertseva-Ostroumova (1960) examined *Atheresthes* reproduction and larval development in the Bering Sea, but spawning data on *A. stomias* was limited and conclusions regarding time and depth of spawning were based primarily on the closely related Kamchatka flounder, *A. evermanni*. More recent genetic and food-habit studies have documented differences between arrowtooth flounder and Kamchatka flounder in the Bering Sea (e.g. Ranck et al., 1986; Yang and Livingston, 1986; Yang, 1988), but none have examined their reproduction. Unpublished arrowtooth flounder size-at-maturity estimates have been made from data collected off Oregon.[3] This study was designed to provide new estimates of size at maturity and a time series of reproductive development and spawning of arrowtooth flounder off Washington.

Methods

Maturity data were collected from three sources: 1) Washington commercial trawl landings ("market"-sized fish) sampled biweekly from July 1991 to July 1992 at shoreside processing plants; 2) fish normally discarded at sea because of their small size, brought in by fishermen

[1] Wilderbuer, T. K., and E. S. Brown. 1992. Flatfish. *In* Stock assessment and fishery evaluation report for the 1993 Gulf of Alaska groundfish fishery, Section 3. N. Pac. Fish. Manage. Counc., Anchorage, AK, 25 p.

[2] Pacific Fishery Management Council. 1993. Status of the Pacific coast groundfish fishery through 1993 and recommended biological catches for 1994: stock assessment and fishery evaluation. (Document prepared for the Council and its advisory entities.) Pac. Fish. Manage. Counc., 2000 SW First Ave., Ste. 420, Portland, OR 97201.

[3] Hosie, M. J., and W. H. Barss. 1977. Age and length at maturity of arrowtooth flounder, *Atheresthes stomias*, in Oregon waters. Oregon Dep. Fish Wildl. unpubl. manuscr., 13 p.

upon request (discards); and 3) survey samples collected at sea from September to November 1992 on the National Marine Fisheries Service (NMFS) triennial bottom trawl and slope surveys off Washington State and Vancouver Island, British Columbia (Table 1). All of the commercial trawlers sampled used larger codend mesh than did the trawl survey (11.4 cm and 8.9 cm, respectively) and reported arrowtooth flounder catch from grounds off northwest Washington (Fig. 1). Commercial trawlers combine catches from different tows so trawl landings and landed discards were sampled on a per trip basis. No samples were obtained in January or February 1992. Up to 100 fish were selected at random for each sample. If fewer than 100 fish were present, all fish were sampled. Each fish was measured to the nearest centimeter fork length (FL), sexed, and assigned a maturity stage based on the macroscopic appearance of the gonads (Table 2). A gonosomatic index (GSI), calculated as ovary weight divided by somatic weight (body weight with ovaries removed and stomach empty), was used to track seasonal changes in ovarian condition. In each sample, the first 10 females encountered at each macroscopic maturity stage were sampled for GSI. Whole ovaries were removed and weighed to the nearest gram, and somatic weight was recorded to the nearest gram. Average monthly GSI's were calculated by maturity stage.

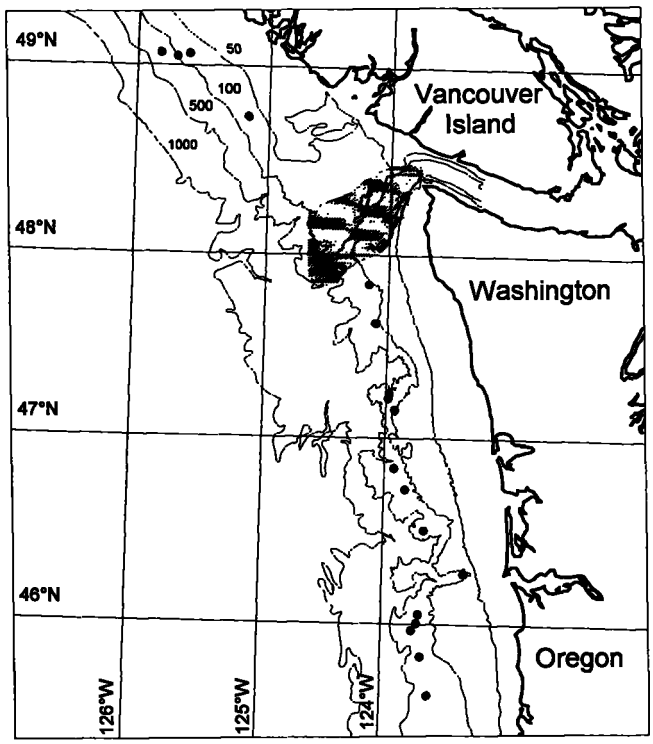

Figure 1

Reported arrowtooth flounder, *Atheresthes stomias*, catch area for sampled commercial bottom trawl trips, and locations of survey tows sampled for maturity, with fathom contours (1 fm=1.83 m).

Fish at any maturity stage other than "immature" were defined as mature. Length at maturity was estimated for each sex by calculating the fraction mature in each 1-cm interval and by fitting a logistic model

$$P_L = \frac{1}{1+e^{(a+bL)}},$$

where P_L = fraction mature at length L, and a and b are constants (Gunderson et al., 1980). The predicted size at which 50% of the fish are mature is

$$L_{50\%} = \frac{-a}{b}.$$

Confidence intervals for $L_{50\%}$ were calculated by using the delta method (Seber, 1982). To see if time of collection affected estimates of $L_{50\%}$, logistic equations were fit to the female length-maturity data that were grouped into the following periods for 1991 and 1992 separately: September–December, January–April, and May–August, corresponding to the prespawning, spawning, and postspawning seasons as determined below.

Ovarian tissue samples were collected from five tows on board the commercial trawler FV *Larkin* in late December 1991, during normal trawl operations off northwest Washington, to compare microscopic and macroscopic staging and provide additional information on arrowtooth flounder reproduction. Immediately after the net was retrieved, arrowtooth flounder were sorted by the crew into discard and market categories and were held alive until they could be sampled. Discard and market categories were maintained for maturity sampling but combined for histology. Length, sex, and maturity stage were recorded, and for the first 10 females encountered at each maturity stage an approximately 3-mm section of ovarian tissue was cut from the anterior third of the blind-side (left) ovary, placed in a tissue cassette, and fixed in Davidson's fixative (Mahoney, 1973). Tissue samples cut from the anterior third of the ovary were assumed to be representative of the arrowtooth flounder ovary as a whole. Weights for GSI were not taken owing to rough weather.

After fixation, tissues were embedded in paraffin, sectioned at 6 μm, and stained with hematoxylin and eosin. Tissue slides were examined under a compound microscope and measurements were taken with a calibrated ocular micrometer. A classification scheme of five stages of oocyte development, two stages of atresia, and a final stage of postovulatory follicles was adopted (Table 3), with terminology proposed by

Table 1

Sources of reproductive data on arrowtooth flounder, *Atheresthes stomias*, with numbers of fish sampled for maturity, and numbers of females sampled for GSI and histology. Samples were collected per trip obtained shoreside or collected per tow obtained at sea; average minimum depth[1] is the average of the minimum depths for tows with arrowtooth flounder from sampled trips and the minimum depth fished for sampled tows. Sampling includes mean fork length (cm) and standard deviation (SD) of fish sampled for maturity with probability *P* for test of difference between means (1-tailed Student's *t*-test, $\alpha = 0.05$).

Sample category	Year	Month	Number of samples		Average minimum depth (m)	Number of fish				Males		Females		
						Maturity								
			Trips	Tows		Males	Females	GSI	Histology[2]	Mean length	SD	Mean length (cm)	SD	*P*
Market	1991	July	2		140	1	199	43		53.0	—	62.1	4.8	—
		August	1		141	1	99	15		45.0	—	60.8	6.0	—
		September	3		196	25	275	70		44.8	2.1	62.1	9.2	0.001
		October	2		240	27	173	56		43.3	4.2	57.8	9.4	0.001
		November	1		265	17	83	25		39.7	1.9	54.2	10.1	0.001
		December	2	4	431	37	330	59	105	35.4	3.9	45.4	8.6	0.001
	1992	March	1		283	15	85	20		37.9	4.9	45.7	9.2	0.001
		April	2		304	46	154	26		43.6	3.1	56.1	10.1	0.001
		May	2		279	32	168	25		44.6	2.8	63.9	9.1	0.001
		June	2		242	24	176	44		45.6	2.2	62.8	8.1	0.001
		July	2		148	91	109	40		44.5	3.0	57.3	7.4	0.001
Discard	1991	December		2	393	74	26		6	29.6	2.4	28.8	1.3	0.050
	1992	May	1		214	10	6	6		37.6	6.9	32.5	6.5	0.083
		June	1		232	24	45			33.2	2.8	31.0	3.5	0.004
Survey[3]	1992	September		4	163	58	63	46		38.9	7.6	46.5	14.6	0.001
		October		7	335	49	85	20		33.6	7.1	40.8	12.5	0.001
		November		7	403	37	59	22		31.0	4.7	41.5	13.9	0.001

[1] Minimum depth is defined as the shallowest depth recorded for either start or end position of a tow.
[2] Histology samples collected at sea.
[3] GSI samples collected at sea, from 4 tows in September, 1 tow in October, and 1 tow in November.

Table 2

Maturity code definitions for arrowtooth flounder, *Atheresthes stomias*, based on the macroscopic appearance of the gonads.

Sex	Stage	Description
Female	Immature	Ovaries are small, pink to red in color, and gelatinous. Little or no visible internal ovarian tissue structure and no oocytes are visible.
	Mature	
	Developing	Ovaries are enlarging. Visible oocytes are white, opaque, and granular.
	Gravid	Ovaries are yellowish and mottled; some oocytes are translucent.
	Ripe/Running	Ripe and running. All oocytes are translucent and may be extruded with light pressure.
	Spent/Resting	Spent ovaries are flaccid, bloodshot, and red to purple. Resting ovary wall looks toughened, pink to beige.
Male	Immature	Testes small and thread-like, brown to pink. No folding or mottled coloration.
	Mature	Testes enlarged, folded, brown to white. Sperm may be visible in cross section or flows with external pressure.

Yamamoto (1956) and stage definitions used by Yamamoto (1956), Wallace and Selman (1981), Hunter and Macewicz (1985), and West (1990). The presence of α and β atretic oocytes was noted, although no attempt was made to differentiate α atretic oocytes by developmental stage. Postovulatory fol-

Table 3

Oocyte developmental stages based on histological criteria.

Stage	Description
Chromatin nucleolar	The oocyte is surrounded by a few squamous follicle cells, and scant cytoplasm surrounds a large nucleus containing a single, large basophilic nucleolus.
Perinucleolar	The oocyte grows, the nucleus increases in size and multiple basophilic nucleoli appear. These arrange themselves towards the periphery of the nucleus; a single dark dot or "Balbiani body" may be visible in the outer surface of the cytoplasm.
Cortical alveoli formation	Spherical vesicles appear in the cytoplasm. Zona radiata present.
Vitellogenic (yolk)	Oocytes are greatly increased in size and ooplasm is filled with yolk globules. Nucleus may be toward the periphery; there is a rapid thickening of the zona radiata.
Hydrated	Yolk globules fuse to form a continuous mass of fluid and the nucleus is not apparent. Postovulatory follicle may be visible.
α atresia	Oocyte is resorbed. Oocyte characterized by an irregular shape and granular, dark basophilic staining. When resorption is complete all that remains is the follicle.
β atresia	Follicle degenerates and is resorbed. Follicle compact, composed of several granulosa cells surounded by a thecal and blood vessel layer. Yellow-brown pigment may be present.
Postovulatory follicle	Collapsing follicle is irregularly shaped; cell layers form loose folds or loops. Degenerating follicle shows fewer loops and is reduced in size.

licles (POF) were identified except in later stages of degeneration when they could not be differentiated from β atresia (Hunter and Macewicz, 1985). Ovaries were staged on the basis of the most developmentally advanced oocyte observed. Proportions of oocyte stages, atretic structures, and POF's were calculated from counts of structures passing under a line horizontally bisecting the tissue slide. Because oocytes at different stages of development differ greatly in size, counts may be biased against smaller, less-developed stages. Average oocyte diameter was determined from the first 10 oocytes encountered at the most advanced developmental stage and sectioned through the nucleus, except hydrated oocytes which were measured as encountered.

Washington commercial bottom trawl logbook data from July 1991 to July 1992 were examined for trends in fishing depth and arrowtooth flounder catch rates. Information on the target fish and estimates of the amount of fish discarded at sea were unavailable. Catch rates were calculated from the set of 14,559 bottom trawl tows in which reported hours fished were greater than 0. Depth of each tow was defined as the shallowest (minimum) depth recorded for either start or end position. Catch rate or catch per unit of effort (CPUE) was computed as the average of the tow-by-tow arrowtooth flounder catch divided by hours fished; catch data were not adjusted to reflect actual fish ticket landings.

Results

Arrowtooth flounder larger than 53 cm FL were all female and the size ranges in each of the sample categories differed (Fig. 2). Females accounted for 85% (by number) of market, 42% of discard, and 67% of survey samples. Males were not well represented and did not show grossly apparent developmental changes over time; therefore, males were categorized only as mature or immature and were not considered further. However, males appeared most developed in July when the testes were largest, brown to whitish and folded. No spawning males were seen.

The average length of males was less than that of females in every month that market and survey samples were taken (Table 1; 1-tailed Student's t-test, α=0.05). Fish size (Table 1) and catch rates (Table 4) were highest in spring and summer. In winter, average length of market-sample fish decreased by approximately 9.0 cm for males and 16.0 cm for females. CPUE peaked (>200 kg/hr) in spring and fall at depths of 183–365 m and decreased in winter, while above 183 m CPUE was highest (about 50–150 kg/hr) in July–August but dropped to at or near 0.0 kg/hr in November–March. There was no apparent seasonal trend in CPUE at depths >366 m.

The proportion of mature females at each macroscopic maturity stage varied seasonally (Fig. 3). Because spring discards included fish that were the

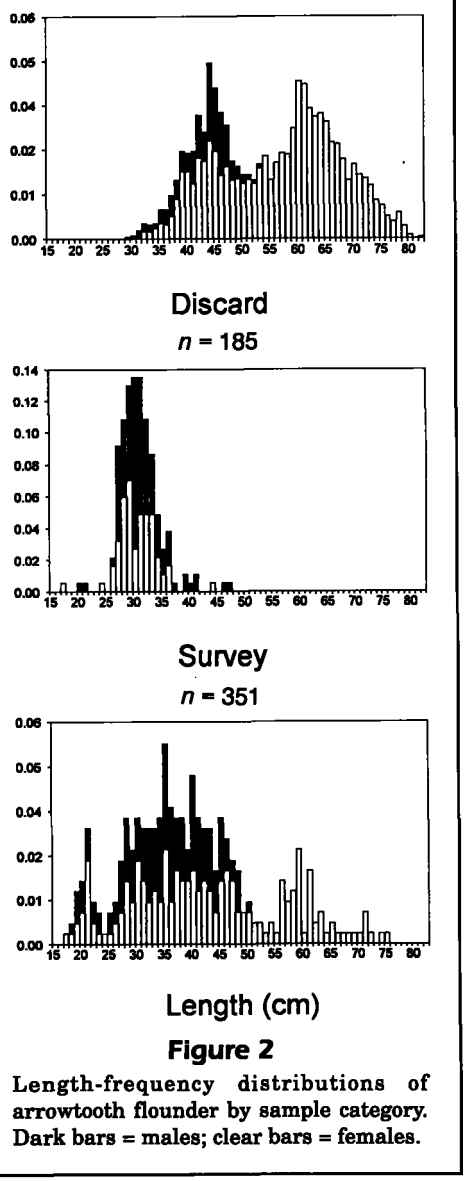

Figure 2
Length-frequency distributions of arrowtooth flounder by sample category. Dark bars = males; clear bars = females.

same size as fish in winter market samples, discard and market samples were pooled by common month and by keeping years separate. Throughout the year, samples almost always included large spent/resting females that did not show signs of ovarian recrudescence. Gravid females first appeared consistently in September 1991. The proportion of developing, gravid, and spent females stayed relatively constant through November. In December the first ripe/running fish and a substantial increase in the proportion of spent females were seen. The next available sample was March 1992 when all the mature females were in the spent/resting stage. Developing females reappeared the following May, and their proportion increased into the fall. In 1992, the first gravid and ripe/running fish were seen in November.

Length at 50% maturity calculated from survey data was 28.0 cm for males and 36.8 cm for females (Table 5). Estimates of $L_{50\%}$ from pooled market and discard ("commercial") data were lower for males and higher for females than estimates from survey data, although confidence intervals for $L_{50\%}$ overlapped. For females, seasonal estimates of $L_{50\%}$ varied widely. The greatest $L_{50\%}$ (>41 cm) was seen before spawning (May–August) and the lowest (<37 cm) during spawning (September–December). Parameters for the logistic function were compared with a likelihood-ratio test (Kimura, 1980). Estimates from commercial data were significantly different from survey estimates for both females (χ^2=145.490, P<<0.001; Fig. 4) and males (χ^2=79.383, P<<0.001). In a comparison of years, logistic curves fit to September–December 1991 (commercial) and September–November 1992 (survey) data were significantly different (likelihood-ratio test, χ^2=143.257, P<<0.001) although again confidence intervals for $L_{50\%}$ overlapped.

Ovarian tissue samples were analyzed histologically from 111 female arrowtooth flounder collected late December 1991 during spawning. Each of the five macroscopic maturity stages was represented and no two macroscopic stages showed the same frequency distribution of oocyte types (Fig. 5). Chromatin nucleolar, perinucleolar, and atretic oocytes were present in all the sampled ovaries. In ovaries of immature fish, none of the oocytes had progressed beyond the perinucleolar stage. Vitellogenic or yolked oocytes were prevalent in developing and gravid stage ovaries, and hydrated oocytes were seen frequently in gravid and ripe/running stage ovaries. Oocytes with cortical alveoli were most frequently seen in spent/resting ovaries.

Atresia was more prevalent in all the ovarian stages of spent/resting fish than in immature fish (Table 6). The percent occurrence of α atretic oocytes was lowest in ovaries from developing fish and highest in ovaries from spent/resting fish. Beta atresia was most common in spent/resting ovaries but also occurred in developing, gravid, and immature ovaries. All the immature and 43.8% of the spent/resting females had perinucleolar stage ovaries. Postovulatory follicles (POF) were present in ovaries from all macroscopic stages except immature. POF were most frequently seen in ripe/running ovaries and were common in gravid and spent/resting ovaries; whereas 7 of 29 developing females examined for histology had ovaries with POF. Postovulatory follicles were also present in 7 of 21 spent/resting

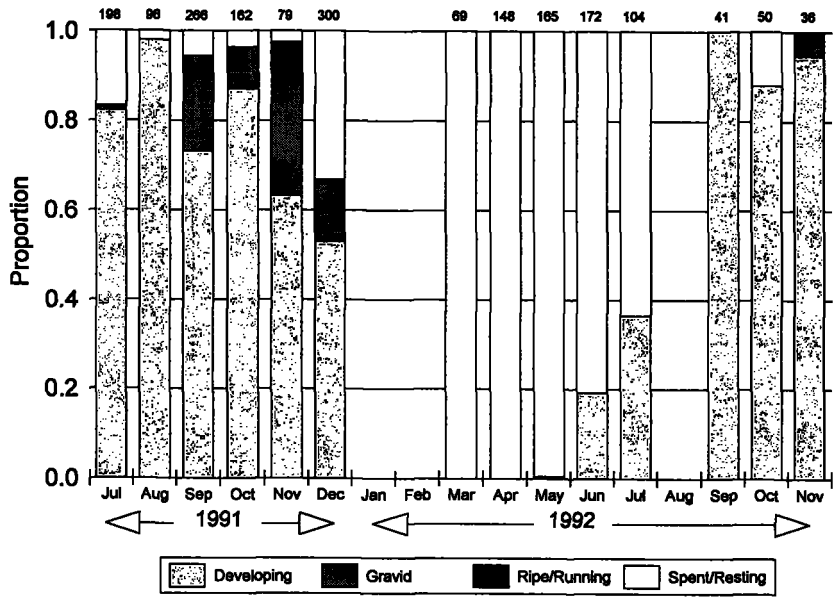

Figure 3

Proportions of mature female arrowtooth flounder at each macroscopic maturity stage by month. Number of females listed at top.

Table 4

Washington commercial bottom trawl catch rates (kg/hr) of arrowtooth flounder, *Atheresthes stomias*, by depth interval based on the minimum depth recorded for each tow. *n* = number of tows.

		1–182 m		183–365 m		366–547 m		547+ m	
Year	Month	*n*	kg/hr	*n*	kg/hr	*n*	kg/hr	*n*	kg/hr
1991	July	1,644	155.7	176	184.0	31	44.6	9	134.5
	August	1,391	54.5	179	130.6	21	3.0	5	0.0
	September	1,362	14.5	187	157.6	54	27.7	7	0.0
	October	860	11.8	274	231.7	56	64.3	4	0.0
	November	210	0.0	95	20.3	37	22.7	3	0.0
	December	187	0.0	126	8.9	82	35.8	7	0.0
1992	January	221	0.1	120	14.9	82	8.9	18	11.0
	February	596	0.0	240	10.7	61	12.2	37	0.4
	March	883	0.3	201	19.5	178	39.8	85	8.9
	April	462	7.4	155	53.9	110	68.5	31	1.7
	May	829	16.3	232	228.2	63	71.0	40	0.0
	June	1,131	19.0	174	344.1	38	16.4	90	0.5
	July	1,246	53.4	134	50.8	13	1.7	82	1.5

females with perinucleolar-stage ovaries. One 41.0-cm gravid female had no POF and 6.3% of its oocytes were hydrated. All other gravid females had POF.

Overall mean oocyte diameters (μm) and standard deviations were as follows: perinucleolar 79.6 ± 34.9 (n=420); cortical alveoli 185.4 ± 23.4 (n=220); vitellogenic 722.9 ± 73.9 (n=290); and hydrated 940.6 ± 206.8 (n=170) (Fig. 6). Chromatin nucleolar stage oocytes were not measured because they never represented the most advanced stage present in an ovary. Mean diameter of perinucleolar oocytes in spent/resting females was about 10 μm greater than that in the immature females (Student's t-test, P<0.003). Some of the variance in hydrated oocyte size

Table 5

Parameter estimates for the logistic model[1] of proportion mature at length (cm), length at 50% mature, and 95% confidence intervals, for arrowtooth flounder, *Atheresthes stomias* from 1991–92 Washington commercial (pooled market and discard), 1992 Washington survey, and 1972–75 Oregon data (See Footnote 3 in the text). For females, results are also given for Washington commercial data grouped by months in relation to the spawning season.

Sex and stratum	a	b	R^2	$L_{50\%}$ (cm)	95% CI for $L_{50\%}$	n
Males						
Washington-survey	24.990	–0.893	0.968	28.0	27.6–28.4	144
Washington-commercial	33.264	–1.197	0.968	27.8	27.5–28.1	424
Oregon	17.397	–0.615	0.971	28.3	27.8–28.8	218
Females						
Washington-survey	19.891	–0.540	0.971	36.8	36.3–37.3	207
Washington-commercial	20.874	–0.559	0.984	37.4	37.0–37.7	1,928
Oregon	15.056	–0.352	0.989	42.8	42.4–43.2	1,628
Females[2]						
Jul–Aug 1991 (before)	13.050	–0.281	0.390	46.5	43.2–49.7	298
Sep–Dec 1991 (during)	14.800	–0.410	0.945	36.1	35.5–36.7	887
Mar–Apr 1992 (after)	61.111	–1.568	0.991	39.0	38.8–39.1	239
May–Jul 1992 (before)	18.194	–0.438	0.928	41.6	40.6–42.6	504

[1] $P_L = 1/(1+e^{(a+bL)})$.

[2] No samples obtained in January–February 1992.

can be attributed to distortion of hydrated oocytes that occurs during histological processing.

Gonosomatic indices (GSI) for immature and spent/resting fish remained fairly constant across seasons, whereas GSI for developing or gravid fish varied considerably over time, reflecting ovarian recrudescence (Table 7). Individual GSI for immature fish ranged from 0.0017 to 0.0154 (average 0.0055), and individual spent/resting GSI ranged from 0.0037 to 0.0259 (average 0.0135). GSI for ripe/running fish (n=4; $\bar{L}$=47.8) was not calculated because loss of eggs in handling precluded accurate gonad weights. From histological analysis, hydrated oocytes and POF were found in "developing" females, indicating some misclassification of spawning females. Because of suspected misclassification, developing and gravid GSI data were pooled by month. GSI for developing or gravid fish showed a rapid increase from about 0.03 in August 1991 and 0.02 in July 1992 to 0.06 in September of both years; the highest annual mean GSI occurred in December 1991 and November 1992. The highest individual GSI was 0.2201 in November 1992 for a 38-cm gravid female.

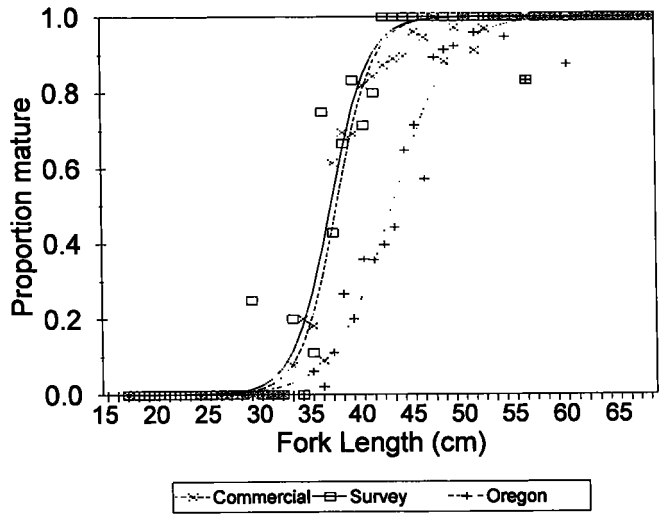

Figure 4

Maturity distributions and logistic curves for female arrowtooth flounder calculated from pooled 1991–92 market and discard (commercial) data, 1992 survey data, and 1973–75 data from Oregon (see Footnote 3 in the text).

Discussion

The progression of gonad maturity stages, increase in GSI, and the appearance of gravid females show that arrowtooth flounder spawn during fall–winter off Washington. Spawning begins as early as September, extends at least through December, and is completed by March. This coincides with the spawning season for *Atheresthes evermanni* in the western

Table 6

Percent occurrence of oocytes in each oocyte developmental stage in arrowtooth flounder, *Atheresthes stomias*, by macroscopic and microscopic maturity stages. Percent occurrences of atresia and postovulatory follicles (POF) among all oocyte structures also included. Microscopic stage reflects the most advanced oocyte type present. n = number of females, L = mean FL in cm; oocyte-stage 1 = chromatin nucleolar; stage 2 = perinucleolar; stage 3 = cortical alveoli; stage 4 = vitellogenic; stage 5 = hydrated; and POF = postovulatory follicle. Samples were collected late December 1991.

Macroscopic stage	Microscopic stage	n	$\bar{L}$ (cm)	Oocyte developmental stage					Atresia		POF
				1	2	3	4	5	α	β	
Immature	Perinucleolar	17	35.7	19.0	81.0	0.0	0.0	0.0	11.5	1.3	0.0
Developing	Vitellogenic	26	43.0	2.4	20.7	0.1	76.8	0.0	3.6	0.9	0.5
Developing	Hydrated	3	39.7	1.0	20.6	0.0	77.0	1.4	6.6	0.9	0.9
Gravid	Hydrated	15	40.4	3.1	25.5	0.2	47.0	24.1	7.2	0.9	7.1
Ripe/Running	Hydrated	2	59.0	3.3	39.6	0.0	1.1	56.0	7.2	0.0	26.8
Spent/Resting	Perinucleolar	21	48.2	15.8	84.2	0.0	0.0	0.0	21.7	7.3	5.4
Spent/Resting	Cortical alveoli	26	61.8	14.5	76.1	9.4	0.0	0.0	20.1	10.2	2.9
Spent/Resting	Hydrated	1	42.0	6.3	34.4	0.0	34.4	25.0	16.7	0.0	7.1

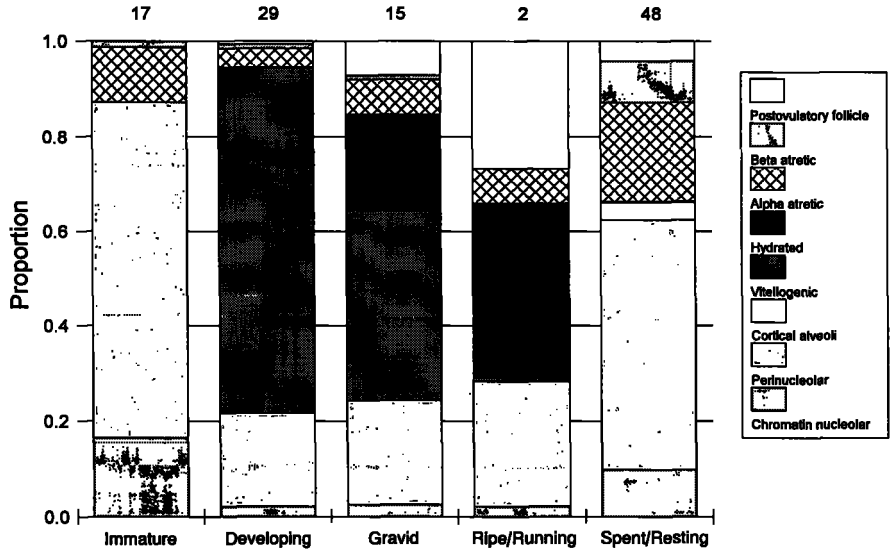

Figure 5

Proportion of arrowtooth flounder oocytes assigned by histological criteria to ovarian developmental stages according to macroscopic maturity stage of the whole ovary. Samples were collected late December 1991. Number of females is listed at top.

Bering Sea reported by Pertseva-Ostroumova (1960). Hirschberger and Smith (1983) found some spawning arrowtooth flounder during spring and summer months in the Gulf of Alaska, but their survey data were insufficient to define the spawning season with any certainty. The appearance of translucent oocytes is usually taken as an indication that spawning is imminent (hours or days) (West, 1990), although there are no laboratory data to indicate the speed at which arrowtooth flounder oocytes ripen and are ovulated. Gravid females were first seen in September 1991 coincident with an increase in GSI. A similar increase in September GSI was seen in 1992, but the first gravid females were observed in November, suggesting that the start of arrowtooth flounder spawning may vary from year to year.

Histological results show arrowtooth flounder are batch spawners, where one female spawns repeat-

Table 7

Arrowtooth flounder, *Atheresthes stomias*, monthly mean fork length ($\bar{L}$, in cm) and mean gonosomatic index (GSI) and standard deviation (SD) for females selectively sampled for GSI by macroscopic maturity stage. July 1991–July 1992 samples were collected shoreside; September–November 1992 samples were collected at sea.

		Immature				Developing/Gravid				Spent/Resting			
Year	Month	*n*	$\bar{L}$	GSI	SD	*n*	$\bar{L}$	GSI	SD	*n*	$\bar{L}$	GSI	SD
1991	July	1	48.0	0.0056	—	22	63.3	0.0277	0.0096	20	61.1	0.0164	0.0021
	August	3	48.0	0.0080	0.0035	10	60.4	0.0290	0.0082	2	63.5	0.0120	0.0028
	September	9	42.8	0.0064	0.0020	46	65.1	0.0587	0.0249	15	53.9	0.0163	0.0047
	October	10	39.4	0.0051	0.0006	40	61.0	0.0738	0.0246	6	56.7	0.0120	0.0066
	November	3	41.7	0.0045	0.0003	20	55.7	0.0883	0.0223	2	54.5	0.0051	0.0003
	December	14	36.3	0.0048	0.0018	33	47.0	0.1160	0.0332	11	45.7	0.0070	0.0060
1992	March	10	35.9	0.0045	0.0017	0	—	—	—	10	49.5	0.0126	0.0015
	April	6	40.5	0.0051	0.0013	0	—	—	—	20	55.3	0.0114	0.0035
	May	9	36.6	0.0048	0.0030	1	67.0	0.0140	—	21	65.4	0.0135	0.0026
	June	4	44.5	0.0067	0.0009	20	61.9	0.0171	0.0042	20	64.4	0.0151	0.0030
	July	5	41.0	0.0071	0.0034	17	57.8	0.0215	0.0046	18	53.8	0.0145	0.0031
	September	18	29.2	0.0063	0.0042	28	55.6	0.0615	0.0292	0	—	—	—
	October	10	35.9	0.0049	0.0017	10	46.0	0.0567	0.0303	0	—	—	—
	November	10	30.0	0.0056	0.0041	11	46.4	0.1004	0.0487	0	—	—	—

edly over a protracted spawning season, as are Pacific halibut, *Hippoglossus stenolepis* (St-Pierre, 1984), and Dover sole, *Microstomus pacificus* (Hunter et al., 1992). Size frequencies of oocyte stages (Fig. 6) show distinct populations of oocytes that indicate a group-synchronous pattern of development. Postovulatory follicles were found in "developing" females, those with no visible translucent oocytes, evidence that these fish had recently spawned and that macroscopic examination of ovaries could not separate all spawning from nonspawning fish. In September 1991, early in the spawning season, gravid mean GSI was significantly greater than developing GSI (Student's *t*-test, $P<<0.001$), but by November and December there was essentially no difference between mean GSI for developing and gravid females (Student's *t*-test, November $P<0.105$, December $P<0.841$); the highest mean GSI was observed in December. Under the macroscopic maturity definitions used, females progress from immature to the developing stage, then cycle between "developing" and "gravid" as successive batches of oocytes ripen and are ovulated. The ripe/running stage corresponds then only to the last and perhaps largest batch of oocytes, suggesting that by December spawning was near completion for some females.

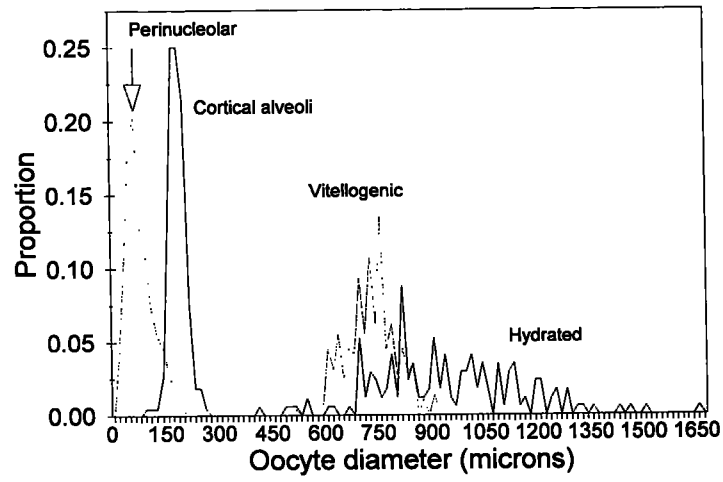

Figure 6

Size-frequency distributions of arrowtooth flounder oocyte developmental stages from ovaries collected late December 1991. Proportions were calculated separately for each oocyte type.

Spent/resting females were seen year-round, evidence that adult arrowtooth flounder may not spawn every year.

Of particular concern is whether small, resting mature fish were misclassified as immature, and vice versa, since errors will bias estimates of size at maturity. Immature male arrowtooth flounder were difficult to identify and errors undoubtedly occurred,

but there was not enough auxiliary information to quantify them. Macroscopically immature females examined for histology did not show signs of recent spawning, and all were microscopically staged as perinucleolar. Out of 48 spent/resting females examined for histology, 43.8% also had perinucleolar ovaries. Seven of these had POF, direct evidence of prior spawning. Of the remaining 14, atretic structures were more than twice as common as in immature females. Hunter et al. (1992) used atresia to distinguish immature from uncertain maturity in Dover sole ovaries defined as inactive but concluded that microscopic examination of oocytes in histological sections may not identify all mature, postspawning females. Relatively high rates of atresia may indicate that fish have finished spawning (Wallace and Selman, 1981), but this alone is insufficient to separate mature from immature fish because atresia can be brought on by stresses not necessarily associated with spawning, such as starvation, pollution, or other environmental conditions (Wallace and Selman, 1981; Hunter and Macewicz, 1985; Hunter et al., 1992). Because histological criteria could not differentiate all mature from immature females and because other microscopic evidence of prior spawning such as ovarian wall thickness (Burton and Idler, 1984) was not available, the degree of misclassification of mature vs. immature females staged macroscopically could not be determined.

Histological processing is known to cause shrinkage of oocytes (West, 1990); therefore oocyte diameters determined from processed tissue sections should be considered an index rather than an absolute measurement of oocyte size. For arrowtooth flounder, Pertseva-Ostroumova (1960) reported whole egg diameters are about 2.5–3.5 mm. Matarese et al. (1989) lists *A. stomias* egg diameter as approximately 3 mm, three times the mean diameter of ripe oocytes determined in this study.

Seasonal bathymetric migrations are a familiar pattern in flatfish. Dover sole, *Microstomus pacificus*, petrale sole, *Eopsetta jordani*, and English sole, *Pleuronectes vetulus*, migrate seasonally across depths (Alverson et al., 1964), and Dover sole tend to reside at deeper depths at older ages (Hunter et al., 1990). Kabata and Forrester (1974) sampled arrowtooth flounder off Vancouver Island in May–June 1968 and found increasing length with depth, and a drop in abundance below 420 m (230 fm) consistent with these results. Trends in arrowtooth flounder catch rates by depth and season (Table 4) indicate arrowtooth flounder move offshore in winter. Arrowtooth flounder were common in shallow water (<183 m) in summer, when the average size of landed fish was large. In winter, smaller numbers and sizes of arrowtooth flounder were caught in deeper water; whereas several hundred tows were reported in shallow water with virtually no arrowtooth flounder. Large, mature, presumably spawning arrowtooth flounder may have moved out of the range of the trawl fishery, possibly to deeper water or north into Canadian waters. However, targeted arrowtooth flounder trips are rare and independent estimates of the amounts of arrowtooth flounder discarded from trawl catches are high, from nearly 76% off Oregon and Washington (Barss and Demory, 1985) to over 80% in the Gulf of Alaska.[1] Large volumes of discards and catch unreported in logbooks may obscure trends in distribution; they certainly result in underestimates of arrowtooth flounder CPUE. Hosie (1976) states that arrowtooth flounder spawn off central Oregon from December through March at about 200 fm. Hirschberger and Smith (1983) reported spawning arrowtooth flounder at depths of over 350 m (191 fm) in the Gulf of Alaska. The full extent of the spawning depth range inhabited by arrowtooth flounder has not been determined, but in this study in 1991 gravid females were found in commercial tows out to 512 m (280 fm) and ripe/running females at 475 m (260 fm). In 1992 gravid and ripe/running females were found at 399 m (218 fm). Since these results also suggest that in winter the bulk of the population was in water as deep or deeper than 366 m, it is likely that the majority of arrowtooth flounder off Washington spawn at depths exceeding 366 m (200 fm).

To examine trends in length at maturity over time, I fitted logistic curves to Oregon trawl survey data from the 1970's[3] to compare with results from Washington (Table 5). The Oregon survey covered the area from Newport, Oregon, south to Cape Blanco and included FL and maturity for 218 male and 1,628 female arrowtooth flounder. Macroscopic criteria used to distinguish mature from immature fish were identical in both studies. Washington maturity samples were collected in all months except January and February. All months except July, August, and November were represented in the Oregon data. Arrowtooth flounder in the present study matured at a smaller size than those collected off Oregon, and likelihood-ratio tests (Kimura, 1980) showed sample nonlinear regressions for Oregon were significantly different when compared with both Washington survey data (male χ^2=74.555, P<<0.001; female χ^2=137.922, P<<0.001) and commercial data (male χ^2=80.539, P<<0.001; female χ^2=147.920, P<<0.001). Distribution of female maturities across lengths (Fig. 4) suggests that female arrowtooth flounder are maturing at a smaller size than they were off Oregon in the early 1970's, or that there are latitudinal

differences in size at maturity. However, differences between results for Oregon and the present study could be explained by differences in sampling distributions across months, or by different interpretations of maturity codes by different observers; therfore they may not represent a biological change.

Size-selectivity and areal or bathymetric sampling biases are critical to estimates of $L_{50\%}$ (Welch and Foucher, 1988; Trippel and Harvey, 1991). Predicted length at maturity may be biased if fish are size-segregated by area or depth (e.g. if immature fish do not migrate to spawning depths while targeted commercial trawl fisheries typically operate where large fish are most likely to be found in quantity, i.e. the spawning grounds). Smaller arrowtooth flounder were not well represented in commercial landings. Size selectivity in commercial fisheries occurs either through net selection (a lesser problem in the trawl survey) or through size-selective targeting and discarding. Net avoidance by larger fish may also be a factor. In the extreme case of male arrowtooth flounder, estimated $L_{50\%}$ was below the size range of fish in market samples though well within the size range of fish in commercial discards and survey catches. Because the trawl survey sampled the widest size range of arrowtooth flounder over a fairly large area and depth range prior to peak spawning in 1992, size-at-maturity estimates from the trawl survey represent the best available.

Hunter et al. (1992) estimated size at maturity for female Dover sole and found samples taken during the spawning season yielded higher estimates of $L_{50\%}$ than did samples taken before spawning. They attributed this to the presence of postspawning females with "highly regressed" ovaries that were histologically indistinguishable from immature females, and they concluded that estimates of length or age at first maturity should always be conducted prior to the onset of spawning, when such females are rare. I found the opposite seasonal pattern in length at maturity for female arrowtooth flounder; lowest $L_{50\%}$ was estimated from commercial samples collected in the fall during spawning, and highest $L_{50\%}$ was estimated from months preceding spawning. Market samples collected in summer (before spawning) tended to underrepresent smaller arrowtooth flounder and yielded extremely high estimates of female length at maturity. In the case where sampling is limited to commercial trawl fisheries, it may be preferable to pool year-round sampling data to generate estimates of $L_{50\%}$ if fish are moving in and out of range of the trawl fleet, rather than to attempt to narrow the sampling window to just prior to spawning as suggested by Hunter et al. (1992). This involves the explicit trade-off of some assumed increase in the misclassification of small fish with the significant bias caused by a seasonal inability to obtain representative samples of the entire size or bathymetric range of a population. Perhaps coincidentally, female length-at-maturity curves generated from the year-round commercial data and the survey data were strikingly similar (Fig. 4), although statistically the curves were different.

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Marine turtle populations on the east-central coast of Florida: results of tagging studies at Cape Canaveral, Florida, 1986–1991*

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Abstract.—Marine turtle tagging records were collected off east-central Florida by a shrimp trawler from May 1986 to December 1991. The data were analyzed to determine species composition, size distribution, seasonal occurrence, movements, morphometrics, and growth of 928 incidentally captured turtles. Loggerhead turtles, *Caretta caretta*, were the most frequently captured species (83% of total catch), while Kemp's ridley, *Lepidochelys kempi*, and green turtles, *Chelonia mydas*, were caught less frequently (12% and 4%, respectively). The loggerhead turtle population consisted of a seasonably variable aggregation of subadult and adult turtles. The Kemp's ridley and green turtle populations were composed of subadult turtles and were captured primarily during winter months. Kemp's ridley and loggerhead turtles appeared to exhibit a seasonal north-south migrational pattern along the Atlantic coast. Regression equations were developed for the morphometric relationships of each species. Average yearly growth rates and estimates for the von Bertalanffy growth interval equation were calculated for loggerhead and Kemp's ridley turtles. These results indicate that the coastal waters of the Cape Canaveral area provide an important developmental habitat for the three species of marine turtle.

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The marine turtle life history is a dynamic progression of stages which includes oceanic dispersal of the offspring and utilization of a series of distinct developmental habitats (Carr, 1980; Hendrickson, 1980). The early in-water stages of marine turtle development have not been as extensively studied as the reproductive stage of females. Information concerning the early life histories of threatened and endangered marine turtles is critical in formulating conservation and recovery strategies as mandated by the Endangered Species Act of 1973 and subsequent amendments.

Inaccessibility of immature turtles in the open ocean is the major factor contributing to the lack of information on the early stages of development. Other than possible current-mediated dispersal scenarios (Carr, 1986; Collard and Ogren, 1990), little is known about the pelagic stage of marine turtle development. However, information concerning the populations of immature turtles foraging in the coastal waters of eastern Florida has been accumulating as a result of data collected through commercial fisheries (fishery-dependent) and fishery-independent activities.

Fishery-independent capture and tagging efforts have characterized the populations of loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, foraging in the northern part of the Indian River lagoon system (Ehrhart and Yoder, 1978; Mendonça, 1981, 1983; Mendonça and Ehrhart, 1982; Ehrhart, 1983). All green turtles collected in the lagoonal habitat were immature, as were almost all of the loggerhead turtles. Aggregations of marine turtles in the Port Canaveral ship channel were first reported in 1978, when two trawlers caught unprecedented numbers of loggerhead turtles while searching for a concentration of shrimp (Carr et al., 1980). This prompted the National Marine Fisheries Service (NMFS) to conduct trawl surveys of the ship channel from 1978 to 1984 (Butler et al., 1987; Henwood, 1987a; Henwood and Ogren, 1987). The surveys provided information on the seasonal occurrence and movement patterns of subadult and adult loggerhead turtles (Henwood, 1987a), as well as subadult Kemp's ridley, *Lepidochelys*

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kempi, and green turtles (Henwood and Ogren, 1987) captured in the vicinity of Cape Canaveral. In addition, the results of research conducted in response to incidental mortality of marine turtles due to dredging in the Port Canaveral ship channel were presented at the Cape Canaveral Sea Turtle Workshop (Witzell, 1987).

In 1986, the NMFS Panama City Laboratory initiated long-term studies of marine turtles found along the northwest (Cedar Keys) and east-central (Cape Canaveral) coasts of Florida (Schmid and Ogren, 1990). The Kemp's ridley turtle was the target species in both study areas. This paper presents the results of NMFS marine turtle studies conducted in nearshore waters of east-central Florida from 1986 to 1991. Information concerning marine turtle species composition, relative abundance, size frequency, seasonal occurrence, movements, morphometrics, and growth is provided.

Materials and methods

Data collection

A commercial shrimp-fishing vessel was contracted by NMFS, from May 1986 to December 1991, to measure, tag, and release marine turtles incidentally captured during trawling. Fishing effort and location were a function of the seasonal abundance of brown shrimp, *Penaeus aztecus*, and white shrimp, *Penaeus setiferus*. Trawling was conducted between St. Mary's Entrance, 30°43'N, and Sebastian Inlet, 27°52'N (Fig. 1), and was concentrated in the Cape Canaveral area, 28°30'N to 28°15'N, as defined by Henwood (1987a). Fishing effort did not extend beyond 24 km offshore and 25.6 m in depth. The majority of effort occurred less than 8 km offshore and 13.4 m in depth. Trawling gear consisted of four 12.2-m or 12.8-m nets (two on each side) for targeting brown shrimp, or two 24.4-m nets (one on each side) for targeting white shrimp.

Captured turtles were double tagged on the trailing edge of the fore flippers with #681 Inconel cattle ear tags. Tagging information for each turtle included: tag codes, species, date, location of capture, latitude and longitude, depth, gear type, standard straight-line carapace length (SSCL; nuchal notch to posterior end of postcentral), and straight-line carapace width. Carapace length and width were measured to the nearest 0.1 inch with forester's calipers and were converted to metric units for analysis. Kemp's ridley and green turtles were weighed with a 15-kg capacity spring scale. Notes on the condition of the turtle were recorded when the animal was injured or deformed (e.g. missing flipper, carapace wounds, etc.).

NMFS issued Sea Turtle Conservation Regulations on 29 June 1987 (Federal Register, 1987) that required vessels 25 feet (7.6 m) long or longer to use Turtle Excluder Devices (TED's) in the Cape Canaveral area beginning 1 October 1987. Subsequently, a NMFS permit was issued authorizing the contract vessel to conduct a TED testing program during fishing operations. The testing procedure consisted of towing a net(s) equipped with a Morrison soft TED on one side of the boat and a net(s) without a TED on the other side. Pounds of shrimp, marine turtle captures, and total catch (when possible) were recorded for the trawl types. Effort data were available for 1989–91, including trawl size and type, number of tows and total tow time, and number of days fished.

Data analysis

The terms "juvenile" and "subadult" used to describe the early stages of the marine turtle life history are

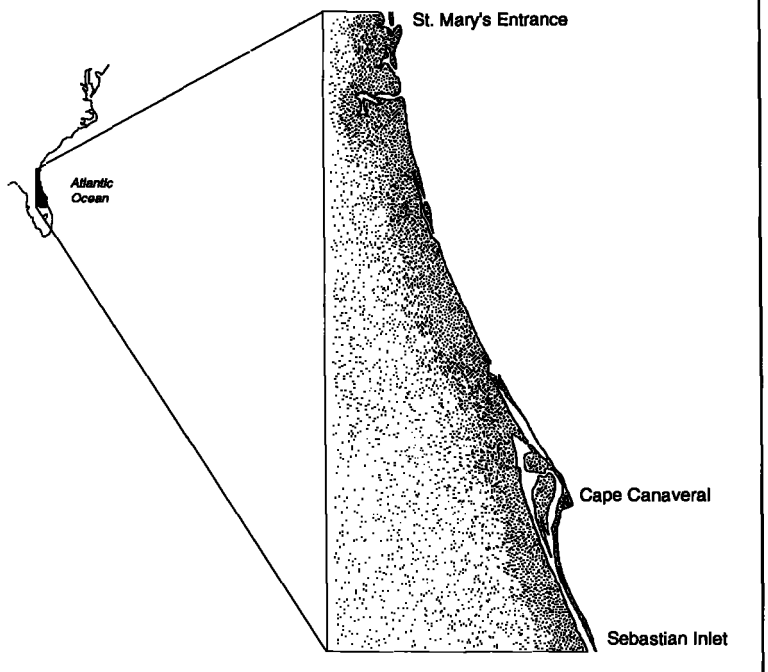

Figure 1

Sampling areas for marine turtles (*Caretta caretta*, *Lepidochelys kempi*, and *Chelonia mydas*) off the Atlantic coast of Florida from 1986 to 1991.

not well defined. In this study, the term "juvenile" has been reserved for immature turtles in the pelagic stage of development. A turtle is considered "subadult" when it has recruited to its respective coastal-benthic habitat and "adult" when sexually mature. Loggerhead turtles greater than 80-cm carapace length were considered adult, based on the length frequencies of Cape Canaveral nesting females (Carr, 1986, and references therein) and earlier investigations of Henwood (1987a). Kemp's ridley turtles greater than 60-cm carapace length were considered adult (Pritchard and Márquez, 1973).

Monthly trawling effort was calculated and standardized according to Henwood and Stuntz (1985) by using the formula

$$E = \left(\frac{Nets \cdot Length}{30.5}\right)\left(\frac{Min}{60}\right),$$

where E is the trawling effort in hours towed by a single 30.5-m headrope length net, *Nets* is the number of nets towed, *Length* is the headrope length (m) of a net, and *Min* is the number of minutes fished.

Capture records were analyzed to evaluate species composition within the study area, length-frequency distribution of each species, and patterns of seasonal distribution and movements. Linear regression analyses were performed for carapace width on length for loggerhead turtles. The morphometric data for loggerhead turtles were subdivided into a subadult group (<80 cm SSCL) and an adult group (≥80 cm SSCL) because the carapace dimensions of this species change as the animals mature (Henwood and Moulding, 1987). Carapace width was regressed on length, and weight regressed on length for Kemp's ridley and green turtles. Turtles with carapace wounds or deformities were not included in the analyses. Regression residuals for length-weight relationships were analyzed graphically to assess the appropriateness of the straight-line model (Sokal and Rohlf, 1981; Kleinbaum et al., 1988).

Curved carapace lengths (CCL) of stranded turtles were converted to straight-line carapace lengths (SCL) by using the following regression equations of Teas (1993):

$$SCL = -1.442 + (0.948 \times CCL)$$
for loggerhead turtles;

$$SCL = 0.013 + (0.945 \times CCL)$$
for Kemp's ridley turtles.

Total straight-line carapace lengths (*TSCL*) of loggerhead turtles were converted to standard straight-line carapace lengths (*SSCL*) with the regression equation of Henwood and Moulding (1987):

$$SSCL = (0.9964 \times TSCL) - 0.775.$$

Yearly growth rates were calculated from the formula

$$G = \left(\frac{\Delta Length}{Days}\right)365$$

where G is the growth rate in cm/yr, *ΔLength* is the difference between the recapture length and the initial length, and *Days* is the number of days out. The von Bertalanffy growth interval equation was fitted to the recapture data with a nonlinear least-squares regression procedure (SAS, 1988). The von Bertalanffy growth interval equation (Fabens, 1965) for recapture is as follows:

$$CL_2 = a - (a - CL_1)e^{-kt},$$

where CL_2 is the carapace length at recapture, a is the asymptotic length, CL_1 is the length at first capture, K is the intrinsic growth rate, and t is the time in years between captures.

Results

Trawling effort

Monthly trawling effort varied from year to year (1989–91); however, monthly totals for all three years indicate that the majority of effort occurred from May to December (Table 1). This corresponds to the summer-fall fisheries for brown and white shrimp, the target species during this study. Monthly turtle capture rates were also variable, probably as a result of the combined seasonal fluctuations in trawling effort and turtle abundance. A structured sampling scheme with equal monthly effort would be required to make accurate calculations of monthly changes in turtle abundance. Loggerhead turtle catch per unit of effort (CPUE) ranged from 0.02 turtles/net hour in October 1989 to 1.09 turtles/net hour in August of 1991. Maximum CPUE of 0.25 turtles/net hour was obtained for Kemp's ridley turtles in May 1990 and 0.05 turtles/net hour was obtained for green turtles in January 1989 (Table 1).

Species composition

A total of 774 (83%) loggerhead, 113 (12%) Kemp's ridley, and 41 (4%) green turtles were captured, tagged, and released during the course of the study. A leatherback turtle, *Dermochelys coriacea*, was also

captured and tagged. Sixty tagged turtles (42 loggerhead, 15 Kemp's ridley, and 3 green) were recaptured by the contract vessel. Additionally, 31 recaptures and recoveries (26 loggerhead, 4 Kemp's ridley, and 1 green turtle) were reported by other investigators.

Loggerhead turtle, *Caretta caretta*—Seven hundred and seventy-four loggerhead turtle captures were recorded off the east coast of Florida. Loggerhead turtles captured in Florida ranged from 38.2 to 110.0 cm SSCL (Fig. 2). Eighty percent (n=616) of the loggerhead turtles captured were subadults and 20% (n=153) were adults. Loggerhead turtles were present year-round in the Cape Canaveral area (Table 2). Total monthly captures were highest during November, December, and January; however, yearly captures for these months varied substantially. Subadult loggerhead turtles were most abundant during all months, except June, and showed a decrease from April to July as adult abundance increases, probably in response to the nesting season (Fig. 3). Peaks in the relative composition of the adult size class during April and June correspond to the peak densities reported by Henwood (1987a) for males and females, respectively.

Sixty-eight tagged loggerhead turtles have been recaptured or recovered since the implementation of this study. Fifty-two (76%) of these turtles were initially tagged by the contract vessel. The remaining sixteen (24%) loggerhead turtle recaptures were tagged by other investigators in Florida and Georgia.[1,2,3,4,5,6,7] Methods of capture included shrimp trawl (69%), beach stranding (22%), pound net (3%), power plant intake canal (3%), nesting female (1%), and SCUBA sighting (1%). The amount of time between tagging and recapture ranged from 1 to 2,499 days. However, 70% (n=45) were recaptured within a year of initial capture.

Twenty-six loggerhead turtles (23 subadults and 3 adults) initially captured

Table 1

Monthly trawling effort (net hours) and turtle capture rates (turtles/net hour) for 1989–91. Cc=*Caretta caretta*, Lk=*Lepidochelys kempi*, and Cm=*Chelonia mydas*.

Year and month	Effort (net hours)	Total turtles/hr	Species		
			Cc/hr	Lk/hr	Cm/hr
1989					
Jan	77.0878	0.3113	0.2465	0.0130	0.0519
Feb	13.1918	0.2274	0.0758	0.1516	0.0000
Mar	25.9838	0.3079	0.2694	0.0385	0.0000
Apr	41.1742	0.2672	0.1700	0.0971	0.0000
May	103.9350	0.0770	0.0673	0.0096	0.0000
June	123.1230	0.1462	0.0568	0.0650	0.0244
July	70.7558	0.1555	0.1555	0.0000	0.0000
Aug	72.7545	0.1924	0.1787	0.0137	0.0000
Sept	19.9875	0.1001	0.1001	0.0000	0.0000
Oct	49.5690	0.0202	0.0202	0.0000	0.0000
Nov	139.1130	0.1006	0.0719	0.0216	0.0072
Dec	56.3648	0.1242	0.1064	0.0177	0.0000
1990					
Jan	27.1830	0.1104	0.1104	0.0000	0.0000
Feb	57.5640	0.2258	0.1737	0.0521	0.0000
Mar	18.3885	0.4894	0.4350	0.0544	0.0000
Apr	23.1855	0.4313	0.3450	0.0863	0.0000
May	15.9900	0.7505	0.5003	0.2502	0.0000
June	31.5802	0.1583	0.1583	0.0000	0.0000
July	147.1080	0.1971	0.1971	0.0000	0.0000
Aug	117.5265	0.0851	0.0851	0.0000	0.0000
Sept	—	—	—	—	—
Oct	—	—	—	—	—
Nov	148.3072	0.1483	0.1079	0.0067	0.0337
Dec	127.5202	0.2666	0.2196	0.0235	0.0235
1991					
Jan	28.7820	0.8686	0.7991	0.0695	0.0000
Feb	23.1855	0.2588	0.2588	0.0000	0.0000
Mar	35.9775	0.1946	0.1668	0.0278	0.0000
Apr	21.5865	0.2780	0.2780	0.0000	0.0000
May	92.7420	0.2588	0.2588	0.0000	0.0000
June	33.5790	0.4467	0.4467	0.0000	0.0000
July	35.7776	0.6988	0.6988	0.0000	0.0000
Aug	21.9862	1.0916	1.0916	0.0000	0.0000
Sept	—	—	—	—	—
Oct	43.3089	0.2309	0.2078	0.0231	0.0000
Nov	77.5515	0.0903	0.0903	0.0000	0.0000
Dec	106.7332	0.1031	0.1031	0.0000	0.0000
Total	2,028.60				

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[5] Martin, E. Applied Biology, Inc., P.O. Box 974, Jensen Beach, FL, 34958. Personal commun., 1991.

[6] Stuntz, W. National Marine Fisheries Service, Pascagoula Laboratory, P.O. Drawer 1207, Pascagoula, MS, 39567. Personal commun., 1991.

[7] Teas, W. National Marine Fisheries Service, Miami Laboratory, 75 Virginia Beach Drive, Miami, FL, 33149. Personal commun., 1991.

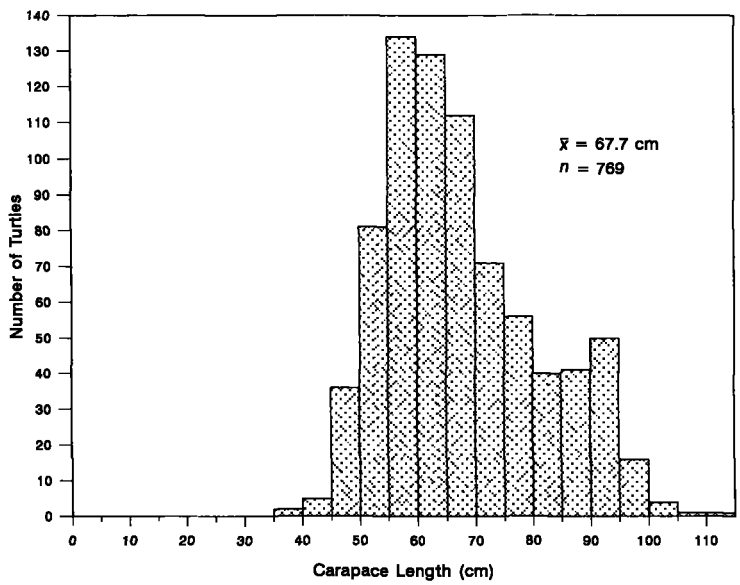

Figure 2

Length frequencies of loggerhead turtles, *Caretta caretta*, collected along the Atlantic coast of Florida from 1986 to 1991.

Table 2

Monthly and yearly trawl captures of loggerhead turtles, *Caretta caretta*, in the nearshore waters of Florida. Dashes indicate trawling effort outside of the study area.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Total
1986					1	5/—	—	—	—/5	37	31	44	123
1987	90	47	31	12	5	11/—	—	—	—	—/3	2	0	201
1988	1	0	16	1	2	0	4	3	2	6	8	15	58
1989	19	1	7	7	7	7	11	13	2	1	10	6	91
1990	3	10	8	8	8	5	29	10	10	10	16	28	145
1991	23	6	6	6	24	15	25	24	—	9	7	11	156
Total	136	64	68	34	47	43/—	69/—	50/—	19/—	66/—	74	104	774

within the Cape Canaveral study area were subsequently recaptured within this area. Of this total, eleven turtles (9 subadults and 2 adults) were captured and recaptured in the Port Canaveral ship channel. Eight loggerhead turtles captured in the Cape Canaveral area during the winter were recaptured or recovered in Georgia, North Carolina, and Virginia during the summer and fall (Fig. 4). All these turtles were subadults ranging from 51 to 61 cm carapace length. Three tagged loggerhead turtles (two subadults and a nesting female) were reported south of Cape Canaveral by fishery-independent sources.

There was a stronger correlation between carapace width and carapace length for subadult loggerhead turtles (r=0.9612; n=508) than for adults (r=0.7724; n=151). Regression equations were computed for the relationship of carapace width (*CW*) to length (*SSCL*) for subadults:

$$CW = 9.0289 + 0.6848\ (SSCL);$$

and adults

$$CW = 22.9153 + 0.5052\ (SSCL).$$

Fifty-one yearly growth rates were calculated for forty-nine loggerhead turtles. Extrapolating annual growth rates from these data is difficult owing to the

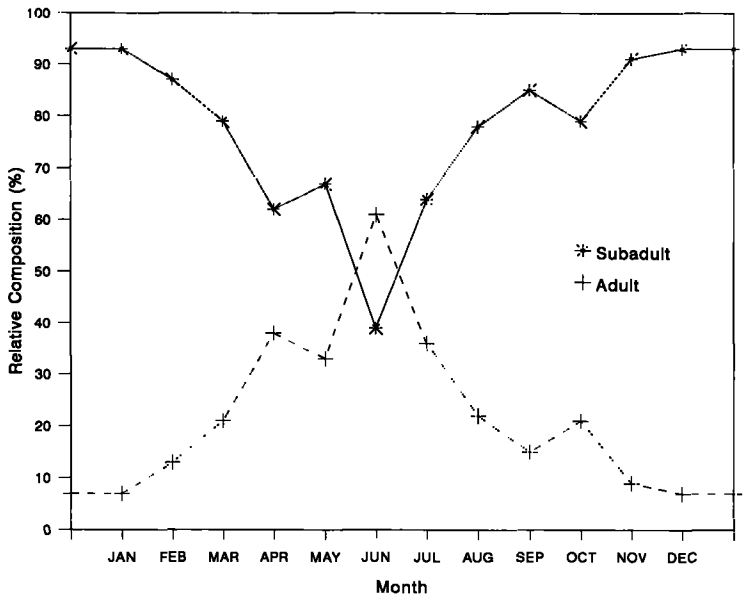

Figure 3

Relative composition of subadult and adult loggerhead turtles collected along the Atlantic coast of Florida from 1987 to 1991.

small sample sizes, measurement errors, and short-term recaptures. A number of treatments were applied to the growth data in an attempt to control for measurement error. However, no single approach was able to account for all the error. Consequently, growth rates were calculated for 1) all data combined, 2) those tag and recapture data recorded by the contracted personnel, and 3) those data with recapture intervals greater than 90 days. A mean growth rate of 5.56 ± 23.91 cm/yr (range: –11.49 to 167.17 cm/yr) was calculated for all loggerhead turtle recaptures. Analysis of the loggerhead turtles tagged and recaptured by the contract personnel indicated a mean growth rate of 1.00 ± 1.23 cm/yr (range: 0.00 to 4.01 cm/yr). Additionally, a mean growth rate of 2.98 ± 7.12 cm/yr (range: –5.96 to 38.44 cm/yr) was calculated for all loggerhead turtle recaptures greater than 90 days at large, 1.84 ± 1.76 cm/yr (range: –0.23 to 8.08 cm/yr) for all recaptures greater than 180 days at large, and 1.77 ± 1.88 cm/yr (range: –0.23 to 8.08 cm/yr) for all recaptures greater than 360 days at large.

The von Bertalanffy growth interval equation was fitted to each of these data treatments. Estimates of asymptotic length (α) for loggerhead turtles ranged from 96.08 cm to 112.52 cm and estimates of intrinsic growth rate (K) ranged from 0.0365 to 0.0588 (Table 3). The growth model for captures and recaptures by the contract vessel had the lowest residual mean square, a criterion commonly used to select the best fit growth model (Dunham, 1978). The estimated parameters for this data treatment (α=112.52 cm; K=0.0365) are similar to Henwood's (1987b) estimated parameters for nonlinear regression of the von Bertalanffy equation (α=110.002 cm; K=0.0313).

Kemp's ridley turtle, *Lepidochelys kempi*—One hundred and thirteen Kemp's ridley turtle captures were recorded on the Atlantic coast of Florida. Kemp's ridley turtles ranged in size from 21.5 to 60.3 cm SSCL (Fig. 5). Sixty-five percent (n=70) of these turtles were early to mid-subadults (20–40 cm). With the exception of a single adult turtle, the Kemp's ridley turtles caught on the east coast were classified as immature. Kemp's ridley turtles were captured year-round in the Cape Canaveral area (Table 4). Their presence in the Cape Canaveral area appeared to be seasonal; 61% (n=69) of the turtles were captured during the winter months of December to March. However, a relatively large number of Kemp's ridley turtles captured in January and February of 1987 and in March of 1988 contributed significantly to this trend. Captures of Kemp's ridley turtles during the following years did not exhibit a pronounced seasonal pattern.

Nineteen tagged Kemp's ridley turtles were recaptured or recovered. Eighty-nine percent (n=17) of the turtles were recaptured by shrimp trawls, and 11% (n=2) were recovered from beach strandings. With the exception of a single turtle captured in the area

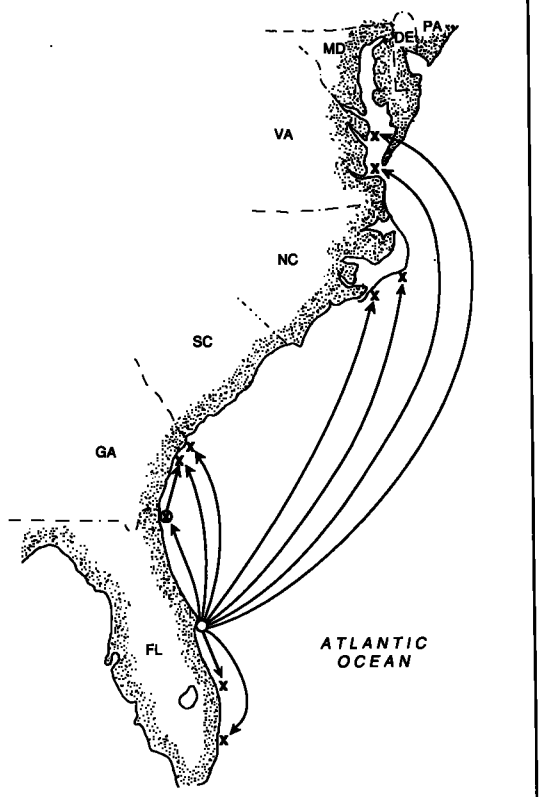

Figure 4

Long-distance recaptures and recoveries of tagged loggerhead turtles. Note: Arrows are not intended to indicate routes traveled by tagged turtles; they are a visual aid to differentiate tagging and recapture sites. O=tagging location; X=recapture location.

of initial tagging after 615 days at large, all Kemp's ridley turtles were recaptured within a year.

Twelve (63%) Kemp's ridley turtles were initially captured in the Cape Canaveral area and subsequently recaptured within this area. Of this total, four turtles were captured and recaptured in the Port Canaveral ship channel. Two Kemp's ridley turtles had multiple recaptures within the Cape Canaveral area, one tagged in November 1986 was caught once in December 1986 and again in May 1987. Another turtle tagged in May 1990 was recaptured twice that September.

Six Kemp's ridley turtles exhibited long-distance movements to and from the Cape Canaveral area (Fig. 6). Two of the recaptures were NMFS Galveston Laboratory headstart turtles released offshore of Padre Island, Texas, in May and captured on the Atlantic coast of Florida in February and March, 0.73 and 1.88 years after release.[8] Two Kemp's ridley turtles displayed seasonal movements northward. The turtles were originally tagged in the Cape Canaveral area in December and February and subsequently recovered in Georgia and South Carolina in July. Another Kemp's ridley turtle exhibited a southerly migration along the Atlantic coast, from Virginia Beach to Port Canaveral.[9]

There was a strong correlation between carapace width and carapace length (r=0.9953; n=105) for Kemp's ridley turtles. Regression of carapace width on length resulted in the equation

$$CW = -2.7157 + 1.0288\ (SSCL).$$

A straight-line equation was applied to the length-weight data; however, graphical analysis of the residuals indicated a curvilinear relationship between the two variables. Power regression was performed through the log-log transformation of weight and length measurements. A strong correlation (r=0.9756; n=88) was calculated for the transformed weight (WT) to length relationship, regression of these variables resulted in the equation

$$\log WT = -8.2837 + 2.8444\ (\log SSCL).$$

Twelve yearly growth rates were computed for ten Kemp's ridley turtles. A mean growth rate of 8.28 ± 9.81 cm/yr (range: 0.00 to 29.16 cm/yr) was calculated for all Kemp's ridley turtle recaptures. Analysis of the Kemp's ridley turtles tagged and recaptured by the contract personnel indicated a mean growth rate of 6.92 ± 9.36 cm/yr (range: 0.00 to 29.16 cm/yr). A mean growth rate of 8.79 ± 10.32 cm/yr (range: 0.00 to 29.16 cm/yr) was calculated for recaptures greater than 90 days at large and 5.94 ± 1.80 cm/yr (range: 4.26 to 7.84 cm/yr) for recaptures greater than 180 days at large.

The von Bertalanffy growth interval equation was fitted to each of these data treatments. Estimates of asymptotic length ranged from 60.66 cm to 77.85 cm and estimates of intrinsic growth rate ranged from 0.0577 to 0.6037 (Table 5). Asymptotic lengths were probably underestimated because of the lack of adult-sized Kemp's ridley turtles in the database.

Green turtle, *Chelonia mydas* —Forty-one green turtles, ranging in size from 24.0 to 55.4 cm SSCL (Fig. 7), were taken from Florida waters. Eighty-one percent (n=33) of the green turtles captured off the east coast of Florida were early subadults less than 40 cm SSCL. No adult green turtles were encountered.

[8] Caillouet, C., Jr. National Marine Fisheries Service, Galveston Laboratory, 4700 Avenue U, Galveston, TX, 77551. Personal commun., 1991.

[9] Keinath, J. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA, 23062. Personal commun., 1993.

The presence of subadult green turtles in the Cape Canaveral area appeared highly seasonal (Table 6); 73% (n=30) were captured from November to January. As with other turtle species, this pattern resulted from a high number of captures in 1987 and a high monthly variation during other years.

Four tagged green turtles were recaptured during this study. Three turtles were originally tagged by contract personnel in the Cape Canaveral area. The tag codes for the fourth green turtle matched a set of NMFS tags that had been distributed to Fort Lauderdale, Florida. Of the three green turtles tagged at Cape Canaveral, one was initially tagged in January 1987 and then recaptured in April, approximately 68 km to the north. Another green turtle that was initially tagged in the Cape Canaveral area in January 1990 was recaptured in this area the following October. A third green turtle was captured off Port Canaveral in September 1990 and found stranded approximately 41 km to the north the following month.

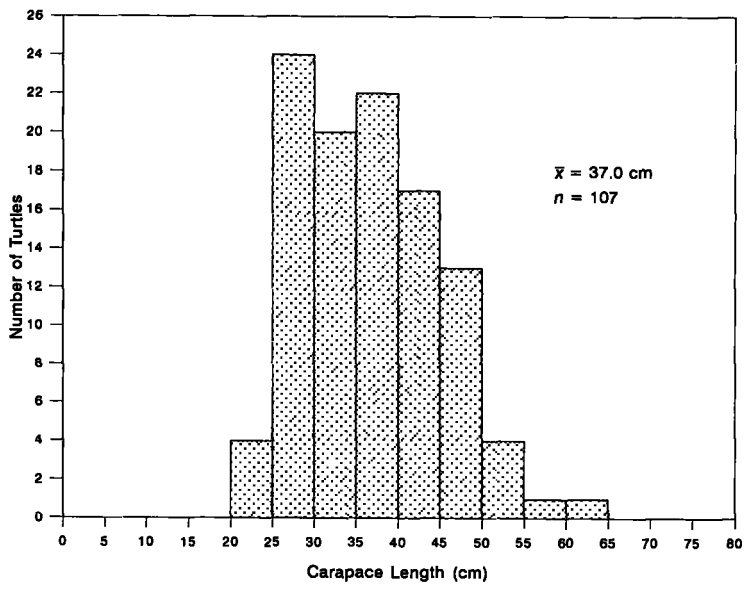

Figure 5

Length frequencies of Kemp's ridley turtles, *Lepidochelys kempi*, collected along the Atlantic coast of Florida from 1986 to 1991.

There was a strong correlation (r=0.9590; n=39) between carapace width and carapace length for green turtles. Regression of carapace width on carapace length resulted in the equation

$$CW = 4.1763 + 0.6847\ (SSCL).$$

Table 3

Estimated values of asymptotic length (a) and intrinsic growth rate (k) from nonlinear regression of von Bertalanffy growth interval equation for loggerhead turtles (one asymptotic standard error in parentheses).

Data treatment	n	a	k
All recaptures	51	96.08 cm (7.07)	0.0586 (0.0149)
	Residual mean square error = 9.1054		
Capture/recapture by contract vessel	17	112.52 cm (24.74)	0.0365 (0.0204)
	Residual mean square error = 0.4088		
All recaptures >90 days	33	96.09 cm (8.72)	0.0588 (0.0185)
	Residual mean square error = 13.8969		
All recaptures >180 days	24	96.40 cm (7.97)	0.0569 (0.0162)
	Residual mean square error = 10.8231		
All recaptures >365 days	19	96.10 cm (8.82)	0.0573 (0.0183)
	Residual mean square error = 13.5947		

Residual analysis of the length-weight relationship indicated the need for curvilinear terms in the regression model. A strong correlation (r=0.9587; n=37) was calculated for the log-transformed weight to length relationship, and regression of these variables resulted in the equation

$$\log WT = 8.8784 + 2.9815\ (\log SSCL).$$

There were no growth data available for green turtles owing to the relatively low number of recaptures and the lack of data for the recoveries.

Discussion

The data for this project were collected incidentally through the commercial shrimp fishery of east-central Florida. Bias in trawling effort oc-

Table 4

Monthly and yearly trawl captures of Kemp's ridley turtles, *Lepidochelys kempi*, in the nearshore waters of Florida. Dashes indicate trawling effort outside of the study area.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Total
1986	1[1]				1	0/—	—	—	—/0	1	1	4	8
1987	13	10	4	1	0	1/—	—	—	—	—/1	1	2	33
1988	1	0	17[1]	0	0	0	2	1	1	1	2	2	27
1989	1	2	1	4	1	8	0	1	0	0	3	1	22
1990	0	3	1	2	4	0	0	0	4	1	1	3	19
1991	2	0	1	0	0	0	0	0	—	1	0	0	4
Total	17	16	24	7	6	9/—	2/—	2/—	5/—	5/—	8	12	113

[1] Recapture of a NMFS Galveston Laboratory Headstart Kemp's ridley turtle.

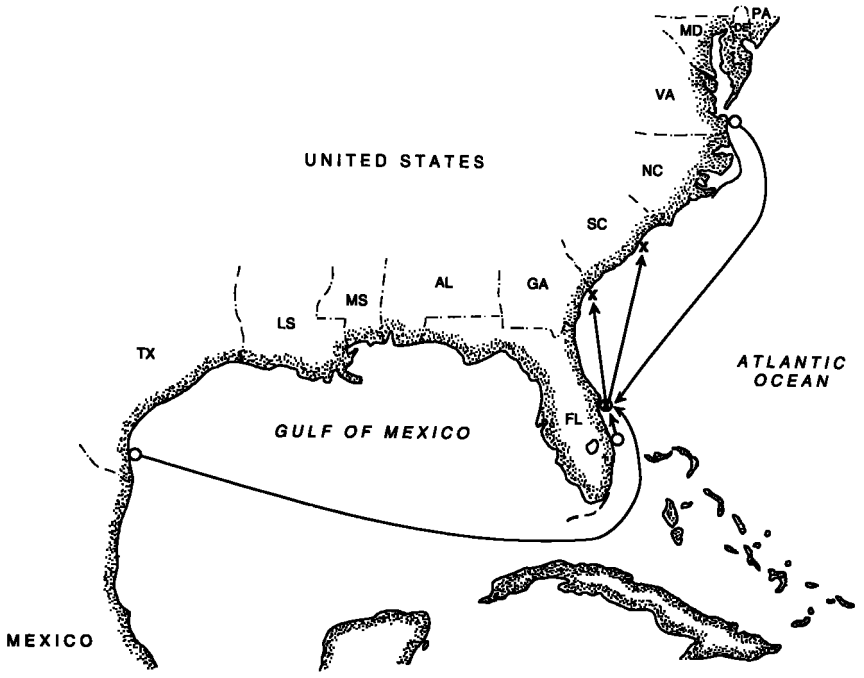

Figure 6

Long-distance recaptures and recoveries of tagged Kemp's ridley turtles Note: Arrows are not intended to indicate routes traveled by tagged turtles; they are a visual aid to differentiate tagging and recapture sites. O=tagging location; X=recapture location.

curred because amount of effort and location of trawling were a function of shrimp abundance. These factors certainly contributed to the annual, and possibly seasonal, variation in turtle captures observed in this study. Restrictions imposed on the shrimping industry during the course of the study also affected data collection. There was a marked reduction in the number of loggerhead captures following NMFS regulations issued in June 1987, requiring the use of TED's in the Cape Canaveral area (Federal Register, 1987). Despite the bias and inconsistencies of data collection, the use of trawl gear allowed access to marine turtle developmental stages not encountered in nesting beach surveys and inshore netting studies. Furthermore, the Cape Canaveral area has a history of trawl studies for general comparison.

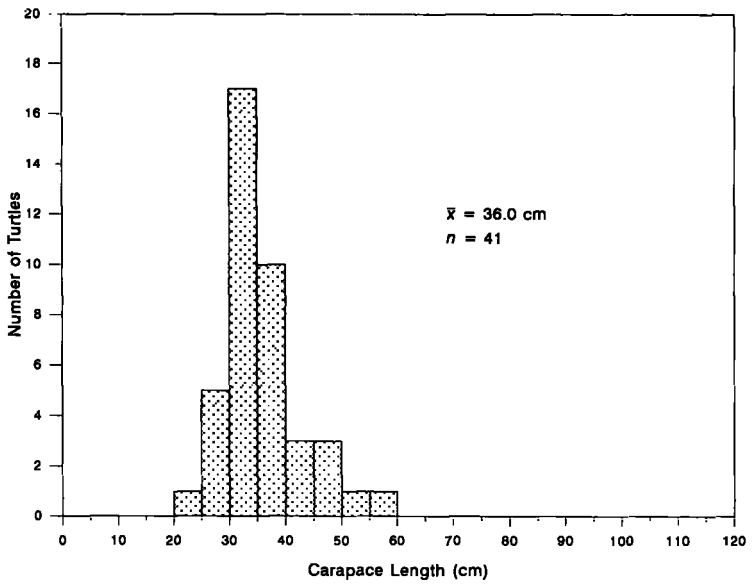

Figure 7

Length frequencies of green turtles, *Chelonia mydas*, collected along the Atlantic coast of Florida from 1986 to 1991.

Trawl surveys conducted by NMFS and the U.S. Army Corps of Engineers from 1974 to 1984 established that marine turtles, especially loggerhead turtles, aggregate in the Port Canaveral ship channel. Henwood (1987a) reported a loggerhead CPUE of 2.00 to 4.86 turtles/hour from July to October 1980, increasing to 12.05 turtles/hour in November. Butler et al. (1987) noted that mean CPUE by month was greater than 10 loggerhead turtles/hour from November 1981 to March 1982 and that there were lower CPUE values from April to September 1982. The CPUE values cited from the previous studies are greater than those in the present analysis, which may be attributable to the different objectives of the present study and the former trawl surveys. The CPUE data presented by Henwood (1987a) were collected during trawl surveys designed to reduce turtle mortality from maintenance dredging in the Port Canaveral ship channel. Butler et al. (1987) conducted surveys of the channel to develop methods of estimating loggerhead abundance. Marine turtles were the target species in both of these studies. The CPUE values reported in this study should be viewed as representative of turtles taken in the commercial shrimp fishery of east-central Florida.

The data on loggerhead turtles collected in the present analysis are similar to the earlier investigations of Henwood (1987a). Most of the log-

Table 5

Estimated values of asymptotic length (a) and intrinsic growth rate (K) from nonlinear regression of von Bertalanffy growth interval equation for Kemp's ridley turtles (one asymptotic standard error in parentheses).

Data treatment	n	a	K
All recaptures	12	61.11 cm (5.43)	0.0577 (0.2176)
	Residual mean square error = 3.4359		
Capture and recapture by contract vessel	10	60.81 cm (5.76)	0.5943 (0.2439)
	Residual mean square error = 4.1701		
All recaptures >90 days	6	60.66 cm (8.04)	0.6037 (0.3549)
	Residual mean square error = 8.2325		
All recaptures >180 days	3	77.85 cm (21.09)	0.2466 (0.1770)
	Residual mean square error = 1.1478		

Table 6

Monthly and yearly trawl captures of green turtles, *Chelonia mydas*, in the nearshore waters of Florida. Dashes indicate trawling effort outside of the study area.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Total
1986					1	0/—	—	—	—/0	0	0	2	3
1987	7	1	0	1	0	0/—	—	—	—	—/0	0	6	15
1988	0	0	0	0	0	0	0	0	1	0	0	2	3
1989	4	0	0	0	0	3	0	0	0	0	1	0	8
1990	0	0	0	0	0	0	0	0	1	3	5	3	12
1991	0	0	0	0	0	0	0	0	—	0	0	0	0
Total	11	1	0	1	1	3/—	0/—	0/—	2/—	3/—	6	13	41

gerhead turtles captured on the east-central coast of Florida were mid-subadults (50–70 cm), typical of immature loggerhead turtles in the western Atlantic Ocean. There was a shift to a larger size class during the spring and summer, a period when reproductively active adults immigrate to the nesting beaches of southeast Florida (Henwood, 1987a). At that time, some immature loggerhead turtles emigrated to foraging grounds as far north as Chesapeake Bay. Captures of adult loggerhead turtles in the coastal waters of Florida declined by late summer with the end of the nesting season. Conversely, the presence of subadult loggerhead turtles increased with the onset of winter.

Kemp's ridley turtles in the northwestern Atlantic are transported from their natal beaches in Mexico by major oceanic currents in the Gulf of Mexico (Collard and Ogren, 1990). The smallest Kemp's ridley turtles captured on the east coast of Florida coincide with the minimum size class for postpelagic turtles in the Gulf of Mexico (Ogren, 1989). Skeletochronological age estimates indicate that these turtles may be two years old (Zug and Kalb, 1989), which may indicate the length of this species' pelagic developmental stage. Recapture data from the present analysis and that of Henwood and Ogren (1987) suggest that Kemp's ridley turtles on the Atlantic coast overwinter in the Cape Canaveral area and migrate to northern foraging grounds during the summer. The lack of significant numbers of adult turtles in the northwestern Atlantic suggests that Kemp's ridley turtles migrate from the U.S. east coast upon reaching sexual maturity. Recently, a Kemp's ridley turtle captured and tagged on the southeast coast of Florida was observed nesting in the western Gulf of Mexico.[10]

Relatively low numbers of green turtles have been captured in the Cape Canaveral area. This observation may be the result of this species preference for a habitat other than the Port Canaveral ship channel and adjacent areas of shrimp trawling. Capture data from fishery-independent studies indicate that early subadult (20–40 cm) green turtles inhabit the nearshore reef tracts off the southeast coast of Florida (Ernest et al., 1989; Wershoven and Wershoven, 1989, 1992; Guseman and Ehrhart, 1990). A slightly larger size class of green turtle was captured on the seagrass shoals of the Indian River Lagoon system (Mendonça and Ehrhart, 1982). Seventy-eight percent of the 108 green turtles captured in Mosquito Lagoon were greater than 40-cm carapace length. Furthermore, green turtles captured in the Indian River Lagoon, south of Sebastian Inlet, were significantly larger than those collected on the reefs offshore of Vero Beach (Guseman and Ehrhart, 1990).

There are a number of problems with the growth data presented in this paper. Extrapolating yearly growth rates from short-term recaptures amplifies measurement error. Extremely large and negative growth values were usually the result of short intervals between capture and recapture. Differences in the measuring techniques used by other investigators was a major source of error when computing growth rates. Length measurements are often reported as "straight-line carapace length" when, in fact, there are four possible straight-line carapace lengths: total, standard, notched, and minimum (Pritchard et al., 1983). Standardized methods of measurement, or a definition of the measurement technique and accurate conversions between the various techniques, are necessary for comparisons between studies (Bjorndal and Bolten, 1988). The growth models presented in this analysis should be interpreted cautiously given the forementioned problems with the database.

In conclusion, the results of this study are indicative of the importance of east-central Florida as a developmental habitat for three species of marine

[10] Martin, E. Applied Biology, Inc., P.O. Box 974, Jensen Beach, FL, 34958. Personal commun., 1994.

turtle. The Cape Canaveral aggregation of loggerhead turtles is composed of significant numbers of subadults. Furthermore, the east coast of Florida supports the second largest rookery for this species (Ross, 1982). Subadult Kemp's ridley and green turtles appear to overwinter in the Cape Canaveral area. The eastern seaboard of North America serves as a vital link between the pelagic stage of marine turtle development and recruitment to the coastal-benthic foraging stages. Continued research in coastal waters is essential to the conservation of these threatened and endangered species.

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Growth rates of captive dolphin, *Coryphaena hippurus*, in Hawaii

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Dolphin, *Coryphaena hippurus*, also known as mahimahi or dolphin fish, are pelagic, predatory fish distributed in tropical and subtropical regions throughout the world (Johnson, 1978; Palko et al., 1982). They are an important resource, supporting commercial and sport fisheries throughout their range (Oxenford and Hunte, 1986) as well as having considerable potential for aquaculture (Hagood et al., 1981; Szyper et al., 1984; Kraul, 1989, 1991).

Gibbs and Collette (1959) and Palko et al. (1982) reviewed the distribution and biology of dolphin, including age and growth data on wild and captive fish. Age and growth of wild (Oxenford and Hunte, 1983) and captive (Uchiyama et al., 1986) fish have been estimated from daily increments on otoliths and scale annuli (Beardsley, 1967; Rose and Hassler, 1968), from modal progression in length-frequency distribution (Wang, 1979), and from fish of known age reared in captivity (Hassler and Hogarth, 1977; Hagood et al., 1981; Szyper et al., 1984; Ostrowski et al., 1989, 1992; Iwai et al., 1992). There is considerable variability in the data, reflecting environmental and nutritional differences associated with experimental designs for captive fish, as well as differences in size, age, and origin of wild fish. In this paper, growth rates of dolphin reared in Hawaii are presented and compared with those of captive and wild dolphin from different populations, as well as other teleost species. The data presented suggest that there are differences in growth rates and morphology between captive and wild dolphin.

Materials and methods

Fish were reared in captivity at The Oceanic Institute, Hawaii, from eggs obtained from wild Hawaiian broodstock fish (F_1; first generation) maintained at Anuenue Fisheries, State of Hawaii. Up to 3 months-of-age juveniles were fed a semi-moist (27.86% moisture) manufactured diet (pellet) twice daily (4% of their body weight per day). The diet contained 53.75% crude protein, 21% crude fat, and a caloric content of 5.13 cal·mg^{-1} (dry matter basis). Between 3 and 9.5 months, fish were fed to satiation once a day on a mixed diet of extruded salmon pellet (Moore-Clarke), frozen squid, and fish. The feed conversion ratio (FCR) is expressed as a ratio between the dry weight of the total amount of food given and the weight gain of live fish.

Up to 3 months-of-age juvenile fish were reared in an outdoor circular tank of 18,800 L (4 m diameter × 1.5 m water column height). After 3 months, fish were transferred to a 28,000-L tank (6 m diameter × 1 m water column height) used for broodstock maintenance. Both tanks had running ambient seawater (25–27°C and 33–35 ppt salinity) at high flow rates (water turnover rate was at 10 tank volumes per day) and under constant aeration.

The initial population was 48 fish, stocked at approximately 3 fish per m^3. Growth data presented correspond to pooled male and female fish periodically sampled during the period studied (1–9.5 months). Data are of individually sampled fish and are not averages. Small fish (1–3 months) were sampled daily. Sampling frequency of intermediate (3–6 months) and large (6–9.5 months) fish was weekly and bimonthly, respectively, owing to difficulties in handling larger dolphin and because there were fewer individuals available for sampling. Since dolphin metamorphosis occurs during the third week after hatching and one month-old fish are fully developed juveniles (Benetti, 1992; Kim et al., 1993), all data corresponding to fish from 1 to 9.5 months-old were combined.

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Results are expressed as:

Absolute growth	$AG = W_2 - W_1$
Absolute growth rate	$AGR = (W_2 - W_1) / (t_2 - t_1)$
Relative growth	$RG = (W_2 - W_1) / W_1$
Relative growth rate	$RGR = (W_2 - W_1) / W_1 (t_2 - t_1)$
Instantaneous growth rate	$IGR = (\ln W_2 - \ln W_1) / (t_2 - t_1)$
Specific growth rate	$SGR = (\ln W_2 - \ln W_1) / (t_2 - t_1) \times 100$
Length-weight relationship	$W = a L^b$
VGBM (length)	$L_t = L_\infty (1 - e^{-K(t-t_0)})$
VGBM (weight)	$W_t = W_\infty (1 - e^{-K(t-t_0)})^b$,

where W_1 = initial wet weight of fish; W_2 = final wet weight of fish; t_1 = time at the beginning of an interval; t_2 = time at the end of an interval; L = fork length in cm; a and b are constants; L_t = fork length (cm) at time t; W_t = total weight (kg) at time t; L_∞ and W_∞ = theoretical asymptotic length and weight, respectively; K = constant indicating the rate of change in length and weight (the Brody growth coefficient); t= time; t_0 = time of hatching; and VBGM is the von Bertalanffy growth model (Ricker, 1975, 1979; von Bertalanffy, 1962; Fabens, 1965):

Results

Fish grew to 4.93 kg and 75.8 cm from hatching in 9.5 months. Absolute growth rates (AGR's) in weight and length were 19.18 g·d^{-1} and 0.227 cm·d^{-1}, respectively (Table 1). Specific growth rate (SGR) of 1–3 month juveniles was 10% of their body weight per day, decreasing to 4.3% throughout the adult stage.

Most of the data correspond to fish younger than 6 months. The calculation of separate growth curves for males and females was not legitimate because sexual dimorphism could not be detected before that age. Therefore, the growth curves and the von Bertalanffy growth parameters were calculated from combined data for all male and female fish. Growth in length of dolphin was best expressed by a linear relationship (r^2=0.98), though an asymptotic curve also fit the data well (r^2=0.90). From Figure 1 it appears that a linear fit is better because of a weighting of the regression by the smaller fish. Growth in weight was best expressed as a quadratic equation (r^2 =0.98, Fig. 2). The length-weight relationship is expressed by the equation

$$W = 0.00836\, L^{3.07}\ (r^2 = 0.98;\ \text{Fig. 3}).$$

The von Bertalanffy growth models (VBGM) were used to estimate dolphin growth beyond the scope of data measured and, therefore, should be interpreted

Table 1

Growth rates of captive dolphin, *Coryphaena hippurus*, in Hawaii, fed a mixture of semi-moist manufactured diet[1] (1–3 months) and Moore-Clarke extruded salmon pellets, squid and fish (3–9.5 months).

Parameter	Value
Absolute growth (g)	4,929
Absolute growth rate (g/day)	19.18
Relative growth	70,413
Relative growth rate	273.98
Instantaneous Growth Rate (g)	0.043
Specific Growth Rate (%/day)	4.33
VGBM[2] Asymptotic length (L_∞) (cm)	169.6
VGBM[2] Asymptotic weight (W_∞) (g)	58,417
t_0 (yr)	0.068
K (annual)	0.72
b (constant; Brody coefficient)	3.07

[1] Manufactured diet contained 27.86% moisture, 53.75% crude protein, 21% crude fat and caloric content of 5.13 cal·mg^{-1} (dry–matter basis).

[2] Von Bertalanffy growth model.

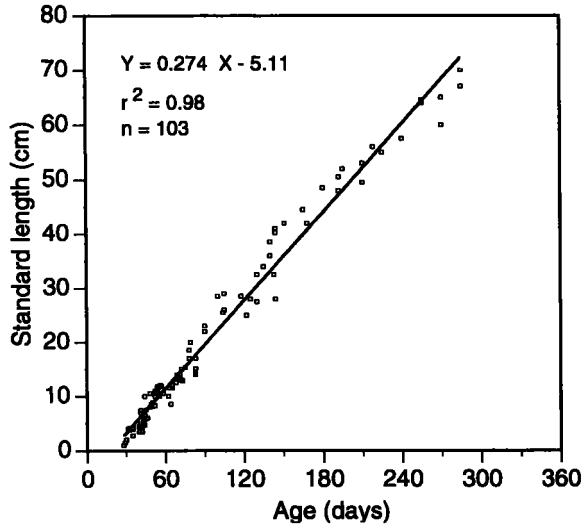

Figure 1

Growth in length of captive dolphin, *Coryphaena hippurus*, in Hawaii.

with caution. The VBGM applied to length-at-age data for captive dolphin in Hawaii is

$$L_t = 169.6 \text{ cm } [1-e^{-0.72\,(t-0.068)}] \text{ (Fig. 4).}$$

The calculated VBGM for weight is

$$W_t = 58.41 \text{ kg } [1-e^{-0.72\,(t-0.068)}]^{3.07}.$$

The feed conversion ratio (FCR) of juveniles up to three months of age was 1.1 (dry feed/live fish), and averaged 1.6 for the entire period studied.

Discussion

There have been several reports of growth rates of wild and captive dolphin, as well as of wild caught fish kept in captivity for various periods of time. Beardsley (1971) reported that a wild caught juvenile kept in captivity grew from one to 35 lb in one year. Schekter (1983) recorded a growth rate of 4.3 kg (from 0.7 to about 5 kg) in 30 days. In Barbados, dolphin may reach lengths of over 80 cm in 5.5 months and over one meter in less than one year (Oxenford and Hunte, 1986). In Hawaii, they also attain a length of over one meter at the end of the first year (Uchiyama et al., 1986). By applying the length-weight regression of Rose and Hassler (1968) to these data, it would correspond to a mass of about 8 kg in one year.

The growth rates presented in this study (4.93 kg and 75.8 cm in 9.5 months) are lower than many of those reported for wild and cultured dolphin in the literature. This may be due to the diet fed to the experimental fish. For instance, Kraul (1989) reported growth rates of 2 kg in 6 months and 9 kg in one year for dolphin that were fed fish and squid in tanks in Hawaii, and of 5.4 kg in 8.7 months for fish reared under identical circumstances but fed commercially available pellets (Kraul and Ako, 1993).

The data suggest that captive dolphin grow slower than their wild counterparts. Yet, even when they are fed artificial diets, growth rates of captive dolphin are among the fastest recorded for teleosts. The specific growth rate (SGR) of dolphin reported in this work (4.3%–10 body weight·d^{-1}), by Ostrowski et al. (1992) (10.7–13.3% bw·d^{-1}), and by Iwai et al. (1992) (9.3–13.0% bw·d^{-1}) are much higher than those of other marine and brackish water fish raised in captivity. For instance, SGR of the common snook, *Centropomus undecimalis*; barramundi, *Lates calcarifer;* hybrid sea bass, *Morone* spp.; Nassau grouper, *Epinephelus striatus;* spotted seatrout, *Cynoscion nebulosus;* red drum, *Sciaenops ocellatus* (Tucker, 1989); three species of mullets, *Liza ramada* (El-Sayed, 1991), *Mugil liza*, and *M. curema* (Benetti and Fagundes Netto, 1991); and the common grouper, *E. guaza* (Fagundes Netto and Benetti, 1984) range from 0.55 to 3.46% of their body weight per day.

The absolute growth rate (AGR) in length of wild and captive dolphin vary between 0.1–0.58 cm·d^{-1}

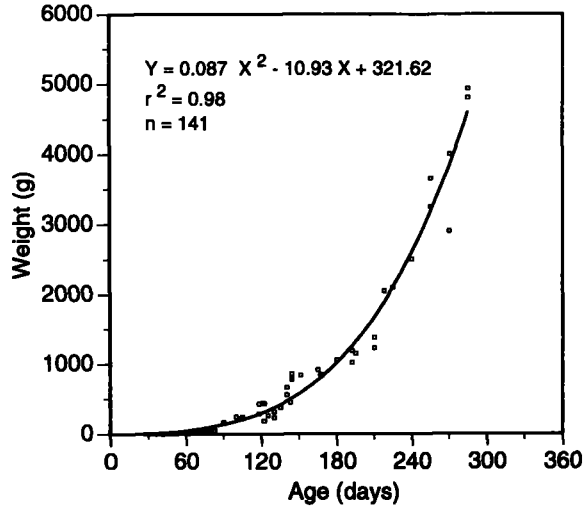

Figure 2

Growth in weight of captive dolphin, *Coryphaena hippurus*, in Hawaii.

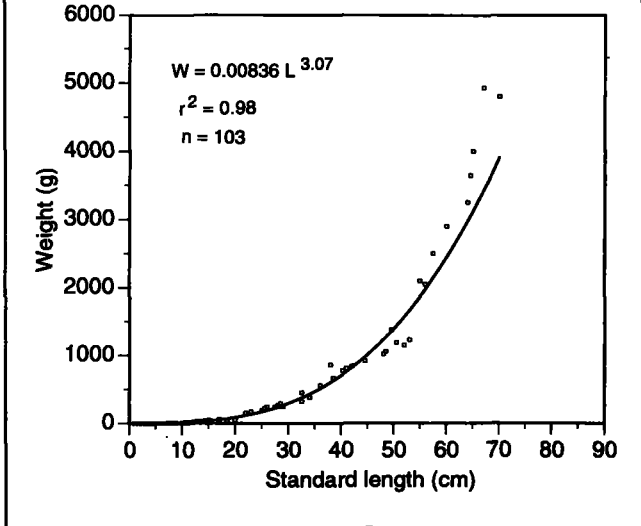

Figure 3

Length-weight relationship of dolphin, *Coryphaena hippurus*, reared in captivity in Hawaii.

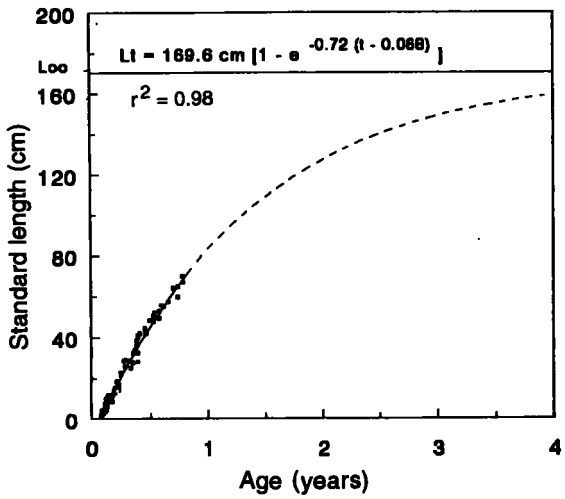

Figure 4

The von Bertalanffy growth model applied to length-at-age data for 1–9.5 month-old captive dolphin, *Coryphaena hippurus*, in Hawaii.

for the first year of life (Oxenford and Hunte, 1983). The AGR value reported in this study (0.227 cm·d^{-1}) is well within this range and the 0.1–0.6 cm·d^{-1} range reported by Brothers et al. (1983) for the Atlantic bluefin tuna, *Thunnus thynnus*, another pelagic teleost. Only a few other pelagic teleosts exhibit growth rates comparable to or higher than dolphin. These include the Atlantic blue marlin, *Makaira nigricans*, and the Atlantic sailfish, *Istiophorus platypterus*, two of the largest North Atlantic pelagic teleosts. Prince et al. (1991) estimated the AGR of young Atlantic blue marlin from otolith microstructure as 1.66 cm·d^{-1}, a value nearly three times higher than that reported for dolphin. From length frequencies of Atlantic sailfish, de Sylva (1957) estimated a maximum absolute growth rate of 1.10 cm·d^{-1}, twice as fast as that reported for dolphin. Although the scope of these comparisons is limited owing to the different age classes of fish, both the blue marlin and Atlantic sailfish exhibit AGR's several times higher than those measured in this work.

In this study, the feed conversion ratio (FCR) was 1.6 (dry feed/live fish). Similarly, Kraul and Ako (1993) obtained a FCR of 1.6 with dolphin fed on a commercially available pellet. FCR's of about 1.0 have been reported for dolphin by Ostrowski et al. (1992), Kraul (1989), and Kraul and Ako (1993), indicating that they are efficient in converting the energy intake from feeds into growth. Relative to other species, dolphin do not appear to require extraordinary food intake to sustain their high growth rates, similar to blue marlin (Prince et al., 1991). In this study, cultured dolphin were fed 4% (dry feed) of their body weight per day. This feeding rate is commonly used for other fish species in captivity, which invariably exhibit slower growth rates and higher FCR. Dolphin appear to exhibit higher energetic efficiency than most other teleosts because they use a proportionally larger portion of the total gross energy ingested for growth and metabolism than for excretion (Benetti, 1992).

Although no spawning was observed, the slight trend of decelerated growth after 180 days (Fig. 1) could be due to the onset of maturation, which in captive dolphin generally occurs in 6 months at 50–55 cm and 2.0–2.5 kg (Kraul, 1991; Ostrowski et al., 1992), but has been observed to occur as early as 3–4.5 months (Uchiyama et al., 1986). Somatic growth rates in teleosts usually decrease after the onset of maturation (Jones, 1976). For dolphin, however, the linear equation fitted the data for the period studied with the highest coefficient of correlation (r^2=0.98). A reason for this may have been the larger sample size during the juvenile stage, when young fish grow very fast. For instance, Hassler and Rainville (1975)[1] found that the length-age relationship of larvae and early juvenile dolphin (13–83 days) was exponential.

The VBGM's were used to model growth beyond the scope of the data and therefore must be considered speculative. Although the data fitted both VBGM's (length and weight) with a high coefficient of determination (r^2>0.98), the asymptotic sizes predicted by the models can not be tested because it has not been possible to keep dolphin alive in captivity for longer than 18 months. In this respect, the age structure of the population should be considered. It is possible that the potential longevity of the Hawaiian dolphin stock may not exceed this maximum age in captivity (about 18 months). For instance, the longevity of dolphin from Florida was estimated to be 4 years, but only 2% of the population was found to be older than 2 years (Beardsley, 1967), and only 4% in North Carolina (Rose and Hassler, 1968). The maximum life span of the Southern Caribbean dolphin stock does not appear to exceed 18 months, and few individuals of the North Caribbean stock live longer than 2 years (Oxenford and Hunte, 1986).

The asymptotic length estimated by the VBGM (L_∞=1.69 m) compares well with existing data for wild fish in the literature (L_∞=1.89 and 1.53 m for males and females, respectively) (Beardsley, 1967). The estimated asymptotic weight (W_∞=58.4 kg), however, is much higher than the maximum weight of 46 kg reported for this species (Florida Sportsman, 1979).

[1] Hassler, N. W., and R. P. Rainville. 1975. Techniques for hatching and rearing dolphin, *Coryphaena hippurus*, through larvae and juvenile stages. Sea Grant Publ. UNC-SG-75-31, 17 p.

This may be explained by the higher value of the exponent (b) of the length-weight relationship calculated for captive dolphin in this study (3.07) compared with wild fish from North Carolina and Florida, $2.58 < b < 2.75$ (Rose and Hassler, 1968). Oxenford and Hunte (1986) reported b values of 2.94 for male and 2.84 for female dolphin from Barbados. These differences indicate that dolphin tend to have shorter, deeper bodies in captivity than in the wild. Blaxter (1988) found that fish reared in captivity tend to be shorter and fatter and have a higher condition factor than fish from the wild, possibly because fish are likely to swim less when confined, diminishing the effect of exercise on growth (Jobling 1990; Christiansen and Jobling, 1990; Benetti, 1992; Christiansen et al., 1992; Boisclair and Tang, 1993). This is consistent with the predictions of the VBGM's in this study, which indicate that it would take longer for dolphin to reach asymptotic length and weight in captivity (6 years) than in their natural environment (4 years or less).

Results presented in this study suggest that captive dolphin grow slower and are less streamlined than in the wild. However, morphological and growth disparities of wild dolphin have been attributed to genetic (Oxenford and Hunte, 1986) and environmental (Rose and Hassler, 1968) differences in unit stocks. The larval development of dolphin from the Gulf of Mexico and from the western Pacific Ocean is similar, but both differ from that off Japan (Ditty et al., 1994). Although Benetti (1992) reported no significant differences between growth rates and development of dolphin larvae in Hawaii from F_1 and F_7 generations inbred in captivity, nothing is known about differences in growth during the juvenile and adult stages among offspring from brood fish from other stocks.

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Modification and comparison of two fluorometric techniques for determining nucleic acid contents of fish larvae

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The ribonucleic acid (RNA) content and the ratio of RNA to deoxyribonucleic acid (DNA) have proven to be reliable indices of the nutritional condition of larval fish (Buckley, 1979, 1980, 1981, 1984; Wright and Martin, 1985; Buckley and Lough, 1987; Clemmesen 1987, 1988; Robinson and Ware, 1988; Canino et al., 1991; Richard et al., 1991; Canino, 1994). Cellular RNA content is correlated with the rate of protein synthesis. DNA content, which remains relatively constant in somatic tissues, may be used as an index of cell number (Bulow, 1987). The RNA/DNA ratio, therefore, reflects the protein synthesizing capability of larval fish and has been used for estimating recent in situ protein growth (see review by Bulow, 1987; Robinson and Ware, 1988; Hovenkamp, 1990; Hovenkamp and Witte, 1991).

Initial methods for determining RNA and DNA concentrations in tissue homogenates, based upon ultraviolet light absorption (Munro and Fleck, 1966; Buckley, 1979), were limited by sample size, requiring about 800 μg dry weight of tissue for a single analysis. The requirement of pooled samples of fish larvae precluded quantitation of variability among individuals. Recent development of highly sensitive fluorometric techniques for direct measurement of nucleic acid contents of marine phytoplankton (Berdalet and Dortch, 1991; Mordy and Carlson, 1991), bacteria (Mordy and Carlson, 1991), and individual fish larvae (Clemmesen, 1988, 1993; Caldarone and Buckley, 1991; Theilacker and Shen, 1993) now provides a greater choice of methods. Several protocols are based upon the fluorescence of the dye ethidium bromide (EB), when bound to nucleic acids. Fluorescence of the nucleic acid-fluorochrome complex is measured before and after digestion of RNA by RNase (Karsten and Wollenberger, 1972, 1977; Robinson and Ware, 1988; Clemmesen, 1993), or after sequential additions of RNase and DNase (Bentle et al., 1981). Total fluorescence is then partitioned into DNA and RNA components and nucleic acid concentrations are calculated indirectly by difference after enzymatic degradation.

A two-dye fluorometric method for nucleic acid analysis of individual fish larvae (Clemmesen, 1988) utilized EB to measure total sample fluorescence and the DNA-specific dye, Hoechst dye H33258 (Hoechst), to measure DNA content directly. A recent modification of this method to a single-dye procedure yields higher DNA estimates and RNA estimates comparable to the previous two-dye method (Clemmesen, 1993). Both protocols require extraction and purification of crude homogenates before analysis. While substances that interfere with sample fluorescence may be reduced or eliminated, the washing and extraction steps of both methods restrict the number of samples that can be processed in a day.

Caldarone and Buckley (1991) developed a two-dye method for determining nucleic acid contents that was coupled with an automated flow-injection analysis (FIA) system in which EB is used to estimate total nucleic acid content and Hoechst is used to measure DNA. This method has the advantage of combining high sensitivity and sample throughput rate with a simple extraction procedure. Unfortunately, an FIA system may be too costly for many laboratories. In this paper, we present an adaptation of the FIA method for conventional static fluorometric analysis (CFA) and compare results using the two procedures.

Methods

Fish larvae and juveniles from laboratory culture and field samples from six species—Atlantic cod, *Gadus morhua*; inland silverside, *Menidia beryllina*; haddock, *Melanogrammus aeglefinus*; tautog, *Tautoga onitis*; winter flounder, *Pleuronectes americanus*; and walleye pollock, *Theragra chalcogramma*—were chosen to provide different species, ages, and nutritional histories for comparison (Table 1). Fish homogenates, except those of walleye pollock, were prepared by homogenizing between 1 and 12 previously frozen individuals with deion-

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Table 1

Fish species, sample abbreviations, and sources used for methods comparison. Fish sampled at discrete ages provided one homogenate at each age. (S) = starved.

Species		Sample name	Source	Age (d)	*n*
Atlantic cod	*Gadus morhua*	C	lab	41–61	3
		C(S)	lab (S)	41–61	3
Inland silverside	*Menidia beryllina*	S	lab	104–108	3
		S(S)	lab (S)	104–108	3
Haddock	*Melanogrammus aeglefinus*	H	lab	11,22,44	3
Tautog	*Tautoga onitis*	T	lab	20	3
Winter flounder	*Pleuronectes americanus*	F	lab	26,41,57	3
Walleye pollock	*Theragra chalcogramma*	P	field	<60	3

ized, distilled water in an Ultra-Turrax homogenizer (Tekmar Co.) with three 15-second pulses at maximum power (Caldarone and Buckley, 1991). Previously frozen walleye pollock larvae were homogenized in prechilled glass homogenizers. Six aliquots of homogenate were pipetted into 1.5-mL polyethylene vials and immediately frozen at –80°C until analysis of three aliquots by FIA and three aliquots by CFA.

Sample extraction procedures followed those outlined by Caldarone and Buckley (1991). Homogenates were extracted in 1% sarcosine (N-lauroylsarcosine), TRIS-EDTA (5.0 mM TRIS-HCl, 0.5 mM EDTA, pH 7.5) buffer for 30 minutes at room temperature, mixed vigorously in a sample vortexer for 10–15 seconds, then extracted for another 30 minutes. Aliquots were diluted with TRIS-EDTA buffer to yield a final concentration of 0.1% sarcosine, then centrifuged at room temperature for 5 minutes at 2,500 times gravity (× g) for CFA and 12,000 × g for FIA. The supernatant was recovered for estimation of nucleic acid concentrations by FIA or CFA. Sarcosine, like other anionic detergents, fluoresces at excitation and emission wavelengths used in the analyses. To reduce this effect, samples extracted in 1% sarcosine required a 10-fold dilution with TRIS-EDTA buffer before FIA (Caldarone and Buckley, 1991). In the modified CFA procedure, a final sample concentration of 0.0125% sarcosine produced an acceptable background fluorescence (blank) value of approximately 5% of the highest nucleic acid standard.

Differences in the total sample volumes required by FIA and CFA procedures required modifications to the concentrations of nucleic acid standards, fluorochrome reagents, and sample volumes of fish homogenates. Nucleic acid standard ranges and homogenate sample volumes were chosen to encompass the typical range of concentrations encountered by each method during routine analysis of individual fish larvae. Working standards of RNA and DNA were prepared as described by Caldarone and Buckley (1991) by serial dilution of previously frozen stock solutions with 0.1% sarcosine in TRIS-EDTA buffer. RNA standards (Sigma Chemical Co., St. Louis, MO, Type IV, calf liver) ranged from 1.97 to 17.68 $\mu g \cdot mL^{-1}$ for FIA and from 0.41 to 13.14 $\mu g \cdot mL^{-1}$ for CFA. DNA standards (Boehringer-Mannheim Corp., Indianapolis, IN, high molecular weight, calf thymus) ranged from 0.16 to 1.52 $\mu g \cdot mL^{-1}$ for FIA and from 0.07 to 2.37 $\mu g \cdot mL^{-1}$ for CFA. Estimates of contamination of the calf liver RNA standard by DNA, determined by fluoresecence in Hoechst, was less than 1% by weight. A 100-μL "spike" of homogenate from walleye pollock larvae was added to serial dilutions of RNA and DNA standards in order to estimate the recovery efficiencies using the CFA protocol.

Fluorochrome working reagents of EB (137.5 $ng \cdot mL^{-1}$) and Hoechst (25 $ng \cdot mL^{-1}$) prepared for FIA in TRIS-EDTA buffer according to Caldarone and Buckley (1991) were modified by reducing the sodium chloride (NaCl) concentration in the Hoechst reagent from 0.2 N to 0.1 N and the pH from 7.5 to 7.0. Working dye solutions of 2.0 $\mu g \cdot mL^{-1}$ EB and 5.0 $\mu g \cdot mL^{-1}$ Hoechst prepared for CFA at the same pH and NaCl concentration as for FIA provided a sensitive linear response to the standards while maintaining a low background fluorescence.

The RNA and DNA concentrations were estimated for each aliquot. In addition, the amount of endogenous fluorescence (sample fluorescence in the absence of fluorochrome dye) was determined for most homogenate samples (21 for FIA, 17 for CFA) by substituting an equal volume of TRIS-EDTA buffer for the fluorochrome working reagent in the assay procedure.

The FIA system for nucleic acid determination is fully described by Caldarone and Buckley (1991). A 50-μL sample is injected into a reagent stream con-

taining one of the fluorochrome dyes. The injected sample is mixed and transported with the reagent to the fluorescence detector which continuously records the fluorescence at 525 nm excitation and 600 nm emission for EB, or 356 nm excitation and 458 emission for Hoechst. The sample fluorescence is displayed as a peak, whose area is proportional to the concentration (Caldarone and Buckley, 1991). Modification of this procedure for CFA required a minimal total volume (sample plus fluorochrome reagent) of 2 mL in order to be measured accurately by the fluorometer (Shimadzu RF–540 spectrofluorophotometer, Shimadzu Corp., Kyoto, Japan), which was adapted to use 12×75 mm borosilicate glass test tubes as cuvettes. For all samples, except the homogenates of larval pollock, a 0.1-mL aliquot of extracted sample was combined with 0.9 mL of TRIS-EDTA buffer and 1.0 mL of fluorochrome working reagent (EB or Hoechst). For larval pollock homogenates, a 0.03-mL aliquot was combined with 0.97 mL of TRIS-EDTA buffer prior to addition of 1.0 mL of the fluorochrome reagents. The sample-fluorochrome mixture was incubated at room temperature for 15–30 minutes before fluorescence was measured at the same excitation and emission wavelengths as in the FIA procedure. Initial trials indicated that maximum sample fluorescence was obtained within 15 minutes and was stable for more than 4 hours at room temperature.

Calculations of nucleic acid concentrations were identical for both methods. First, endogenous sample fluorescence was subtracted from total sample EB or Hoechst dye fluorescence. Sample DNA concentrations were estimated directly from fluorescence in Hoechst dye by using a DNA-Hoechst standard curve. The computed DNA concentration was used to estimate the fluorescence contribution by DNA to the total sample EB-fluorescence by using a DNA-EB standard curve. Fluorescence due to DNA-EB was subtracted from the total sample fluorescence and the remaining fluorescence was assumed to be due to RNA. The RNA concentration was then estimated by using an RNA-EB standard curve.

The relationships between mean RNA and DNA concentration and RNA/DNA ratios of the fish homogenates predicted by FIA and CFA methods were analyzed by using a geometric mean regression procedure (Ricker, 1984) that describes the linear central trend between two independent estimates of the variate.

Results

Standard calibration curves indicated that detection limits for CFA are about 0.07 $\mu g \cdot mL^{-1}$ for RNA and 0.03 $\mu g \cdot mL^{-1}$ for DNA, similar to the values detectable with automated FIA (Caldarone and Buckley, 1991). The precision of both methods was comparable; mean coefficients of variation, V_x (standard deviation as a percentage of the mean), for triplicate determinations from each homogenate averaged 5 to 7% for RNA and 3 to 4% for DNA over a broad range of estimated sample concentrations. Recovery of DNA standards from six replicate "spikes" of larval pollock homogenate with the CFA method averaged 99.5 ± 0.9% in Hoechst and 99.2 ± 2.9% in EB, and recovery of "spiked" RNA standards averaged 94.8 ± 6.0% in EB.

Mean nucleic acid concentrations and RNA/DNA ratios of fish homogenates were generally lower when estimated by CFA relative to FIA (Fig. 1). RNA concentration was most strongly correlated between the two methods and DNA concentration less so (Table 2). The ratio of RNA to DNA was only moderately correlated between the two methods and provided the poorest basis for comparison. Intermethodological calibration between FIA and CFA results was achieved by the application of regression coefficients (Table 2) to mean nucleic acid concentrations and RNA/DNA ratios estimated by CFA (Fig. 2).

Homogenates prepared from larval stages of the gadid species (*Gadus morhua*, *Melanogrammus aeglefinus*, and *Theragra chalcogramma*), tautog, *Tautoga onitis*, and winter flounder, *Pleuronectes americanus*, exhibited negligible endogenous fluorescence, regardless of fluorochrome, over a 3- to 4-fold range of nucleic acid concentrations (Table 3). Endogenous fluorescence was highest for juvenile inland silverside and juvenile winter flounder.

Discussion

Modification of the FIA method described by Caldarone and Buckley (1991) to conventional fluorometry produced an assay protocol with comparable

Table 2

Geometric mean functional regression coefficients describing mean RNA and DNA concentrations ($\mu g \cdot mL^{-1}$ homogenate) and RNA/DNA ratios of 24 fish homogenates determined by conventional fluourometric analysis (CFA) regressed upon estimates obtained by flow injection analysis (FIA).

Variate	Y-intercept	Slope	r^2
RNA	–5.318	0.652	0.972
DNA	–1.795	0.991	0.808
RNA/DNA	–0.309	0.733	0.569

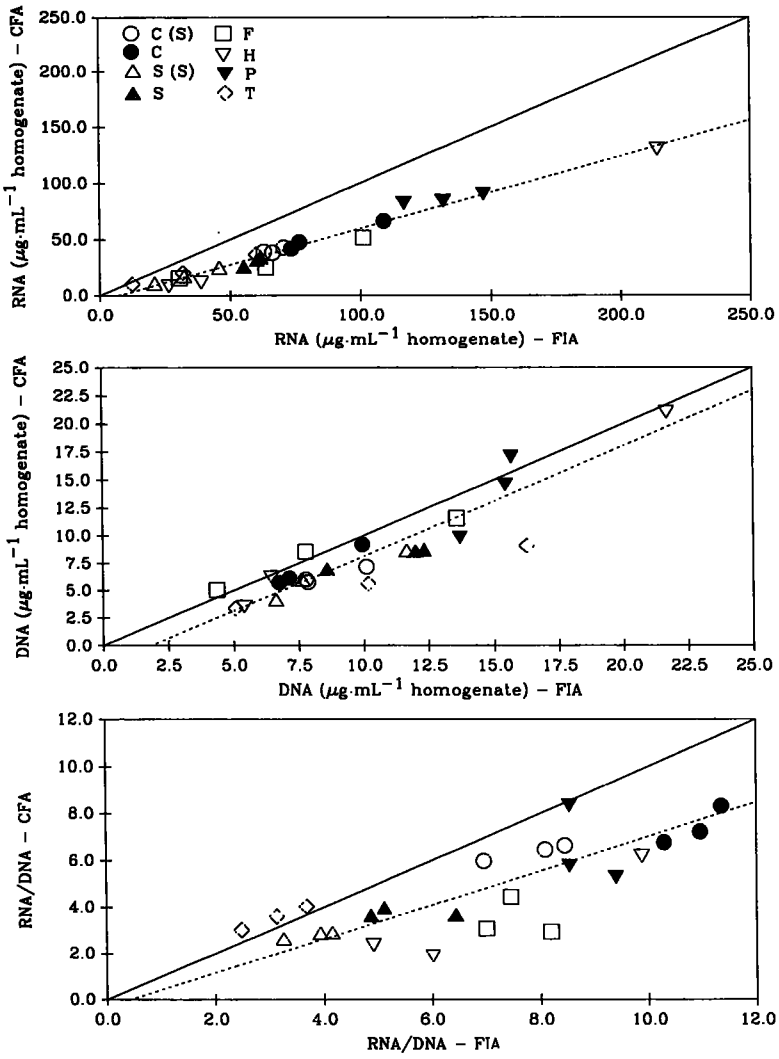

Figure 1

Mean RNA and DNA concentrations and RNA/DNA ratios of 24 crude fish homogenates obtained by flow injection analysis (FIA) versus conventional fluorometric analysis (CFA). Solid line represents a 1:1 correspondence between the two methods. Dashed line is the geometric mean regression between the two estimates. Species abbreviations as in Table 1.

sensitivity, precision, and sample throughput. Mean coefficients of variation (V_x) for DNA concentration estimated by FIA and CFA in this study (3 to 4%) are similar to those reported for replicate assays of a pooled fish homogenate using FIA (Caldarone and Buckley, 1991), another two-dye procedure (Clemmesen, 1988), and a single-dye method (Clemmesen, 1993). In this study, the mean V_x values for RNA concentration were 3 to 5% higher when determined by FIA and CFA for multiple homogenates than for FIA estimates of a single, pooled homogenate (Caldarone and Buckley, 1991) but are comparable to those reported by Clemmesen (1993) for RNA estimates of pooled fish homogenate using a single-dye technique.

The RNA and DNA concentrations of fish homogenates were consistently lower when estimated by CFA compared with FIA. Calibration between the two methods by functional regression relationships established a reasonable basis for comparison of results (Fig. 2), although considerable differences in mean estimated nucleic acid concentrations and RNA/DNA were still evident. We emphasize that sample homo-

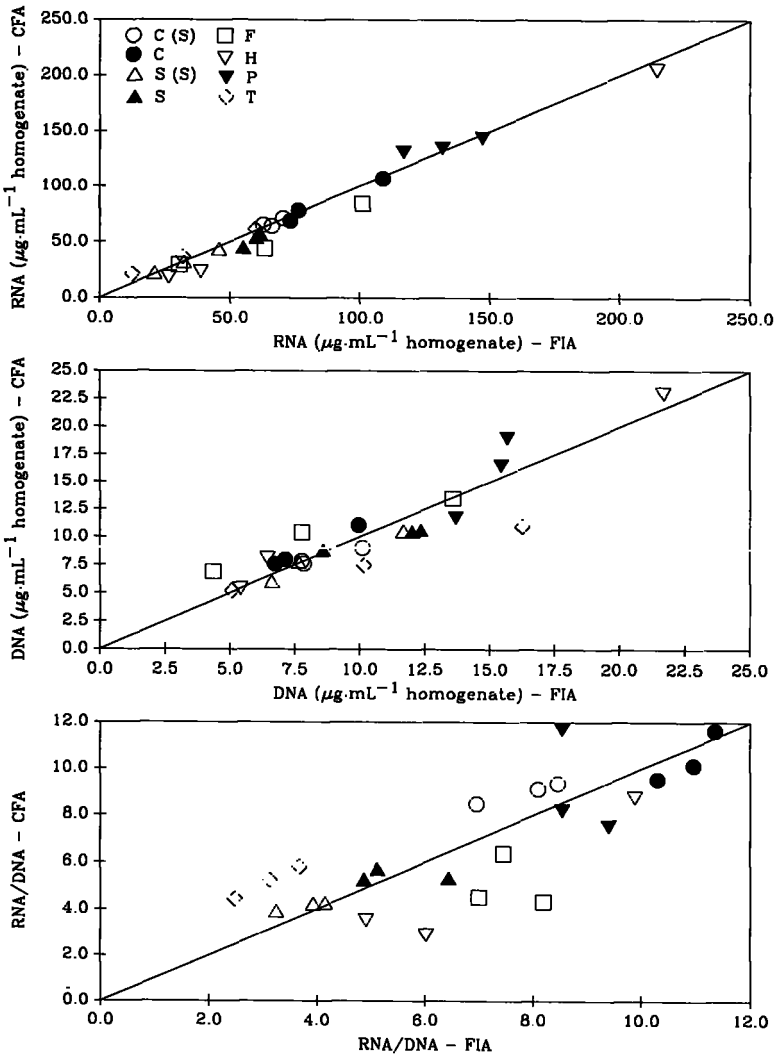

Figure 2

Mean RNA and DNA concentrations and RNA/DNA ratios of 24 crude fish homogenates obtained by flow injection analysis (FIA) versus values transformed from conventional fluorometric analysis (CFA) by functional regression coefficients in Table 2. Solid line represents a 1:1 correspondence between the two methods. Species abbreviations as in Table 1.

genates for this study were chosen from six fish species and assayed across far greater ranges of age and nucleic acid concentrations than reported previously (Clemmesen 1988, 1993; Caldarone and Buckley, 1991; McGurk and Kusser, 1992) in order to broaden the scope of comparison and statistical inference. A comparative study of FIA and CFA techniques within the more limited range of sample concentrations encountered during routine processing of individual larvae of a single species would have undoubtedly yielded higher correlations between estimates.

The FIA and CFA procedures differ primarily in the choice of instrumentation as both use sample extraction by sarcosine. Caldarone and Buckley (1991) reported that nucleic acids in larval fish samples (<200 μg dry weight) were completely extracted in one hour at room temperature. Sample nucleic acid concentrations of fish homogenates in this study were prepared to be similar to those obtained from assays of individual larvae, suggesting that incomplete or differential extraction of homogenates by sarcosine between FIA and CIA is un-

Table 3

Mean endogenous fluorescence[1] of fish homogenates as a percentage of total fluorescence in Hoechst 33258 (Hoechst) or ethidium bromide (EB) fluorochromes. Samples are from larvae unless otherwise noted. (S) = starved.

Species	Sample name	Age (d)	Hoechst		EB	
			FIA	CFA	FIA	CFA
Atlantic cod	C	41–61	<3	<2	<1	3
Atlantic cod (starved)	C(S)	41–61	<3	<2	<1	3
Inland silverside (juvenile)	S	104–108	38	33	<1	12
Inland silverside (juvenile, starved)	S(S)	104–108	40	37	<1	12
Haddock	H	11	<3	<2	<1	<2
		22	<3	<2	<1	<2
		44	<3	<2	<1	2
Tautog	T	20	<3	<2	<1	<2
Winter flounder	F	26	<3	<2	<1	<2
		41	<3	<2	<1	<2
Winter flounder (juvenile)		57	19	14	<1	6
Walleye pollock	P	<60	<3	<2	<1	2

[1] Endogenous sample fluorescence occurs in the absence of fluorochrome dye.

likely. The consistently lower estimates of nucleic acids with the CFA method, relative to the FIA method, implies a lower ratio of fluorescence yield of samples to standards. One possibility is that the effective sample concentration at the detector may be greater in CFA compared with FIA. In FIA, the time between the mixing of dye and sample is precisely controlled but the ratio of dye to sample is unknown. The concentrations of the fluorochrome working reagents used in FIA were increased (14× and 100× for EB and Hoechst, respectively) in order to saturate the standards for the CFA modification. A higher effective sample concentration at the detector (possibly making the samples less available to the dye), coupled with a longer pathlength, may explain the lower fluorescence yield of the CFA samples relative to the standards. The higher correlation between the methods for RNA estimates than for DNA was an unexpected result; RNA content is calculated indirectly (total sample fluorescence minus estimated fluorescence due to DNA) and, presumably, is more subject to measurement error than is direct fluorometric determination of DNA.

Fluorescence by compounds other than nucleic acids represents a potential source of interference in any fluorometric assay. The level of endogenous sample fluorescence should be determined by preliminary analyses when a new fish species or developmental stage is being investigated. Crude tissue homogenates exhibit fluorescence characteristics not found in commercial preparations of nucleic acids that appear to be related to tissue type and developmental stage of the fish. Caldarone and Buckley (1991) found that winter flounder and American sand lance, *Ammodytes americanus*, larvae and the nucleic acids used as standards exhibited negligible amounts of endogenous or residual fluorescence, whereas winter flounder postlarvae and juvenile muscle and liver had levels ranging from approximately 5 to 55% of total fluorescence in EB or Hoechst dyes. Clemmesen (1993) reported endogenous fluorescence values ranging up to 40% in Hoechst determinations of the DNA content of herring, *Clupea harengus*, larvae. In this study, only homogenates of the juvenile inland silverside and juvenile winter flounder exhibited high levels of endogenous fluorescence in Hoechst dye or EB (Table 3), providing further evidence of an ontogenetic effect. Gadid larvae, of approximately the same age as the juvenile winter flounder, displayed negligible amounts of endogenous fluorescence, suggesting that systematic differences may also exist.

Interference in nucleic acid estimation from contaminants of crude homogenate preparations has been reported previously (Brunk et al., 1979; Mordy and Carlson, 1991; Clemmesen, 1993). McGurk and Kusser (1992) compared three fluorescence methods for quantitating nucleic acids in Pacific herring, *Clupea pallasi*, larvae. Of the three, the method incorporating the most extensive purification steps (Clemmesen, 1988) resulted in higher estimates of RNA content and RNA/DNA ratios than the other two methods, suggesting that higher yields may have resulted from the elimination of substances interfering with accurate fluorometric quantitation. However, quenching of nucleic acid fluorescence by contaminants in the samples does not appear to be sig-

nificant in either the CFA or FIA techniques using the sarcosine extraction procedure with larval fish. Recoveries of crude homogenate "spikes" added to nucleic acid standards by FIA (Caldarone and Buckley, 1991) and CFA (this study) are similar to those reported for more purified extracts (Clemmesen, 1993). McGurk and Kusser (1992) reported higher RNA contents and RNA/DNA ratios for yolk-sac herring larvae analyzed with the Clemmesen method (1988) and suggested that fluoresecence absorbance by yolk components may be reduced by the purification steps in that assay. However, when a homogenate of winter flounder yolk-sac larvae was "spiked" with nucleic acid standards and subjected to FIA with a sarcosine extraction procedure, recoveries of calf thymus DNA standards remained unchanged and those for calf liver RNA standards only declined by 3 to 5% (Caldarone, Unpubl. data).

RNA/DNA indices have proven useful as indicators of condition in a wide variety of fish species. When coupled with data on water temperature, and calibrated with laboratory-reared larvae, estimates of recent growth in the field can be obtained (Buckley, 1984). However, this study and others illustrate a common problem with the application of fluorescent techniques to estimation of nucleic acid levels in fish and other biosamples, and the need for intercalibration. Given the disparity in estimates of RNA and DNA contents due to the method of analysis (McGurk and Kusser, 1992; this study) and choice of nucleic acid standards (Caldarone and Buckley, 1991), no direct intermethodological comparisons of data can be made without intercalibration between analytical methods, as done by McGurk and Kusser (1992), Clemmesen (1993), Mathers et al. (1994), and this study. It is inappropriate to compare RNA/DNA ratio values with published data unless the same methods and standards are used. Also, the generalized growth equation in Buckley (1984) uses RNA/DNA ratios determined with an ultraviolet light absorption method that cannot be directly applied to ratios determined with other analytical procedures without running an intercalibration between the two methods. Alternatively, the relation between RNA/DNA, temperature, and growth must be determined for laboratory-reared larvae by using the analytical method of choice before a growth equation can be applied to fish larvae collected in the field.

A general assay protocol for FIA and CFA is presented in Figure 3. For this study, fish larvae were pooled and homogenized to provide adequate replicates for methods comparison. On a routine basis, individual larvae may be frozen in 1.5-mL microcentrifuge vials, then extracted in the same vial, reducing processing time and errors associated with sample transfer. The actual volumes of 1% sarcosine and TRIS-EDTA buffer may have to be determined empirically depending upon the larval fish size and sample volume required for spectrofluorometric analysis. A trained operator can process approximately 80 samples for RNA and DNA determinations as well as standards in eight hours using CFA and in five hours with FIA. We do not routinely assay replicate sample aliquots or correct for endogenous sample fluorescence when preliminary estimates are less than 3% of total sample fluorescence.

The "best" method for nucleic acid analysis of larval fish may well be determined by sample size, instrumentation, the presence of interfering substances, or the need to compare values to previously published data. Flow-injection analysis (Caldarone and Buckley, 1991) is a sensitive, precise assay with a simple extraction procedure and high sample throughput. The modified CFA protocol presented here retains those advantages, extends them to a more inexpensive method using static fluorometry, and provides an intercalibration between the two methods.

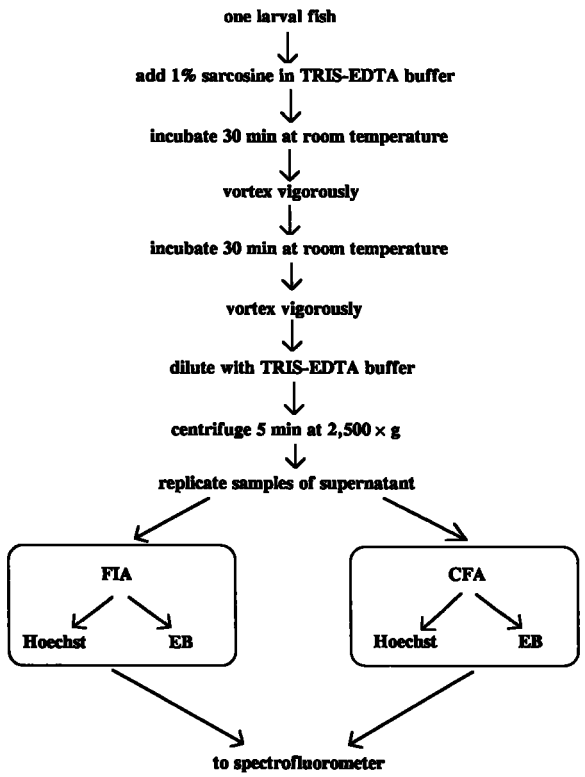

Figure 3

Generalized flowchart of the sarcosine extraction, flow injection analysis (FIA), and conventional fluorometric analysis (CFA) procedures.

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The potential use of otolith characters in identifying larval rockfish (*Sebastes* spp.)

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Rockfish of the genus *Sebastes* are commercially important in the northeast Pacific Ocean, where more than 60 valid species are recognized (Eschmeyer et al., 1983). Although morphological and chromatic characters are used routinely to identify adults of the genus, such traits are frequently ineffective for young of the year, especially larvae. Like most fish, early developmental stages of *Sebastes* spp. have less pigmentation, fewer hard structures (e.g. fin rays), and show less differentiation when compared with adults. However, an ability to discriminate among the larvae of the many rockfish species is critical to the advancement of early life history studies in this group.

A variety of methods have been used to identify larval and juvenile rockfish (Kendall, 1991). Although pigmentation is the most frequently used character (Moser et al., 1977; Laroche and Richardson, 1980; Moser et al., 1985; Kendall and Lenarz, 1987), size at extrusion (Moser et al., 1977), meristic counts (Moser et al., 1977), morphometrics (Morris, 1956), size at specific life history events (Stahl-Johnson, 1985), time of parturition in conjunction with geographic location (Moser et al., 1977), and electrophoretic patterns (Seeb and Kendall, 1991) have all been used to identify larval and juvenile rockfish.

A problem with many of these techniques, however, is that larval characters often undergo ontogenetic change. To overcome this problem, the larvae of many species have been reared in captivity and sequentially sacrificed. This is not only technically demanding, expensive, and time consuming, but differences in development between laboratory and wild fish may affect the number, size, and distribution of the attributes under investigation. Thus, permanent identifiable characters would be useful. A static trait, which retained its characteristics throughout early life, would increase our ability to positively identify rockfish larvae. Otoliths, being acellular aragonitic concretions, are good candidates to retain features produced during the larval stage. Likewise, otoliths have been shown to contain sufficient variation among species (Hecht and Appelbaum, 1982; Akkiran, 1985; Victor, 1987) and stocks (Messieh, 1972; Postuma, 1974; McKern et al., 1974; Neilson et al., 1985; Smith, 1992) to assign with accuracy group membership to individuals.

This study investigates the potential of using otolith microstructure to assist in the identification of larval rockfish. We assume that no change occurs to early larval otolith microstructure once it is deposited (Brothers, 1984; Stevenson and Campana, 1992). Otolith characteristics (nuclear shading patterns, nuclear radius, and first increment width) produced during the early larval period were described and measured from late larval and pelagic juvenile stage specimens of eight species of rockfish: *Sebastes auriculatus*, *S. entomelas*, *S. flavidus*, *S. goodei*, *S. jordani*, *S. mystinus*, *S. paucispinis*, and *S. saxicola*. These species were the most numerous rockfish species collected off the central California coast during the study period.

Methods

Field collections

Samples of young-of-the-year pelagic juveniles and late larvae were collected with a midwater trawl (12 × 12 m) from the National Oceanic and Atmospheric Administration RV *David Starr Jordan*. From 1983 to 1989 nine cruises were conducted off central California (lat. 36°30'–38°10'N) during the months of April-June. Pelagic juvenile rockfish were frozen at sea and returned to the laboratory for final identification. Wyllie Echeverria et al. (1990) have described cruise sampling methodology in detail.

Laboratory procedures

Pelagic juveniles were identified to species from external characteristics, including pigmentation, fin-ray counts, and gill-raker counts (Laidig and Adams, 1991). The sagittal otoliths were removed and affixed whole to microscope slides and were prepared for viewing with the methods outlined in Laidig et al. (1991).

Otoliths were examined with a video image interfaced with a digitizer (Laidig et al., 1991). Distinct reoccurring shading patterns in the

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nucleus (i.e. the otolith core) were noted for each species. Increment counts were made beginning at the first clearly defined mark that completely encircled the primordium (see also Penney and Evans, 1985). This "extrusion" check forms at parturition (Ralston, unpubl. data) and defines the outer edge of the nucleus; the distance from the primordium to this mark is the nuclear radius (Fig. 1), and the increment immediately following the extrusion check is the first growth increment.

Data analysis

The mean radius of the nucleus and the mean width of the first growth increment were compared among species and years. An overall analysis of variance (ANOVA), incorporating separate pairwise *t*-tests, equivalent to Fisher's least-significant difference, was performed to detect differences in the size of the nuclear radius and the width of the first increment among species and years. We used a two-way factorial analysis and calculated least square means (Searle et al., 1980) to evaluate treatment effects among species, years, and the interaction of species and years. A parametric discriminant analysis, assuming a multivariate normal distribution with pooled covariance matrix, was used to determine the percentage of each species that was correctly classified by nuclear radius and first increment width, alone and in combination with each other.

To further evaluate species-specific differences in nuclear radius and first increment width, the data were pooled over years; however, we recognized the difficulty in isolating the effect of species alone. *Sebastes auriculatus* and *S. saxicola* were only sampled in one year; therefore they were not included in the annual variation analysis. For comparison, we treated these single-year studies as the pooled data for the other species.

A blind test was performed to determine the accuracy of the otolith characters in distinguishing between the eight rockfish species used in this study. One hundred otoliths representing all eight species (*S. auriculatus* [n=5]; *S. entomelas* [n=13]; *S. flavidus* [n=15]; *S. goodei* [n=14]; *S. jordani* [n=25]; *S. mystinus* [n=9]; *S. paucispinis* [n=11]; and *S. saxicola* [n=8]) were given to a reader. No other information (e.g. species, fish length, etc.) about the individual samples was provided. The reader then attempted to identify the correct species of rockfish, using both measured distances and shading patterns. The results of the tentative classification were compared with the actual species identities to determine percent agreement. The significance of this result was evaluated against a null multinomial distribution, by assuming assignments at random to species.

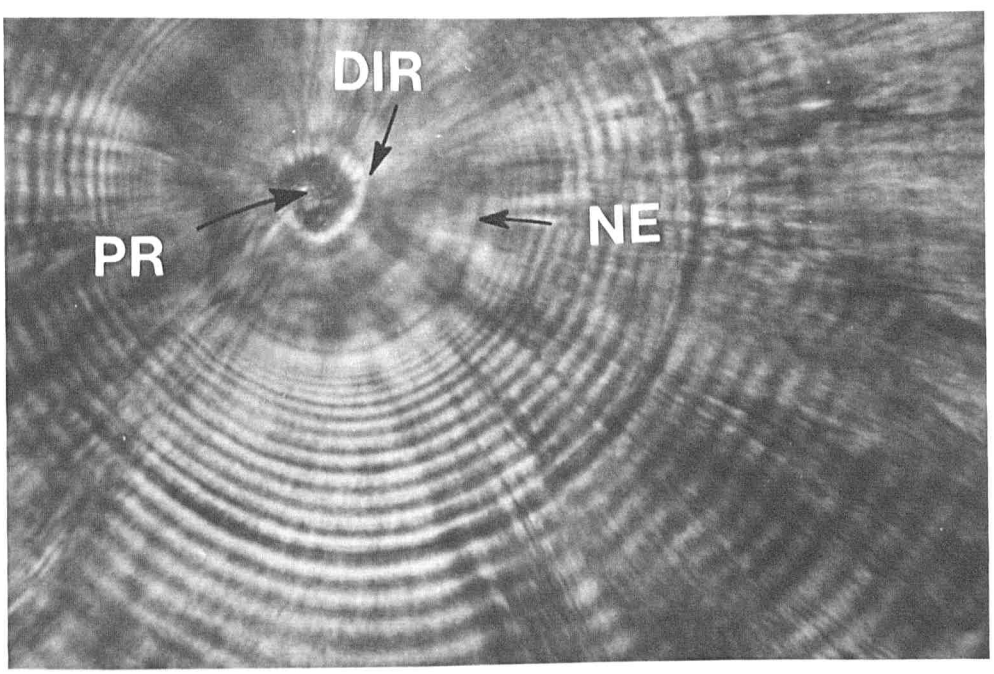

Figure 1

A *Sebastes goodei* otolith displaying the characteristic dark inner ring (DIR) around the primordium (PR). NE = nuclear edge.

Results

Seven specific nuclear shading characters were identified (Table 1): 1) the opacity of the primordium; 2) the opacity of the markings inside the nucleus; 3) the opacity of the increments directly outside the nucleus; 4) the opacity of the nuclear edge; 5) the existence of a dark inner band near the nuclear edge; 6) the existence of a light inner band near the nuclear edge; and 7) the existence of a dark inner ring encircling the primordium.

In some cases, combinations of the shading patterns were sufficient to characterize a species. For example, 84% of the otoliths of *S. goodei* were found to have a dark primordium, a dark nuclear edge, and a dark inner ring surrounding the primordium, while this combination was never found in the other species examined (Fig. 1). Likewise, in *S. jordani*, a light penumbra was regularly found (76% occurrence) adjacent to the inner edge of the nucleus, along with a dark primordium and many inner rings (faint microstructure occurring inside the nucleus). In *S. paucispinis* and *S. flavidus*, there was usually a dark inner band next to the edge of the nucleus (87% and 73% occurrence, respectively) . No annual variation was observed for the nuclear shading patterns. However, in the remaining species, the shading patterns were too variable to establish consistent identifiable character states that would distinguish species.

Annual variations in nuclear radius and the width of the first increment were examined (Fig. 2). Annual variation in nuclear radius among the species was not significant; however, annual variability in the width of the first increment was significant ($P<0.05$). In addition, there was a significant interaction ($P<0.05$) between year and species. The mean width of the first increment of *S. paucispinis*, for example, declined from 1984 to 1989, whereas that of *S. flavidus* increased (Fig. 2A).

Sebastes jordani was found to have the largest average nuclear radius (Table 2; Fig. 2B). The rank order for the remaining species, from largest to smallest average nuclear radii, was *S. goodei*, *S. auriculatus*, *S. paucispinis*, *S. flavidus*, *S. entomelas*, *S. saxicola*, and *S. mystinus*. Individually, the nuclear radii of *S. jordani*, *S. goodei*, *S. auriculatus*, and *S. mystinus* were significantly different ($P<0.05$) from all other species and from each other.

Sebastes jordani was also found to have the largest average first increment of all species studied (Table 2; Fig. 2A). The rank order of the other species, from largest to smallest average widths of the first increment, was *S. paucispinis*, *S. goodei*, *S. auriculatus*, *S. saxicola*, *S. flavidus*, *S. entomelas*, and *S. mystinus*. *Sebastes jordani* and *S. paucispinis* had significantly larger average first increment widths ($P<0.05$) than all other species studied (0.97 μm and 0.91 μm, respectively) (Table 2).

A discriminant analysis was performed on the classification of species by using nuclear radius and the width of the first increment as predictor variables (Table 3). *Sebastes goodei*, *S. jordani*, *S. mystinus*, and *S. paucispinis* were correctly identified from 57 to 83% of the time; *Sebastes auriculatus* and *S. flavidus* were classified correctly 33.9% and 41.8% of the time, respectively. Although these values are less than 50% correct, they represent the largest single classification for each species. Two species, *S. entomelas* and *S. saxicola*, were not often classified correctly (9.5% and 0%, respectively).

In a blind test, the reader correctly classified 70 of the 100 otoliths (70% correct; Table 4), demonstrating that otoliths provide useful information in species identification ($P<0.001$). Greater than 90% of *Sebastes*

Table 1

Observed shading patterns of otolith nuclei for the eight species studied. An F means the attribute was faint, a D means it was dark, and a blank means that it was either variable or did not exist. For the last three attributes, an X means the character was present. aur = *S. auriculatus*, ent = *S. entomelas*, fla = *S. flavidus*, goo = *S. goodei*, jor = *S. jordani*, mys = *S. mystinus*, pau = *S. paucispinis*, and sax = *S. saxicola*.

	Species							
Attribute	aur	ent	fla	goo	jor	mys	pau	sax
Primordium opacity	D	F	F	D	F	D	D	D
Inner ring opacity	F	F		D	F	F	F	
Outer increment opacity	F			D		F		
Nuclear edge opacity	F	F		D		D		
Dark inner band			X				X	
Light inner band			X		X			
Dark primordial ring				X				

goodei and *S. paucispinis* were correctly classified, whereas the remaining species showed lower accuracy varying from 56 to 68%.

Discussion

Otolith characteristics have been shown to vary among species and among stocks. Rybock et al. (1975) and Postuma (1974) used nuclear dimensions to identify different fish stocks. McKern et al. (1974) used otolith dimensions to separate seasonal stocks of steelhead trout, and Victor (1987) used otolith dimensions to separate different species of pomacentrids and labrids. Postuma (1974) related otolith opacity to nuclear size and compared this relationship between stocks. Messieh (1972) used otolith shape to distinguish among stocks of herring. Hecht and Appelbaum (1982) and Gago (1993) also used otolith shape to distinguish between species.

We have found that otolith characteristics can effectively distinguish certain species of *Sebastes*. Four of the species examined, *S. jordani*, *S. goodei*, *S. auriculatus*, and *S. mystinus*, had significantly different nuclear radii from each other and from the other species examined. *Sebastes jordani*, *S. goodei*, *S. paucispinis*, and *S. flavidus* each had unique shading patterns that may help in species identifications. *Sebastes jordani* and *S. paucispinis* were correctly classified over 90% of the time in the blind test, displaying the usefulness of otolith characteristics for identification.

Table 2

Mean nuclear radius and first increment width of otoliths (all years combined) of *Sebastes*. SD = standard deviation. *n* = sample size.

Species	*n*	Nuclear radius (μm)	SD	First increment (μm)	SD
S. auriculatus	56	14.07	1.48	0.82	0.20
S. entomelas	147	11.81	0.94	0.72	0.13
S. flavidus	122	12.09	0.69	0.72	0.16
S. goodei	230	15.15	0.89	0.85	0.17
S. jordani	541	16.96	0.99	0.97	0.23
S. mystinus	106	10.93	1.05	0.65	0.14
S. paucispinis	277	12.20	1.14	0.91	0.18
S. saxicola	12	11.58	0.90	0.73	0.23

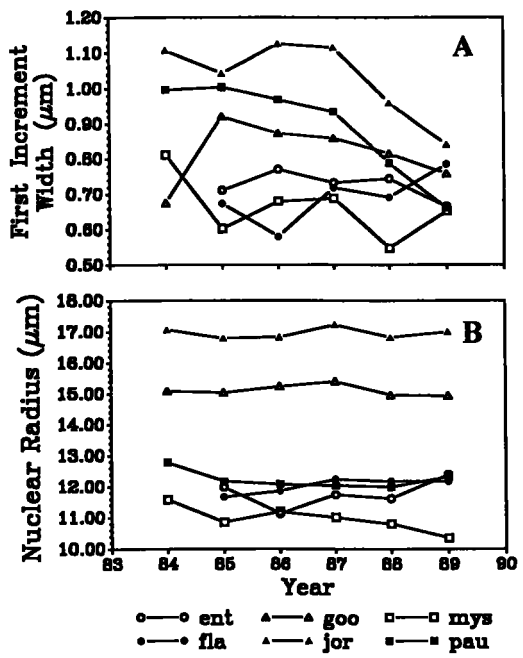

Figure 2

Annual variation in average nuclear radius and first increment width for the six species of *Sebastes* that had multiple year observations. ent = *S. entomelas*, fla = *S. flavidus*, goo = *S. goodei*, jor = *S. jordani*, mys = *S. mystinus*, and pau = *S. paucispinis*.

The specificity of otolith characters gives researchers an opportunity to separate larvae using these characters alone. Without otolith data, the separation of *S. mystinus* larvae from other rockfish larvae is difficult. Although larval *S. jordani* are relatively easy to identify on the basis of pigmentation (Moser et al., 1977), identifications can be confirmed with a few additional otolith measurements.

We suggest from these findings that the difficult task of identifying rockfish larvae can be facilitated in some cases by employing otolith characters in combination with more traditional traits like pigmentation. Of the eight species examined, six species (*S. auriculatus*, *S. flavidus*, *S. goodei*, *S. jordani*, *S. mystinus*, and *S. paucispinis*) had distinctive otolith characters that allowed separation from other species. Many of the larval stages of the more than 60 species of rockfish found in the northeast Pacific Ocean are very similar, and pigmentation alone cannot always reliably separate species. Otolith character examination may be one further method that can aid researchers in accurately identifying species in this group.

Acknowledgments

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Table 3

Discriminant analysis for nuclear radius and first increment width of otoliths for all years combined showing percent classified as each species of *Sebastes*. aur = *S. auriculatus*, ent = *S. entomelas*, fla = *S. flavidus*, goo = *S. goodei*, jor = *S. jordani*, mys = *S. mystinus*, pau = *S. paucispinis*, and sax = *S. saxicola*.

	Classification							
Species	aur	ent	fla	goo	jor	mys	pau	sax
aur	33.9	0.0	17.9	23.2	10.7	0.0	12.5	1.8
ent	1.4	9.5	38.8	1.4	0.0	22.5	12.9	13.6
fla	5.7	14.8	41.8	0.0	0.0	11.5	18.9	7.4
goo	23.5	0.0	0.9	59.6	14.4	0.0	1.7	0.0
jor	0.9	0.0	0.0	15.9	83.2	0.0	0.0	0.0
mys	0.9	4.7	6.6	0.0	0.9	72.6	6.6	7.6
pau	7.6	2.5	13.7	4.3	0.7	6.5	57.4	7.2
sax	0.0	8.3	25.0	0.0	0.0	33.3	33.3	0.0

Table 4

Results of blind test showing classification rates of *Sebastes* by species category. Bold numbers along the diagonal indicate correct classifications. aur = *S. auriculatus*, ent = *S. entomelas*, fla = S. *flavidus*, goo = *S. goodei*, jor = *S. jordani*, mys = *S. mystinus*, pau = *S. paucispinis*, and sax = *S. saxicola*.

	Classified as:								
Actual	AUR	ENT	FLA	GOO	JOR	MYS	PAU	SAX	% Correct
AUR	**3**	2							60%
ENT	2	**8**			1	2			61%
FLA		1	**9**			1	2	1	60%
GOO	1			**13**					92%
JOR	2			1	**17**	3	1	1	68%
MYS		1	1	1		**5**		1	56%
PAU							**10**	1	91%
SAX		2					1	**5**	63%

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Changes in the spatial patchiness of Pacific mackerel, *Scomber japonicus*, larvae with increasing age and size

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Several investigators have suggested that the spatial patchiness of fish eggs and larvae may be an important factor in the recruitment process (Smith, 1973; Lasker, 1978; Hewitt, 1981; Houde and Lovdal, 1985; McGurk, 1986). Patchiness has been linked to success in foraging (Hewitt, 1981), ontogeny of schooling behavior (Hewitt, 1981), and predation mortality (McGurk, 1986, 1987). Contagion in the dispersion of ichthyoplankton has been described for Pacific sardine, *Sardinops sagax*, eggs (Smith, 1973); northern anchovy, *Engraulis mordax*, and jack mackerel, *Trachurus symmetricus*, larvae (Hewitt, 1981); haddock, *Melanogrammus aeglefinus*, eggs (Koslow et al., 1985); several taxa found in Biscayne Bay including bay anchovy, *Anchoa mitchilli*, eggs and larvae (Houde and Lovdal, 1985); Atlantic herring, *Clupea harengus harengus*, larvae (Henri et al., 1985); Pacific herring, *Clupea harengus pallasi*, larvae (McGurk, 1987); bluefin tuna, *Thunnus maccoyii*, larvae (Davis et al., 1990); Brazilian sardine, *Sardinella brasiliensis*, larvae; and scaled sardine, *Harengula jaguana*, larvae (Spach, 1990).

The patchy distribution of fish eggs and larvae is initially introduced by the spawning behavior of adult fish. In order to guarantee successful fertilization in a pelagic environment, eggs must be laid when the adults are highly aggregated, and spawning and fertilization must occur almost simultaneously (Hewitt, 1981). Alternately, demersal spawners may deposit their eggs in batches that incubate on a substrate before releasing a cohort of larvae into the pelagic environment (McGurk, 1987). Thereafter, eggs or hatching larvae, or both, disperse, principally in horizontal directions; distribution patterns during this period are primarily influenced by dispersal, diffusion, and transport (Smith, 1973). After a few days or weeks, larvae begin to reaggregate, an activity that becomes more evident in the juvenile stages of most schooling pelagic fishes.

Patchiness-at-age curves for several species of pelagic schooling fishes have been shown to exhibit a characteristic "U" shape: high initial patchiness, followed by a rapid decline as the eggs or newly hatched embryos, or both, passively disperse, followed by an increase in patchiness as the developing fish begin to aggregate in schools (Hewitt, 1981; McGurk, 1987; Spach, 1990). Patchiness-at-age curves for fish eggs and larvae have been interpreted in terms of species-specific differences in life history traits such as adult reproductive behavior and larval feeding ecology, size, growth, and mortality (Smith, 1973; Hewitt, 1981; Koslow et al., 1985; McGurk, 1987). Insight into the function of patchiness may be improved by comparing how patchiness changes with age and size for species with different life histories.

In this note, we present patchiness-at-age and patchiness-at-size curves for Pacific mackerel, *Scomber japonicus*, larvae and compare them with similar curves for other pelagic fish larvae.

Material and methods

Data base

The data used in this work came from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton data base. These data are available from the CalCOFI on-line data system (Anon., 1988). Details of station and ichthyoplankton data were published in a series of CalCOFI ichthyoplankton data reports (NOAA Tech. Memo., NMFS, SWFSC, numbers 70–88, 92–100, and 102–105). Size-specific catches of Pacific mackerel larvae, collected from 1953 through 1981, were extracted and summarized for the analyses reported here.

Pacific mackerel larvae were collected with 1-m ring nets from 1953 through 1975 and with bongo nets thereafter. Sampling methods and laboratory procedures were described by Kramer et al. (1972). Out of 23,963 CalCOFI stations sampled from 1953 to 1981, plankton samples from 1,011 stations contained at least one Pacific mackerel larva. The 1,011 stations where larva were collected were assumed to define the Pacific mackerel's

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habitat, and these stations comprised the data set used in the analyses.

Size-frequency analysis

Frequency distributions of larval catches by size were assembled and a negative binomial model was fit to each distribution. The negative binomial has been used to describe aggregated distributions of ichthyoplankton (Hewitt, 1981; Zweifel and Smith, 1981; Smith and Hewitt, 1985). The model is specified by the mean (m) and the index of dispersion (k); the variance (σ^2) is related to m and k as

$$\sigma^2 = m + \frac{m^2}{k}.$$

Lloyd's (1967) index of patchiness (P) was used to describe the intensity of the distribution pattern at various larval sizes where

$$P = 1 + \frac{\sigma^2 - m}{m^2}.$$

The index has been used by several investigators to describe ichthyoplankton patchiness (Smith, 1973; Hewitt, 1981; Houde and Lovdal, 1985; McGurk, 1987) and may be considered as a measure of how many times more crowded an average individual is relative to an individual in a population with the same mean density, but one which is randomly dispersed. The index is independent of density and the scale of sampling (Pielou, 1977; Hewitt, 1982) which allows comparisons of patchiness between relatively abundant yolk-sac larvae and less abundant older larvae. By substituting the expression for the variance of the negative binomial,

$$P = 1 + \frac{1}{k},$$

where k was estimated by using a maximum likelihood estimate expression (Bliss and Fisher, 1953; Smith and Hewitt, 1985). The standard error of the sample estimate of patchiness was estimated by following Lloyd (1967):

$$se(P) \cong \frac{1}{\hat{k}^2}\sqrt{\widehat{\text{var}(k)}},$$

where $\widehat{\text{var}(k)}$ is the sampling variance of k.

Adjusting for shrinkage and converting to age

Initial size measurements were obtained from larvae preserved in 5% buffered formalin. Preserved size was converted to live size by using the shrinkage rate obtained for jack mackerel larvae from Theilacker (1980). To convert from larval size to larval age, we used the growth curve obtained from laboratory reared larvae with water temperature ranging from 16.8 to 19.2°C (Hunter and Kimbrell, 1980):

$$t = \frac{\ln(SL/3.4432)}{0.05968},$$

where t = age in days since hatching (= 0 age), and SL = standard length in live size (mm). The incubation period (from spawn to hatch) was assumed to be 2.3 days.

Results and discussion

Frequency distributions of larval catches by size are presented in Table 1. The corresponding live sizes, ages, mean abundances per tow, and patchiness parameters are also presented in Table 1. Larvae less than 3.5 mm in length appear to be undersampled in comparison to larger sizes. Pacific mackerel larvae grow rapidly through the first two size classes and therefore are vulnerable to capture for a relatively short period of time; small larvae are also more likely to be extruded through the meshes of the sampling net (Smith and Richardson, 1977).

The change in patchiness with age suggests that recently hatched Pacific mackerel larvae were highly aggregated and dispersed rapidly until approximately five days after spawning (Fig. 1). Patchiness gradually increased with age until 9.2 days, then decreased slightly and continued to increase with age thereafter.

Morphological and behavioral changes of developing Pacific mackerel larvae are summarized in Table 2 and illustrated in Figure 2. A functional visual sensory organ is formed in Pacific mackerel larvae at 6.0–6.5 mm and completed at approximately 8 mm.[1] Although caudal and pectoral fins begin development at 3.5 mm, swimming speed increases rapidly with size only after the pelvic, anal, and dorsal fins are formed at approximately 9.6 mm (Watanabe, 1970; Hunter and Kimbrell, 1980). Hunter and Kimbrell (1980) reported that schooling behavior did not begin until 14 mm, although an increase in patchiness at 4.6 mm is apparent from the plankton catches. It may be that the ontogeny of schooling behavior in Pacific mackerel involves a prolonged period of contact between larvae that is necessary for the successful integration of approach-withdraw and approach-orient behaviors (Shaw, 1960, 1970; Williams and Shaw, 1971). This phenomenon may be statistically recognizable as an increase in patchiness but not visually recognizable as coordinated social behavior.

[1] O'Connell, C. Southwest Fisheries Science Center, Nat. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, California.

Table 1

Size-specific catch statistics for *Scomber japonicus* larvae collected during CalCOFI surveys from 1953 through 1981. A total of 8,396 larvae were caught at 1,011 stations out of a total of 23,963 CalCOFI stations.

	Preserved size (mm) / Live size (mm) / Age since spawn (days)											
Catch	2.00	2.50	3.00	3.50	4.00	4.50	5.00	5.75	6.75	7.75	8.75	9.75
	3.10	3.30	3.50	4.00	4.60	5.20	5.70	6.50	7.70	8.50	9.60	10.70
	2.3	3.0	3.3	5.0	7.2	9.2	10.7	13.0	15.7	17.5	19.5	21.3
Number of larvae/sample												
0	825	671	571	698	774	806	849	836	908	970	980	995
1	93	149	195	143	112	113	90	99	80	26	28	13
2	34	66	81	63	56	35	34	39	9	10	2	2
3–4	28	42	70	52	36	29	23	17	5	3	1	1
5–8	18	31	42	29	18	16	11	15	6	2	0	0
9–16	5	30	27	15	11	8	3	4	2	0	0	0
17–32	4	15	14	10	2	2	1	1	1	0	0	0
33–64	3	4	5	1	1	2	0	0	0	0	0	0
65–128	1	2	4	0	1	0	0	0	0	0	0	0
129–256	0	1	2	0	0	0	0	0	0	0	0	0
Total larvae	709	1,823	2,334	1,088	762	762	350	400	193	67	36	21
Number of samples	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011
Mean per sample	0.701	1.803	2.309	1.076	0.754	0.754	0.346	0.396	0.191	0.066	0.036	0.021
Variance	13.101	67.540	97.629	10.823	13.885	7.421	1.415	1.936	0.933	0.155	0.050	0.036
k	0.092	0.152	0.209	0.189	0.140	0.102	0.139	0.139	0.097	0.048	0.106	0.030
Patchiness	11.91	7.57	5.79	6.30	8.15	10.76	8.21	8.19	11.33	21.98	10.42	34.28
SE (patchiness)	1.09	0.48	0.32	0.44	0.67	0.94	0.91	0.86	1.71	18.42	4.54	39.78

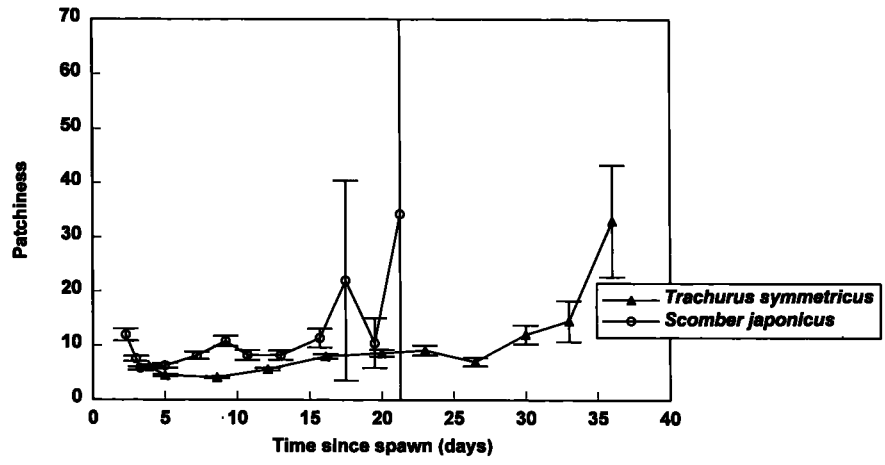

Figure 1

Lloyd's index of patchiness as a function of larval age for *Scomber japonicus* and *Trachurus symmetricus* in the California Current region.

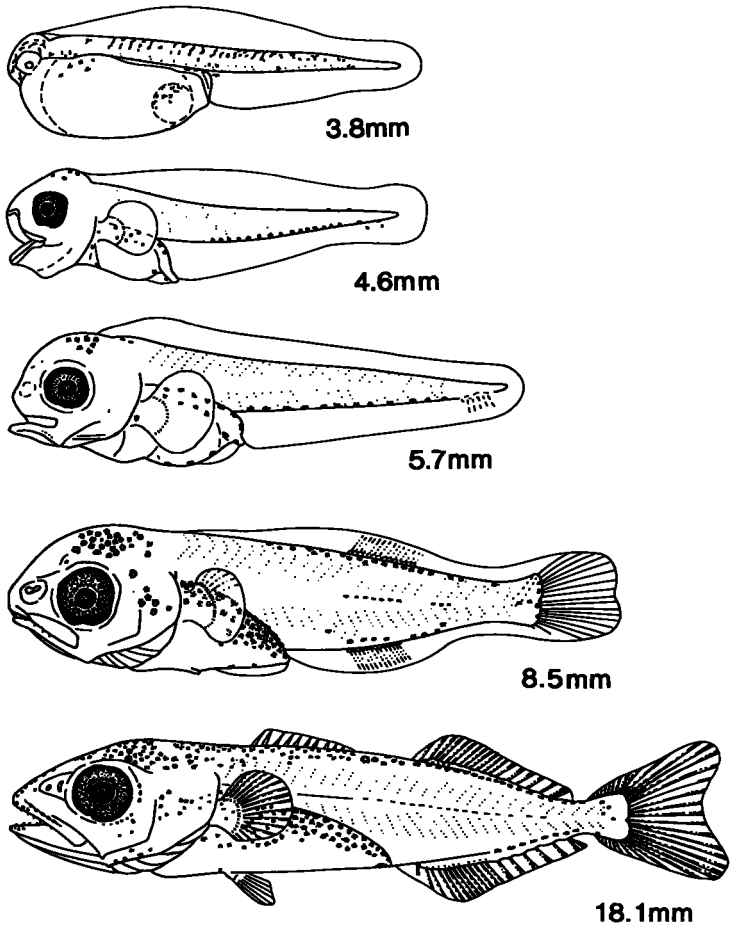

Figure 2

Developmental stages of *Scomber japonicus* larvae (from Matarese et al., 1989). Sizes shown are estimated live sizes.

Table 2

Behavioral and morphological changes in developing *Scomber japonicus* larvae.

	Measurements																	
Live size	3.1	3.3	3.5	4.0	4.6	5.2	5.7	6.5	7.7	8.5	9.6	10.7	11.8	12.9	14.0	15.1	16.2	17.3
Swimming speed (cm/sec)[1]		0.4	0.6	0.7	0.9	1.0	1.3	1.8	2.1	2.6	3.1	3.7	4.4	5.0	5.7	6.5	7.3	
Cannibalism[1]								sibling cannibalism between 8 and 15 mm										
Schooling[1]														oriented swimming				
Patchiness		11.9	7.6	5.8	6.3	8.2	10.8	8.2	8.2	11.3	22.0	10.4	34.3					
Feeding ability[2]				Mouth opening and yolk absorption at 4 mm														
Fin formation[2]			CF, PF at 3.5 mm								PvF, AF, DF at 9.6 mm							
Visual sensory organ[3]								developed between 6.5 and 7.7 mm										

[1] Hunter and Kimbrell (1980).
[2] Watanabe (1970); CF = caudal fin, PF = pectoral fin, PvF = pelvic fin, AF = anal fin, DF = dorsal fin.
[3] O'Connell (unpub. data).

Patchiness-at-age curves for six species (*Engraulis mordax* and *Trachurus symmetricus*, Hewitt, 1981; *Clupea harengus pallasi*, McGurk, 1987; *Sardinella brasiliensis* and *Harengula jaguana*, Spach, 1990; and *Scomber japonicus*, reported here) describe a similar sequence: a high index is observed at the youngest larval ages, a low index is observed at one or two weeks after spawn, and thereafter the index increases suggesting the onset of schooling behavior (Fig. 3). The highest index of patchiness at early larval age was observed for *S. brasiliensis* (P=14.5). This can be attributed to intensive spawning behavior of adult sardine, short incubation time (Matsuura, 1983), and fast larval growth (Yoneda, 1987) relative to the other species. The lowest index of patchiness was observed for *C. harengus pallasi* (P=3.5) collected in a small inlet on the west coast of Vancouver Island, British Columbia; McGurk (1987) noted that this may be a reflection-dispersed prey. Houde and Lovdal (1985) reported that fish larvae in Biscayne Bay, Florida, were only slightly more patchy (P=1.3) than their prey, which was abundant and not aggregated (P=1.06). Henri et al. (1985) also reported low patchiness values (P=1.63–3.52) for *Clupea harengus harengus* larvae collected in the St. Lawrence estuary, Quebec. Hewitt (1981) discussed differences in patchiness-at-age curves for *E. mordax* and *T. symmetricus* in terms of their prey availability and foraging strategies. In contrast to *T. symmetricus*, *E. mordax* exhibited an initial high degree of patchiness and slowly dispersed before showing a rapid increase in patchiness at about 18 days of age. *Trachurus symmetricus* larvae were approximately 1/10 as abundant, exhibited lower initial patchiness, and achieved maximum dispersion at an earlier age. *E. mordax* depend on small, but abundant, prey; they have poorly developed swimming capabilities and can effectively forage only through a small volume of water. In contrast, *T. symmetricus* depend on large, but rare, prey items; they have well-developed swimming capabilities and are able to search through relatively large volumes of water.

In comparison to the four clupeoid species, the increase in patchiness was observed to occur at an early age for both *S. japonicus* and *T. symmetricus*. *Scomber japonicus* and *T. symmetricus* larvae share similar morphologies and life history traits. Hunter and Kimbrell (1980) noted that Pacific mackerel larvae may be characterized as having fast growth, rapid swimming abilities, high metabolism, a dependence on increasingly larger prey, and a tendency for cannibalism. Sibling cannibalism may be an important survival strategy for mackerel larvae, where larger individuals prey on smaller ones. Grave (1981) reported that by the time Atlantic mackerel, *Scomber scombrus*, larvae were 12 mm long, 83% of the food items in their diet were other mackerel larvae. High initial dispersal, followed by aggregation of similar-sized larvae may be mechanisms for reducing sibling cannibalism. Although the patchiness-at-age curves for *S. japonicus* and *T. symmetricus* are distinct (Fig. 1), the patchiness-at-size curves are almost coincident (Fig. 4), suggesting that change in patchiness

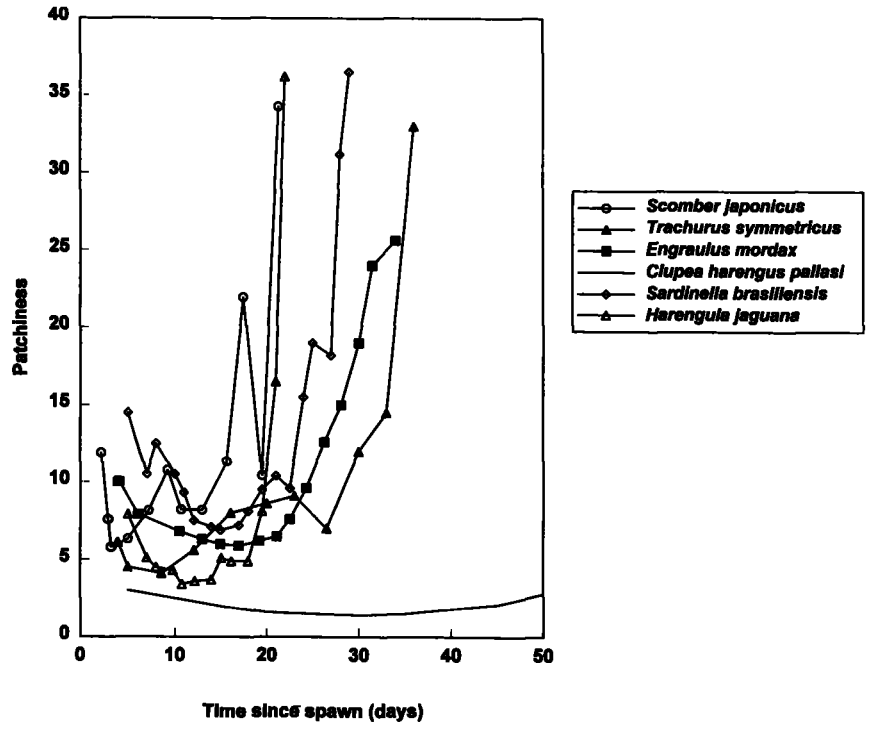

Figure 3

Patchiness-at-age curves for three species from the California Current (*Engraulis mordax*, *Trachurus symmetricus*, and *Scomber japonicus*), two species from southern Brazil (*Sardinella brasiliensis* and *Harengula jaguana*), and one species from British Columbia (*Clupea harengus pallasi*).

may be a size-dependent phenomenom.

Acknowledgments

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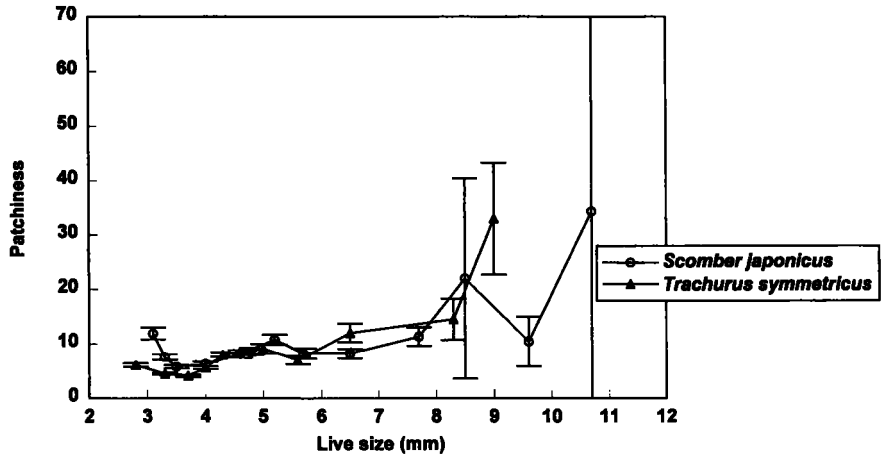

Figure 4

Lloyd's index of patchiness as a function of larval size for *Scomber japonicus* and *Trachurus symmetricus*.

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Growth and morphology of larval and juvenile captive bred yellowtail snapper, *Ocyurus chrysurus**

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The snappers (Lutjanidae) are major components of the reef fish fishery in the Gulf of Mexico (Nakamura, 1976), and recent declines in their populations have prompted interest in a number of management practices including limited catches, size limits, area closures, and additions of artificial reef habitat to improve survival of wild stocks (Leis, 1987; Munro, 1987). Studies on the spawning, distribution, larval and juvenile ecology, and stock assessment of new recruits are crucial to the development of management strategies for reef species since little is known about their early life history (Grimes, 1987). During most developmental stages, snapper larvae are pelagic and widely dispersed, limiting the numbers of specimens to be found in taxonomic collections (Munro, 1987). The similarity in size and pigmentation of small larval lutjanids (<5 mm) and the paucity of species-specific details of size at age and morphological development has made identification of individuals in ichthyoplankton samples difficult (Leis, 1987). Of the fourteen species of snappers that are found in the Gulf of Mexico,[1] larval development has been fully described for only three species: red snapper, *Lutjanus campechanus*, from both laboratory spawned (Rabalais et al., 1980) and wild caught larvae (Collins et al., 1980); gray snapper, *L. griseus*, from wild eggs reared in the laboratory (Richards and Saksena, 1980); and vermilion snapper, *Rhomboplites aurorubens*, from wild preserved specimens (Laroche, 1977). A recent NOAA report by Richards et al.[2] summarizes the larval lutjanid descriptions listed above and introduces some newly available descriptive material for several additional species of snappers including some stages of yellowtail snapper, *Ocyurus chrysurus*. In their report, the yellowtail snapper is included in the genus *Lutjanus*, a change suggested as a result of two recent treatments by Loftus (1992) and Domeier and Clark (1992).

The commercial and recreational importance of snappers has also been recognized by the aquaculture industry, and efforts are underway to culture several of these species in captivity. In this paper we describe the development and growth of laboratory spawned and reared yellowtail snapper. This species is found from Massachusetts through the Caribbean and south to Brazil (Hoese and Moore, 1977). Laboratory culture allowed us to document growth and development of the critical larval and juvenile stages of yellowtail snapper that will aid identification and ageing of larval snappers collected in the field. We have also included information on the effects of a commonly used preservative (ethyl alcohol) on length measurements and pigmentation characteristics of laboratory-cultured larvae for purposes of comparative use with wild-collected larvae.

Materials and methods

Young adult *Ocyurus chrysurus* were collected by hook and line in July 1990 from the Florida Keys and were transported to the laboratory where they were matured and cycled for one year following the methods described by Arnold (1988). Adults began spawning in July 1991 and continued to March 1994.

Eggs were stocked at a density of 50/L in fiberglass tanks (300 and 600 L) with internal biofilters. Larvae were reared at 27–28°C with 12 hours light at salinities of 33–38 ppt on a diet of zooplankton (collected from the Corpus Christi Ship Channel), rotifers (*Branchionus plicatilis*) and brine shrimp nauplii (*Artemia salina*).

The description of larval development is based on larvae from multiple spawns of two different groups of broodstock (15 adults/tank). Larvae were measured live (SL=tip of snout to posterior tip of notochord) to the nearest 0.01 mm on a stereomicroscope equipped with a drawing tube and digitizing

* Contribution 907 of the Marine Science Institute, University of Texas at Austin.

[1] Lyczkowski-Shultz, J., and B. H. Comyns. 1992. Early life history of snappers in coastal and shelf waters of the northcentral Gulf of Mexico (late summer/fall months, 1983–1989). Final Rep. to MARFIN, NA90AA-H-MF730.

[2] Richards, W. J., K. C. Lindeman, J. L. Shultz, J. M. Leis, A. Ropke, M. E. Clark, and B. H. Comyns. 1994. Preliminary guide to the identification of the early life history stages of lutjanid fishes of the western central Atlantic. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFSC-345, 49 p.

Manuscript accepted 29 August 1994.
Fishery Bulletin 93:179–185 (1995).

pad. Drawings were made with a dissecting scope and camera lucida attachment of live, anesthetized larvae before they were preserved in 80% ethyl alcohol (ETOH). To determine laboratory shrinkage rates, the larvae were remeasured after at least one month in ETOH, and preserved lengths were compared to those of the previous, live measurements. Since larvae were drawn from living specimens, no staining or special preparations were required for observation of spines, rays, or other details of morphology.

Results

Pigmentation and overall development

Daily measurements and developmental milestones are presented in Table 1. The pelagic eggs were spherical, averaged 0.96 mm diameter, had a single oil globule, and hatched in 22–24 hours at 27°C. Eggs were essentially transparent, the only pigment observed was a series of small chromatophores on the dorsal surface of the embryo (Fig. 1A). After hatching and through the two day yolk-sac stage, larvae possessed a single unpigmented oil globule in the anterior end of the yolk-sac, an unpigmented finfold, and 24 myomeres. Within 12 hours after hatching (Fig. 1B), the dorsal chromatophores of the embryo had migrated to form a series along the ventral surface of the body and tail; a single stellate chromatophore was present on the gut anterior to the anus, and a light scattering of dark pigment was found on the yolk-sac and lateral surfaces of the head. Exogenous feeding coincided with development of eye pigmentation, functional jaws, and gas bladder inflation at 3.36 mm (age 3 days, Fig. 1C). Pigmentation at this stage included a large dark chromatophore on the ventral surface of the gut, four chromatophores over the dorsal surface of the gut and gas bladder, and a single, dark chromatophore on the ventral tip of the notochord. In live specimens at this stage, we first observed the development of a yellow chromatophore (indicated by arrow on Fig. 1C) located on the lateral surface of the body at about midgut. Larvae 3.67–3.82 mm (Fig. 2A) showed dramatic developmental changes. The development of numerous yellow chromatophores (indicated on illustrations by solid arrows) scattered on the lateral surfaces of the head, gut, and upper body near the base of the pectoral fin, as well as dark stellate chromatophores on the hindbrain and on the ventral edge of the cleithrum coincided with eruption of the pelvic fin buds and the appearance of preopercular spination. Larvae 4.10–4.53 mm (Fig. 2, B–D) were characterized by daily increases in the number of dorsal spines and by elongation of the pelvic fins, as well as by an increase in the density of yellow chromatophores on the lateral head region. Notochord flexion occurred when larvae reached 4.40 mm at 15–16 days posthatch (Fig. 3A) and was followed by full fin formation. Changes in pigmentation consisted primarily of increasingly dense concentrations of yellow pigment on the lateral upper body and head, dark web-like pigment in the membranes of developing fins, and diffuse internal pigment over the gut surface (Fig. 3B). The first indication of adult coloration was visible on early juveniles approximately 14.00 mm SL (Fig. 3C) where yellow chromatophores formed a horizontal line through the eye onto the snout and were also interspersed with the dark chromatophores lining the dorsal and ventral margins of the body at the fin bases. Yellow pigment was also present along the lateral midline of the tail. Near-adult pigmentation was present by 16.00 mm (age 62 days) at which time juveniles were fully scaled (Fig. 3D).

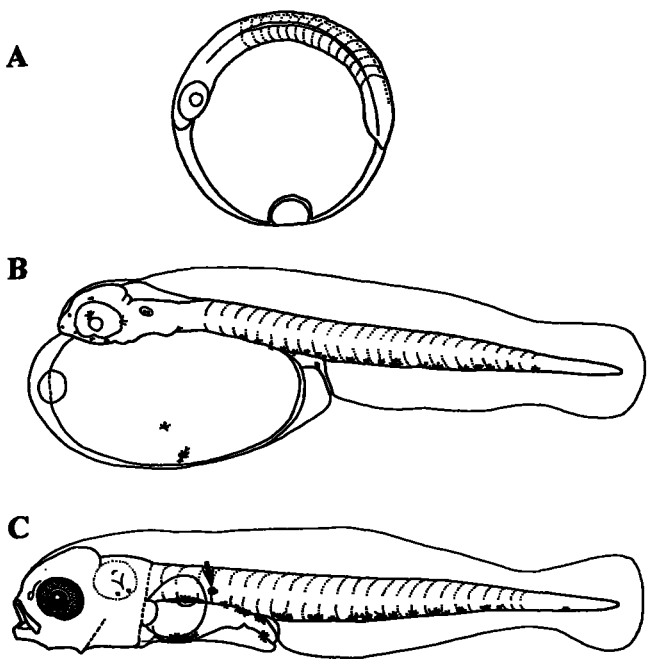

Figure 1

Early developmental stages of yellowtail snapper, *Ocyurus chrysurus*, illustrated from live specimens. (A) late embryo egg, 0.96 mm diameter; (B) 2.23 mm SL newly hatched larva; (C) 3.36 mm, 3 days posthatch. Dark arrows indicate location of yellow chromatophore.

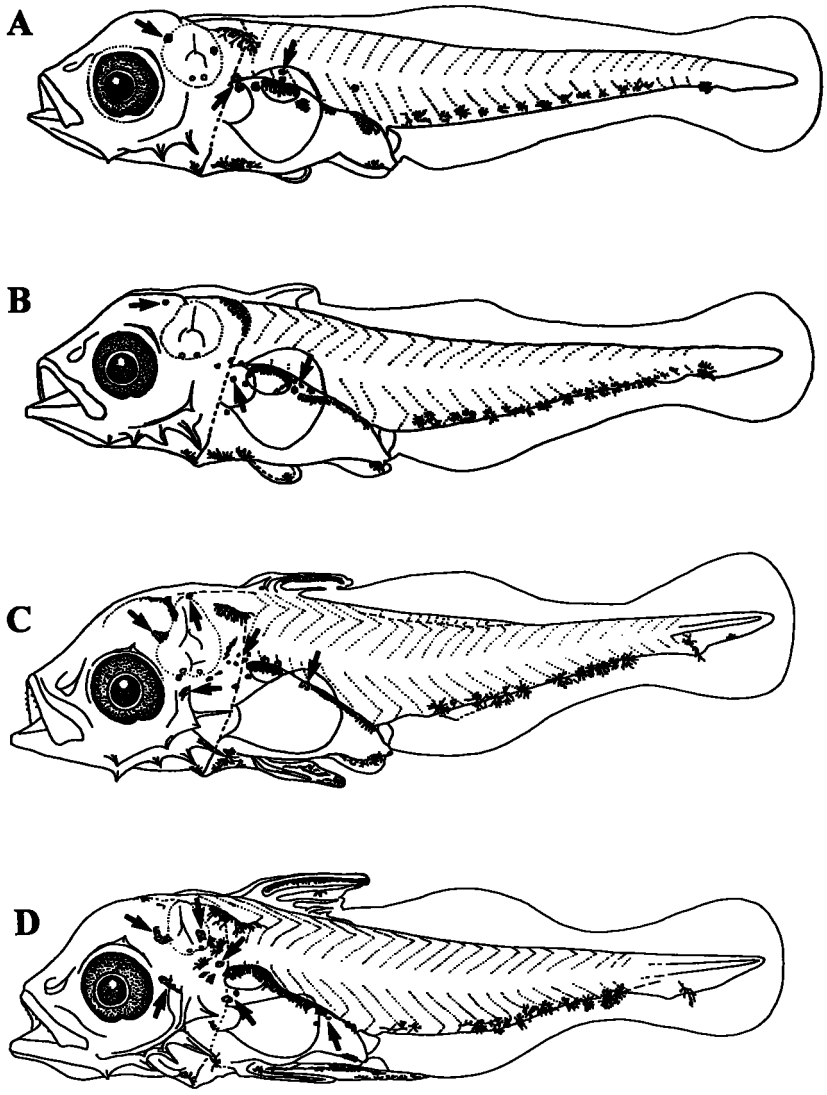

Figure 2

Developmental stages and mean live lengths of yellowtail snapper. Dark arrows indicate location of yellow chromatophores. (**A**) 3.67–3.82 mm SL, days 7-9 posthatch; (**B**) 4.10–4.53 mm SL, days 10-11 posthatch; (**C**) 4.51 mm SL, day 12 posthatch; (**D**) 4.11 mm SL, day 13 posthatch.

Head spination

One or two paired, smooth spines on the posterior edge of the preoperculum first occurred in larvae 3.67–3.82 mm (Fig. 2A). Preopercular spination increased to four and a supraocular ridge with one spine was present at 4.10 mm (Fig. 2B). At 4.50 mm (Fig. 2C), 5 or 6 elongated preopercular spines were present, the longest of which occurred at the preopercal angle. Larvae at 4.80 mm and 16 days of age (Fig. 3A) had a fully formed supraocular ridge with 4 short, smooth spines and 3 supracleithral spines. A reduction in the length of all head spines began at approximately 6.00 mm, but some short, opercular spines remained on the oldest juveniles.

Fin formation

The adult meristic complement of *O. chrysurus* is X+12–14 dorsal, 9 + 8 caudal, I + 5 pelvic, III + 8–9 anal, and 15 or 16 pectoral (Hoese and Moore, 1977). In laboratory-reared larvae, fin development oc-

curred in the following sequence: pelvic and dorsal spines, caudal, dorsal and anal soft rays, pectoral rays (Table 1). The spinous pelvic and dorsal fin formation occurred simultaneously at 4.10 mm. Dorsal and anal fin analage were first visible at 4.51 mm and ray bases were fully formed by 5.35 mm. Caudal flexion and caudal ray formation occurred in larvae between 4.40 and 4.75 mm and was followed by development of the soft rays of the dorsal and anal fins (Fig. 3A); additionally, the spines of the dorsal and pelvic fins were strongly serrated. By 6.23 mm SL, all juveniles had the full adult complement of fin spines and rays (Fig. 3B); however, serrated spines, characteristic of larvae, were still present on juveniles 14.66 mm.

Growth and shrinkage

Laboratory-reared yellowtail snapper showed large variation in size among larvae of the same age (Table 1), and key developmental events were tightly linked to larval size more than to age. Growth rates prior to flexion averaged 0.31 mm/day and decreased to only 0.18 mm/day during the process of transformation to juveniles (4.83–7.00 mm SL, ages 14–28 days). During the last month and a half of recorded development, juvenile growth averaged 0.25 mm/day.

Mean daily lengths of postpreservation larvae are listed on Table 1. Shrinkage after preservation was greatest in larvae prior to any fin development (<4.00 mm), averaging 10.36% through the first 13 days. Larvae with partial fin development (4.83–5.72 mm SL) shrank an average of 9.32%. Once larvae attained complete development of the dorsal and pelvic fins (>5.00 mm); shrinkage was reduced to an average of 7.24% throughout the remaining juvenile stages examined.

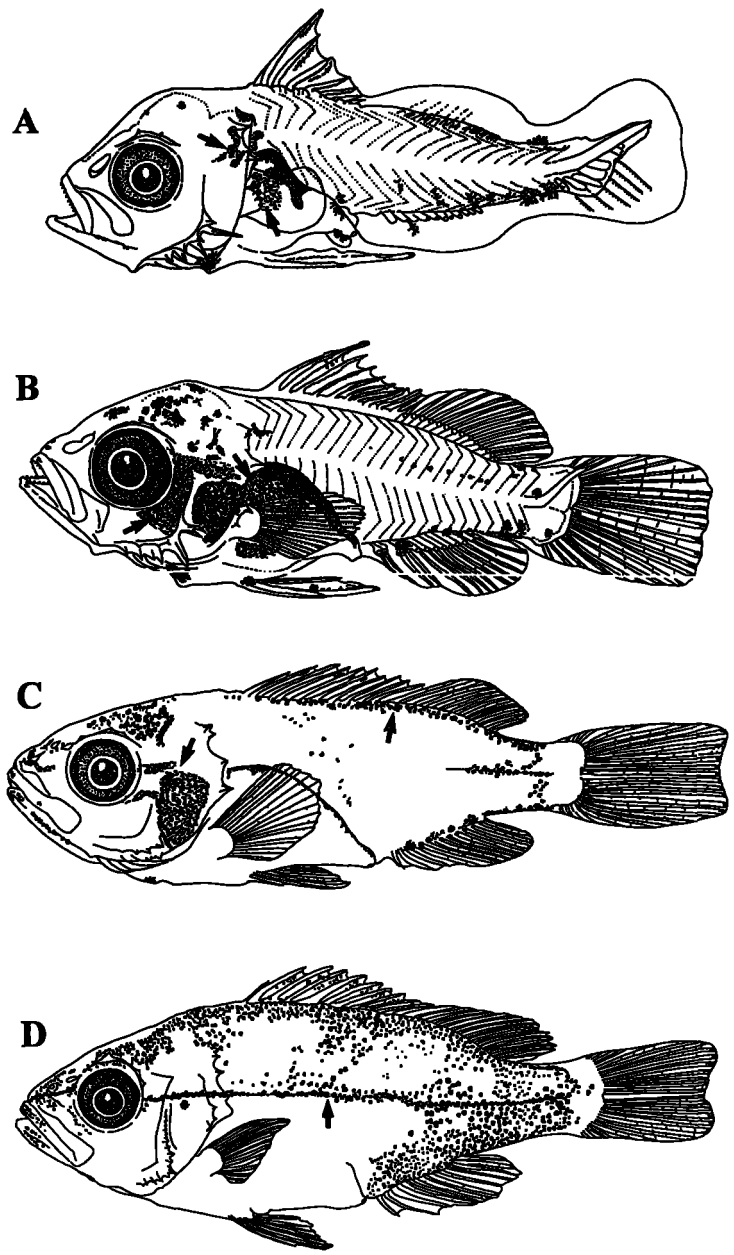

Figure 3

Late developmental stages and mean lengths of yellowtail snapper. Dark arrows indicate location of yellow chromatophores. (**A**) 4.64–4.80 mm SL, days 15–16; (**B**) 6.23–6.73 mm SL, days 18–28; (**C**) 14.66 mm SL, day 31, drawn from preserved specimen; (**D**) 16.05 mm SL, day 62, from preserved specimen.

Discussion

Ocyurus chrysurus have similar larval characteristics to the previously described snappers *Lutjanus campechanus* (Collins et al., 1980), *L. griseus* (Richards and Saksena, 1980), and *Rhomboplites aurorubens* (Laroche, 1977). Preflexion larvae of each of the four species have a series of chromatophores along the ventral midline and have pigment covering the dorsum of the gut and gas bladder. All have

Table 1

Sizes and meristic characteristics of laboratory-spawned and reared larval and juvenile yellowtail snapper, *Ocyurus chrysurus*. All ages listed are in days except for NH = newly hatched < 1 hr old, *n* = number of individuals examined, SD = standard deviation, Shrinkage = % decrease in mean SL after preservation.

	Live SL (mm)					Preserved SL (mm)		Dorsal fin		Pelvic fin		Anal fin		Caudal fin		Pectoral fin	
Age	*n*	Min	Max	Mean	SD	Mean	SD	Spines	Rays	Spines	Rays	Spines	Rays	Principal	Rays	Rays	Notocord flexure
EGG	30	0.92	0.99	0.96	0.02	0.94	0.02	0	0	0	0	0	0	0	0	0	—
NH	42	1.99	2.78	2.23	0.16	2.09	0.23	0	0	0	0	0	0	0	0	0	straight
1	56	2.47	3.60	3.14	0.25	2.85	0.16	0	0	0	0	0	0	0	0	0	straight
2	42	3.09	3.99	3.57	0.26	3.00	0.21	0	0	0	0	0	0	0	0	0	straight
3	39	2.76	3.72	3.36	0.23	3.07	0.20	0	0	0	0	0	0	0	0	0	straight
4	23	3.12	3.68	3.44	0.16	3.05	0.28	0	0	0	0	0	0	0	0	0	straight
5	20	3.24	3.76	3.49	0.18	3.08	0.36	0	0	0	0	0	0	0	0	0	straight
6	23	3.33	3.92	3.64	0.15	3.21	0.28	0	0	0	0	0	0	0	0	0	straight
7	34	3.18	4.22	3.67	0.27	3.35	0.22	0	0	0	0	0	0	0	0	0	straight
8	21	3.51	4.46	3.92	0.25	3.43	0.36	0	0	0	0	0	0	0	0	0	straight
9	13	3.44	4.38	3.82	0.23	3.66	0.46	1	0	1	0	0	0	0	0	0	straight
10	21	3.59	4.76	4.10	0.34	3.67	0.38	1	0	1	0	0	0	0	0	0	straight
11	12	3.88	5.13	4.53	0.37	4.03	0.36	2–3	0	1	0	0	0	0	0	0	straight
12	14	3.50	5.45	4.51	0.59	3.84	0.66	3–4	0	1	0	0	0	0	0	0	straight
13	24	3.77	5.40	4.11	0.35	3.77	0.41	3–4	0	1	0	0	0	0	0	0	straight
15	14	3.95	5.47	4.69	0.57	4.01	0.80	5	0	1	3	0	0	8	4	0	flexed
16	4	3.80	5.52	4.80	0.76	4.59	0.61	5	0	1	3	0	0	9	4	0	flexed
18	6	5.70	6.56	6.22	0.31	5.63	0.33	8	13	1	3	3	9	9	8	0	flexed
21	8	4.80	7.46	5.72	0.86	5.34	0.82	8–9	13	1	4	3	9	9	8	16	flexed
25	11	5.31	8.86	6.69	1.12	6.05	0.82	10	13	1	4	3	9	9	8	16	flexed
28	7	5.68	9.32	7.00	1.28	6.75	1.15	10	13	1	5	3	9	9	8	16	flexed
31	4	7.80	14.66	11.52	3.31	12.19	1.75	10	13	1	5	3	9	9	8	16	flexed
62[1]	5	14.48	17.71	—	—	16.05	1.32	10	13	1	5	3	9	9	8	16	flexed

[1] = Preserved lengths only

large solitary chromatophores on the cleithral symphysis, gut ventrum, anus, and on the notochord at the point of flexure, and all undergo flexion within a narrow size range of 4.2–5.2 mm SL.

There are, however, a few distinctive characteristics that can be used to separate the larvae of these species. Immediately following flexion at 4.40 mm, larvae of *O. chrysurus* and *R. aurorubens* (flexion at 4.7 mm, Laroche, 1977) possess large serrations on both the anterior and posterior margins of the dorsal spines, but these are not present on larvae of *L. campechanus* (Collins et al., 1980) or *L. griseus* (Richards and Saksena, 1980). Preopercular spination is also a useful character in that the longest spine (located at the preopercle angle in each described species) is serrated in *R. aurorubens* but not in *L. campechanus*, *L. griseus* (Laroche, 1977), or *O. chrysurus* (present study). Lyczkowski-Shultz and Comyns[1] compared small, preserved larval *R. aurorubens* and *L. campechanus*, and found that both species had two dorsal spines and 4 or 5 preopercular spines at 3.3 to 3.9 mm SL. Yellowtail snapper differ in having fewer or no dorsal spines and only three preopercular spines at the same preserved sizes (corresponding to days 7–11, Fig. 2, A and B). Lyczkowski-Shultz and Comyns[1] also examined pigmentation differences in <4.0 mm larvae and identified a characteristic pigment spot in *R. aurorubens* located on the branchial chamber and visible through the operculum; they also observed pigment on the anterior surface of the gut (at the level of the pectoral fin base) in *L. campechanus*. Larval *O. chrysurus* of the same size range were devoid of pigment in either of these locations. Larval *R. aurorubens* (Laroche, 1977) had numerous, dark chromatophores located on both the midbrain and hindbrain regions in all sizes of larvae examined, however, the two species of *Lutjanus* and *O. chrysurus* had head pigment only on the hindbrain area. The yellow chromatophores found on live or recently preserved specimens of *O. chrysurus* are definitive characteristics for identification of this species; unfortunately, this light-colored pigment was not visible after the 30-day preservation period in larvae <7.00 mm SL and would not likely be detected in ichthyoplankton samples preserved in ETOH. The yellow chromatophores were faintly visible on the snout, operculum, and lateral line of the larger preserved individuals. Larval *O. chrysurus* can be distinguished from the other described lutjanid species by utilizing combinations of the above characteristics including the presence of heavy serrations on both the anterior and posterior margins of the dorsal spines at the time of flexion, lack of serrations on the longest preopercle spine, reduced number of preopercle spines and dorsal spines at comparable sizes, and lack of internal pigment on the anterior surface of the gut or branchial chamber.

Newly hatched and early developmental stages of larval fishes are rarely collected or retained in net samples.[3] Those larvae that are collected show significant handling effects (Theilacker, 1980; Hay, 1981; McGurk, 1985), including distortion and size reduction that result in less than optimal depictions of size at critical stages of development. In contrast, laboratory-reared specimens provide more realistic size values and information on age and pigmentation not available to studies with field-caught larvae. The shrinkage rates at each age and phase of morphological development in *O. chrysurus* are conservative measures because field-collected larvae show additional shrinkage from net damage. In small unossified larvae, reduction in SL as a result of net collection alone increased shrinkage rates of laboratory-preserved northern anchovy by 19% (Theilacker, 1980) and in Pacific herring by about 8% (Hay, 1981). From these results it is clear that some additional allowance for net shrinkage should be applied to the laboratory-preserved lengths of *O. chrysurus* when compared to those of field-caught individuals; however, shrinkage rates may be variable between species; therefore the value to be used is unclear. Shrinkage rates have been shown to decrease with increasing age and size of larvae (Theilacker, 1980; McGurk, 1985) and to become equivalent to that of larvae exposed to laboratory handling only (e.g. no net damage) once larvae are completely ossified. Shrinkage rates of laboratory *O. chrysurus* also decreased in postflexion larvae, stabilizing at <10% in early juveniles. Therefore, to make predictions regarding the live size or age of field-collected larval snappers, an additional, though unknown, rate of shrinkage due to net damage should be taken into account in preflexion stages but not in postlarvae and juveniles.

The nomenclatural status of the yellowtail snapper has come under review recently. After describing the morphology of the natural hybrid between *O. chrysurus* and *Lutjanus synagris* (Loftus, 1992) and the laboratory-produced hybrids of *O. chrysurus* and *L. synagris* (Domeier and Clarke, 1992), the authors of these studies concluded that the morphological and meristic data indicated that *Ocyurus* is probably not a distinct genus from *Lutjanus*. The larval morphology described in this study of *O. chrysurus* also confirms the very similar size and developmental characteristics of this species with the previously described members of the genus *Lutjanus*.

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Acknowledgments

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Validation of otolith-based ageing and a comparison of otolith and scale-based ageing in mark-recaptured Chesapeake Bay striped bass, *Morone saxatilis*

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Anadromous striped bass, *Morone saxatilis*, populations in the mid-Atlantic region comprise important commercial and recreational fisheries (ASMFC[1]). Stock assessments for these fisheries depend upon age estimates using annular structures of scales (Merriman, 1941; Mansueti, 1961; Kahnle et al.[2]; Hornick et al.[3]). Age estimation for large adults (>91 cm) has been problematic owing to the presence of false annuli and to difficulty in interpreting narrow annuli in peripheral fields of the scale (Scofield, 1928a; Merriman, 1941; Tiller, 1950; Mansueti, 1961). Recent work on otolith microchemistry to decipher environmental histories of migratory striped bass has provided age estimates that were considerably greater than those previously reported (Secor, 1992). Longevity of female Chesapeake striped bass was estimated to exceed 31 years based on examination of otolith microstructure (Secor et al.[4]).

An investigation of the rate of annulus formation in the otoliths of Chesapeake Bay striped bass was performed to verify estimates of growth and longevity (Secor et al.[4]). For otolith microchemistry applications (Secor, 1992), it also was critical to verify that annuli formed at a yearly rate so that seasonal patterns in Sr/Ca ratio (exposure to varying salinity) could be interpreted. Heidinger and Clodfelter (1987) reported yearly rates of annulus formation in otoliths of striped bass from one to four years in age in a midwest reservoir, but no specific measurements of accuracy or precision were presented. No other studies have been published on annulus formation in striped bass otoliths.

A mark-recapture study on hatchery-produced striped bass (Rago et al., 1993; Hornick et al.[3]) provided samples of known-age resident and migratory fish that were 3 to 7 years old. From 1985 to 1992, approximately 5.5 million juvenile striped bass were stocked in Chesapeake Bay tributaries (Rago et al., 1993). All fish were implanted with a binary-coded wire tag which indicated year of origin and provided information on their hatchery source and release date and site. The objective of this study was to verify the rate of annulus formation by comparing annulus counts with the known age of recaptured hatchery fish. A second objective was to compare scale and otolith ages of large striped bass (>91 cm, total length [TL]) to determine the accuracy of age estimates derived from scales.

Methods

Known-age study

Striped bass otolith ageing techniques were verified by using two sets of known-age, coded-wire tagged (CWT) adults. A group of 24 CWT fish was obtained from a collaborative study of migratory striped bass conducted by the Maryland Department of Natural Resources (DNR); the National Marine Fisheries Service; the North Carolina Department of En-

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vironment, Health, and Natural Resources; and the U.S. Fish and Wildlife Service. Between 6 and 8 February 1993, migratory fish were captured off the North Carolina coast by the crew of the NOAA vessel *Chapman* by means of a 90-ft, 2-seam fish trawl that was towed for a maximum of 30 minutes (Laney and Cole, 1993). A second group of 13 CWT fish was obtained from DNR commercial drift gillnet and poundnet surveys between 5 October 1992 and 23 February 1993. Pound nets and drift nets were located in shoal areas of the upper Chesapeake Bay, off Kent Island, MD.

Fish in the study group had been tagged with binary coded wire tags as age-0+ juveniles. Tags were removed from recaptured fish and decoded by personnel at the U.S. Fish and Wildlife Service laboratory in Annapolis, MD, to determine their ages.

Otoliths were extracted, soaked in 10% sodium hypochlorite solution, rinsed with deionized water, and embedded within a Spurr epoxy (Secor et al., 1991). Transverse sections, approximately 1 mm thick, were then cut through the otolith cores with a Buehler Isomet saw. The sections were mounted on glass slides, polished on 600-grain sandpaper, and polished again on a slurry of 0.3-μm alumina until their surfaces were free of pits and abrasions. Polished sections were viewed under a light microscope, and otolith annuli were counted by two independent readers. Annuli comprised a narrow opaque zone and a wide translucent zone under transmitted light microscopy (magnification at 60 or 150×). Annuli were counted along the sulcal ridge in transverse sections. The otolith ages were compared with each other and with the known age of the fish.

Scale vs. otolith study

Scales and otoliths were sampled from recreational landings of striped bass (>91 cm TL) during the May 1992 Maryland "Trophy Striped Bass Fishery." These fish were assumed to have spawned recently in upper Chesapeake Bay tributaries. Five additional fish, large females (>100 cm) collected in 1991 and 1992 from the Patuxent and Nanticoke Rivers by DNR for hatchery propagation purposes, were included in the comparisons. Scales and otoliths were aged independently by a reader at Chesapeake Biological Laboratory (otoliths) and at DNR (scales). Otoliths were prepared and aged as described above. Scale samples for ageing had been removed from the left side of the fish above the lateral line and below the first dorsal fin. Age was determined from either direct interpretation of the scale's annuli or from acetate impressions of the scales. Otoliths and scales were coded so that fish length was unknown to readers.

Results

Known-age study

Striped bass collected in pound nets and drift gill nets in Upper Chesapeake Bay were 3- to 7-year-old males and females. The migratory hatchery striped bass from offshore samples tended to be older, ranging in age from 4 to 7 years old (Fig. 1).

Agreement between known and estimated age for resident striped bass was 100% for both otolith readers (n=13). Exact agreement between estimated and known age for migratory fish (n=24) was 79% and 87% for reader 1 and reader 2, respectively. All migratory fish were estimated to be within one year of their true age. The mean age difference between readers for migratory fishes was not significantly different from 0 (paired t-test: n=37; P=0.66). The mean absolute difference between ages estimated by reader 1 and known-age, a measure of precision, was estimated at 0.13 years. Precision estimated for reader 2 was 0.08 years. Error in age estimates was not related to fish length or age.

Scale vs. otolith study

Age estimates from scales and otolith sections were not significantly different for fish with otolith-estimated ages of 5 to 11 years (Fig. 2; paired t-test: n=30; P=0.41). However, fish with otolith-estimated ages of 22 to 31 years had scale-estimated ages which were, on average, 9 years less than otolith age estimates (Fig. 2; paired t-test: n=30; P<0.0001).

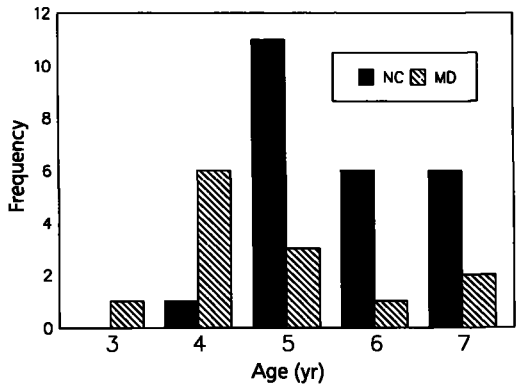

Figure 1

Age-frequency distribution of known-age striped bass from Upper Chesapeake Bay, Maryland (MD) and coastal North Carolina (NC).

Discussion

Annulus formation in otoliths and scales

We verified age estimates of striped bass from annuli observed in sectioned otoliths of fish 3 to 7 years old. Annuli precisely and accurately reflected ages in both resident and migratory Chesapeake Bay striped bass. Annulus appearance at 6 and 7 years was similar to that of annuli from otoliths of much older individuals (Fig. 1 in Secor, 1992). Therefore, we believe that annuli also are formed at a yearly rate in older individuals (e.g. >20 years). Tagged hatchery striped bass represent over 5% of the striped bass population which over-winters in coastal waters off North Carolina (Laney and Cole, 1993). Thus, these fish will continue to provide a pool of known-age material to verify age estimates in older fish. In the next decade it will be possible to verify annulus formation in the oldest fish of the population.

The timing of annulus formation in otoliths was not quantitatively evaluated; samples among months of the year were insufficient to conduct a marginal increment analysis (see Beckman et al., 1988, 1990, 1991). However, we did consistently observe that samples collected during the Maryland Trophy Striped Bass Season in May 1991 and 1992 (see Secor, 1992) contained a newly formed annulus and that no such annulus was observed in otoliths of resident or migratory fish collected in February 1993. Therefore, annulus formation probably occurs during the February–April period. This observation agrees with observations on season of annulus formation in striped bass scales (Merriman, 1941; Heidinger and Clodfelter, 1987).

On the basis of evidence that annuli in otolith ages represent true age in older fish, we believe that scales significantly underestimate age in fish older than 20 years. Scale ages were not significantly different from otolith ages for fish aged 5 to 11 years, ages that corresponded to fish 91 to 110 cm TL. Scale ages were, on average, 9 years less than otolith ages in fish older than 20 years that corresponded to fish >120 cm TL. Because samples were unavailable for ages 12 to 19 years owing to the scarcity of individuals from these year classes (Secor et al.[4]), we could not determine the accuracy of scale ages for this period. In a similar study on southeastern U.S. riverine and reservoir striped bass, Welch et al. (1993) observed that scale ages were in good agreement with otolith ages for fish <90 cm TL but that scale ages were significantly lower than otolith ages for fish 90–10 cm TL. For Sacramento-San Joaquin striped bass, Scofield (1928a) found good agreement between age estimates made from either hardpart for the first eight years of fish life.

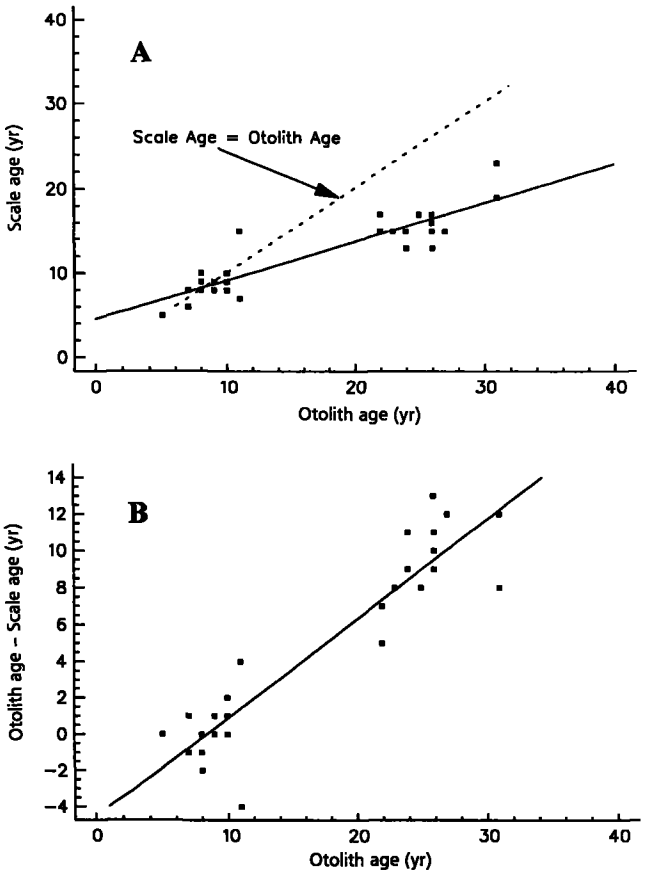

Figure 2

(A) Scale-estimated age vs. otolith-estimated age for Maryland Trophy striped bass (>91 cm TL). Scale age = 4.55 + 0.46 otolith age; n=45; r^2=0.85. For reference, a line corresponding to scale age = otolith age has been plotted. (B) Discrepancy between otolith-estimated and scale-estimated age vs. otolith-estimated age for Maryland Trophy striped bass (>91 cm TL). (Otolith age-Scale age) = −4.55 + 0.54 otolith age; n=45; r^2= 0.88.

Ageing in striped bass stock assessments

Errors in ageing can result in large biases in stock assessments and in mismanagement of fishery resources (Beamish and McFarlane, 1983; Richards et al., 1992). Scientists at the turn of the century recognized that otoliths often provide more accurate and precise estimates of age than do other hard parts (Heinke, 1904; Cunningham, 1905; Haempel, 1910). Indeed, early verification of age estimation based on scales of striped bass relied upon comparisons of age estimates with those based on otoliths

(Scofield, 1928, a and b). However, the popularity and ease of age estimations using scales caused investigators to overlook the importance of verifying ageing methodology (Beamish and McFarlane, 1983).

All stock assessments on migratory populations of striped bass currently rely on interpreting annular features on scales, a largely unvalidated method. Annulus formation in scales of striped bass has been verified for fish up to age three (Humphreys and Kornegy, 1985) and four years (Heidinger and Clodfelter, 1987) in nonmigratory striped bass. Our data indicated that annuli in scales may adequately estimate age for fish less than 12 years of age. Thereafter, scales provided a continuous age distribution between 11 and 20 years of age, and otolith ageing indicated an absence of fish corresponding to these ages (Fig. 2). Therefore, we inferred that otolith-based age determination will provide more accurate estimates after 12 years of age.

A major disadvantage of using otoliths for age determinations is that fish must be sacrificed. Because large and old members of coastal populations have potentially high reproductive values and may be important contributors to annual recruitments (Rago and Goodyear, 1987; Zastrow et al., 1989; Secor et al., 1992; Cowan et al., 1993), it may be undesirable to sacrifice large numbers of these individuals for stock assessment purposes. An alternative approach would be to correct the age estimates from scales by using an otolith vs. scale calibration curve (Fig. 2). Our reported relationship was somewhat variable (r^2=0.85), but with additional otolith samples, reliable prediction of age from scale annuli may be possible.

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An evaluation of six marking methods for age-0 red drum, *Sciaenops ocellatus**

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Mark-recapture studies of fishes can reveal valuable information on movement, mortality, and growth rate (Parker et al., 1990). Despite the many successful methods that have been developed for adult fish, marking of small juvenile fishes is problematic (Chapman and Bevan, 1990). Age-0 fish are typically too small and delicate for many marking methods.

A few methods for marking age-0 fishes have been developed: coded wire microtags (Thrower and Smoker, 1984; Brodziak et al., 1992; Bumguardner et al., 1992); spray paint marking (Phinney et al., 1967; Pierson and Bayne, 1983); fluorescent staining (Hettler, 1984; Secor et al., 1991a; Szedlmayer and Able, 1992); and external plastic minitags (Floy Tag and Mfg. Co., Inc., Seattle, WA). All of these methods have advantages and disadvantages based on the attributes of each species. Thus, there is a need to test different marking methods on small size classes of different species to determine the most suitable methods.

Two marking methods have been reported for age-0 red drum, *Sciaenops ocellatus*: 1) spray paint marking,[1] and 2) coded wire microtags (Bumguardner et al., 1992). Fluorescent staining is another method that may be useful for age-0 *S. ocellatus* and has been successfully applied to juvenile red sea bream, *Pagrus major* (Tsukamoto et al., 1989), and to larval and juvenile striped bass, *Morone saxatilis* (Secor et al., 1991a). However, it is not possible from these studies to determine the most useful marking method for age-0 *S. ocellatus*. Hence, we examined mortality, mark retention, and growth in age-0 *S. ocellatus* that were marked by one of six different methods: 1) coded wire microtags, 2) external plastic minitags, 3) alizarin complexone, 4) oxytetracycline dihydrate [OTC], 5) red fluorescent spray paint, and 6) green fluorescent spray paint.

Materials and methods

We marked 614 cultured age-0 *S. ocellatus* (mean standard length [SL] ± standard deviation [SD]=67.4 ± 8.7 mm; range=48–95 mm SL) on 4–5 February 1993. Fish were anesthetized with tricane methanol sulfate (50 mg MS222/L seawater), weighed, measured, and randomly assigned to one of the following treatments: red fluorescent paint (red), green fluorescent paint (green), external plastic tags (plastic), binary coded wire microtags (wire), oxytetracycline-dihydrate (250 mg OTC/L 25 ppt seawater for 15 h), and alizarin-complexone (250 mg alizarin/L 25 ppt seawater for 15 h).

Wire tags were injected into the left epaxial muscle with a specially designed hypodermic needle (Northwest Marine Technology, Shaw Island, WA). The plastic tags (numbered disk: 0.5×3×7 mm) were attached posterior to the dorsal fin with elastic thread sewn through the left and right epaxial muscles. Red and green paints were applied at a pressure of 70 to 100 psi from a distance of 30 to 50 cm (Phinney et al., 1967). A total of 614 fish were marked and classified as follows: 100 OTC, 114 alizarin, 100 red, 100 green, 100 plastic, and 100 wire. All fish were held in a 7,570-L closed seawater system, and differentially marked fish were separated by flow through partitions. Ammonia, nitrite, and nitrate levels were controlled with an oyster shell biological filter (mean ± standard error [SE]: NH_3=0.018 ±0.003 ppm; NO_2=0.253 ± 0.047 ppm; NO_3=47.4 ± 1.9 ppm). Particulates were removed with a sand filter. Salinity was held constant by addition of artificial seasalts or freshwater (mean salinity ± SE=25.0 ± 0.2 ppt). Temperature was held constant with three 1,000-W heaters (mean temperature ± SE=20.8 ± 0.2°C).

Fish mortalities were counted and removed daily for 68 days. All fish were fed daily at 5% body weight per day with Zeigler salmon crumbles no. 2 pellet food (Zeigler Bros. Inc., Gardners, PA). At 25, 48, and 68 days, all fish from each treatment were anesthetized, weighed, measured, and food was adjusted for growth to maintain the daily 5% body weight ration. Red and green paint marks were verified with an ultraviolet light (paint was not visible under white light). Fish were considered marked if at least one granule of pigment was observed. Also, when fish were anesthetized and measured, we randomly sacrificed 20 fish from

* Contribution 8-944903 of the Alabama Agricultural Experiment Station, Auburn University, Mobile, Alabama 36615.

[1] McMichael, Robert H., Jr. Florida Department of Natural Resources, St. Petersburg, FL. Personal commun., 1992.

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each treatment: from OTC and alizarin treatments for otolith mark examination, from wire treatments for wire removal, and from other treatments for future otolith analysis. All samples were preserved by freezing. In estimating percent survival, it was assumed that all fish that were sacrificed (alive and healthy at time of sample) would have survived the 68-d experimental period. The actual survival of sacrificed fish would be lower than 100%, but the difference in survival rate among treatments would be expected to increase if actual survival rates for all fish were known.

Whole sagittal otoliths were removed from OTC and alizarin treatments and viewed with an Olympus BH–2 compound microscope under 100-W ultraviolet light. When fluorescent marks were not visible on whole otoliths, they were sectioned and polished for increased resolution (Secor et al., 1991b; Szedlmayer and Able, 1992). Wire tags were located by making a sagittal incision of the epaxial muscle and examined under a Nikon stereo-microscope. If wire tags were not located by dissection, fish were X-rayed to locate tags.

We compared instantaneous mortality rates with analysis of covariance (ANCOVA) and percent tag retention with a randomized block analysis of variance (ANOVA) with day as blocks and marking method as the factor (Zar, 1984). We compared standard lengths (SL) and weights over marking method with ANOVA for each sample date. If significant differences ($P<0.05$) were detected, we compared the means (ANOVA) or slopes (mortality; ANCOVA) with Newman-Keuls range test (Zar, 1984).

Results

Instantaneous mortality rates (log percent survival=$-Zd + Y$) for OTC ($-Z=0.0013$, $r^2=0.92$), alizarin ($-Z=0.0014$, $r^2=0.80$), and wire ($-Z=0.0016$, $r^2=0.78$) marking were significantly less than those for plastic ($-Z=0.0023$, $r^2=0.90$), red ($-Z=0.0025$, $r^2=0.96$), and green treatments ($-Z=0.0033$, $r^2=0.92$; Fig.1). Survival curves showed similar patterns with higher mortality in the first 40 days; thereafter mortality was reduced (Fig. 1).

Percent mark retention of alizarin, OTC, and wire tags were significantly greater than those of other treatments. The highest mark retention was observed for OTC- and alizarin-marked fish (100%; Table 1). Wire-marked fish also showed high retention rates (85–100 %). Red-, green-, and plastic-marked fish showed significant declines in tag retention over the 68 days (Table 1).

Mean SL and weight showed no significant difference among treatments on day 1, 25, 48, and 68 (Tables 2 and 3). Growth rates were similar among all treatments: 1.0–1.1 mm SL/d and 0.5–0.6 g wet wt/d (Tables 2 and 3).

Discussion

Wire tags provided the best overall performance of the marking methods tested over this two-month

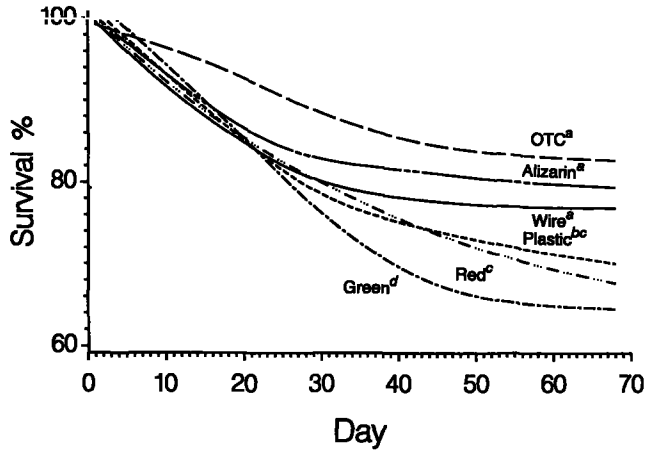

Figure 1

Percent survival of age-0 red drum, *Sciaenops ocellatus*, marked by six methods. Treatments with different letters were significantly different ($P<0.05$).

Table 1

Percent mark retention among sample days of age-0 red drum, *Sciaenops ocellatus*, marked by one of six methods: wire = coded wire microtag; plastic = external plastic tag; red = red fluorescent paint; green = green fluorescent paint; OTC = oxytetracycline dihydrate; and Ali = alizarin complexone. Numbers in parenthesis are sample sizes. Treatments with different letters are significantly different ($P<0.05$).

	Marking method					
Day	OTC[a]	Ali[a]	Wire[a]	Red[b]	Plastic[b]	Green[b]
25[a]	100.0(21)	100.0(20)	90.0(20)	80.5(82)	78.2(78)	42.3(78)
48[ab]	100.0(20)	100.0(20)	100.0(20)	55.8(52)	49.1(53)	39.1(46)
68[c]	100.0(19)	100.0(21)	85.0(20)	14.8(27)	24.1(29)	16.0(25)

study. Wire-marked fish showed low mortality and high tag retention compared with those marked by the plastic and paint methods. Also, individual fish are identifiable with wires which can be more useful than batch marking with OTC and alizarin. Of particular interest were the high tag-retention rates of wires (85–100 %). In past studies of wire tags injected in the cheek muscle of age-0 *S. ocellatus*, considerable tag loss was shown over the first 114 d: 67.3% tag retention after 24 h, 47% from 2 to 23 d, and 45%

Table 2

Mean standard lengths and growth rates of age-0 red drum, *Sciaenops ocellatus*, marked by one of six methods: wire = coded wire microtag; plastic = external plastic tag; red = red fluorescent paint; green = green fluorescent paint; OTC = oxytetracycline dihydrate; and Ali = alizarin complexone. Treatments were not significantly different ($P<0.05$). SL=standard length, SE=standard error, n=sample size.

		Mark method					
Day	Measure	Wire	Plastic	Red	Green	OTC	Ali
1	SL (mm)	65.9	66.9	66.8	67.1	68.9	67.6
	SE	0.8	0.9	0.9	0.9	0.9	0.7
	n	100	100	100	100	100	114
25	SL (mm)	90.5	91.6	88.8	90.5	90.7	91.6
	SE	1.0	1.1	1.1	1.1	1.1	1.0
	n	80	78	82	78	88	95
48	SL (mm)	116.7	117.9	112.5	118.1	117.5	114.0
	SE	1.3	1.7	2.0	1.6	1.6	1.4
	n	57	53	52	46	64	71
68	SL (mm)	131.1	134.7	134.4	134.3	128.7	129.1
	SE	2.2	2.9	2.0	2.3	1.8	2.1
	n	37	29	27	25	44	50
	Growth (mm/d)	1.1	1.1	1.1	1.1	1.0	1.0
	r^2	0.86	0.83	0.83	0.85	0.80	0.83

Table 3

Mean weights and standard error (SE) of age-0 red drum, *Sciaenops ocellatus*, marked by one of six methods: wire = coded wire microtag; plastic = external plastic tag; red = red fluorescent paint; green = green fluorescent paint; OTC = oxytetracycline dihydrate; and Ali = alizarin complexone. Treatments were not significantly different ($P<0.05$). WT=weight, n=sample sizes.

		Mark method					
Day	Measure	Wire	Plastic	Red	Green	OTC	Ali
1	WT (g)	4.9	5.2	5.2	5.2	5.7	5.2
	SE	0.2	0.2	0.2	0.2	0.2	0.2
	n	100	100	100	100	100	114
25	WT (g)	12.9	13.5	14.0	13.5	13.4	13.1
	SE	0.4	0.5	1.1	0.5	0.5	0.4
	n	80	78	82	78	88	95
48	WT (g)	30.1	29.5	27.9	28.2	27.8	27.2
	SE	1.1	1.3	1.4	1.1	1.1	1.0
	n	57	53	52	46	64	71
68	WT (g)	41.9	44.7	45.1	42.2	37.6	38.1
	SE	2.1	2.8	2.2	2.5	1.7	2.0
	n	37	29	27	25	44	50
	Growth (g/d)	0.6	0.6	0.6	0.6	0.5	0.5
	r^2	0.80	0.77	0.69	0.80	0.74	0.72

from 24 to 114 d (Bumguardner et al., 1992). A similar wire tag loss rate was observed in striped bass tagged horizontally in the cheek muscle (22.2–30.7% retention over the first 70 d; Dunning et al., 1990). However, Dunning et al., (1990) also reported that wire retention rates substantially increased when stripped bass were tagged in the snout (63–98.5%), nape (93.8–99.3%), or vertically in the cheek (82.7–87.0%) over the first 70 days. Also, Klar and Parker (1986) showed 99% tag retention after 90 days if wires were injected into the epaxial muscle of striped bass. Our results agree with the higher tag retention rates reported by Dunning et al., (1990) and Klar and Parker (1986); there was little indication of tag loss in the first days after marking. We suggest that higher wire retention resulted from mark location, because current wires were injected deep (4–5 mm) into the epaxial muscle and had little chance of expulsion.

Although wire tags showed the best overall performance compared with other tags, the method was the most labor intensive of all methods, because of the required dissection, removal, and reading of wires. If individual growth rates are needed and both personnel and budget are limiting, plastic tags may be useful. Plastic tags can be read directly without harm to the fish, but they also showed significant tag loss compared with other methods and should be limited to short experiments of no more than 25 days.

Paint marking methods showed greater mortalities and lower retention times compared with other methods but are useful in situations where fish can only be held for short periods (1–2 h, see Weinstien et al., 1984). However, paint marking methods should also be limited to short-term experiments because of significant mark loss after 25 days.

If fish movements or survival are the objectives and fish can be held for long (≈15 h) marking periods, then OTC or alizarin may be the best marking methods. Both methods showed higher tag retention (100%) and lower mortality rates compared with plastic minitags or paint methods. Other studies have shown long-term retention for these chemicals: for example, OTC marks in chum salmon, *Oncorhynchus keta* (Bilton, 1986) and alizarin marks in *P. major* (Tsukamoto et al., 1989) were both detected two years after marking. Another advantage of OTC and alizarin staining was that handling was minimal and probably caused the least amount of stress among all the marking methods, as reflected in the lower mortality rates. Therefore, these fluorescent stains would be most suitable for long-term studies where individual growth rates are not needed and for batch marking large numbers of fish, for example prior to release of hatchery reared fish (Tsukamoto et al., 1989; Secor et al., 1991a).

One difference in the present study was the use of oxytetracycline-dihydrate instead of oxytetracycline-hydrochloric acid (HCL), as used in other studies. (Hettler, 1984; Tsukamoto and Shima, 1990; Secor et al., 1991a). The dihydrate form of OTC was advantageous in that it did not cause a reduction in pH as observed with the HCL form. This difference may account for the low mortality observed after 15 hours in the OTC bath (i.e. no fish died during the 15-h marking period). One advantage of the alizarin stain over the OTC marker was the ease in detecting the fluorescent marks. When whole otoliths were examined only 2 of 91 alizarin otoliths needed further cutting and polishing to detect the stain, whereas 23 of 83 OTC otoliths needed sectioning before OTC marks were visible.

As indicated by growth rates, fish acclimated well to the closed seawater system. Although we did not have a control group of fish, growth rates in the present study (1.0–1.1 mm SL/d) were similar to or greater than previous studies of unmarked *S. ocellatus* of similar sizes and temperatures as the current study: 0.8 mm/d from Tampa Bay (Peters and McMichael, 1987), 0.8 mm/d from Charleston Harbor (Daniel, 1988), and 1.0 mm/d for reared fish in Texas (Colura et al., 1990). Also, we were not attempting to compare growth rates of marked fish with those of wild populations or those of unmarked laboratory fish but rather to determine the most useful tag of the methods tested.

Thus, we recommend wire tags when individual marks are needed because of lower mortality and higher mark retention compared with those from plastic minitags. We recommend alizarin when batch-marking methods are needed and individual growth rates are not critical, because of lower mortality and higher retention compared with those from paint methods and because of ease of detecting mark compared with OTC marking.

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Stranding and mortality of humpback whales, *Megaptera novaeangliae*, in the mid-Atlantic and southeast United States, 1985–1992

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Marine mammal strandings are a result of, or result in, mortality that may be attributed to natural or anthropogenic factors. As such, stranding data can provide insight on spatial distribution, seasonal movements, and mortality factors pertaining to marine mammal populations (Woodhouse, 1991; Mead[1]).

The general distribution and migratory movements of humpback whales, *Megaptera novaeangliae*, in the western North Atlantic are well known from numerous studies based on the identification of individual animals and on other techniques. Humpbacks feed in high latitude areas during the summer months, including waters of the Gulf of Maine, eastern Canada, West Greenland, and Iceland (Hain et al., 1982; Martin et al., 1984; Perkins et al., 1984; Katona and Beard 1990). In the winter, whales from all populations migrate to breeding grounds in the West Indies (Balcomb and Nichols, 1982; Mattila and Clapham, 1989; Mattila et al., 1989; Katona and Beard 1990). Between these migratory end points, little is known of the distribution of the species. In recent years, however, there has been an apparent increase in the frequency of sightings of humpback whales off the mid-Atlantic coast of the United States (Swingle et al., 1993). Furthermore, a considerable number of strandings have been documented along the mid-Atlantic and southeast coasts, many in midwinter, a time when the majority of humpbacks are thought to be located in tropical waters. In this paper, we analyze data from these strandings, discuss implications regarding distribution and possible spatial segregation by age class, and examine apparent causes of mortality.

Methods

Study area and period

The study covers the coastal area of eastern North America extending from New Jersey(40°28'5N, 74°00'0W) to southern Florida (25°12'N, 80°13'W), consisting of 2,319 km of coastline (Fig. 1). The eight-year period from 1 January 1985 through 31 December 1992 was investigated. Stranding data were obtained from the United States Museum of Natural History, Smithsonian Institution's Marine Mammal Events Program (MMEP). This information was confirmed and augmented by comparison with data from stranding response personnel involved with the Northeast and Southeast Regional Stranding Networks and with data published in newspaper reports. Organizations involved in the regional stranding networks operate under a permit issued by the National Marine Fisheries Service. The names and organizations of investigators responding to specific stranding events are on file.

Analyses

The following data were recorded for each stranding: date, location, sex, body length, and the presence or absence of body markings that may indicate a possible anthropogenic cause of mortality (e.g. ship strike or fishery interaction).

Stranding incidents among states were compared by using a ratio of the number of strandings in the state to

[1] Mead, J. G. 1979. An analysis of cetacean strandings along the eastern coast of the United States. *In* J. R. Geraci and D. J. St. Aubin (eds.), Biology of marine mammals: insights through strandings, p. 54–68. Report to U.S. Marine Mammal Comm. Contract MM7AC020. U.S. Dep. of Commer., Natl. Tech. Info. Serv. PB-293 890.

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the length of coastline along the state. This is referred to as the stranding incidence ratio (SIR). Length of coastline was calculated from Ringold and Clark (1980).

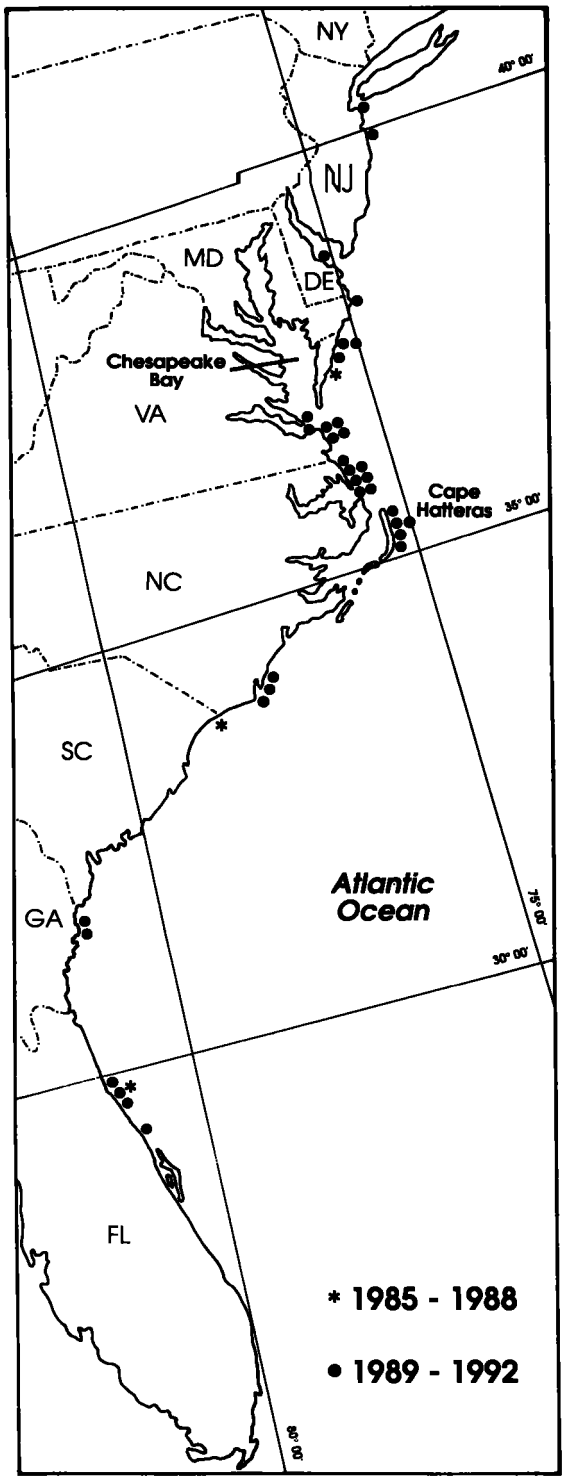

Figure 1

Locations of humpback whale, *Megaptera novaeangliae*, strandings from New Jersey to southern Florida, 1985 through 1992.

Reproductive class was inferred from body-length data. Animals of less than 8 m in length were considered to be dependent, nursing calves (Nishiwaki, 1959; Rice, 1963). We considered newly independent calves to be animals greater than 8.0 m but less than 9.9 m (calculated from Katona et al., 1983[2]). Males between 9.9 m and 11.6 m and females between 9.9 m and 12.0 m were considered sexually immature but not newly independent. Animals greater than 11.6 m (males) and 12.0 m (females) were considered sexually mature (Nishiwaki, 1959; Rice, 1963).

The Mann-Whitney *U*-test (Sokal and Rohlf, 1981) was used to test for differences between the number of strandings that occurred in the period 1985–88 versus 1989–92. Time periods were chosen to coincide with reported changes in observations of live animals in the same region (Swingle et al., 1993). The hypothesis that strandings occurred randomly throughout the study area was tested by chi-square analysis in a 2×2 contingency table (Sokal and Rohlf, 1981). The hypothesis that stranding events were not influenced by season was tested by chi-square analysis. Seasons were winter (January–March), spring (April–June), summer (July–September) and fall (October–December). Seasonal groupings were constructed so that the winter season would approximately coincide with the period of peak humpback occupancy of the breeding grounds, as reported by Mattila and Clapham (1989). The hypothesis that stranding occurrence was not influenced by sex was tested by chi-square analysis in a 2×2 contingency table.

Factors relating to mortality were taken from the written reports of on-site stranding response personnel from the Northeast and Southeast Regional Stranding Networks or, when not available, from the synthesis of such reports contained in the MMEP. The experience of stranding network response personnel is variable, and factors contributing to death or interpretation of bodily injury can be subject to debate. If on-site investigators recorded references to rope marks, propeller marks, broken bones, large gashes, etc., or directly suggested ship strike or entanglement as a potential cause of death, we attributed the death to possible anthropogenic causes. All mortality not suggesting anthropogenic trauma were grouped into a "natural" mortality category. This included animals that were euthanized but showed no other indications of human interaction. If a necropsy was conducted and no mention was made of body trauma, we assumed natural mortality. Carcasses that were reported to be in advanced stages of decomposition were eliminated from consideration.

[2] Calculated as length at birth, 4.5 m; growth rate, 45 cm per month; 12 month growth period = 9.9 m.

Results

A total of 38 stranded humpback whales were recorded between 1 January 1985 and 31 December 1992 (Table 1). One animal (4/14/85) was not included in the analyses because body condition ("mummification") indicated death or stranding, or both, occurred prior to the study period. The number of strandings by year was as follows: 0 in 1985, 2 in 1986, 0 in 1987, 1 in 1988, 3 in 1989, 8 in 1990, 7 in 1991, and 16 in 1992. Significantly more animals stranded during the period 1989 to 1992 (n=34), than from 1985 to 1988 (n=3) (Mann-Whitney U: Z=–2.32, P=0.02). Of the strandings recorded in our database, 92% (34/37) occurred after January 1989.

Significantly more strandings occurred along 170 km of coastline between Chesapeake Bay, Virginia, and Cape Hatteras, North Carolina (χ^2=70.67, df=1, P<0.01), than occurred in the rest of the study area. In this region, which represents 7.3% (170 km/2,319 km) of the coastline within the study area, 43% (16/37) of all strandings occurred. A second cluster of strandings occurred along the coast of northern Florida; however, this grouping was not found to be significant (χ^2=5.98, df=1, P=0.25). The region, which represents 4.7% (110 km/2319 km) of the study area's coastline, contained 13.5% (5/37) of all strandings.

The number of strandings per state was highly variable (Table 2). Numerically, the highest number of strandings occurred in North Carolina (n=15), but the incidence of strandings (strandings per kilometer of coastline) was greatest in Virginia (SIR=0.055, n=10), followed by North Carolina (SIR=0.031). South Carolina had the lowest incidence of strandings (SIR=0.003, n=1). The stranding incidence ratio for the entire study area was 0.016. All states recorded at least one stranding.

There were no significant differences in stranding occurrence by season (χ^2=4.22, df=3, P=0.24) (Fig. 2). However, only 8% (3/37) of all strandings occurred during the summer (July-September). Strandings occurred with the greatest frequency in April (n=6) followed by February, March, and October (n=5 each), and least in July and August (n=0 each). In 1992 (the most recent year of the study), strandings were spread over a greater number of months than any of the seven previous years.

Data on body length were available for 25 animals. Body length indicated all animals were sexually immature but none were dependent calves. Sixty-eight percent (17/25) of the animals were considered newly independent calves. Information on gender was available for 26 animals. Fifty percent (13/26) were female and 50% (13/26) were male.

Mortality

Of the 37 animals, an advanced stage of decomposition eliminated 13 from analysis for potential cause of death. Four additional animals were insufficiently examined or information was inadequately reported to determine a cause of death or the presence or absence of injury or scars. Of the 20 remaining animals, 30% (6/20) had major injuries potentially attributable to a ship strike and 25% (5/20) had injuries consistent with possible entanglement in fishing gear. One animal exhibited scars consistent with past entanglement or ship strike, or both, and was emaciated at the time of stranding. Thus, up to 60% (12/20) of the sufficiently inspected animals showed signs that anthropogenic factors may have contributed to or been directly responsible for their death. However, the possibility that some animals sustained body trauma after death can not be ruled out. Unfortunately, few animals were sufficiently necropsied to establish an unequivocal cause of death.

Discussion

These results suggest that stranding of humpback whales along the mid-Atlantic and southeast coastal areas of the United States has increased. All stranded animals were sexually immature and males and females stranded with equal frequency. However, natural mortality may show a gender bias that has been obscured by the high number of deaths potentially due to anthropogenic factors. Strandings occurred throughout the fall, winter, and spring seasons, but few strandings occurred during the summer months.

There are several possible explanations for the apparent increase in strandings, including changes

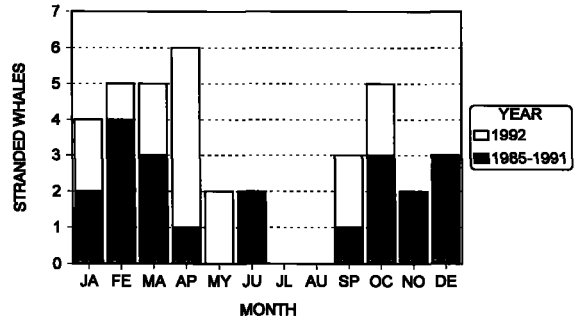

Figure 2

Humpback whale, *Megaptera novaeangliae*, strandings by month, 1985 through 1992.

Table 1

Humpback whale, *Megaptera novaeangliae*, strandings, New Jersey to south Florida, 1985–1992. unk = unknown; est = estimated.

Date	Location	Sex	Length	Necropsy	Carcass analyses	Potential cause of death
14 Apr 85	Carolina Beach, NC 34°02'--" N 078°53'--" W	unk	unk	no	old carcass (mummy or skeleton) not included in analyses	unknown
15 Feb 86	Cobb Island, VA 37°2-'--" N 075°4-'--" W	F	10.8 m	partial	fresh, no obvious sign of external trauma or disease	natural
07 Mar 86	N. Myrtle Beach, SC 33°48'--" N 078°44'--" W	F	11.7 m	yes	live stranding; euthanized	natural
08 Dec 88	St. Johns, FL 29°54'--" N 081°20'--" W (est)	unk	7.8 m (est)	no	advanced decomposition	unknown
14 Jan 89	St. Augustine, FL 29°55'3-" N 081°17'3" W	F	7.6 m (est)	unknown	advanced decomposition	unknown
18 Sep 89	Monmouth Beach, NJ 40°19'55" N 073°57'17" W	unk	8.0 m (est)	no	entangled in gear, apparently anchored by gear to bottom	entanglement
18 Dec 89	Assateague Island, VA 37°50'--" N 075°20'--" W	F	8.7 m[1]	yes	live stranding, no external injuries noted	natural
27 Jan 90	New Smyrna Beach, FL 29°00'0-" N 080°52'2-" W	M	7.9 m	yes	advanced decomposition	unknown
05 Feb 90	Nags Head, NC 35°56'5-" N 075°36'5-" W	unk[2]	11.1 m	partial	broken jaw bone, head damaged[3]	ship strike
24 Feb 90	Corolla Beach, NC 36°15'--" N 075°46'--" W	unk	9.0 m (est)	unknown	fresh, insufficient information	unknown
24 Mar 90	Sanderling, NC 36°11'5-" N 075°45'2-" W	unk	7.6 m – 8 m (est)	no	advanced decomposition	unknown
01 Apr 90	Virginia Beach, VA 36°4-'--" N 075°5-'--" W	F	9.6 m	yes	fresh, net/line marks on tail stock, right half of fluke had line marks	entanglement
19 Jun 90[4]	Virginia Beach, VA 36°56'15" N 076°03'30" W	F	8.3 m	yes	fresh, no evidence of scars or injuries	natural
20 Jun 90	Virginia Beach, VA 36°45'15" N 075°56'30" W	F	8.2 m	yes	live stranding; euthanized, rope marks on flukes, emaciated	entanglement

Table 1 (continued)

Date	Location	Sex	Length	Necropsy	Carcass analyses	Potential cause of death
19 Nov 90	Norfolk, VA 36°56'00" N 076°11'30" W	M	9.5 m	no	various rope burns, abrasions on tail stock, rope scars on left flipper	entanglement
05 Feb 91	St. Johns, FL 29°59'06" N 081°18'48" W	M	9.4 m	partial	moderately decomposed, no external injuries noted	natural
02 Mar 91	Bald Head Island, NC 33°55'0-" N 077°56'4-" W	M	8.5 m	no	inaccessible	unknown
15 Oct 91	Kill Devil Hills, NC 36°01'--" N 075°39'--" W	unk[5]	9.3 m[6]	partial	no external injuries noted	natural
25 Oct 91	Nags Head, NC 35°56'5-" N 075°37'0-"	M	9.1 m (est)	no	no external injuries noted	natural
27 Oct 91	Bodie Island, NC 35°46'0-" N 075°29'1-" W	unk	10.0 m	no	advanced decomposition	unknown
08 Nov 91	Island Beach State Park, NJ 39°50'00" N 074°05'12" W	M	9.0 m	yes	four propeller cuts, one through the occipital condyle, were cause of death	vessel strike
25 Dec 91	Carolina Beach, NC 34°01'--" N 077°54'--" W	F	9.9 m	no	insufficient information	unknown
03 Jan 92	Salvo, NC 35°20'9-" N 075°21'8-" W	M	10.4 m	no	no external injuries noted	natural
30 Jan 92	Oregon Inlet, NC 35°46'5-" N 075°31'9-" W	unk	unk	no	inaccessible	unknown
14 Feb 92	Virginia Beach, VA 37°01'--" N 076°07'--" W (est)	M	8.5 m[1]	yes	left eye socket and left mandible fractured, signs of healing from injuries at point of fractures	vessel strike
10 Mar 92	Avon, NC 35°20'--" N 075°21'--" W	F	10.7 m	partial	left fluke "scalloped" possibly due to ship strike or entanglement, evidence of healed rope/net scars on caudal peduncle	past entanglement or ship strike
19 Mar 92	North Core Banks, NC 35°01'1-" N 076°06'0-" W	M	11.0 m	no	advanced decomposition	unknown

Table 1 (continued)

Date	Location	Sex	Length	Necropsy	Carcass analyses	Potential cause of death
14 Apr 92	St. Johns, FL 29°45'--" N 081°10'--" W (est)	unk	8.6 m existing length	no	advanced decomposition	unknown
16 Apr 92	Assateague Island, MD 38°12'--" N 075°08'--" W	F	8.9 m	yes	no external trauma, but skull disarticulated, blunt trauma to left side	vessel strike
18 Apr 92	Southport, NC 33°42'8-" N 77°55'4-" W	M	9.5 m	no	advanced decomposition	unknown
22 Apr 92	Hatteras, NC 35°11'4-" N 075°46'3-" W	F	8.9 m	yes	no external trauma, but extensive skeletal damage, "probably struck by boat"	vessel strike
30 Apr 92	Nags Head, NC 35°22'--" N 075°29'--" W	unk	9.2 m (est)	no	advanced decomposition inaccessible	unknown
16 May 92	Ossabaw Island, GA 31°45'7-" N 081°05'0-" W	M	> 7.2 m	no	advanced decomposition	unknown
17 May 92	St. Catherines Island, GA 31°38'2-" N 081°08'2-" W	unk	unk	partial	advanced decomposition	unknown
22 Sep 92	Prime Hook National Wildlife Refuge, DE 38°55'--" N 075°05'--" W	F	8.3 m (est)	yes	advanced decomposition	unknown
28 Sep 92	Assateague Island, VA 37°53'--" N 075°22'--" W	M	8.9 m (est)-part of head buried	yes	advanced decomposition	unknown
09 Oct 92	Metompkin Island, VA 37°46'--" N 075°32'--" W	F	8.7 m	yes	"probably boat strike," 3 areas of hemorrhage noted	vessel strike
22 Oct 92	Virginia Beach, VA 36°46'15" N 075°57'02" W	M	9.1 m	yes	"obvious entaglement scars" on leading edge of fluke and around caudal peduncle	entanglement

[1] Animal towed prior to measurement, therefore measured length may be greater than actual length.

[2] Discrepancy in reported gender. Original stranding report stated female. MMEP reported male.

[3] Discrepancy in reported body condition. Original stranding report stated broken jaw bone and head damage. MMEP had no report of body condition.

[4] Discrepancy in reported date. Original stranding report stated 19 June 1990. MMEP reported 19 May 1990.

[5] Discrepancy in reported gender. Original stranding report stated female. MMEP reported as unknown.

[6] Discrepancy in reported body length. Original stranding report stated 9.3 m. MMEP reported an estimated length of 660 cm.

Table 2

Humpback whale, *Megaptera novaeangliae*, strandings by state; 1985 through 1992.

State	Number of strandings	Kilometers of coastline	SIR: Number of strandings / km of coastline
Virginia	10	180.6	0.055
North Carolina	15	485.5	0.031
Delaware	1	45.2	0.022
Maryland	1	50.0	0.020
Georgia	2	161.3	0.012
New Jersey	2	209.7	0.010
Florida	5	935.5	0.005
South Carolina	1	301.6	0.003

in observer effort, mortality factors, and whale distribution. That increased observer effort could account for the increase seems unlikely. The size of stranded humpback whales and both the public and media interest in such events results in few carcasses escaping notice. Additionally, strandings of finback whales, *Balaenoptera physalus*, over the same time period have remained relatively constant (1985 to 1988, n=10; 1989 to 1992, n=9)) (calculated from MMEP, Smithsonian Institution). An increase for this large baleen species might also be expected if the reported humpback change were due solely to increased observer effort.

If the reported increase in strandings is not an artifact of observer effort, it may be due to an increase in factors resulting in mortality, an increase in the number of animals inhabiting the study area, or both. While the tonnage of cargo moving through Atlantic ports in 1989 showed a 9% increase over the mean of the previous four years (calculated from Anon., 1991), the number of vessels using the Chesapeake Bay area, and probably the rest of the Atlantic coast, has decreased because ships capable of carrying greater tonnage are being used (Pringer[3]). While a decline in vessel traffic may result in a decreased risk to whales, it is possible that these larger, faster, deeper draft vessels pose a greater danger than the slower, shallower draft vessels of the past. In addition to commercial shipping, some areas, such as near Chesapeake Bay and northern Florida, are subject to substantial use by military vessels. However, data pertaining to trends in military vessel traffic were not available.

Evidence also indicates that as much as 25% of the reported mortality may be attributable to interaction with commercial fishing activity, such as gill netting. North Carolina's coastal sink gillnet fishery expanded dramatically during the 1980's (Ross[4]). South Carolina, the state with the lowest SIR, banned the commercial use of gill nets in 1987 (with the exception of a tended shad net fishery) (Moran[5]). However, fishing effort in the entire study area is inadequately monitored to determine trends (Read, in press; Bisack[6]).

While changes in shipping and commercial fishing activity may represent increased hazards to animals inhabiting the study area, they seem inadequate to account for the dramatic change in stranding levels reported. Each of these hazards existed prior to 1989, the period when strandings began to increase. The most likely explanation for the reported increase in mortality appears to be increased use of this area by juvenile humpback whales that are then exposed to such hazards.

Although few standardized marine mammal surveys consistently cover the study area, anecdotal and published observations point to a recent increase in live sightings of humpback whales in coastal waters of Florida and Georgia (Kraus[7]), North Carolina (Barrington[8]), Virginia (Swingle et al., 1993), and Maryland (Driscoll[9]). Although reliable estimation of the length of free-swimming whales is difficult, there is general agreement among observers that most, if not all, of the animals frequenting the area are small.

Changes in humpback whale distribution in relation to changes in prey composition and abundance have been demonstrated elsewhere (Payne et al., 1986; Piatt et al., 1989; Payne et al., 1990), and such a prey shift may account for or be an important fac-

[3] Pringer, Captain M. Association of Maryland Pilots, Baltimore, MD 21228. Personal commun., January 1993.

[4] Ross, J. L. 1989. Assessment of the sink net fishery along North Carolina's Outer Banks, fall 1982 through spring 1987, with notes on other coastal gill net fisheries. Special Sci. Rep. 50, North Carolina Dep. of Environ., Health and Nat. Resour., Moorehead City, NC, 54 p.

[5] Moran, J. South Carolina Wildlife and Marine Resource Department, Charleston, SC 29422. Personal commun., September 1993.

[6] Bisack, K. 1992. Sink gill net fishing activity in the North Atlantic as reflected in the NEFSC weightout database: 1982–1991. U.S Dep. Commer., NOAA, Natl. Mar. Fish.Serv. Northeast Fish. Sci Cent., Woods Hole, MA 02543. Unpubl. manuscr., 4 p.

[7] Kraus, S. New England Aquarium, Boston, MA 02110. Personal commun., March 1993.

[8] Barrington, P. North Carolina Aquarium, Fort Fisher, Kuri Beach, NC 28449. Personal commun., April, 1993.

[9] Driscoll, C. NMFS, Office of Protected Resources, Silver Spring, MD 20910. Personal commun., March 1993.

tor in the change in whale distribution suggested here. While data on changes in prey distribution were not available, the first observations of winter feeding humpbacks were documented in the nearshore waters of Maryland (deGroot[10]) and Virginia (Swingle et al., 1993), during the winters of 1991 and 1992.

An additional possibility is that the humpback whale population in the western North Atlantic may be increasing and expanding its range such that habitats historically occupied are being recolonized. Several authors (Katona and Beard, 1990; Sigurjonsson and Gunnlaugsson, 1990) have reported numerical increases for this population, although this may be due to increased effort resulting in more accurate estimates of abundance.

Humpback whales may have always been present during winter in offshore waters of the study area, but a shift in prey abundance or distribution, or both, may have brought them into areas where death would result in stranding, rather than have caused them to be lost at sea. However, offshore concentrations were not detected during 1978–82 aerial surveys (CeTAP[11]) or during 1980–88 ship board surveys (Payne et al.[12]).

While juvenile whales can be expected to exhibit higher mortality than adults (Sumich and Harvey, 1986; Kraus, 1990a), the absence of adult animals from the stranding record may provide support for the suggestions of Swingle et al. (1993) that winter or migratory segregation, or both, is occurring. Foraging opportunities on the breeding grounds are rare (Dawbin, 1966; Baraff et al., 1991), and it may be adaptive for some juvenile animals to remain and feed in mid-latitude areas, rather than to migrate with adults. If occupying the breeding grounds is the preferred behavior, individuals remaining in higher latitude areas may be those that failed to obtain sufficient resources during the feeding season. Such nutritionally stressed animals may be more susceptible to all forms of mortality, natural or anthropogenic. Nutritionally stressed juveniles and newly weaned calves in particular may be vulnerable to the effects of the parasitic nematode *Crassicauda boopis* (Lambertsen, 1992).

If winter foraging opportunities are sufficient, juveniles may delay their return to traditional feeding areas and may eventually occupy new habitat. This may be one mechanism by which a species establishes itself in new areas or reoccupies historic sites. This process may be reflected in the stranding record. There seems to be a progressive trend not only for an increased number of strandings but for strandings to take place in a greater variety of months.

A high percentage of animals exhibited signs that anthropogenic interactions could be implicated in their death. However, there are reasons to believe that mortality estimates based on available stranding data could under- or overestimate the impact of human interaction. For example, stranded animals on 16 and 22 April 1992 exhibited no external signs of trauma. However, necropsies indicated internal injuries consistent with a ship strike (McLellan[13]; Thayer[14]), suggesting that such injuries could have escaped notice during more cursory examinations. The lack of external body trauma on animals which thorough necropsy revealed to have been killed by a ship strike has also been noted for the northern right whale, *Eubalaena glacialis* (Kraus[15]).

Alternatively, references to rope or net marks did not always specify whether such marks were of recent origin or due to past entanglement from which the animal escaped. Baleen whale entanglement does not always lead to immediate mortality (Kraus, 1990a); however, the effect of escaped entanglement on long-term survivorship or reproductive success, or both, is unknown. If rope or net marks noted in the stranding reports were of past origin, they may have been independent of the animal's death or the animal may have succumbed to the long-term effects of past entanglement. Reduced foraging efficiency during the entanglement period may be a factor influencing animals to engage in winter feeding behavior, such as that observed in the study area by Swingle et al. (1993).

The apparent high rate of interaction with commercial fishing and shipping, may be due, in part, to the age class inhabiting the area. Juvenile animals, and newly independent calves in particular, may be more susceptible to ship strikes or fishing gear entanglements, or both, owing to a lack of experience with either factor (Lien, in press). Commercial shipping and military traffic to and from the Chesapeake Bay passes by much of the area where strandings

[10] deGroot, G. 1992. A fluke of nature. The Annapolis Capital-Gazette. 10 March, p. 1.

[11] CeTAP. 1982. A characterization of marine mammals and turtles in the mid- and North Atlantic areas of the U. S. outer continental shelf. Final Rep. to the Cetacean and Turtle Assessment Program, Univ. Rhode Island, Bur. Land Manage., Contract AA551-CT8-48. U.S. Dep. Int., Wash., DC, 450 p.

[12] Payne, P. M., W. Heinemann, and L. A. Selzer. 1992. A distributional assessment of cetaceans in shelf/shelf-edge and adjacent slope waters of the northeastern United States based on aerial and shipboard surveys, 1978–1988. Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent,, Woods Hole, MA 02543. Unpubl. manuscr., 108 p.

[13] McLellan, W. James Madison Univ., Harrisonburg, VA 22807. Personal commun., March 1993.

[14] Thayer, V. Natl. Mar. Fish. Serv., Beaufort, NC 28516. Personal commun., March 1993.

[15] Kraus, S. New England Aquarium, Boston, MA 02110. Personal commun., March 1993.

occur most frequently (Virginia and North Carolina), often in water depths of less than 20 m. In Florida, the concentration of strandings occurs in the vicinity of active commercial and military shipping and where ship strikes have been reported to represent a hazard to northern right whales (Kraus and Kenney, 1991).

Entanglement in commercial fishing gear has been the most frequently identified anthropogenic cause of injury and death in humpback whales; gillnet-type gear most often was implicated (O'Hara et al., 1986). Coastal gillnet fisheries exist in the study area on a year-round basis, but effort may peak in late winter/spring (NMFS, 1992; Swingle et al., 1993; Brooks[16]). Over 2,200 gillnet licenses have been issued for the mid-Atlantic coastal region. However, fishermen may hold more than one permit and some coastal fisheries do not require permits (NMFS, 1992). In the study area, coastal gill nets and whales concurrently occupy waters of less than 15 m in depth (observed by RAA and DPG), and whales have been observed trailing such gear (Swingle[17]). The association of young, inexperienced whales with gill nets in shallow waters may increase the potential for entanglement incidents. Since entanglement mortality is inversely related to body size (Lien et al., 1989; Kraus 1990b), juvenile humpbacks may be more susceptible to fatalities.

Data contained in this paper suggest that mid-Atlantic and southeast coastal areas of the United States are becoming increasingly important habitat for juvenile humpback whales and that anthropogenic factors may negatively impact these animals. However, there are a number of factors that suggest caution should be used in interpretation of these data. The site of stranding is not necessarily the site of death, as the body of a large whale can be carried considerable distances by wind and currents before beaching occurs. Cause of death in the stranded animals was rarely determined with certainty and in most cases was inferred from observations of the presence or absence of surface body trauma, not from thorough necropsy by experienced individuals. A greater emphasis should be placed on complete necropsies of stranded animals to determine not only the immediate cause of death but also whether there is an underlying factor in the fatality. This would allow a more reliable investigation into mortality and provide greater ability to evaluate and alleviate the impact of anthropogenic interactions. This is particularly important for an endangered species, such as the humpback whale.

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Publication Awards, 1993

National Marine Fisheries Service, NOAA

The Publications Advisory Committee of the National Marine Fisheries Service is pleased to announce the awards for best publications authored by NMFS scientists and published in the Fishery Bulletin for Volume 91 and in the Marine Fisheries Review for Volume 54. Eligible papers are nominated by the Fisheries Science Centers and Regional Offices and are judged by the NMFS Editorial Board. Only articles that significantly contribute to the understanding and knowledge of NMFS-related studies are eligible. We offer congratulations to the following authors for their outstanding efforts.

Fishery Bulletin, Volume 91

Outstanding Publication

Ambrose Jearld Jr., Sherry L. Sass, and Melinda F. Davis

Early growth, behavior, and otolith development of the winter flounder *Pleuronectes americanus*. Fish. Bull. 91:65–75.

Ambrose Jearld is with Northeast Fisheries Science Center, Woods Hole, Massachusetts. Sherry Sass is with the Division of Marine Fisheries, Sandwich, Massachusetts. Melinda Davis is with Fort Valley State College, Fort Valley, Georgia.

Honorable Mention

Michael H. Prager and Alec D. MacCall

Detection of contaminant and climate effects on spawning success of three pelagic fish stocks off southern California: Northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus*. Fish. Bull. 91:310–327.

Michael Prager is with the Southeast Fisheries Science Center, Miami, Florida. Alec MacCall is with the Southwest Fisheries Science Center, Tiburon, California.

Marine Fisheries Review, Volume 54

Outstanding Publication

Thomas K. Wilderbuer, Gary E. Walters, and Richard G. Bakkala

Yellowfin sole, *Pleuronectes asper*, of the eastern Bering Sea: biological characteristics, history of exploitation, and management. Mar. Fish. Rev. 54(4):1–18.

Thomas Wilderbuer and Gary Walters are with the Alaska Fisheries Science Center, Seattle, Washington. Richard Bakkala is a retired fishery biologist who was formerly with the Alaska Fisheries Science Center, Seattle, Washington.

Honorable Mention

Carl. J. Sindermann

Disease risks associated with importation of nonindigenous marine animals. Mar. Fish. Rev. 54(3):1–10.

Carl Sindermann is with the Northeast Fisheries Science Center, Oxford, Maryland.

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Confidence of otolith ageing through the juvenile stage for Atlantic menhaden, *Brevoortia tyrannus*

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Abstract.—The periodicity of increment formation and our ability to enumerate increments in sagittal otoliths of Atlantic menhaden are evaluated from hatching through a nine-month period. We studied otoliths from one group of field-collected larvae that was marked by immersion in oxytetracycline (OTC) and from a second group that was marked by immersion in alizarin complexone (ALC). Additionally, otoliths from known-age juveniles resulting from an Atlantic menhaden laboratory spawning and rearing experiment were examined. We determined that, on the average, larval and juvenile Atlantic menhaden form one growth increment per day. We were able to age juvenile menhaden reliably up to 200 days old within a confidence interval (CI) of about 7 days and up to 250 days old within a CI of about 16 days. We hypothesized that growth rates may have impacted the periodicity of increment formation, as well as our ability to count them accurately. The statistically strongest results were obtained from the ALC-marked fish, which were reared outdoors and displayed growth rates (0.67 to 0.95 mm·day^{-1}) similar to higher rates observed for juveniles captured from estuarine nursery areas. The periodicity of increment counts for the ALC-marked fish was less than one per day when growth rates were observed to be less than 0.3 mm·day^{-1}. Increments in otoliths from the known-age and OTC-marked fish, which were reared indoors, had lower contrast than their outdoor-reared counterparts. Otoliths were sectioned for enumeration on both a transverse and oblique-transverse plane. With minor exception, no differences in age estimation could be attributed to the orientation of the sections.

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The daily age information obtained from larval and juvenile fish otoliths is a valuable tool for studies of early life history and factors affecting recruitment (Jones, 1992). Daily age information is necessary for backcalculating cohort-specific spawning dates and is the best approach for estimating mortality and growth rates in young fish (Essig and Cole, 1986; Pepin, 1989; Jones, 1992). A prerequisite, however, is the validation of the temporal periodicity of otolith increment formation (Geffen, 1992). While the otolith approach to determination of vital rates has successfully been applied to larval fish, use of otoliths for the juvenile stage has been more controversial, often because of additional requirements of otolith preparation, including sectioning and polishing of otoliths, and because of increased uncertainty in age estimations and back-calculations of size at age (cf. Rice, 1987; Mosegaard, 1990; Jones, 1992).

Many validation studies have determined that increments are, on average, daily in periodicity (cf. Jones, 1986), but conditions affecting a low growth rate, for example, can result in increment periodicity other than a daily one (Geffen, 1992) or can result in difficulty in the detection of daily increments (Campana, 1992). Therefore ageing error commonly increases with age and otolith size as increment widths decrease with decreasing growth rates, resulting in greater uncertainty of ages, growth rates, and birthdates (Rice et al., 1985; Rice, 1987; Campana and Jones, 1992). We examined conditions where confidence about the assumption of daily ring deposition may be low and what the consequence would be of increased ageing error on age estimation for Atlantic menhaden, *Brevoortia tyrannus*.

Larger, older otoliths are more difficult to prepare and read. To address this issue, we also exam-

ined the efficacy of sectioning and polishing juvenile menhaden otoliths on two orientations of transverse planes. Greater attention to otolith preparation can significantly improve ageing accuracy (Campana and Moksness, 1991), and section orientation can affect the ability to read otoliths (Secor et al., 1992).

Previous menhaden validation studies have used only a minor amount of otolith processing, and the material has been examined on the sagittal plane. Maillet and Checkley (1990) and Warlen (1992) used known-age, lab-spawned and reared larvae, whereas Simoneaux and Warlen (1987) examined the outermost growth increments of juvenile Atlantic menhaden injected with oxytetracycline (OTC). Maillet and Checkley (1990) examined growth/increment formation from hatching through 36 days of age, Warlen (1992) through 41 days of age, and Simoneaux and Warlen (1987) used juveniles (63–98 mm in fork length) with an experimental duration of 7–14 days after marking with OTC. With the exception of one test group (Maillet and Checkley, 1990), results of all studies indicated that, on average, one growth increment was formed daily.

However, these approaches have not resulted in a method that will permit precise and accurate ageing of older juvenile Atlantic menhaden otoliths. While Simoneaux and Warlen (1987) were able to validate the daily periodicity of increment formation for a short period of time, their otolith processing method could not be used to determine the actual age of the juveniles examined. The periodicity of increment formation in otoliths should be validated over the ranges in age and size that can potentially be encountered with unknown-age, field-collected material.

We use two of the preferred validation methods, known-age and otolith-marking, to bridge the gap in age and size among the studies of Maillet and Checkley (1990), Warlen (1992), and Simoneaux and Warlen (1987) and to provide an estimate of the uncertainty in deriving age from older juveniles. Our known-age study provides a continuous validation from first feeding through metamorphosis, to juveniles up to 9 months old.

Materials and methods

Known-age fish

Atlantic menhaden brood stock were held in the laboratory and induced to spawn in February 1987 by Hettler's (1981) methods. Eggs were hatched and larvae were reared under laboratory conditions as described by Warlen (1992). Samples of postlarvae and later juveniles were sampled periodically from 52 to 136 days after hatching, then preserved in 70% ethyl alcohol.

Oxytetracycline (OTC) marked fish

In 1988, larval Atlantic menhaden collected at Pivers Island, Beaufort, North Carolina, were acclimated to 100-L indoor laboratory tanks and immersed on 7 April in OTC by a procedure modified from Hettler (1984). Salinity was slowly reduced to 0‰ by adding tap (well) water over several hours. A premixed, buffered (sodium bicarbonate) stock solution of OTC was added to the tank. The resulting treatment conditions were 300 $mg \cdot L^{-1}$ OTC at pH 6.3. After four hours of immersion, ambient seawater flow was restored; the test solution was thus diluted within an hour and salinity slowly increased. The fish remained in this tank for the duration of the study. Samples of postlarvae and juveniles were taken periodically, 13 to 147 days following treatment, and preserved in 95% ethyl alcohol.

Alizarin complexone (ALC) marked fish

In 1992 we conducted validation trials with marked fish under high and low feeding rations to examine further the effect of growth rate on increment deposition. Larval menhaden were captured with a neuston net at Pivers Island, NC, on 1 April 1992 and held at ambient temperatures and salinities until 21 April, then immersed for 14 hours in 100 $mg \cdot L^{-1}$ ALC buffered with sodium bicarbonate to pH 6.5. After immersion, 1,026 larval menhaden were divided between two 2,100-L outdoor holding tanks and sampled monthly, May through December. The larvae were fed cultured, live *Artemia franciscana* and increasing additions of dry food until 29 May, when only dry food (Ziegler salmon starter) was added in a ratio of 3 (high food tank) to 1 (low food tank). The amount of dry food initially added for the low food treatment was 25 $mL \cdot day^{-1}$ in April; this amount was increased to approximately 90 $mL \cdot day^{-1}$ by July and held constant after this period.

Otolith preparation and increment counting

Some otoliths from late larvae were mounted whole in a mounting medium (Flo-tex) on glass microscope slides. After increments were counted on the sagittal plane, many were removed from the mounting medium and sectioned on one of two planes as described below.

We generally followed the sectioning techniques described in Epperly et al. (1991) and Secor et al. (1992). Our processing techniques for the ALC-

marked group were altered: otoliths were dissected from each fish without bleaching (i.e. without a 5% sodium hypochlorite solution to remove tissue) and serial sectioning was used for the transverse sections rather than single cuts with dual blades. Two sectioning orientations were used: a transverse section, taken with the primordium (and focus) as the centerline, on a proximal-distal plane 90° to the anterior-posterior axis, and an oblique-transverse section on a proximal-distal plane from a posterior and dorsal position through the focus to the anterior ventral(most) portion (Fig. 1). (Some otoliths were also examined on an unsectioned, sagittal plane.) Transverse sections were taken on the right sagitta and oblique sections were taken on the left, with the exception of the 1992 ALC-marked material for which selection of the right or left sagitta was randomized. Resulting sections were then ground and polished according to the methods of Epperly et al. (1991) and Secor et al. (1992). For otolith terminology and increment interpretation we followed Pannella (1980) and Campana (1992).

Oxytetracycline and alizarin complexone marks were located with blue light epifluoresence on prepared otolith sections and viewed directly on a compound microscope or on a video image analysis system. The OTC-marked increment(s) fluoresced yellow-green when illuminated with blue light (Fig. 2) and the ALC-marked zone fluoresced orange. The position of each fluorescing mark was fixed with the aid of an ocular micrometer (scope viewing) or with a pointer on the viewing screen; increment counts were made with white or polarized light. Otolith sections viewed on a video monitor were magnified to 1,500×. Since only a fraction of a section would fill the screen at this magnification, increment counting was done stepwise between distinguishable features or "landmarks," and counts were summed when interpretation was complete. An additional series of increment counts was performed with the microscope at 1,000× and by tallying counts blindly on a handheld counter. Agreement between the two methods on enumeration generally was better than 95%. Final counts were means from the two enumeration

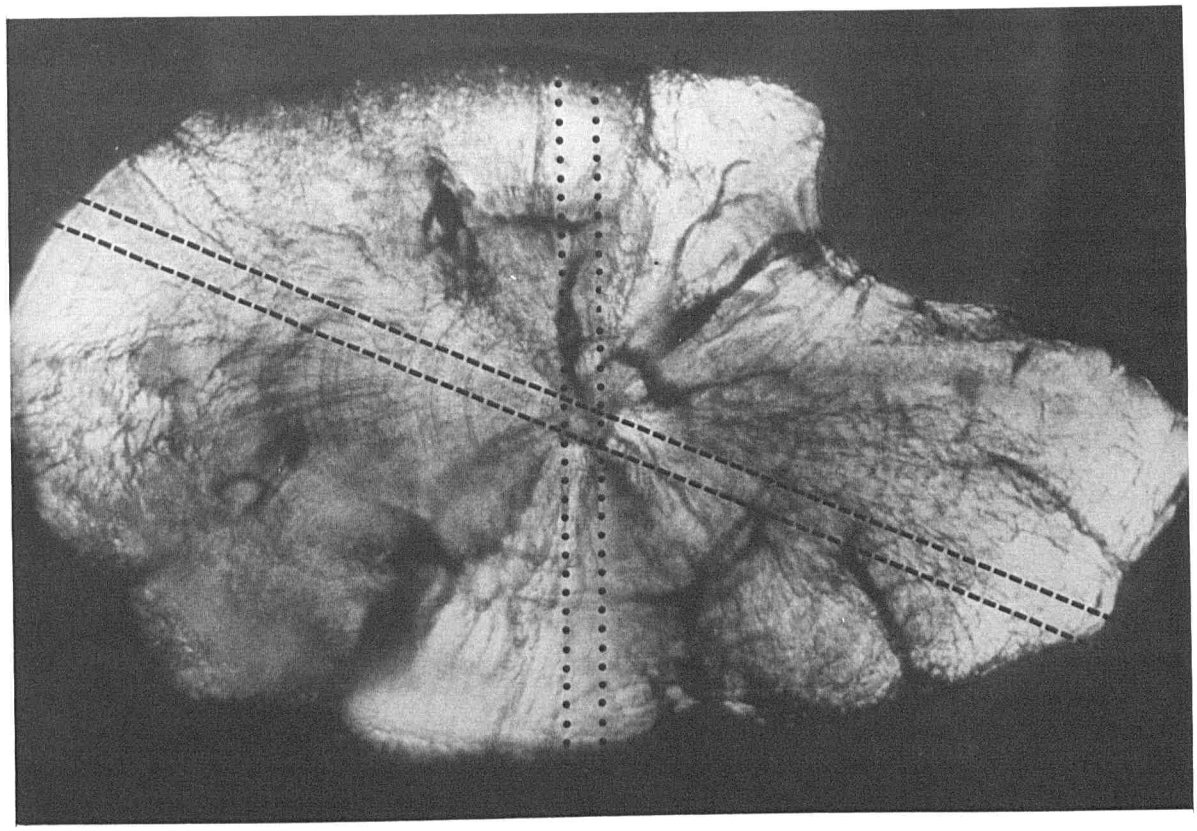

Figure 1

A whole sagittal otolith from a 39.0-mm (0.481-g) juvenile Atlantic menhaden, *Brevoortia tyrannus*, is shown to demonstrate the orientation of sectioning for this study. Transverse (dotted lines) and oblique-transverse (dashed lines) sections are displayed. The otolith is oriented with the dorsal edge up and the anterior to the right.

methods. Mean counts from the known-age fish were increased by five to estimate time from spawning rather than from first feeding (Warlen, 1992). ALC-marked material was viewed under a microscope at 400–1000×, counted with a hand-held counter, and the median of five serial counts was taken.

Statistical analysis

Regression and analysis of covariance (ANCOVA) computations were conducted with SAS statistical programs (SAS Institute, Inc., 1985). Analysis of covariance was used to test for common regression parameters (ring count versus known days) for the low and high food treatments and between transverse and oblique-transverse sectioned material for each marking-validation method (Ott, 1977). Mean growth rates were estimated as the slopes of simple linear regressions of length on age.

We tested the null hypothesis that growth increments in otoliths of larval and juvenile Atlantic menhaden are formed daily. The null hypothesis is accepted if the regression of estimated increment count on known age in days since marking is significant, the slope is not significantly different from one, and the intercept is not significantly different from zero. We also calculated the appropriate statistical power to detect a relatively small difference from a slope of one (Rice, 1987). Student's-*t* test was used to test for significance of the slope and intercept. Statistical power to determine a deviation of 0.1 (α=0.05) from a slope of one was estimated for each linear regression (Rice, 1987; Neter et al., 1989).

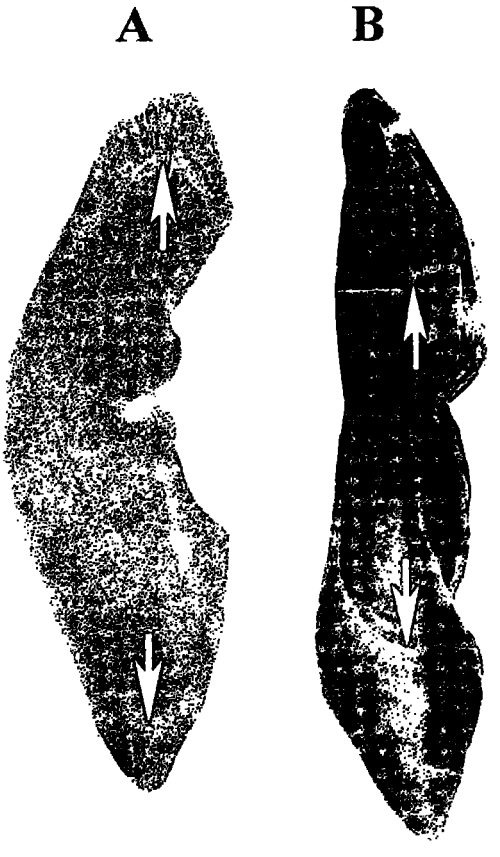

Figure 2

Photomicrographs of juvenile Atlantic menhaden, *Brevoortia tyrannus*, sagittal otolith sections showing fluorescent marks (arrows). (**A**) Transverse section of otolith from a post-larval fish 12 days after immersion in alizarin complexone solution (ALC). The maximum dimension of this section (dorsal/ventral) is 462 μm. (**B**) Oblique-transverse section of otolith from a juvenile 42 days after immersion in oxytetracycline solution (OTC). The maximum dimension of this section (posterior-dorsal/anterior-ventral) is 938 μm.

Results

Otolith preparations were generally readable for the ranges in sizes and ages for the elapsed times. Known-age fish were sampled at ages 52, 66, 81, 122, 131, 132, and 136 days; they ranged from 10 to 64 mm in fork length. Mean growth for the known age group was 0.55 mm·d^{-1}, with a standard error (SE) of 0.048 over the interval from March to June. OTC-treated fish were sampled 13, 18, 42, 110, and 147 days after treatment; they ranged from 27 to 98 mm in fork length and ranged in estimated age from 62 to 130 days with a mean age of 103 days at marking, resulting in mean growth of 0.49 mm·d^{-1} (SE=0.011) for the interval April to August. ALC-marked fish were sampled 12, 42, 71, 100, 131, 161, 190, 205, and 237 days after treatment; they ranged from 26 to 175 mm FL and were approximately 70 days old at marking. Mean growth rates of the ALC-marked fish were 0.67 and 0.95 mm·d^{-1} (SE=0.020 and 0.015) through day 131 postmarking in low and high food tanks respectively. Growth visibly declined for the interval from day 161 to day 237 postmark and was 0.29 mm·d^{-1} for both the low and high food treatments (SE=0.037 and 0.195).

It was readily apparent from scatter plots that the ALC growth-increment count beyond day 131 (day 161 to day 237) postmark was less than one per day and the variance about an individual sampling date substantially greater. We pooled data up through day 131 postmark from the ALC high and low food treatments because tests for homogeneity of the resulting slopes (P=0.667) and intercepts (P=0.831) for age-

increment count regressions (transverse sections) revealed that these parameters were not significantly different between treatments.

We tested for the homogeneity of slopes for the increment count-age regressions between sectioning orientations separately for the known-age experiment and both of the marking experiments. None of the slopes were significantly different (P for known age=0.0583, for OTC=0.188, and for ALC=0.667). Tests for differences in intercepts for the same experimental sets revealed none (P for known age=0.345, for OTC=0.082, and for ALC=0.526). Therefore we pooled the increment count results within each experiment.

We used regressions to compare the results for the known-age and chemically marked otoliths for about the same time duration (i.e. 136 days for known-age fish, 147 days for the OTC group, and 131 days for the ALC group; Table 1, Fig. 3). The intercepts of the three increment-count regressions were not significantly different from zero, and none of the three slope estimates were significantly different from 1.0 (Table 1). The results for the ALC and the OTC groups had sufficient power (>0.80) to detect a difference in slope of 0.1 from a value of 1.0. The standard error of the slope was relatively greater for the known-age group, and thus the power estimate was less than that for the ALC and OTC groups (Table 1).

We examined the results from day 161 to 237 for the ALC experiment in parallel fashion. A test for homogeneity of slopes for increment count on days postmark revealed a (marginally) significant difference between the sectioning orientations (P=0.044). Estimates of the slopes from separate regressions for the oblique-transverse and transverse sections were significantly different from 1 (P=0.016 and P<0.001). While these observations begin to define limits for applying daily ageing techniques to juvenile Atlantic menhaden, they do not reduce the usefulness of the technique over a relatively broad time period. With the minor exception of the period when increment counts were less than daily in the ALC trial, the results for the ALC-marked and OTC-marked test groups were equivalent for either section orientation with slopes near one and with good statistical power to detect a small deviation from one (Fig. 3, Table 1).

Discussion

Atlantic menhaden, on the average, form one growth increment per day through at least an estimable age of 200 days (131 days postmark + approximately 70 days in age at marking) and a size of nearly 150 mm fork length. We could reliably age menhaden up to 200 days old to within about 7 days when juvenile growth rates were high (e.g. above 0.6 mm·d^{-1} over summer months). At moderate juvenile growth rates (approximately 0.5 mm·d^{-1}), we still detected increments at approximately one per day through a 250 day time period for the OTC fish (147 days postmark + an average of 103 days of age at marking), but the variability of an individual age estimate increased in comparison with fish with higher growth rates. For the OTC and known-age test groups respectively, 95% confidence intervals increased to approximately ±16 and 21 d for similar-aged menhaden with slower growth rates (Table 1, Fig. 3). As growth rates declined further (below 0.3 mm·d^{-1}), our increment counts declined to less than one per day, and variability in estimated age increased; this may be due to decreases in increment width or to reduced periodicity as has been found for starved larval Atlantic menhaden (Maillet and Checkley, 1990). After day 131 postmark (ALC), declining growth rates and an increment periodicity of less than one per day (Fig.

Table 1

Least squares linear regression analysis for increment counts from known-age, oxytetracycline (OTC) marked and alizarine (ALC) marked Atlantic menhaden, *Brevoortia tyrannus*, otolith sections. The null hypotheses tested are that the intercept=0 and the slope=1. (SE=standard error.)

Test group	n	r^2	Intercept	SE	P	Slope	SE	P	%Power[1]	95%CI[2]
Known-age	37	0.92	–5.853	5.149	0.263	1.036	0.053	0.501	45.1	21
Tetracycline-marked	34	0.97	1.796	2.139	0.407	0.949	0.027	0.068	94.9	16
Alizarine-marked[3]	84	0.99	0.634	0.701	0.368	0.990	0.008	0.215	>99.9	7

[1] Estimate of percent statistical power to detect a deviation of 0.1 from a slope of one at the P = 0.05 level.
[2] 95% confidence interval (±days) for an age estimate based on individual ring counts. The 95% confidence intervals for individual age estimates were constant over the range of values used to generate the regression.
[3] Through day 131 postmark.

3, bottom graph) corresponded with declining tank temperatures (beginning in September; Fig. 4). However, age could still be estimated within about 3 weeks up to 300 days after hatching (230 days postmark plus about 70 days in age at marking; Fig. 3). If this relationship were consistently repeatable, it would still be a useful tool for estimating ages of older juveniles, even though the age-ring count relationship was well below 1:1. However, we suspect that this change was not so much a function of age as it was a result of reduced growth rate, possibly in conjunction with declining temperature, which affected our ability to accurately estimate ages. Savoy and Crecco (1987) also showed that reduced rearing temperatures can reduce growth rate and subsequently result in a count-age slope below 1.0 for larval American shad, *Alosa sapidissima*.

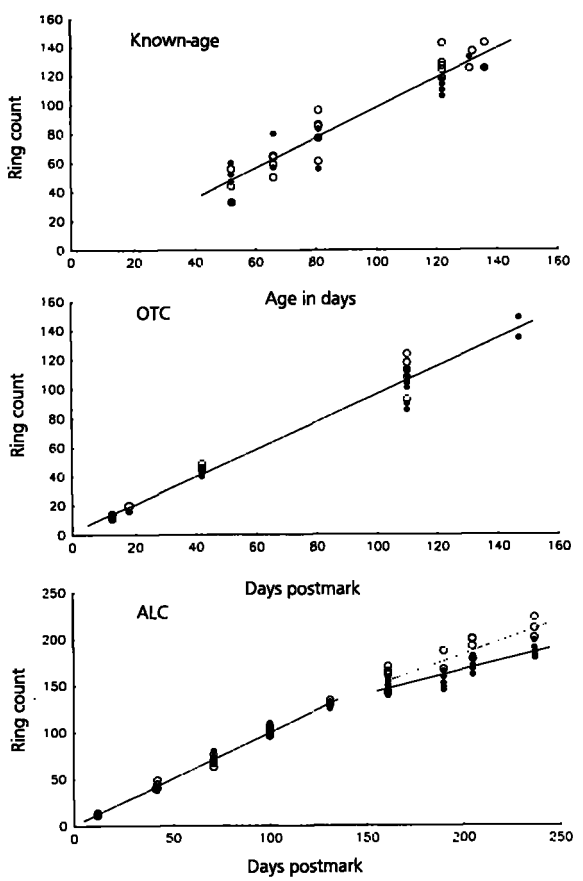

Figure 3

Estimated number of otolith growth increments against elapsed time in days (known age) or days postmark (oxytetracycline [OTC] or alizarin complexone [ALC]) of juvenile Atlantic menhaden, *Brevoortia tyrannus*. Results from oblique-transverse sections (open circles) and transverse sections (closed circles) are pooled for the regression lines shown. The regression coefficients are given in Table 1. (Results for the alizarin-complexone trial for days 161–237, where increment formation rates were less than daily, are shown on the upper right of the bottom graph. Regression parameters for the oblique-transverse (dashed line) and the transverse (solid line) data sets respectively, are r^2=0.81 and 0.79, intercept=39.62 and 62.76, and slope=0.73 and 0.52.)

The growth rates of fish treated with ALC (through day 131 post-ALC-mark) are comparable with observations for upper growth rates of juveniles in tidal creeks, spring through fall (0.7 to 0.83 mm·d^{-1}; Kroger et al., 1974). The laboratory-reared fish had lower growth rates, but their rates were still greater than those for the ALC fish following postmarking day 131. Therefore it appears that reduced growth rate was a contributing factor for the higher variance of our estimates of the slope of counts versus days for our known-age and OTC test groups. Similarly, the variances for the ALC group were highest during the period when increments displayed a less than daily periodicity (Fig. 3).

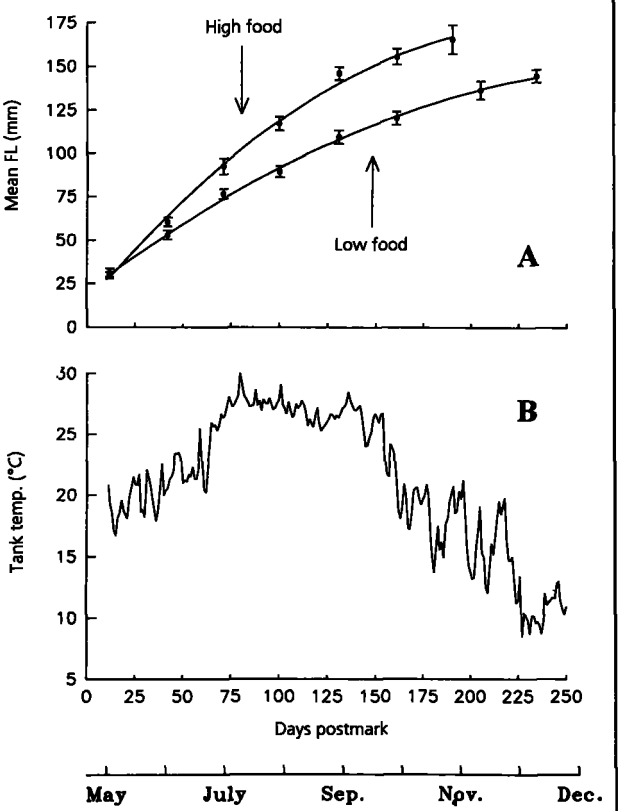

Figure 4

(A) Mean fork length of juvenile Atlantic menhaden, *Brevoortia tyrannus* (error bars represent ±1 standard deviation), and (B) tank water temperatures for the alizarin complexone rearing trial (see bottom graph on Fig. 3).

The otolith sections of the laboratory-reared material, which includes the OTC fish following marking, generally had less contrast between alternating bands than did field material. Warlen (1988) noted similar results for gulf menhaden. This was not the case for the ALC fish, where contrast more closely resembled field material. OTC and known-age specimens were raised indoors in relatively small (100 L) containers, as compared with the larger (2,100 L) outdoor containers used for the ALC fish. (All groups were reared in ambient sea water.) Problems in validating otoliths with laboratory-reared fish have been noted for other species (Campana and Moksness, 1991; Toole et al., 1993). Pannella (1980) notes that the transition between increments are unclear with respect to chemical or structural changes in some laboratory-reared material. It may be that otoliths from laboratory-reared specimens are less typical because of confounding effects from container size, growth rates, and other aspects of the rearing conditions. The poorer contrast may result in lower accuracy and precision in increment counting, and the slower growth may result in more variable increment counts for a given time period.

We obtained detectable OTC and ALC marks in viewing otoliths with the dosages used for immersing larvae. Because of the color contrast of the orange-against-blue background, ALC was visibly easier to detect under blue light fluoresence than was OTC. ALC has been used for marking eggs and hard parts in fish; it leaves a brilliant mark, does not adversely affect growth at low dosages, and does not require dilution procedures as does OTC (Tsukamoto, 1988; Kishiro and Nakazono, 1991).

Although we obtained similar results using either oblique-transverse or transverse sections for those periods when increment formation is on the average one per day, one orientation or the other may be preferred for various reasons. The oblique-transverse method of sectioning may be easier to complete in polishing because the primordium and focus can be detected from a greater distance (thickness) when the material is viewed. This reduces processing time and minimizes the number of overground, unusable preparations. On transverse sections of larger or older individuals, or both, the focus is located more by the outline shape than by early optical discovery. However, some investigators using increment measurements for size back calculation or discriminant analysis may prefer the transverse section for ease in keeping the same plane of measurement from otolith to otolith. The two section orientations were useful for cross comparisons and interpretation of certain growth zones. Therefore choice of orientation should depend upon the material being examined and the questions being addressed.

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Description of the starving condition in summer flounder, *Paralichthys dentatus*, early life history stages

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Abstract.—The nutritional status of laboratory-reared summer flounder, *Paralichthys dentatus*, larvae and early juveniles was assessed by morphometric, biochemical, and histological criteria. Conditions of food deprivation were imposed on 6-, 16-, and 33-day-old larvae as well as on 60-day-old juveniles. Samples of ad-libitum-fed or starved individuals were analyzed with regard to standard length, dry weight, eye diameter to head height ratio, pectoral angle, RNA:DNA ratio, total protein content, histological appearance of selected organs, and cell height of the anterior and posterior intestinal mucosae. In general, tolerance to starvation increased with age: 60 h in 6-day-old-larvae, 72 h in 16-day-old larvae, 8 d in 33-day-old-larvae, and 10 d in 60-day-old-juveniles. The results of this study demonstrate that morphological criteria are either not good indicators of nutritional status (eye:head ratio), good only for larvae (pectoral angle), or require extensive calibration (standard length and dry weight). They also show that biochemical criteria are either not good indicators (protein content) or are sensitive to starvation only in juveniles (RNA:DNA ratio). Among the histological criteria, thickness of the posterior intestinal mucosa was the most sensitive and consistent indicator of starvation in summer flounder larvae and early juveniles. The most salient attributes of this histological analysis were sensitivity, objectivity, ease of interpretation, and exemption from shrinkage calibration. These results suggest the use of the histological approach in the face of uncertainties associated with the other methods examined. On the other hand, application of either morphological or histological criteria is appropriate for an aquaculture setting in which age of larvae is known.

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It is currently accepted that starvation and predation are the main agents of marine fish larval mortality (Hunter, 1976; Bailey and Houde, 1989). However, the relative magnitudes of the processes controlling prerecruit mortality are, for the most part, either unknown or controversial (Pepin, 1988/1989; Miller et al., 1991). Furthermore, these forces may at times operate concurrently, adding an additional level of complexity. For instance, although intense food limitation of fish larvae can be lethal per se, it could also be regarded as a sublethal agent that exposes weakened individuals to selective predation by reducing their growth rates (Laurence, 1985; Houde, 1987; Fogarty et al., 1991), reaction capabilities (Hunter, 1972, 1981), or ability to maintain a preferred depth in the water column (Blaxter and Ehrlich, 1974).

Nutritional condition of teleost larvae has been measured and described in a number of ways. The physical deterioration of larvae resulting from experimental conditions of food deprivation has been interpreted by means of morphometric and gravimetric (e.g. Hempel and Blaxter, 1963; Ishibashi, 1974; Ehrlich et al., 1976), biochemical (e.g. Ehrlich, 1974, a and b; Buckley, 1980, 1982, 1984; Fraser et al., 1987; Clemmesen, 1987; Richard et al., 1991), and histological (e.g. Ehrlich et al., 1976; O'Connell, 1976, 1980; Theilacker, 1978; Martin and Malloy, 1980; Watanabe, 1985; Theilacker and Watanabe, 1989) criteria. In some cases, several of these techniques were tested concurrently to determine their relative utility as indicators of starvation (Martin and Wright, 1987; Setzler-Hamilton et al., 1987). Martin and Wright (1987) proposed the combined application of two or three techniques to any given study because of differences in response time of the measure to actual nutritional status.

The summer flounder, *Paralichthys dentatus*, is a temperate paralichthyid flatfish occurring in Atlantic estuaries and continental shelf waters from Nova Scotia to Florida (Rogers and Van Den Avyle, 1983; Able et al., 1990). During 1983–91, the average landings from the commercial and recreational fishery were 11,400 metric tons. Recent surveys revealed that the stock biomass is currently at the lowest average level since the early 1970's which, combined with calcu-

lated present fishing mortality rates, indicates that summer flounder stocks are overexploited (NMFS, 1993). The decline in the natural fishery, together with recent success in culturing other flatfish species, such as the Japanese flounder, *Paralichthys olivaceus* (Sproul and Tominaga, 1992), and the European turbot, *Scophthalmus maximus* (Person-Le Ruyet et al., 1991), stimulated interest in the development of technology for the culture of summer flounder.

Basic information on the ability to distinguish starving from feeding *P. dentatus* larvae and juveniles will be useful for studies of both natural and cultured populations. Studies on the occurrence or frequency of starvation in either field populations or aquaculture operations must be preceded by an experimental study in which specific starvation indicators are validated for fish of known nutritional history. Therefore, the aim of our research was to evaluate and compare alternative criteria for assessing starvation effects at several stages during the early life history of *P. dentatus*. We characterize *P. dentatus* larvae and recently metamorphosed juveniles subjected to conditions of starvation or ad libitum feeding, using biochemical, morphometric, and histological criteria.

Materials and methods

Adult broodstock *P. dentatus* were collected from Narragansett Bay, Rhode Island, and Long Island Sound, Connecticut, and were held in laboratory facilities. They were spawned after artificial induction with repeated carp pituitary injections (2.5 mg/kg) during 8 to 12 consecutive days (Smigielski, 1975). The fertilized eggs were distributed in 38-L glass aquaria covered with opaque black plastic. Each tank was filled with UV-treated filtered (1 μm) Narragansett Bay seawater (adjusted to 34 ±1‰ salinity by brine addition). Antibiotic (200 mg erythromycin activity dissolved in 23 liters of water) was added at one time in each tank, and water changes were performed every 2–3 days to maintain water quality. During the first week, the alga, *Tetraselmis suecica,* was added to the water. No artificial substrate was added to the aquaria. Water temperature was maintained at 19 ±1°C throughout the experiment. Overhead illumination adjusted to a natural photoperiod and aeration were provided.

Hatching began 55 hours after fertilization. During the next 4 days the larval digestive system became morphologically ready to process external food at the time of mouth opening (Bisbal and Bengtson, in press). Since yolk resorption and mouth opening are almost simultaneous, flounder larvae were fed daily on rotifers, *Brachionus plicatilis,* cultured on *T. suecica* (Lubzens, 1987) after day 4. Newly hatched Reference *Artemia* III nauplii (Collins et al., 1991) were offered for the first time 18 days later, and the rotifer supply was progressively reduced. Settlement to the bottom began on day 45 after hatching.

Available literature on the early life stages of fish and previous direct observations on flounder cultures directed our interest toward four developmental stages (Al-Maghazachi and Gibson, 1984; Blaxter, 1988; Youson, 1988). The effects of starvation were evaluated at day 6 (early food ingestion, yolk completely resorbed), day 16 (these larvae have positively ingested and processed food at least once or else they would have died within 10 days after hatching), day 33 (at the beginning of metamorphic eye migration), and day 60 (bottom-dwelling juveniles have metamorphosed) after hatching. At these times, subsamples of the larvae pool were randomly placed in one of two 5-L tanks (25 larvae/L): one (control group) receiving food ad libitum (i.e. *Brachionus* or *Artemia*); the other (starved group) devoid of food. Although the presence of food in the gut was not systematically recorded, the performance of feeding motions and active swimming were visually confirmed on an individual basis. An extra subsample was processed as described below in order to establish the basal levels of the several parameters measured prior to the initiation of the imposed starvation (time 0). Based on previous observations on the progression of starvation at different age intervals and constant visual monitoring of behavioral changes, each group (control and starved) was sampled at least three times, from the beginning of the experimental exposure until the onset of mortality. A larva was considered dead if it did not respond to gentle probing with a glass rod. If that was the case, the larva was captured and placed under the dissecting microscope for a confirmation of its status. At each sampling time the same protocol was followed: 6 to 10 individuals from each group were sampled for histological analysis, 10 for morphometric and dry weight measurements, and 10 for biochemical analyses.

Morphometric measurements consisted of standard length, eye diameter, head height, and the pectoral girdle angle as defined by Ehrlich et al. (1976). Measurements of live larvae were taken under a dissecting microscope equipped with an ocular micrometer accurate to 0.7 μm. Pectoral angles were traced under a camera lucida and measured on a digitizing pad. Each fish was then rinsed in deionized water and placed in a 60°C oven until a constant dry weight was obtained. Weight was measured, on either a Mettler AE 240 balance or a Cahn C–31 electrobalance.

Samples for biochemical analysis were rinsed in deionized water and individually preserved in Eppen-

dorf vials in a –80°C freezer for no more than 45 days until RNA, DNA, and protein determinations were performed. Owing to the extremely small size of the 6-day-old larvae, each determination was performed on samples consisting of two larvae pooled in the same vial. This was the only case where pooling was necessary.

Determinations of RNA and DNA were performed according to the methodology described by Bentle et al. (1981) as modified for individual larvae of small size (Nacci et al., 1992). Total protein determination was assessed by a dye-binding assay (Bradford, 1976) in which bovine serum albumin was the reference standard. Volumes were adjusted to 96-well microtitration plates and, after completion of the colored reaction, absorbances were read at 600 nm in an EL 312 Bio-Tek automated microplate reader.

The fraction of the sample destined for histological examination consisted of 6 to 10 specimens preserved in Dietrich's fixative, embedded in paraffin blocks, and completely sectioned every 4–5 μm on a rotary microtome. Light microscopy analysis was performed after staining with Cason's trichromic (Cason, 1950).

The qualitative histological examination concentrated on the liver, pancreas, musculature, and intestinal mucosae. For quantitative purposes, measurements of the cell height of the anterior and posterior intestinal mucosae were performed as described by Theilacker and Watanabe (1989). These measurements consisted of the distance from the basal membrane to the tip of the brush border and were obtained under a microscope equipped with an ocular micrometer eyepiece accurate to 0.02 μm. In the anterior intestine, the site for this measurement was the ventral row of cells located just cranial of the intestinal valve complex (see Fig. 6, A and B). A similar measurement on the posterior intestine mucosa was performed caudal of the intestinal valve (see Fig. 6, A and B).

Control and starved group parameters at each sampling time were compared by using Student's *t*-tests. The overall level of significance (α) for each data set was fixed at a nominal value of 0.05. The critical *t*-value for *k* number of tests was adjusted through Bonferroni's correction as α/k (Sacks, 1978). All values were plotted as arithmetic means and standard errors.

Results

Morphometry and biochemistry

Sampling of 6-day-old larvae was conducted at 24, 48, and 60 hours after initiation of starvation (Fig. 1). Mortality in starved larvae began about 60 hours after food deprivation. The mean standard length of starved larvae was lower than their fed counterparts at all sampling times (t_{18}=3.39, P=0.003, at 24 h, Fig. 1A). Mean dry weight (Fig. 1B) and the mean eye to head ratio (Fig. 1C) did not differ significantly (dry weight, t_{18}=2.39, P=0.028, at 24 h; eye/head ratio, t_{18}=1.31, P=0.208, at 60 h). The mean pectoral angle of starved larvae decreased relative to the fed larvae after 24 hours (t_{18}=3.53, P=0.002; Fig. 1D). Mean RNA:DNA ratios of starved larvae were lower than those of fed larvae (t_{18}=2.68, P=0.015, at 60 h; Fig. 1E). After 60 hours, mean RNA:DNA ratios had decreased from an initial value of 3.75 to 2.74 and 2.31 in fed and starved larvae, respectively. Levels of protein remained fairly constant throughout the experimental period (Fig. 1F).

Sampling of 16-day-old larvae was conducted at 24, 48, and 72 hours after initiation of starvation (Fig. 2). Starved 16-day-old larvae began to die after 72 hours. Mean standard length of both groups was not statistically different at any time (t_{18}=2.25, P=0.037, at 72 h; Fig. 2A). However, differences in mean dry weight were significant at 72 hours (t_{18}=3.04, P=0.007; Fig. 2B). A comparison of the mean dry weight at the beginning of the experiment and that for each group after 72 hours indicates that fed larvae incorporated body mass at a daily specific rate of 7.9%/day, whereas starved larvae lost weight at a rate of 10.4%/day. Similarly, the ratio of eye diameter to head height became significantly different only after 72 hours of starvation (t_{18}= 4.41, P<0.001; Fig. 2C). Little difference was observed in the mean pectoral angle between the groups until 48 h (t_{18}=4.59, P<0.001) and 72 hours (t_{18}=8.25, P<0.001; Fig. 2D). For three days, the mean RNA:DNA ratio of fed animals (2.97–2.99) remained near the mean value at time 0 (2.81; Fig. 2E). During the same period, starved fish showed a steady decline in RNA:DNA ratio to a final value of 1.93, although differences were only significant at 72 hours (t_{18}=3.47, P=0.003). Mean protein content initially decreased in both groups but became fairly constant and indistinguishable between groups thereafter (Fig. 2F).

Sampling of 33-day-old larvae was conducted at 24, 72, 120, and 192 hours after initiation of the experiment (Fig. 3). Larvae began to die after approximately 8 days of food deprivation. Starved larvae were significantly shorter than fed ones after 72 hours (t_{18}=3.32, P=0.004; Fig. 3A). Daily specific growth in length of fed larvae progressed at a rate of 2.5%/day but remained almost constant in starved fish. Dry weight of fed larvae also increased significantly relative to starved larvae (Fig. 3B). At the end of the experimental period, the fed larvae had in-

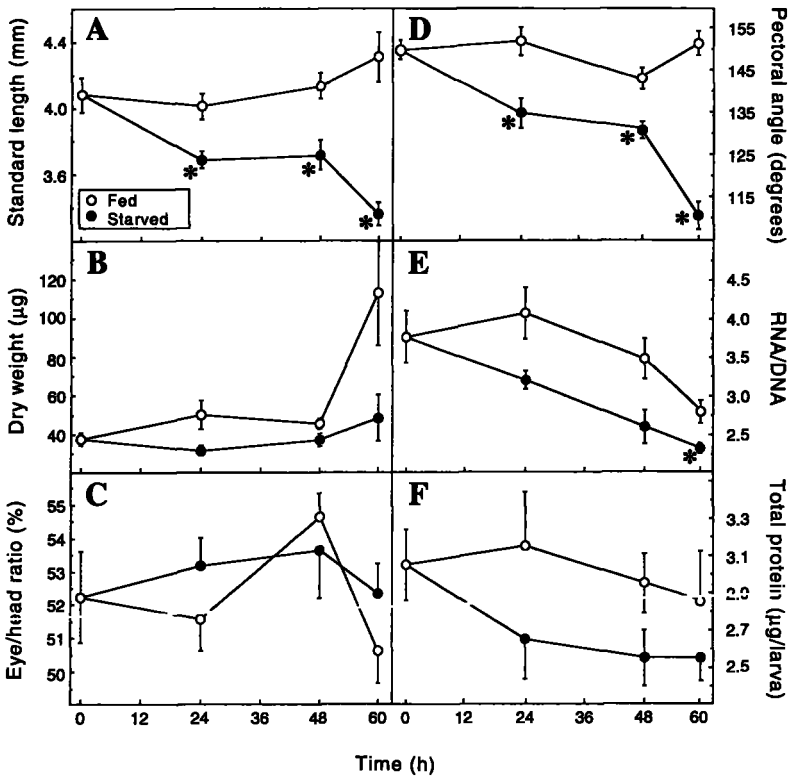

Figure 1

Summer flounder, *Paralichthys dentatus*, 6-day-old larvae. Morphometric, gravimetric, and biochemical changes during ad libitum feeding (○) or starvation (•). (**A**) standard length; (**B**) dry weight; (**C**) eye diameter/head height ratio; (**D**) pectoral angle; (**E**) RNA:DNA ratio; (**F**) total proteins. Symbols represent the arithmetic mean of samples of 9–10 animals ±Standard Error. Asterisks indicate a statistically significant difference between fed and starved groups at a particular sampling time.

creased their dry weight by more than 206% of the initial value, whereas the starved group remained unchanged. This weight difference was significant at 72 hours (t_{18}=4.46, P<0.001), 120 hours (t_{18}=5.54, P<0.001), and 192 hours (t_{18}=4.06, P<0.001). The eye:head ratio of both groups differed at 192 hours (t_{18}=4.28, P<0.001; Fig. 3C). At 72 hours (t_{18}=5.38, P<0.001), 120 hours (t_{18}=7.89, P<0.001), and 192 hours (t_{18}=6.85, P<0.001) the starved group had a lower mean pectoral angle than did the fed group (Fig. 3D). The RNA:DNA ratio showed an initial rise from 2.88 to 3.41 and to 3.26 in fed and starved larvae, respectively (Fig. 3E). After 24 hours, both groups showed a decline, but starved larvae declined to a much greater extent, resulting in significant differences between the two groups at 120 hours (t_{18}=4.85, P<0.001) and 192 hours (t_{18}=5.18, P<0.001). By day 8, starved larvae had ratios 62.4% lower than those of fed larvae. Mean total protein of starving larvae was also significantly lower than that in fed fish, a difference detectable after 192 hours (t_{18}=4.19, P<0.001; Fig. 3F).

Samples of 60-day-old metamorphosed juveniles were taken at 72, 144, and 216 hours (Fig. 4). Mortality in the starved group began after 10 days. While the mean standard length of both groups was different at 216 hours (t_{18}=4.01, P<0.001; Fig. 4A), mean dry weights of the starved and fed groups were significantly different from each other at each sampling time (t_{18}=2.95, P=0.009, at 72 h; Fig. 4B). In 9 days, fed juveniles grew in length at a daily specific rate of 3.1%/day, whereas starved larvae grew at 0.7%/day. During the same time, fed fish gained weight at a rate of 10.1%/day, whereas starved fish lost 1.9% of their body mass every day. The eye diameter to head height ratio in both groups varied in a similar manner (Fig. 4C). A significant difference in the shape of the pectoral angle was only detected at 216 hours (t_{18}=3.15, P=0.006; Fig. 4D). Mean RNA:DNA ratios

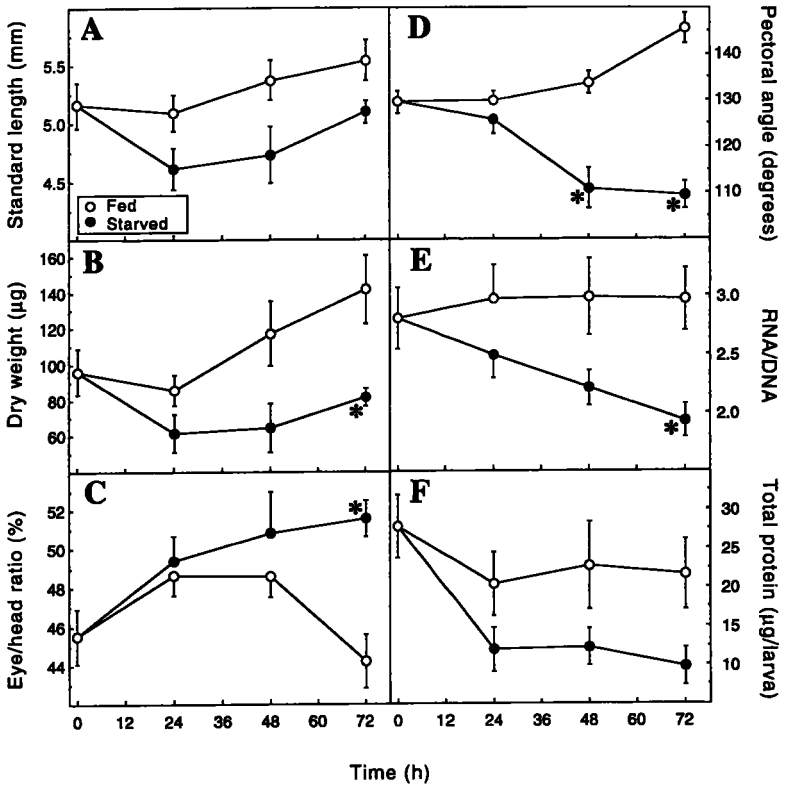

Figure 2

Summer flounder, *Paralichthys dentatus*, 16-day-old larvae. Morphometric, gravimetric, and biochemical changes during ad libitum feeding (○) or starvation (•). (**A**) standard length; (**B**) dry weight; (**C**) eye diameter/head height ratio; (**D**) pectoral angle; (**E**) RNA:DNA ratio; (**F**) total proteins. Symbols represent the arithmetic mean of samples of 9–10 animals ±Standard Error. Asterisks indicate a statistically significant difference between fed and starved groups at a particular sampling time.

of starved juveniles remained consistently lower than those of fed juveniles at all times (t_{17}=3.05, P=0.007, at 72 h; Fig. 4E). During the experimental period, fed fish maintained a mean ratio between 8 and 9. In contrast, the ratio in starved fish dropped from an initial value of 8.49 to a final value of 4.86, a 68% difference from the fed group. Differences in mean total proteins were significant at 72 hours (t_{17}=3.46, P=0.003) and 216 hours (t_{18}=2.71, P=0.014; Fig. 4F).

Histology

The trunk musculature in fed larvae was striated, closely packed, and composed of parallel myofibrils over the lateral surfaces of the notochord (Fig. 5A). However, under starving conditions, the fibrils were not distinguishable and their parallel orientation was disrupted. Further, muscle fibers were widely separated because of shrinkage of the cells (Fig. 5B). In 6 and 16-day-old larvae, degradation of skeletal muscle was evident after 24 hours of starvation. In 33-day-old larvae and 60-day-old juveniles, this effect was detected after 72 and 144 hours of starvation, respectively.

Hepatic tissue of fed larvae appeared continuous and compact, composed of hepatic cells organized in typical liver cords (Fig. 5C). The hepatocytes had a bulky cytoplasm with low staining affinity, several vacuolar inclusions, and round nuclei in their centers. Conversely, liver tissue of starving larvae was fractionated and exhibited loss of the cellular cord arrangement and contained wide intercellular spaces (Fig. 5D). The cytoplasm was severely collapsed and deeply stained (there were no vacuolar spaces) and contained heavily pigmented eccentric nuclei of irregular shape. Liver deterioration was detected after 24, 48, 120, and 144 hours of food deprivation in 6, 16, 33-day-old larvae, and 60-day-old juveniles, respectively.

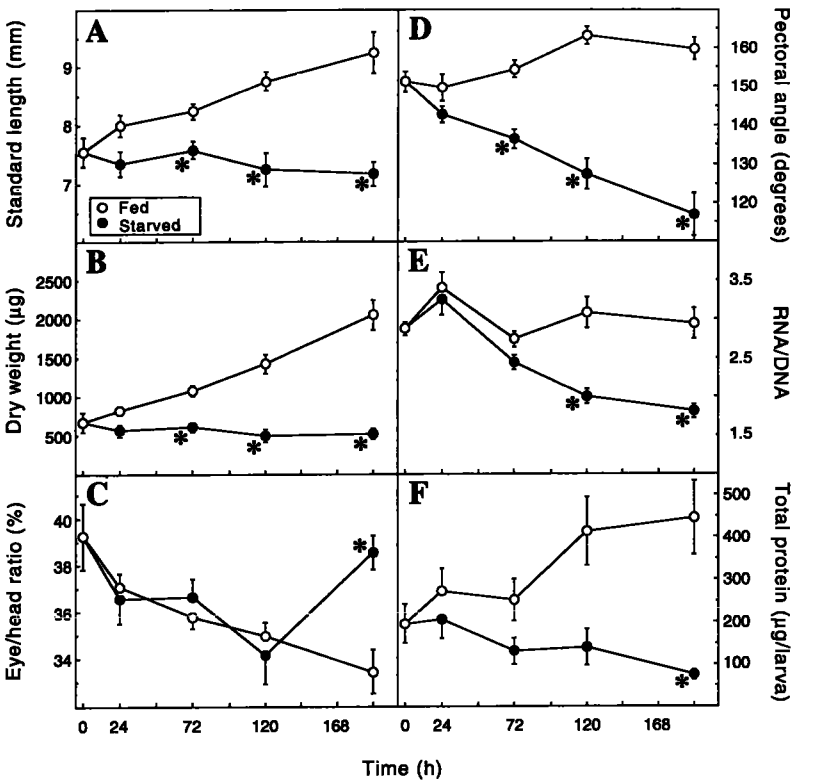

Figure 3

Summer flounder, *Paralichthys dentatus*, 33-day-old larvae. Morphometric, gravimetric, and biochemical changes during *ad libitum* feeding (○) or starvation (●). (**A**) standard length; (**B**) dry weight; (**C**) eye diameter/head height ratio; (**D**) pectoral angle; (**E**) RNA:DNA ratio; (**F**) total proteins. Symbols represent the arithmetic mean of samples of 9–10 animals ±Standard Error. Asterisks indicate a statistically significant difference between fed and starved groups at a particular sampling time.

The acinar arrangement of pancreatic cells was sensitive to starvation. In fed larvae, the typical acinar structure was well defined and symmetrical; cells were arranged around central intercellular lumina (Fig. 5E). Under food deprivation, the acinar structure became increasingly disorganized (Fig. 5F). In 6, 16, and 33-day-old larvae, symptoms of pancreatic degeneration were discernible as early as 24 hours after food deprivation. In 60-day-old juveniles, this effect was detectable after 144 hours of starvation.

The intestinal mucosa of fed larvae was continuous and uninterrupted. A distinct brush border composed of microvilli was evident. The intestinal lumen was wide and the columnar enterocytes were systematically arranged and deeply folded. Cytoplasmic vesicles and vacuoles, suggestive of pinocytosis and intracellular protein digestion, were present in varying numbers and sizes (Fig. 6C). In the starved group, the intestinal mucosa was discontinuous, less compact, and had irregular cells and intercellular spacing. The brush border was not smooth and signs of cell sloughing were evident from the necrotic debris in the lumen. The enterocytes were shrunken and collapsed resulting in a severe reduction of the entire mucosal thickness. The intestinal lumen was comparatively occluded. Cytoplasmic vesicles were not present (Fig. 6D).

The mean cell height of the anterior intestinal mucosa was significantly different between starved and fed groups of all ages. In all cases, these differences were detectable from the first sampling time (t_{18}=2.99, P=0.008, at 24 h in 6-day-old larvae; t_{18}=8.20, P<0.001, at 24 h in 16-day-old larvae; t_{18}=6.06, P<0.001, at 24 h in 33-day-old larvae; and t_{10}=11.0, P<0.001, at 72 h in 60-day-old juveniles; Fig. 7, A, C, E, and G, respectively).

Differences in the cell height of the posterior intestinal mucosa of starved and fed groups were also

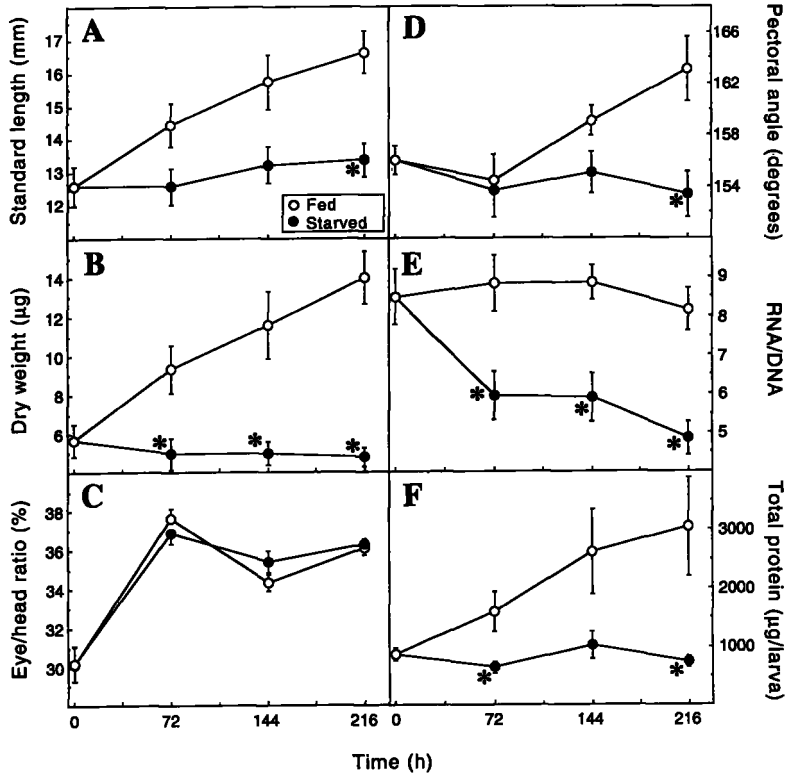

Figure 4

Summer flounder, *Paralichthys dentatus*, 60-day-old juveniles. Morphometric, gravimetric, and biochemical changes during ad libitum feeding (○) or starvation (●). (**A**) standard length; (**B**) dry weight; (**C**) eye diameter/head height ratio; (**D**) pectoral angle; (**E**) RNA:DNA ratio; (**F**) total proteins. Symbols represent the arithmetic mean of samples of 9–10 animals ±Standard Error. Asterisks indicate a statistically significant difference between fed and starved groups at a particular sampling time.

significant from the first sampling time in 16-day-old larvae (t_{18}=6.86, P<0.001, at 24 h), 33-day-old larvae (t_{18}=2.87, P=0.010, at 24 h), and in 60-day-old juveniles (t_{10}=3.05, P=0.012, at 72 h; Fig. 7, D, F, and H, respectively). In the case of 6-day-old larvae, these differences were significant after 48 hours (t_{18}=10.49, P<0.001; Fig. 7B).

Discussion

In summer flounder, the onset of mortality due to starvation occurred later in older ontogenetic stages, similar to observations made by Ivlev (1961) and Wyatt (1972). Response to starvation may depend not only on energy reserves stored in the liver, muscles, and other body tissues but also on more efficient catabolic capabilities attained during ontogenesis (Ehrlich, 1974b). Yin and Blaxter (1987) argued that the relative tolerance to lack of food is the result of reduced energy costs for metamorphosing flounder that increasingly spend more time lying on the bottom.

Morphometric, biochemical, and histological measurements all showed significant differences between starved and fed summer flounder at some point during development. The question then becomes the following: Which individual measurement or combination is the most useful indicator of nutritional status as development proceeds? We define usefulness both in terms of ease and practicality of application. Because of the relatively low resistance to starvation in younger larvae, it is imperative to select an indicator with the sensitivity to respond quickly to changes in nutritional status.

While mean length and dry weight of fed summer flounder showed a steady increase, starving fish shrank or did not grow. Only in 6-day-old larvae did standard length decrease, presumably representing

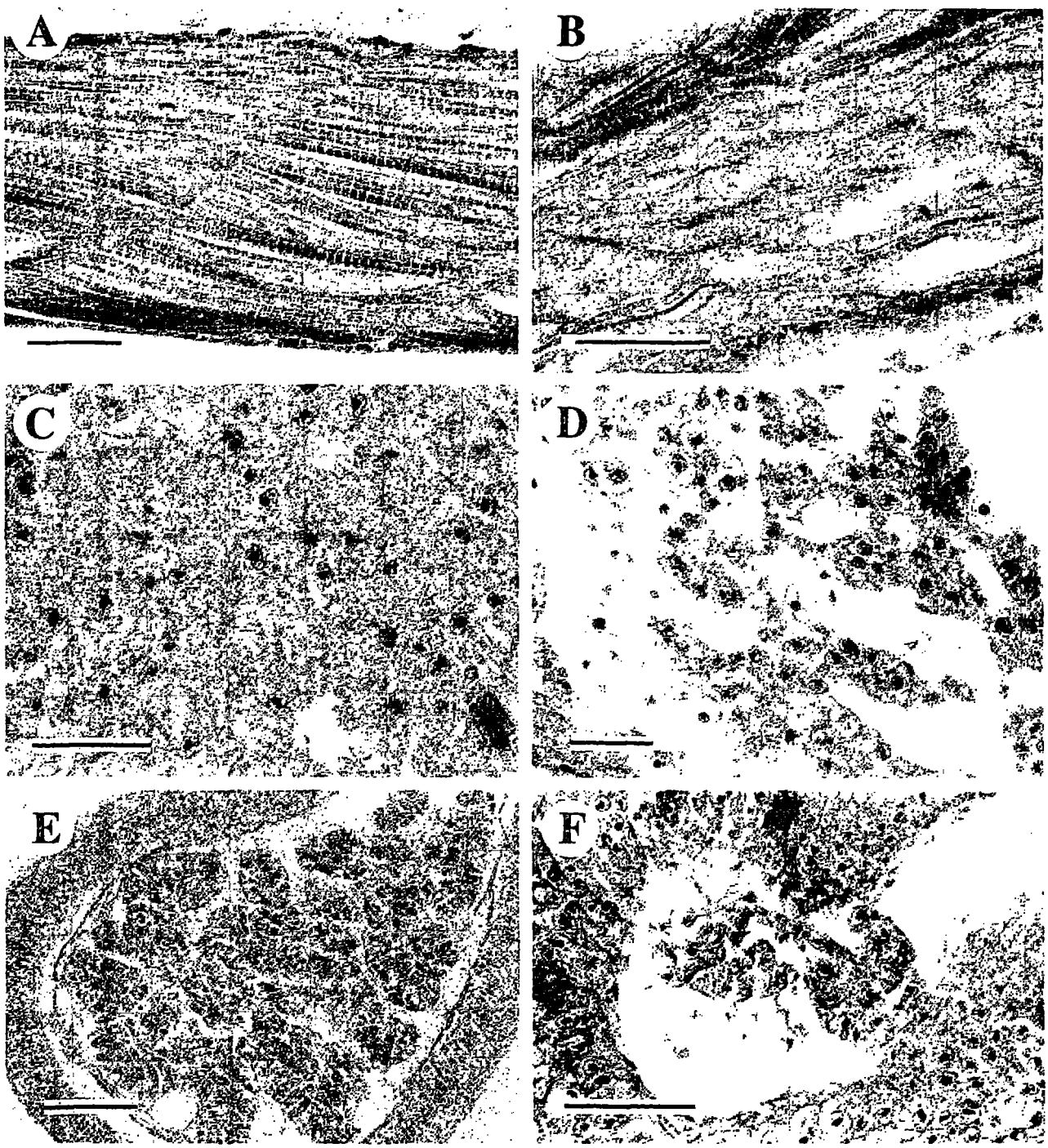

Figure 5

Histological comparisons of ad-libitum-fed and starved summer flounder, *Paralichthys dentatus*, larvae. (**A**) 16 days after hatching (DAH), skeletal musculature, ad-libitum-fed control (bar=20 µm). (**B**) 19 DAH, skeletal musculature, after 72 hours of starvation (bar=35 µm). (**C**) 18 DAH, hepatic tissue, ad-libitum-fed control (bar=25 µm). (**D**) 19 DAH, hepatic tissue, after 72 hours of starvation (bar=20 µm). (**E**) 19 DAH, pancreatic tissue, well-fed control (bar=55 µm). (**F**) 19 DAH, pancreatic tissue, after 72 hours of starvation (bar=30 µm).

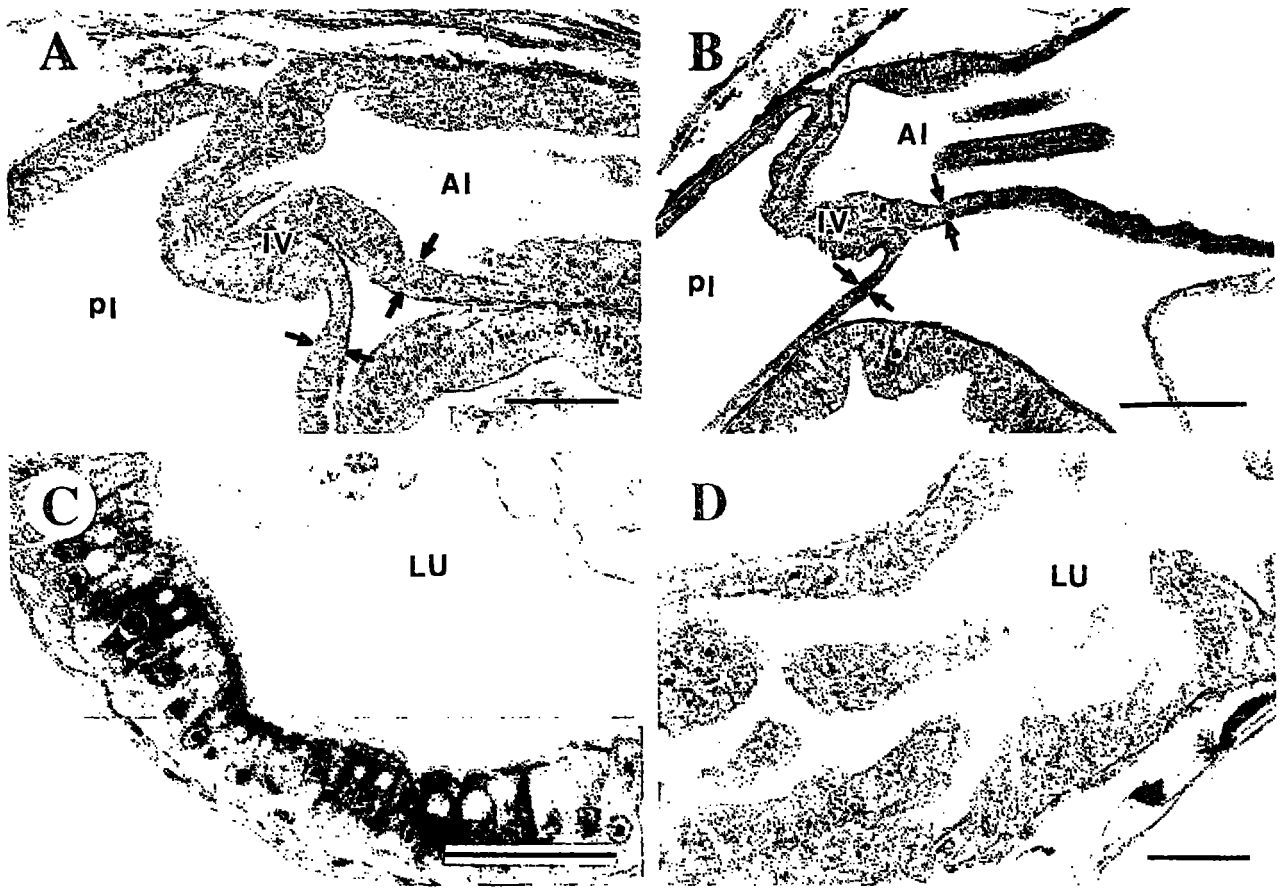

Figure 6

Histological comparisons of well-fed and starved summer flounder, *Paralichthys dentatus*, larvae. (**A**) 19 days after hatching (DAH), intestinal mucosae at the intestinal valve, ad-libitum-fed control (bar=50 μm). (**B**) 19 DAH, intestinal mucosae at the intestinal valve, after 72 hours of starvation (bar=60 μm). The arrows indicate the mucosal height in each intestinal segment. (**C**) 16 DAH, detail of enterocytes showing absorptive inclusions, ad-libitum-fed control (bar=35 μm). (**D**) 19 DAH, detail of enterocytes showing cellular sloughing into the lumen, after 72 hours of starvation (bar=20 μm). Abbreviations: AI=anterior intestine, IV=intestinal valve, LU=lumen, PI=posterior intestine. The arrows indicate the mucosal height in each intestinal segment.

shrinkage of the larvae after yolk absorption. Shrinkage of starved early stage larvae has been reported in herring (Ehrlich et al., 1976) and striped bass (Eldridge et al., 1981). Additionally, large variation in the extent of shrinkage has been reported in preserved larvae as a consequence of capture and fixation (Theilacker, 1980; Hay, 1981). The time of sampling must also be considered to account for changes in dry weight associated with the diurnal rhythms of visual feeders (Arthur, 1976). The dry weight of a larva with a full digestive tract will obviously be greater than that of the same larva with an empty digestive tract. Because extensive calibration between laboratory and field experiments is necessary to compare small larvae at the same developmental stage, length and dry weights are not useful indicators of nutritional status.

The pectoral angle accurately identified the nutritional condition of earlier larval stages. The variability within each group was low and significant differences were established early in the sampling protocol. However, these attributes progressively vanished at later stages. The eye length to head diameter ratio was not a good indicator of the feeding condition at any stage because of large variability within each group. Ehrlich et al. (1976) found the pectoral angle to be a good indicator of starvation in both herring, *Clupea harengus*, and plaice, *Pleuronectes platessa*, but the eye:head ratio was a good indicator in herring only.

Morphological characteristics are relatively simple to measure, inexpensive, and require little time, but the validity of laboratory-derived criteria is uncer-

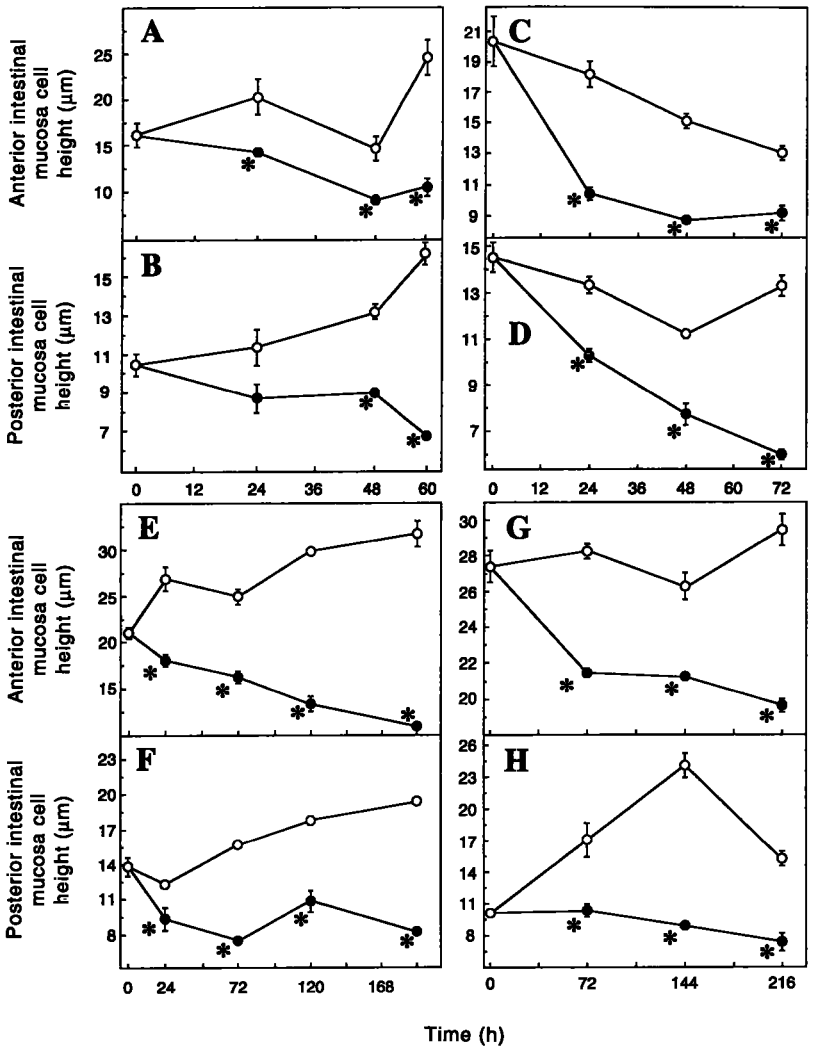

Figure 7

Anterior and posterior intestinal mucosal cell height in summer flounder, *Paralichthys dentatus*, during ad libitum feeding (○) or starvation (●). (**A–B**) 6-day-old larvae; (**C–D**) 16-day-old larvae; (**E–F**) 33-day-old larvae; (**G–H**) 60-day-old juveniles. Symbols represent the arithmetic mean of samples of 9–10 animals ±Standard Error. Asterisks indicate a statistically significant difference between fed and starved fish groups at a particular sampling time.

tain for populations in nature (O'Connell, 1976; Theilacker, 1986; Fraser et al., 1987; Setzler-Hamilton et al., 1987). Confinement in experimental tanks influences growth rates and morphometrics of laboratory-reared larvae (Blaxter, 1975; Arthur, 1976). At present, the applicability of morphometric indices seems more reliable and feasible for reared larvae, where age and historic information are known and feeding can be controlled.

Given the inherent problems of laboratory-to-field calibration and the dynamic changes in body proportions due to allometric growth and progressive ossification of developing larvae, Theilacker (1978) concluded that no single morphological feature can be singled out as a consistent indicator of larval condition. Because some of the variability associated with field-collected larvae is accounted for by differences in age of larvae, interpretation of the data requires the ability to determine age. Ageing of summer flounder from daily growth ring deposition is difficult on field-collected larvae of mixed age (Dery, 1988, Szedlmayer and Able, 1992). Therefore, the use of

length as an estimate of age is a coarse alternative when age data are not available. If this is the case, then the analysis should be restricted to a limited size range (Martin and Wright, 1987).

Among the biochemical criteria, protein data had the largest associated variability. Similar variation in the protein content of winter flounder, *Pleuronectes americanus*, larvae has been obtained by Cetta and Capuzzo (1982). Other studies have shown that protein breakdown is the major source of energy during starvation of herring (Ehrlich, 1974a) and plaice (Ehrlich, 1974b), at least during early larval stages, when lipid reserves are negligible or nonexistent.

The RNA:DNA ratio showed less individual variability and provided a more sensitive index to feeding condition than did protein. The ratio of total RNA to DNA in tissues has been extensively used as an indicator of recent growth rate and changes in feeding levels of various larval fish (Buckley, 1984; Bulow, 1987). In recent years, the relative ease and sensitivity of this analysis have stimulated the development of several procedural variations of the technique. Thus, discretion should be exercised in directly comparing RNA:DNA values obtained with different methods and standards (Caldarone and Buckley, 1991). In addition, it has been demonstrated that temperature can affect the RNA:DNA ratio in fish larvae (Buckley, 1982, 1984; Buckley and Lough, 1987). In the 6-day-old larvae used in our study, the RNA:DNA ratio declined by about 30% over the 60-hour experiment, even in fed larvae. After that decline, which was similar in magnitude to that observed in fed winter flounder larvae 4 days after yolk absorption (Buckley, 1980), the mean RNA:DNA ratio of fed larvae remained within a narrow range (2.7 to 3.1) for the remainder of the larval period. Therefore, it appears that a mean RNA:DNA ratio of less than 2.7 strongly suggests food limitation in flounder. The equilibrium RNA:DNA ratio for *P. dentatus* larvae reared at 14, 16, or 18°C has been reported to be 2.4, 3.1, and 2.6, respectively (Buckley, 1984). Winter flounder and striped bass, *Morone saxatilis*, larvae also appear to establish narrow RNA:DNA equilibrium ranges (Buckley, 1980; Wright and Martin, 1985). After metamorphosis, the RNA:DNA ratio of summer flounder increased to between 8.2 and 8.9, whereas that of starved fish was never above 6. A similar increase in RNA:DNA ratio after metamorphosis has been observed in fed winter flounder (Buckley, 1980).

Although RNA:DNA ratio and pectoral angle were both able to discriminate fed from starved summer flounder, pectoral angle was more sensitive to starvation than was the RNA:DNA ratio in larvae, whereas the opposite was true for juveniles. The quick response of RNA:DNA ratio to food deprivation noted by Buckley (1980), Wright and Martin (1985), and Martin and Wright (1987) was not apparent in summer flounder. An advantage of biochemical methods for field use is that larvae damaged by sampling gear can still be analyzed (Fraser et al., 1987) and distortions due to chemical fixatives are avoided. We conclude, therefore, that RNA:DNA ratios may be useful as indicators of nutritional limitation in summer flounder larvae and juveniles.

Histological analyses indicated that food deprivation of summer flounder larvae and early juveniles had a marked effect on several internal structures. Starvation was readily manifest in the intestine, followed in time by changes in the pancreas, liver, and skeletal musculature, as previously seen in other teleost larvae (Umeda and Ochiai, 1975; Ehrlich et al., 1976; O'Connell, 1976, 1980; Theilacker, 1978, 1986; Cousin et al., 1986; Margulies, 1993). The nutrient shortages that result from food deprivation have an almost immediate manifestation in the intestinal epithelium. In starved summer flounder, lipid and protein inclusions progressively disappeared from the intestinal epithelial cells until they were no longer visible, similar to the previous observations of Ehrlich (1974a), Ciullo (1975), Watanabe (1985), and Govoni et al. (1986). By contrast, Kjørsvik et al. (1991) reported that pinocytic inclusions were visible at all stages of starvation in cod larvae.

Mucosal cell height in summer flounder was extremely sensitive to starvation when applied to the posterior intestine, whereas the height of the anterior intestinal mucosa varied with increasing size or age, or both. The mean height of the posterior intestinal mucosa showed a stable boundary for discrimination of fed and starved individuals (above 10 μm for fed larvae, below for starved) regardless of individual size or age. This criterion therefore provides the best tool to assess starvation in summer flounder during the first 60 days of life. Previous investigators have noted the utility of histological examination of intestinal mucosa, especially cell height, for determination of starvation (Ehrlich et al., 1976; Theilacker, 1978, 1980; Watanabe, 1985; Umeda et al., 1986; Theilacker and Watanabe, 1989; Kjørsvik et al., 1991). The discriminating power of the mucosal cell height criterion incorporates the well known advantages of other traditional histological evaluation procedures. As with the biochemical criteria, specific equipment and some technical proficiency are required to process the samples. One advantage to this criterion is that samples can be preserved on a ship and no subsequent calibration is necessary for shrinkage due to capture or fixation, or for individual size or age.

To summarize, this study has demonstrated that 1) morphological criteria were either not good indicators of nutritional condition (eye:head ratio), good only for larvae (pectoral angle), or require extensive calibration (standard and dry weight); 2) biochemical criteria are either not good indicators (protein content) or are sensitive only in juveniles (RNA:DNA ratio); and 3) the histological criterion of posterior intestinal mucosa cell height is the most sensitive and consistent indicator of starvation in young summer flounder over the stages examined. Although the current study needs to be applied to field-collected larvae, the laboratory data indicate that the additional time and expense of histological sample preparation and analysis is justified in the face of uncertainties associated with the other methods examined. On the other hand, application of either morphological or histological criteria is appropriate for an aquaculture setting in which age of the larvae is known.

Acknowledgments

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Abstract.—Species diversity and abundance of fish eggs in shelf waters of the western Gulf of Alaska were similar in both surface neuston net tows and subsurface bongo net tows, but a unique group of fish larvae appear to be associated with the neuston in this region. The dominance of larvae of an osmerid, several hexagrammids, cottids, bathymasterids, *Anoplopoma fimbria*, *Cryptacanthodes aleutensis*, and *Ammodytes hexapterus* in this group resembles the neustonic assemblage of fish larvae found in the California Current region along the U.S. west coast and most of these taxa are considered obligate members of the neuston. Several taxa, however, appear to be abundant in the neuston only at night suggesting a facultative association with the neuston through a diel pattern of vertical migration. The facultative association of certain species of larvae with the neuston varies with larval size.

The distribution patterns observed for most taxa of fish larvae in the neuston during this study suggest that during spring, spawning and emergence of larvae into the plankton and subsequently into the neuston take place mainly around Kodiak Island (except along the seaward side) and along the Alaska Peninsula to the southwest. Analysis of multispecies spatial patterns using recurrent group analysis and numerical classification did not reveal the existence of more than one neustonic assemblage of fish larvae in the study area. Apart from perhaps *Pleurogrammus monopterygius* larvae, which are known to occur throughout the Gulf of Alaska, and to a lesser extent *A. fimbria* and *Hemilepidotus hemilepidotus*, members of this neustonic assemblage of larvae are not commonly found in the oceanic zone.

The ecological significance of a neustonic existence for larvae of fish that are primarily demersal spawners in the Gulf of Alaska is considered to be trophic in nature. Neustonic fish larvae seem to be able to exploit to their advantage the unique feeding conditions which exist at the sea surface.

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Neustonic ichthyoplankton in the western Gulf of Alaska during spring*

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The Fisheries Oceanography Coordinated Investigations (FOCI) is a long-term cooperative research program conducted by National Oceanic and Atmospheric Administration (NOAA) biological and physical scientists to describe processes leading to recruitment variability of commercially important fish and shellfish stocks of the Gulf of Alaska and Bering Sea (Schumacher and Kendall, 1991). To date, most effort has concentrated on walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska, specifically in Shelikof Strait and along the Alaska Peninsula. Understanding the dynamics of the spring spawning of this species in Shelikof Strait and the subsequent hatching, drift, growth, and survival of the larvae, in interaction with the physical and biological oceanographic environment, have been the primary goals of FOCI.

Ancillary to the information collected on the early life history stages of walleye pollock, are data on the distribution and abundance patterns of eggs and larvae of other fishes that spawn in the coastal waters and adjacent deeper waters of the western Gulf of Alaska. These observations can contribute to our understanding of the biology and ecology of fish populations in this region and the relationships between their life history strategies and the environment.

Prior to the onset of FOCI investigations in the early 1980's, plankton collections in the vicinity of Kodiak Island were generally limited in scope but still yielded information on species composition and spatio-temporal patterns in abundance of fish eggs and larvae (Rogers et al., 1979; Kendall and Dunn, 1985; Kendall et al.[1]). Based on early FOCI plankton collections, large-scale patterns in the ichthyoplankton have been documented for a more extensive portion of the continental shelf along the Alaska Peninsula (Rugen and Matarese[2]; Rugen[3]). There remains, however, considerable data from the more recent FOCI spring cruises, the analysis of which may improve our understanding of the ecological relationships among the fish populations inhabiting this region.

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[1] Kendall, A. W., Jr., J. R. Dunn, R. J. Wolotira Jr., J. H. Bowerman Jr., D. B. Dey, A. C. Matarese, and J. E. Munk. 1980. Zooplankton, including ichthyoplankton and decapod larvae, of the Kodiak Shelf. U. S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA 98115. Proc. Rep. 80-8, 393 p.

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During the 1970's and 1980's, several investigations of ichthyoplankton in the neuston were conducted in the northeast Pacific Ocean, primarily off the coasts of Washington and Oregon but also extending to southern California waters (Ahlstrom and Stevens, 1976; Shenker, 1988; Brodeur, 1989; Doyle 1992). These studies established that larvae of many fish are abundant at the surface as well as deeper in the water column and that an additional group of species is almost exclusively neustonic. Doyle (1992) identified obligate and facultative members of the neuston among the larvae and juveniles of fish collected off Washington, Oregon, and northern California and attributed their association with the neuston primarily to the unique trophic conditions that prevail in this environment. Clearly, the neustonic realm is important in the early life history of many fish species (Zaitsev, 1970; Hempel and Weikert, 1972; Moser, 1981; Tully and O'Ceidigh, 1989; Doyle 1992). The level of importance, however, varies with geographical area and local conditions.

Rogers et al. (1979), Kendall and Dunn (1985), Kendall et al.[1], and Rugen[3] identified a unique surface component in the ichthyoplankton of the western Gulf of Alaska and concluded that the larvae of several species, mainly hexagrammids and cottids, are primarily neustonic. This finding merits further investigation concerning the ecological significance of a neustonic existence, particularly in this shelf area where there is a dynamic surface zone with a vigorous flow field (Reed et al., 1988; Reed and Schumacher, 1989). The present paper focuses on the neustonic ichthyoplankton in the western Gulf of Alaska. During seven of the spring cruises (1981–86), neuston as well as subsurface bongo net sampling was carried out. Data from these collections were used 1) to examine species composition and relative abundance of ichthyoplankton taxa in the neuston and to compare these with subsurface ichthyoplankton collected concurrently; 2) to identify obligate and facultative members of the neustonic ichthyoplankton; 3) to investigate diel variation in catches of larvae in the neuston; 4) to compare size distributions among the neustonic and subsurface larvae; and 5) to describe horizontal distribution patterns of the dominant neustonic ichthyoplankton species and to relate these to the oceanography of the western Gulf of Alaska.

Methods

In 1981, the National Marine Fisheries Service (NMFS) initiated studies on the early life history of walleye pollock in the northwestern Gulf of Alaska. These studies included cooperative cruises with the Soviet Pacific Research Institute (TINRO, Vladivostok). Although the primary purpose of these cruises was to assess the spatial distribution and abundance of walleye pollock and to understand the dynamics of their planktonic stages, all taxa collected were identified and measured. For the present study, we used data from seven cruises during which both neuston net and bongo net samples were collected at each station. These cruises were conducted during spring months of the years 1981 to 1986 (Table 1). The survey area extended from the Kenai Peninsula (145°W), southwest along the Alaska Peninsula and Kodiak Island to Unimak Pass (165°W). The topography of the study area in the western Gulf of Alaska is characterized by numerous troughs and shallow banks (Fig. 1). The shelf area, as defined by the 200-m isobath, is generally wide (65–175 km) and drops abruptly to depths of 5,000–6,000 m in the Aleutian Trench, which parallels the shelf break (Fig. 1). A detailed description of the physical oceanography of the region is provided by Reed and Schumacher (1986).

The neuston was sampled at a total of 898 stations (Table 1). Station locations varied for each cruise because of specific objectives and are given in Dunn and Rugen.[4] Neuston net samples were collected with a Sameoto sampler (Sameoto and Jaroszynski, 1969)

[4] Dunn, J. R., and W. C. Rugen. 1989. A catalog of Northwest and Alaska Fisheries Center ichthyoplankton cruises, 1965–1988. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA, 98115. Proc. Rep. 89–04, 197 p.

Table 1

Summary of neuston collections by cruise conducted during spring of 1981 to 1986 in the western Gulf of Alaska.

Cruise	Inclusive dates	Number of collections	Longitudinal range (°W)
1SH81	5–18 March 1981	130	148–164
2SH81	16–24 April 1981	60	151–159
1CH83	16–31 May 1983	62	154–159
1SH84	17 April–9 May 1984	157	145–159
1PO85	29 March–21 April 1985	151	150–158
2PO85	16 May-8 June 1985	189	148–168
1GI86	30 March–20 April 1986	149	138–166

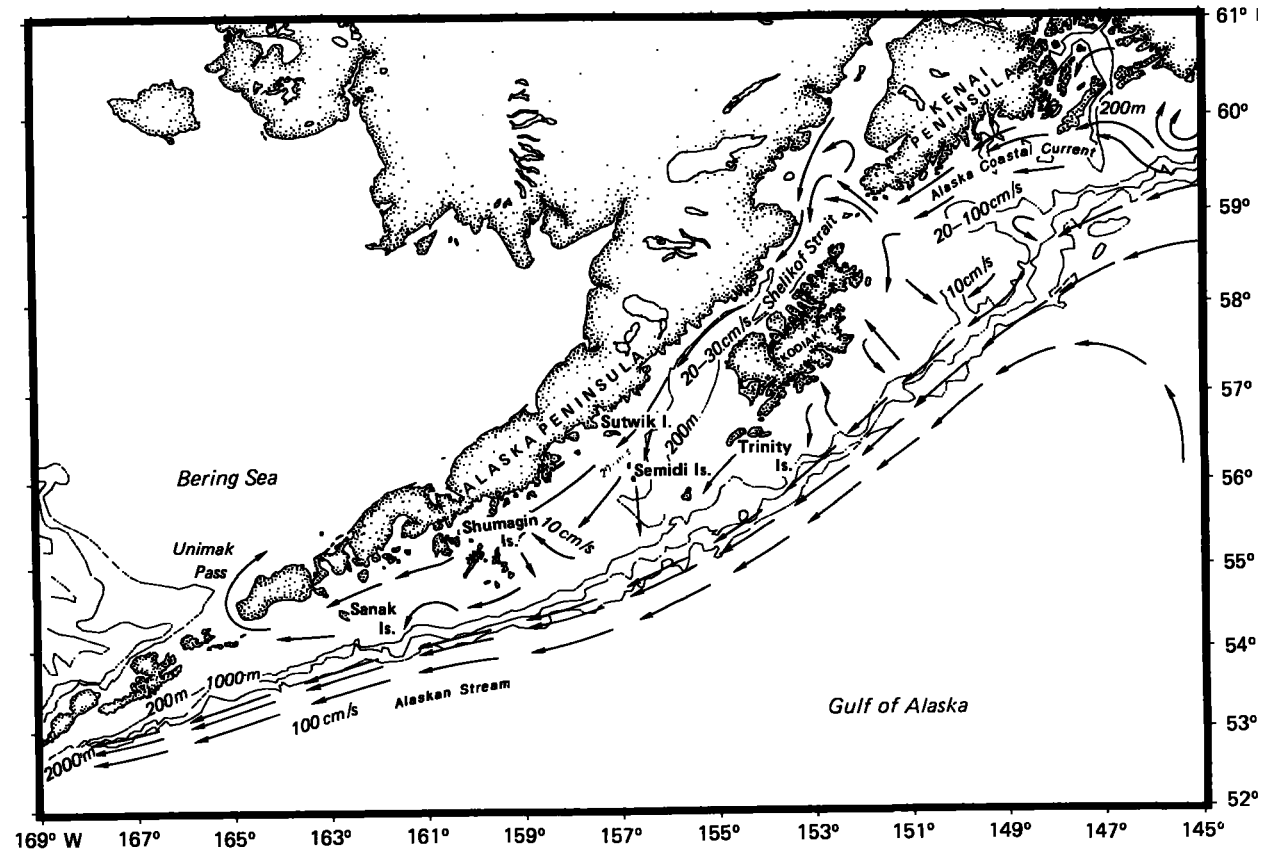


Figure 1

Near surface currents and some geographic and bathygraphic features of the western Gulf of Alaska. Currents based on Reed and Schumacher (1986).

with a mouth opening of 0.3 m × 0.5 m and with a 0.505-mm mesh net. Ship speed was 2 knots. Standard MARMAP (Marine Resources Monitoring Assessment and Prediction) oblique tows (Smith and Richardson, 1977) were conducted to sample subsurface ichthyoplankton with 60-cm bongo samplers fitted with 0.505-mm mesh nets. In shelf waters, tows were made to a depth close to the bottom, usually around 5 m above, and in deep water to a maximum depth of approximately 200 m. Calibrated flowmeters in the mouths of the samplers were used to determine the volume of water filtered by each net.

Counts of fish eggs and larvae were converted to densities per 1,000 m^3 for neuston collections, as follows:

$$(n)(1{,}000)/[(h)(w)(l)],$$

where n = number of organisms in sample;
h = effective fishing height of net opening (0.15 m);
w = width of net opening (0.5 m);
l = length of tow in meters (calculated from flowmeter).

In order to determine the importance of the neustonic layer relative to that of the entire water column, we compared the paired catches of neuston and bongo tows from the same stations following the approach derived by Hobbs and Botsford (1992). This approach accounts for the differences in surface area sampled between the neuston tows and the bongo tows. The method solves for the density of larvae per unit area in the ith sample (λ_i) and the portion of total water column larvae in the neuston (θ) simultaneously in an iterative fashion. We first calculated the surface area (in m^2) sampled by the neuston (A_{ni}) and bongo (A_{bi}) net as:

$$A_{ni} = \frac{h \times w \times l}{d}$$

and

$$A_{bi} = \frac{r^2 \times \pi \times l}{d},$$

where r = radius of net opening (0.3 m for bongo net);
d = depth of water column sampled.

The maximum likelihood estimates of λ and θ for k sample pairs are derived as follows:

$$\hat{\lambda} = \frac{S_{ni} + S_{bi}}{A_{ni}\hat{\theta} + A_{bi}}$$

and

$$\hat{\theta} = \min\left(1; \frac{\sum_{i=1}^{k} S_{ni}}{\sum_{i=1}^{k} A_{ni}\hat{\lambda}_i}\right),$$

where S_{ni} = number of larvae in the ith neuston sample;
S_{bi} = number of larvae in the ith bongo sample.

This method assumes that the sample pairs are drawn from a population that is distributed randomly in the horizontal plane but stratified vertically (Hobbs and Botsford, 1992).

Plankton samples were preserved in the field with a 5% formalin-seawater solution buffered with sodium tetraborate. Ichthyoplankton were sorted at the Polish Plankton Sorting Center in Szczecin, Poland. All fish eggs and larvae were removed and identified to the lowest possible taxa. Identifications were later verified at the NMFS laboratory in Seattle. Up to 50 larvae per taxon per station were measured to the nearest 0.1 mm standard length (SL).

Since sampling patterns and positions were different for each cruise, the study area was subsequently divided into 298 sectors of approximately 215 mi^2 (347 km^2). Data from stations within each sector were pooled so that average distribution patterns could be determined for the dominant neustonic taxa. The number of tows in each sector over all seven cruises are illustrated by various levels of stippling (Fig. 2). The mean densities of individual taxa were calculated for each sector by dividing the summed

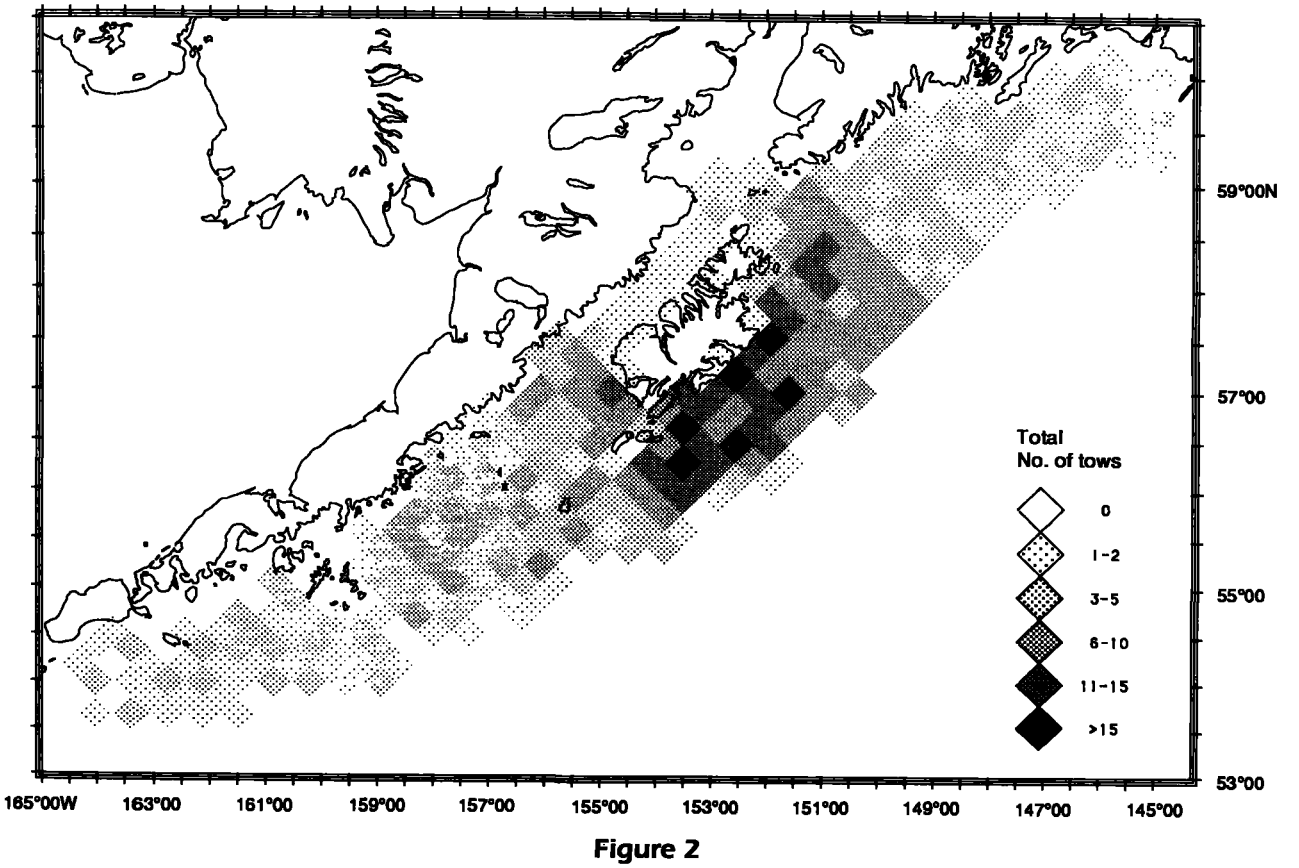


Figure 2

Neuston sampling coverage and intensity per sector for all seven cruises combined (1981–86).

abundance in each sector by the total number of stations sampled within that sector.

Cooccurrences of larval fish taxa in the neuston net samples were determined by using recurrent group analysis (Fager, 1957). This analysis identifies groups of taxa that occur together relatively frequently and considers only joint occurrences and not abundance. The procedure involves two steps: the calculation of indices of affinity for each pair of taxa and the formation of groups of taxa based on a chosen minimum index value. The equation for the affinity index is

$$I = \frac{N_j}{\sqrt{N_a N_b}} - \frac{1}{2\sqrt{N_b}},$$

where I = the affinity index (range 0–1);
N_j = the number of joint occurrences;
N_a = the number of occurrences of taxon a, the less common taxon;
N_b = the number of occurrences of taxon b, the more common taxon.

For this study, minimum index values for the formation of recurrent groups were set at 0.3 and 0.4, respectively, for two separate runs of the analysis. One or both of these values have been chosen previously by other workers who applied this method to ichthyoplankton data (Kendall and Dunn, 1985; Moser et al., 1987).

Numerical classification was used to investigate multispecies spatial patterns among the fish larvae in the neuston. It involves grouping similar entities based on numerical data such as, in this instance, species abundance at a range of stations (Clifford and Stephenson, 1975). An agglomerative, hierarchical technique was chosen. Normal and inverse classifications were carried out on the data sets (i.e. both the species and stations were classified into groups). Only the dominant larval fish taxa occurring in >4% of the samples were included in this analysis, as scarce taxa did not contribute significantly to spatial patterns overall. The numerical classification was performed on each individual data set from the seven neuston cruises, as well as on data combined for all the cruises (i.e. mean abundance of larval fish species in each of the previously chosen geographical sectors). The data were log-transformed prior to analysis.

The first step in the classification procedure comprised the calculation of correlation coefficients for each pair of species or stations in a data set. The Bray-Curtis dissimilarity measure was used. An agglomerative, hierarchical sorting strategy produced dendrograms depicting clusters of stations and species. The "flexible sorting" strategy was used and a recommended value of –0.25 was chosen as the clustering intensity coefficient (Lance and Williams, 1967).

To aid in identification of groups from the dendrograms, the original data sets (species abundance × stations) were rearranged into two-way tables according to the order that species and stations appeared in the dendrograms. In this manner, it was possible to see how a group of stations was characterized by the occurrence or definitive range of abundance of a particular species or group of species. After the final species and station groups were chosen, the two-way tables were reduced by calculating the mean abundance of each species, within the different species groups, for each station group. The station groups were then plotted on maps of the sampling area to aid in the identification of geographically distinct groups of fish larvae.

Results

Taxonomic composition and density

A total of 24,327 fish eggs were collected in the neuston samples. Eggs of 12 species representing five families were identified from the samples (Table 2). The numerically dominant taxa included the gadid *Theragra chalcogramma* and several pleuronectids, mainly *Errex zachirus*, *Hippoglossoides elassodon*, *Microstomus pacificus*, and other unidentified Pleuronectidae. *Theragra chalcogramma* was the only taxon whose eggs occurred in greater than 10% of all the samples. Although the density of *Clupea pallasi* eggs was relatively high, this taxon occurred in less than 1% of the samples. It is likely that the presence of these demersal eggs in the neuston was due to clumps of eggs breaking off the substrate and floating to the surface. The low diversity and generally low density of fish eggs in the neuston (relative to the diversity and density of fish larvae) was indicative of the scarcity of species that spawn pelagic eggs in this region.

In total, 41,157 specimens of larvae or early juveniles were caught in the neuston. The taxonomic diversity and overall density were higher than for the eggs (Table 3). Thirty-five species were identified representing a total of 18 families. Apart from *T. chalcogramma* and *Anoplopoma fimbria*, which spawn pelagic eggs close to the bottom, the numerically dominant taxa among the larvae were demersal spawners.

Among the dominant larvae, the families Hexagrammidae and Cottidae were best represented. The

Table 2

Summary of all fish eggs collected in neuston gear during spring cruises from 1981 to 1986 in the western Gulf of Alaska.

Scientific name	Common name	Percent occurrence (n=895)	Mean abundance (no./1000m^3)
Clupea pallasi	Pacific herring	0.37	22.83
Theragra chalcogramma	walleye pollock	28.12	205.59
Sebastalobus spp.	unidentified thornyhead	1.39	1.04
Chirolophis nugator	mosshead warbonnet	0.09	0.03
Trachipterus altivelis	king-of-the-salmon	0.74	0.16
Eopsetta exilis	slender sole	0.09	0.01
Errex zachirus	rex sole	6.38	5.50
Hippoglossoides elassodon	flathead sole	7.12	10.69
Microstomus pacificus	Dover sole	5.46	33.50
Platichthys stellatus	starry flounder	1.57	1.22
Pleuronectes asper	yellowfin sole	0.09	0.03
Pleuronectes isolepis	butter sole	0.37	0.20
Pleuronectes quadrituberculatus	Alaska plaice	5.83	12.67
Pleuronectes vetulus	English sole	0.46	0.49
Pleuronectidae	unidentified flounder	5.83	12.67
Teleost Type A	unidentified teleost	4.07	2.07
Teleost Type H	unidentified teleost	0.09	0.01

most abundant species by far was the hexagrammid *Hexagrammos decagrammus*, which was present in 71% of all the samples collected and had a mean density of 234 larvae/1,000 m^3 (Table 3). Less abundant were the hexagrammids *H. stelleri* and *Pleurogrammus monopterygius*. The category *Hexagrammos* spp. was also numerically important. Many of these larvae were most likely *H. decagrammus*, but the condition of the specimens made specific identification impossible. The most important taxa among the cottids were *Hemilepidotus hemilepidotus*, *H. jordani*, *H. spinosus*, *Hemilepidotus* spp., and *Myoxocephalus* spp. *Hemilepidotus hemilepidotus* was the third most abundant species overall, present in 20% of the samples with a mean density of 60 larvae/1,000 m^3. *Ammodytes hexapterus* was the second most abundant taxon with a mean density of 148 larvae/1,000 m^3 and was present in 14% of the samples. With a mean density of 43 larvae/1,000 m^3, *Cryptacanthodes aleutensis* was ranked as the fourth most abundant larval taxon and it was present in 21% of the samples collected. The remaining larval taxa each were found in less than 10% of the samples and had a mean density of less than 20 larvae/1,000 m^3. Most important among these were *Mallotus villosus*, *Theragra chalcogramma*, the hexagrammids and cottids mentioned above, *Bathymaster* spp., and the family Stichaeidae. The rest were scarce, mostly with a mean density of less than 1 larva/1,000 m^3 and a percent occurrence of less than 2%.

A comparison of the occurrence of dominant taxa of ichthyoplankton in the neuston samples with their occurrence in bongo samples, and estimates of the fraction of each taxon in the neuston, indicate that most of the dominant larval taxa in the neuston were scarce or absent in the subsurface zone (Table 4). In contrast, the dominant taxa of eggs were the same for both neuston and subsurface samples. *Theragra chalcogramma* eggs were by far the most abundant and accounted for 69% of all eggs caught in the neuston and 95% in the bongo samples. Eggs of pleuronectids, mainly of *Microstomus pacificus*, *Hippoglossoides elassodon*, and *Errex zachirus*, were the only other eggs to be significantly abundant in either gear, again indicating the paucity of pelagic spawners in this region. The estimated fractions (θ) of these eggs occurring in the neuston were moderately high (9–26%) merely showing that positively buoyant eggs tend to accumulate in the surface layer.

The only taxa of larvae well represented in both neuston and bongo samples were *T. chalcogramma*, *A. hexapterus*, and *Bathymaster* spp. (Table 4). All three occurred in much fewer of the neuston net than the bongo net samples, however. In addition, the fractions of these taxa occurring in the neuston were low (<13%) suggesting that they were only occasionally abundant in the neuston. Among the less abundant taxa in the neuston, *Mallotus villosus*, Stichaeidae, *Zaprora silenus*, and *Myoxocephalus* spp. were only slightly better represented in neuston net than in

Table 3

Summary of all fish larvae collected in the neuston during spring cruises from 1981 to 1986 in the western Gulf of Alaska.

Scientific name	Common name	Percent occurrence (n=895)	Mean abundance (no./1000m^3)
Mallotus villosus	capelin	5.83	8.90
Osmeridae	unidentified smelt	0.09	0.03
Nansenia candida	bluethroat argentine	0.09	0.01
Oncorhynchus keta	chum salmon	0.09	0.01
Bathylagidae	unidentified deepsea smelt	0.09	0.01
Stenobrachius leucopsarus	northern lampfish	0.09	0.01
Gadus macrocephalus	Pacific cod	0.65	0.15
Theragra chalcogramma	walleye pollock	6.75	13.66
Gadidae	unidentified gadid	0.56	0.24
Sebastes spp.	unidentified rockfish	1.67	2.68
Hexagrammos decagrammus	kelp greenling	59.11	194.84
Hexagrammos lagocephalus	rock greenling	0.46	0.09
Hexagrammos octogrammus	masked greenling	1.85	0.26
Hexagrammos stelleri	whitespotted greenling	8.14	1.87
Ophiodon elongatus	lingcod	1.76	0.53
Pleurogrammus monopterygius	Atka mackerel	3.61	1.76
Hexagrammos spp.	unidentified greenling	3.52	5.94
Hexagrammidae	unidentified greenling	0.28	0.04
Anoplopoma fimbria	sablefish	5.00	15.37
Blepsius bilobus	crested sculpin	0.09	0.01
Enophrys bison	buffalo sculpin	0.09	0.01
Hemilepidotus hemilepidotus	red Irish lord	16.84	50.25
Hemilepidotus jordani	yellow Irish lord	5.55	3.63
Hemilepidotus spinosus	brown Irish lord	6.38	5.80
Hemilepidotus spp.	unidentified Irish lord	3.70	5.47
Leptocottus armatus	Pacific staghorn sculpin	0.09	0.01
Myoxocephalus spp.	unidentified sculpin	2.59	1.04
Radulinus boleoides	darter sculpin	0.09	0.01
Cottidae	unidentified sculpin	0.65	0.10
Agonidae	unidentified poacher	0.28	0.04
Cyclopteridae	unidentified snailfish	0.37	0.06
Bathymaster spp.	unidentified ronquil	4.63	6.68
Chirolophis decoratus	decorated warbonnet	0.19	0.05
Chirolophis spp.	unidentified warbonnet	0.56	0.16
Lumpenella longirostris	longsnout prickleback	0.09	0.02
Stichaeidae	unidentified stichaeid	1.57	4.90
Cryptacanthodes aleutensis	dwarf wrymouth	17.76	36.13
Cryptacanthodes giganteus	giant wrymouth	1.67	0.53
Zaprora silenus	prowfish	2.78	1.09
Ammodytes hexapterus	Pacific sand lance	11.75	123.75
Atheresthes stomias	arrowtooth flounder	0.19	0.04
Errex zachirus	rex sole	0.46	0.08
Hippoglossoides elassodon	flathead sole	0.93	0.15
Hippoglossus stenolepis	Pacific halibut	1.67	0.48
Microstomus pacificus	Dover sole	0.09	0.01
Platichthys stellatus	starry flounder	0.19	0.05
Pleuronectes bilineatus	rock sole	0.56	0.12
Pleuronectes vetulus	English sole	0.09	0.01
Psettichthys spp.	unidentified sole	0.19	0.02
Reinhardtius hippoglossoides	Greenland turbot	1.48	0.55

Table 4

Comparison of percent occurence and percent of total abundance (based on no./1000 m^3) of the dominant taxa in the neuston and bongo collections and fraction of each taxon occurring in the neustonic layer (θ). Taxa ranked in order of percent occurrence in neuston.

	Neuston		Bongo		
Taxa	Percent occurrence	Percent total abundance	Percent occurrence	Percent total abundance	Fraction in neuston
Eggs					
Theragra chalcogramma	33.85	69.40	46.90	95.10	0.013
Hippoglossoides elassodon	8.69	3.61	21.06	0.72	0.091
Errex zachirus	7.68	1.86	18.07	0.77	0.155
Pleuronectidae	7.02	4.28	8.54	2.10	0.261
Microstomus pacificus	6.57	11.31	13.08	0.87	0.209
Larvae					
Hexagrammos decagrammus	71.16	40.15	4.99	0.22	0.930
Cryptacanthodes aleutensis	21.38	7.44	3.22	0.08	0.861
Hemilepidotus hemilepidotus	20.27	10.35	2.33	0.09	0.890
Ammodytes hexapterus	14.14	25.50	73.84	29.92	0.053
Hexagrammos stelleri	9.80	0.79	0.11	<0.01	0.989
Theragra chalcogramma	8.13	2.82	48.78	46.05	0.009
Hemilepidotus spinosus	7.68	1.19	0.55	0.01	0.932
Mallotus villosus	7.02	1.83	5.10	0.18	0.568
Hemilepidotus jordani	6.68	0.75	0.00	0.00	1.000
Anoplopoma fimbria	6.01	3.17	2.33	0.04	0.689
Stichaeidae	5.79	0.32	2.33	0.10	0.728
Bathymaster spp.	5.57	1.38	17.74	6.47	0.121
Hemilepidotus spp.	4.45	1.13	2.33	0.04	0.638
Pleurogrammus monopterygius	4.34	0.38	0.11	<0.01	0.974
Hexagrammos spp.	4.23	1.22	0.00	0.00	1.000
Zaprora silenus	3.34	0.22	2.55	0.05	0.541
Myoxocephalus spp.	3.12	0.22	1.88	0.08	0.596

bongo net samples perhaps also reflecting a facultative association with the neuston (i.e. concentrated at the surface only during certain hours). However, the high (54–73%) fraction occurring in the neuston suggests a strong association by these species with the surface zone.

The remaining dominant taxa of larvae in the neuston were absent or scarce in the bongo samples and all except *Hemilepidotus* spp. had a θ value of >85% (Table 4). It seems that their association with the neuston was obligative (i.e. permanent presence in the surface zone). These obligative taxa included the hexagrammids and cottids as well as *Cryptacanthodes aleutensis* and *Anoplopoma fimbria*. They formed a unique community of fish larvae in the neustonic realm.

Most of the dominant taxa of fish larvae that inhabit the subsurface zone of the western Gulf of Alaska were absent or rare in the neuston, including *Gadus macrocephalus* and *Sebastes* spp., and species of Bathylagidae, Myctophidae, Cyclopteridae, Agonidae, and Pleuronectidae (Kendall and Dunn, 1985; Rugen[3]).

Diel variation in catches of larvae

To examine diel variation in catches of larvae for both the neuston and bongo samplers, stations were grouped by hour of the day, and mean densities of larvae for each of the 24 hours were calculated. Because of the substantial variability in day length over the 3-month sampling period, it was not possible to assign a specific sunrise and sunset time that could be used for all cruises. For the purposes of this analysis, we assumed that the daytime period lasted from 0700 to 1900 hr and the nighttime from 2200 to 0400 hr. The intervening periods of 0400 to 0700 h and 1900 to 2200 h were presumed to have been twilight, including dawn and dusk, respectively.

For all neuston catches combined, both the total mean density and the number of hauls in which larvae were caught were higher at night than during

the day (Fig. 3A). This pattern was not apparent for the bongo catches taken from the same stations (Fig. 3B). Some of the highest catches of larvae in the bongo samples were taken during daylight. The ratio of night:day catches for the neuston was 9.1:1, whereas it was 1.6:1 for the bongo tows. The high ratio of night:day catches in the neuston may be attributed to two factors: 1) vertical migration of larvae into the neuston at night and 2) enhanced avoidance of the neuston sampler during daylight. One or both of these factors may operate among the species of larvae in the neuston.

Diel variation in catches among all the dominant taxa of neustonic larvae suggested a daytime decrease in density in the neuston. All larvae, except *Hexagrammos decagrammus* and *Theragra chalcogramma*, had lowest occurrences in neuston samples during the day (Fig. 4). Sampler avoidance by the larvae during daylight probably contributed significantly to this pattern. The taxa *Hemilepidotus jordani*, *H. spinosus*, *Myoxocephalus* spp., *Bathymaster* spp., and *Zaprora silenus* were absent from neuston samples during most daylight hours but were relatively abundant in twilight or nighttime samples. Because the latter three of these taxa were relatively common in bongo samples (Table 4), indicating a facultative association with the neuston, their scarcity in the neuston during the day may have been at least in part due to a diel pattern of vertical migration with larvae moving toward the surface zone at night. This may have also been true for *T. chalcogramma* and *Ammodytes hexapterus* whose larvae were extremely abundant in the bongo net samples (Table 4) but abundant in the neuston samples only at night (Fig. 4). *Mallotus villosus* larvae were also relatively common in bongo samples (Table 4), although they were most abundant in the neuston at night (Fig. 4).

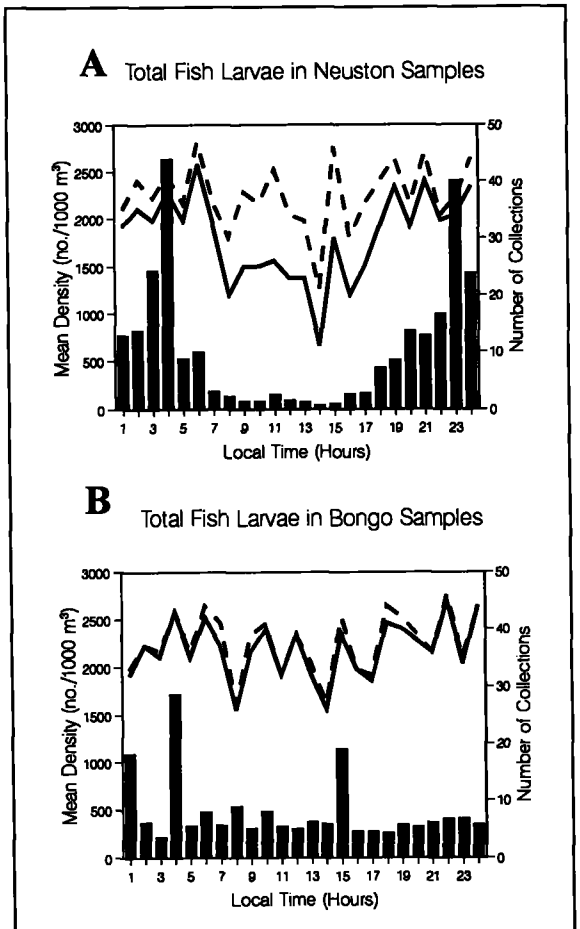


Figure 3

Diel variation in density and occurrence of total fish larvae in (**A**) neuston samples and (**B**) bongo samples for all cruises combined (1981–86). Bars represent mean density of fish larvae; dashed line represents total number of collections; solid line represents the number of hauls that collected fish larvae.

As expected, catches of *T. chalcogramma* eggs showed no discernable diel variation in either density or frequency of positive hauls. The large mean densities during two periods of the day are most likely due to spatial variation of egg densities rather than to any biological factor.

Length distributions of dominant neustonic taxa

Standardized length distributions were plotted for the dominant neustonic taxa (Fig. 5). Comparisons were made with the corresponding length distributions of larvae in the subsurface zone for six of these taxa that were sufficiently represented in the bongo samples. For all these six taxa, greater median lengths were documented for larvae in the neuston than in the bongo hauls, especially in the case of *Mallotus villosus* and *Ammodytes hexapterus*. *Mallotus villosus* seemed unusual in that all larvae caught in both neuston and bongo net samples were >25 mm SL indicating a predominance of postflexion larvae. This is most likely due to species identification capabilities, as it is not possible to identify small osmerids to species until the pectoral fin rays are completely developed. With the exception of *Bathymaster* spp., the larvae caught in the neuston were also significantly larger than those caught in the bongo collections (Kolmogorov-Smirnov (*K-S*) 2-sample tests; all $P<0.01$). For *A. hexapterus*, it seemed that only the large postflexion larvae and early juveniles (mostly >20 mm SL) migrated into the neuston, mainly at night; most *A. hexapterus* larvae

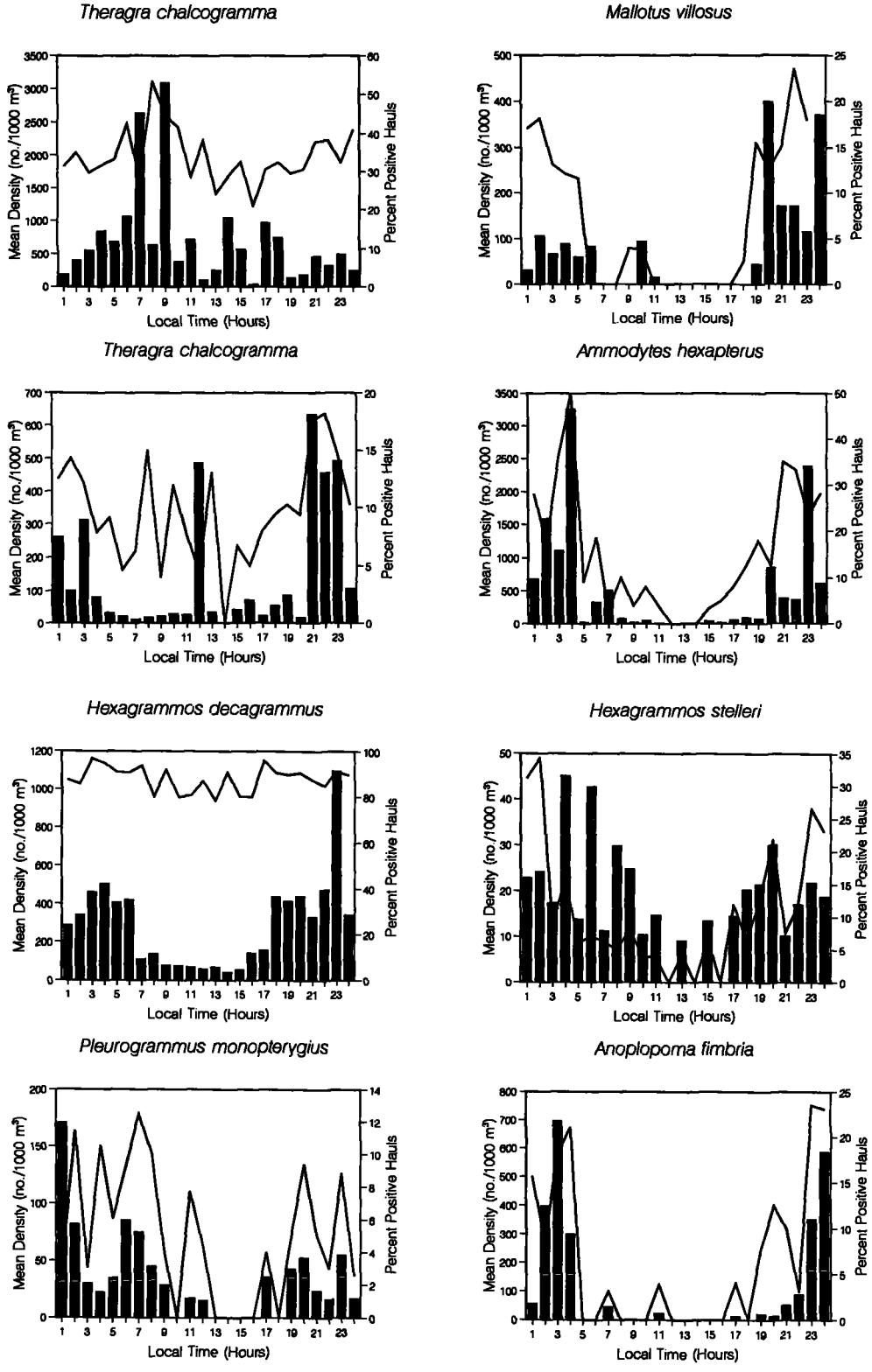
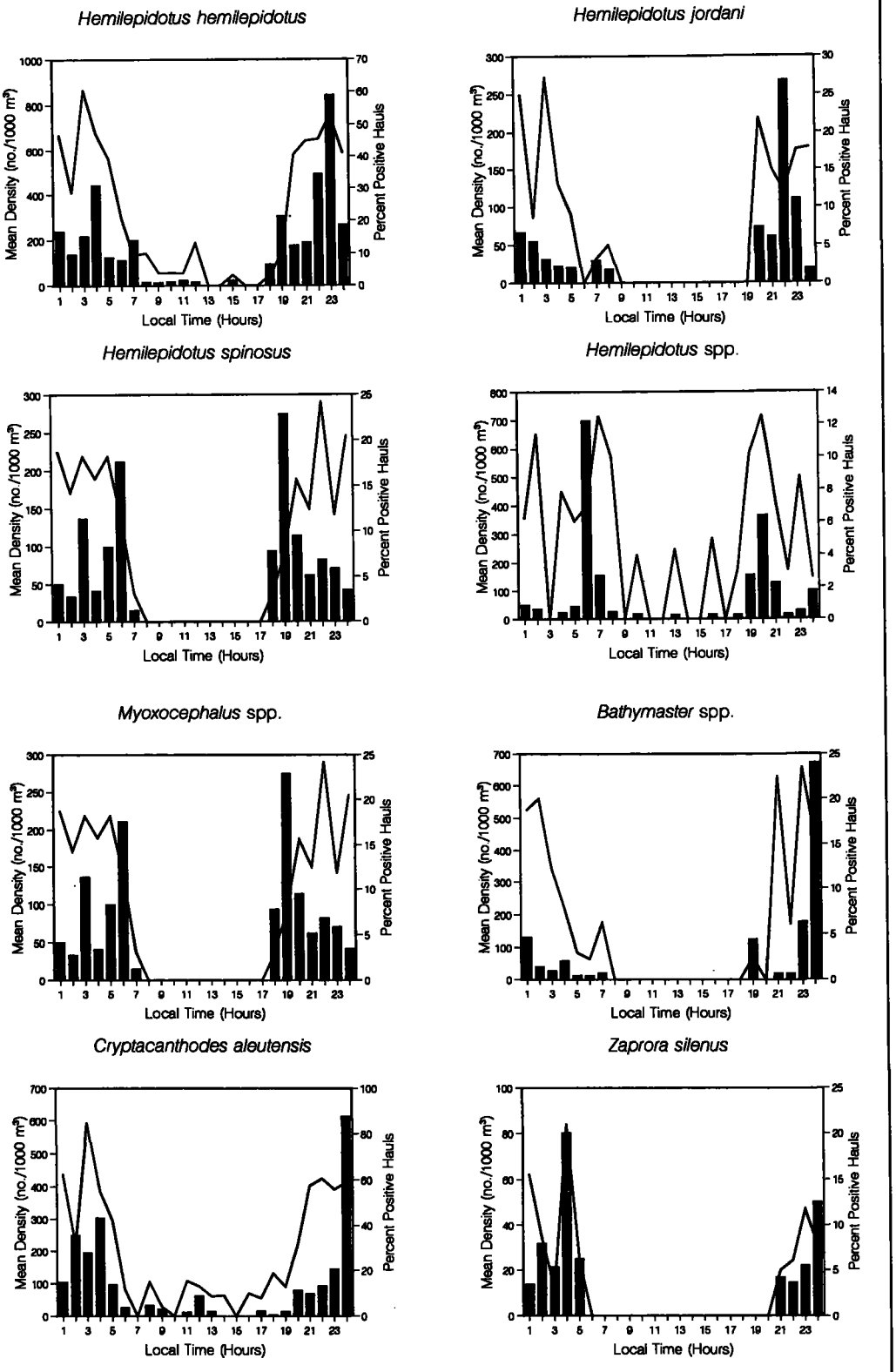


Figure 4

Diel variation in density and occurrence of walleye pollock, *Theragra chalcogramma*, eggs and individual dominant taxa of fish larvae in neuston samples, for all cruises combined (1981–86). Bars represent mean density; solid line represents the percent of hauls that caught larvae.



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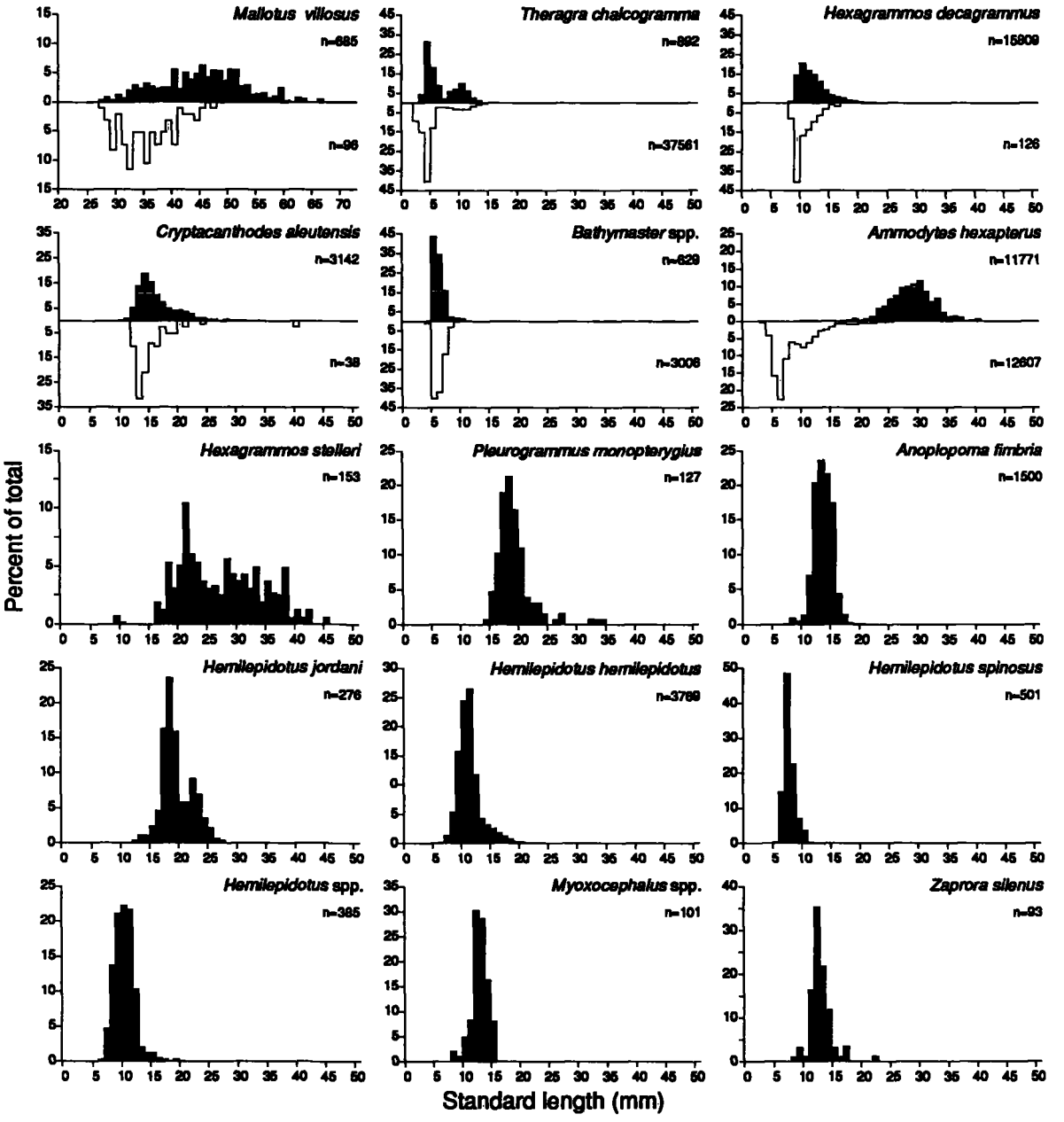

Figure 5

Length-frequency distributions for the dominant taxa of fish larvae in neuston samples and, where comparable, in bongo samples (open histograms), for all cruises combined (1981–86).

caught in the bongo samples were <15 mm SL. In contrast, larvae of *Bathymaster* spp. that were common in the neuston at night did not differ significantly in size from those occurring in the bongo samples; all were small, mostly <10 mm SL. *Theragra chalcogramma* larvae were also relatively small (all <15 mm but mostly <10 mm SL) both in bongo and neuston catches.

Among the remaining neustonic taxa, most larvae caught were >10 mm SL, and length distributions generally displayed one dominant mode within a relatively short length interval. The predominant length range for the taxa *Hexagrammos decagrammus*, *Cryptacanthodes aleutensis*, *Anoplopoma fimbria*, *Hemilepidotus hemilepidotus*, *Myoxocephalus* spp.,

and *Zaprora silenus* was 10–20 mm. *Hexagrammos stelleri*, *Pleurogrammus monopterygius*, and *Hemilepidotus jordani* larvae were larger with predominant length ranges of 15–40 mm, 15–25 mm, and 15–30 mm, respectively. In contrast, larval sizes for the cottids, *Hemilepidotus spinosus* and *Hemilepidotus* spp., were relatively small with a predominant length range of 5–15 mm.

Daytime catches of larvae in the neuston were sufficient to make diel comparisons in length distributions for only three of the dominant taxa. There was no significant day-night difference in the length distribution of *Hexagrammos decagrammus* larvae (*K-S* test; $Z=0.07$, $P>0.05$). *Theragra chalcogramma* larvae caught at night (median length=6 mm) were slightly, but significantly, larger (*K-S* test; $Z=1.52$, $P=0.02$) than those caught during the day (median length=5 mm). Day-night differences were much greater for *Ammodytes hexapterus* larvae for which the median length caught at night was 24 mm and the median day length was 13 mm (*K-S* test; $Z=4.99$, $P<0.001$). Migration of the larger larvae and juveniles to the surface at night may have been the cause of this difference, but it is also likely that enhanced sampler avoidance during daylight by large larvae and juveniles reduced the daytime median larval length significantly.

Horizontal patterns of distribution

Patterns of distribution illustrated here for total and individual dominant taxa of neustonic larvae were based on data combined for all cruises. The distribution maps therefore represent general patterns of horizontal distribution for these species during spring in this region and did not take into account day-night, monthly, or interannual differences in catches.

The pattern for total fish larvae in the neuston indicated that highest concentrations generally occurred to the southwest of Kodiak Island, in Shelikof Strait, and off the northern tip of Kodiak Island (Fig. 6A). Southwest of the Shumagin Islands and northeast of Kodiak Island, high densities of larvae were more scattered. Despite the high intensity of sampling seaward of Kodiak Island (Fig. 2), mean larval concentrations tended to be low in this region. Based on data which incorporated sampling during all seasons, Kendall and Dunn (1985) and Rugen[3] frequently recorded high concentrations of various species of larvae in the neuston seaward of Kodiak Island. The apparent scarcity of larvae here may therefore be characteristic of spring in the sampling area.

Larvae of the osmerid *Mallotus villosus* were taken primarily southwest of Kodiak Island along the Alaska Peninsula as far southwest as the Shumagin Islands (Fig. 6b). They were scarce southwest of the Shumagin Islands and seaward of Kodiak Island and absent in the northeastern part of the sampling area. This pattern is similar to that described by Rugen[3] except that the latter study plus Kendall and Dunn's (1985) observations indicated a greater presence of larvae seaward of Kodiak Island. These studies also showed that *M. villotus* larvae were relatively scarce both in bongo and neuston samples during spring; the main spawning season seems to be late summer through fall (Kendall and Dunn, 1985).

Theragra chalcogramma larvae were usually most abundant in the upper 50 m of the water column in the southern Shelikof Strait area and along the Alaska Peninsula during spring (Schumacher and Kendall, 1991). Spawning takes place primarily in the sea valley in Shelikof Strait during late March and early April. Rugen[3] has also documented the occurrence of pollock larvae on occasions in large concentrations to the northeast of Kodiak Island. These patterns were reflected in the distribution of pollock larvae in the neuston documented during the present study (Fig. 6C). The scarcity of larvae within Shelikof Strait may have been due to the low number of samples from that region. Pollock larvae were absent or scarce along the outer shelf and slope indicating that most of the larvae in the surface zone were retained on the shelf.

Neustonic larvae of *Anoplopoma fimbria* were most abundant during late spring and summer in the western Gulf of Alaska where they were associated with the shelf edge (Kendall and Dunn, 1985; Rugen[3]). The general distribution pattern documented here for the spring months showed them to be most abundant close to the shelf edge southwest and northeast of Kodiak Island, as well as around the northern and northwestern perimeter of Kodiak Island (Fig. 6D). As with pollock, this species is a pelagic spawner in deep water, and the distribution pattern of larvae suggested that spawning occurred mainly in outer shelf and slope waters, a pattern which is consistent with what is known about the early life history of this species (Kendall and Matarese, 1987; Doyle, 1992).

The dominant hexagrammid species whose larvae were abundant in the neuston of the sampling area all spawn in coastal waters (Matarese et al., 1989). In the Gulf of Alaska region, spawning of these species seems to occur from fall through spring (Kendall and Dunn, 1985; Rugen[3]). Larvae of the most abundant species, *Hexagrammos decagrammus*, were found to be dominant in the neuston during most of the year; during the summer months there was a large decrease in density. They were distributed widely throughout the sampling area, but greater concentrations were found in the southwestern re-

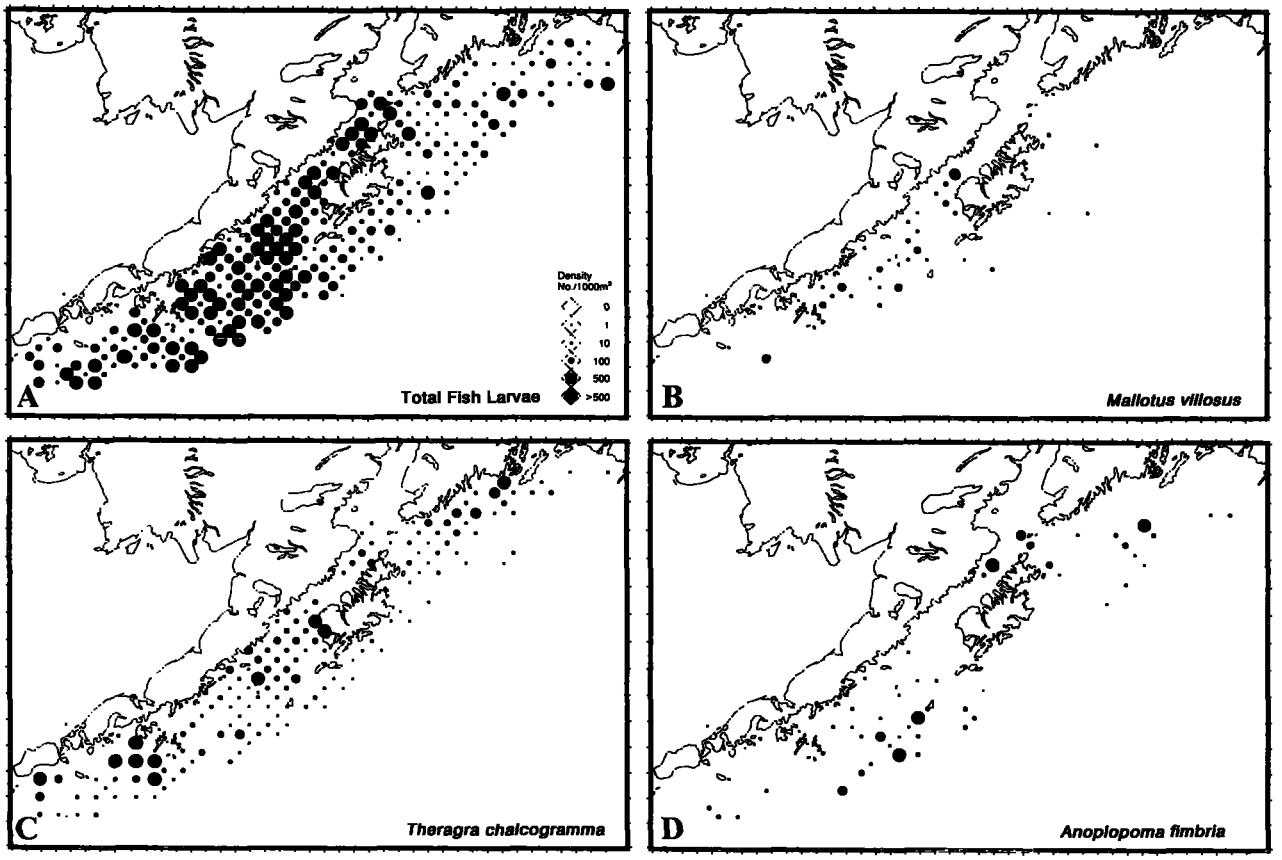

Figure 6

Distribution maps for total and individual dominant taxa of fish larvae in the neuston for all cruises (1981–86). Mean density of a particular taxa is superimposed on each sector in the form of a dot the area of which is proportional to the mean number of larvae/1,000 m^3.

gion than northeast of Kodiak Island (Rugen[3]). The same pattern was apparent from the spring data presented here (Fig. 6E). Larvae were most abundant to the north of Kodiak Island and to the southwest beyond the Shumagin Islands, whereas densities were lowest to the northeast and offshore of Kodiak Island. Kendall and Dunn (1985) documented widespread distribution around Kodiak Island but mainly at nearshore and midshelf stations early in the spawning season during fall. Advection of larvae in the neuston is probably extensive throughout winter and spring months in this region. Patterns in seasonal occurrence and spatial distribution of *H. stelleri* larvae were similar to those for *H. decagrammus* (Fig. 6F), and as found in previous studies (Kendall and Dunn, 1985; Rugen[3]), densities were much lower than those for *H. decagrammus*.

The third dominant hexagrammid species, *Pleurogrammus monopterygius*, was also considerably less abundant in the neuston than was *H. decagrammus*. Although the spawning season appears to extend from fall through spring, maximum densities of these larvae have been recorded during late October in the Kodiak Island region (Kendall and Dunn, 1985). The distribution of *P. monopterygius* larvae during the spring months of the present study extended from the Kodiak Island region southwest to the Shumagin Island area; most records were in the vicinity of the shelf edge from Kodiak Island to the Shumagin Islands (Fig. 6G). Kendall and Dunn (1985) and Rugen[3] also recorded highest densities of these larvae over the outer shelf and slope in the Kodiak Island region. The former authors also documented fingers of occurrence of these larvae extending shoreward associated with the troughs seaward of Kodiak Island. Although the larvae of this species usually display an offshore and oceanic distribution, spawning is known to take place in shallow water where currents

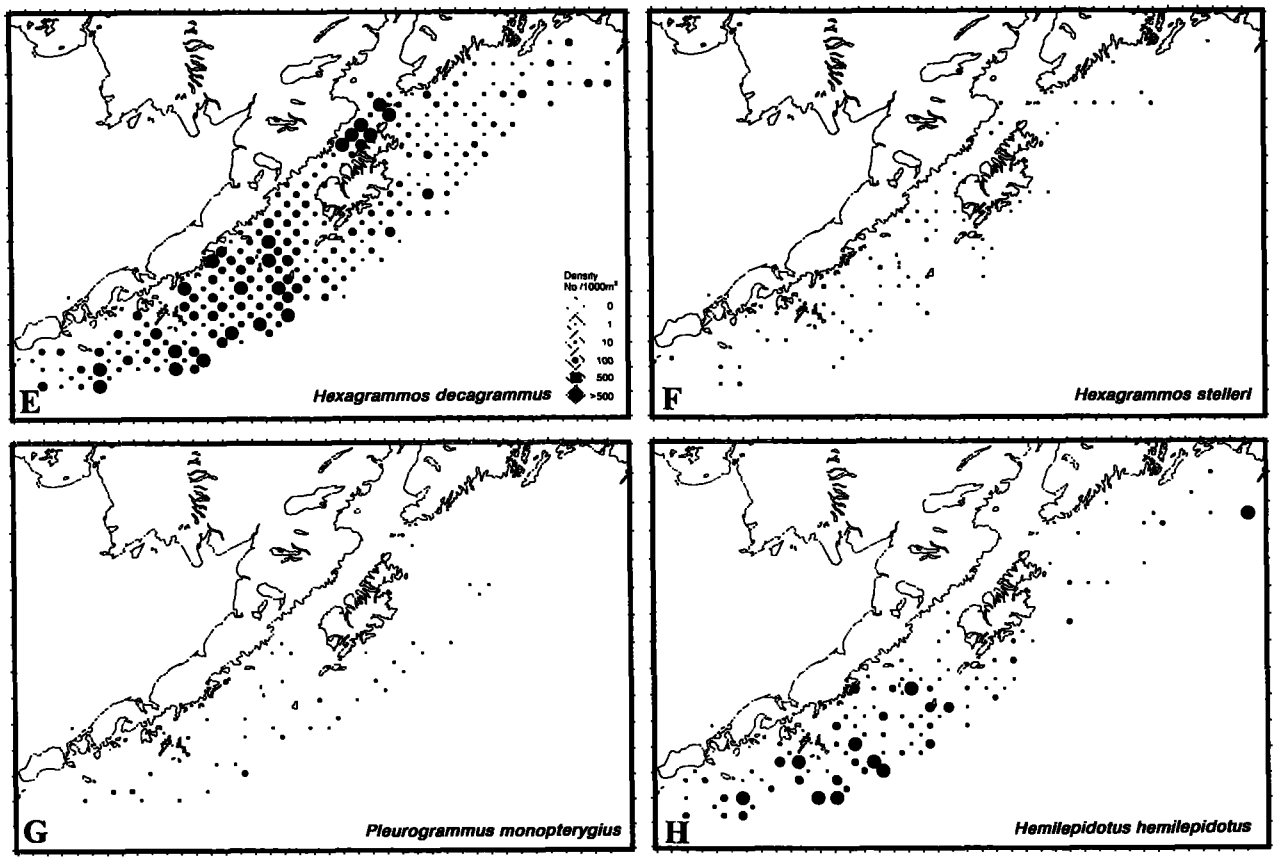

Figure 6 (continued)

are strong, primarily at 10–30 m depth, following an onshore migration by the mature adult fish during summer (Gorbunova, 1962; Macy et al.[5]). Gorbunova (1962) describes the oceanic occurrence of *P. monopterygius* larvae in the Pacific Ocean and Bering Sea and suggests that they migrate out to sea after hatching in shallow water, thus explaining the primarily offshore distribution pattern observed for these larvae.

The predominant cottid species in the sampling area were members of the genus *Hemilepidotus*. As with the hexagrammids, these species are inshore coastal dwellers that spawn demersal eggs and have neustonic larvae (Matarese et al., 1989). In the study area, spawning seems to occur from fall through spring; peak densities of larvae occur in the neuston during fall (Kendall and Dunn, 1985). The most abundant cottid recorded during the present study was *H. hemilepidotus*. Highest densities of this species occurred to the southwest of Kodiak Island, extended beyond the Shumagin Islands, and had a tendency to be associated with the mid- to outer-shelf region (Fig. 6H). Larvae were scarce northeast of Kodiak Island. The same pattern of distribution was observed for this species by Rugen[3] from samples taken during all seasons. The less abundant *H. jordani* displayed a similar distribution pattern (Fig. 6I) as did *Hemilepidotus* spp. (Fig. 6K). *Hemilepidotus spinosus*, however, had a more northerly distribution. Most larvae were caught northeast of Kodiak Island (Fig. 6J), suggesting that this is the main spawning area for this species.

Kendall and Dunn (1985) found larvae of the cottid *Myoxocephalus* spp. to be most abundant during summer to the south of Kodiak Island. The samples from the present study yielded low numbers of these larvae; when present they were found in the mid-shelf region

[5] Macy, P. T., J. M. Wall, N. D. Lampsakis, and J. E. Mason. 1978. Resources of the non-salmonid pelagic fishes of the Gulf of Alaska and eastern Bering Sea. Part 1: Introduction, general fish resources and fisheries, and review of literature on non-salmonic pelagic fish resources. Part of Final Report for Contracts R7120811 and R7120812, Task A-7, Research Unit 64/354, Outer Continental Shelf Environment Assessment Program, U.S. Dep. Interior, Bureau of Land Management, 355 p.

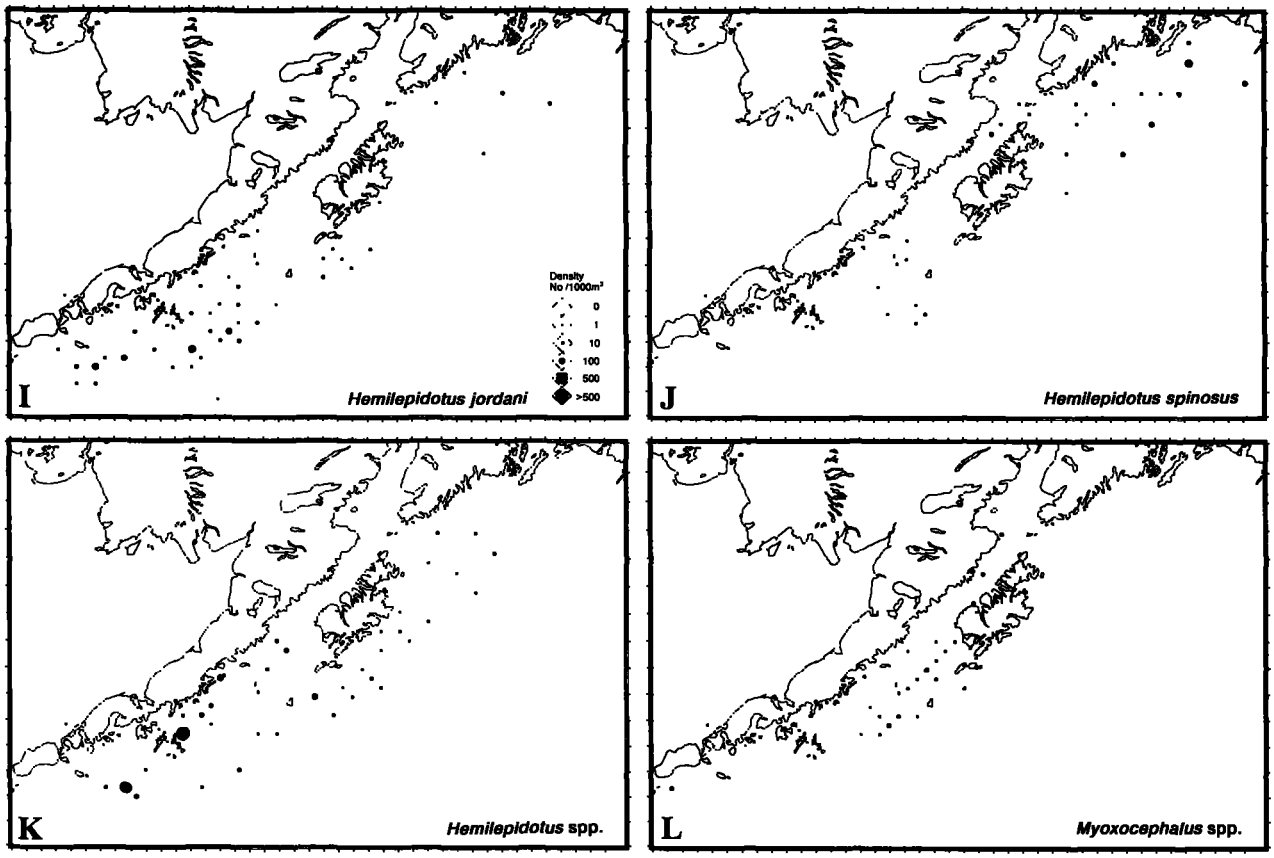

Figure 6 (continued)

between Kodiak Island and the Shumagin Islands (Fig. 6L). Spawning may be centered in this region.

Three species of bathymasterids belonging to the genus *Bathymaster* are known to occur in the sampling area: *B. caeruleofasciatus*, *B. leurolepis*, and *B. signatus* (Rogers et al., 1979; Rugen[3]). They are coastal demersal spawners. At the larval stage, it is not possible to identify these to species and they are included here in the taxon *Bathymaster* spp. The distribution of these larvae during spring was centered southwest of Kodiak Island (Fig. 6M) suggesting that this may be a primary spawning area. Occurrences were scarce northeast of Kodiak Island and southwest of the Shumagin Islands. It seems, however, that spring is a period when *Bathymaster* larvae are relatively scarce in the neuston. Previous studies have found these larvae to be most abundant in subsurface samples from May to October with a peak in summer (Kendall and Dunn, 1985; Rugen[3]). In the neuston, however, larvae did not become abundant until late June. Although Rugen[3] found *Bathymaster* larvae to be most abundant from Kodiak Island to the Shumagin Islands, he also found them to be abundant seaward of Kodiak Island, particularly during the summer, as did Kendall and Dunn (1985). There may be a northeasterly progression in spawning activity in the sampling area from spring to summer.

The wrymouth *Cryptacanthodes aleutensis* is epi- and meso-benthic in shelf and slope waters and spawns demersal eggs during spring and summer (Matarese et al., 1989). Larvae are associated mainly with the neuston (Kendall and Dunn, 1985; Doyle, 1992; Rugen[3]). The distribution of *C. aleutensis* larvae during the spring months of the present study was associated primarily with Kodiak Island and southwest to the Shumagin Islands (Fig. 6N), similar to that documented by Rugen.[3] Densities were higher in the inner- and mid-shelf region than along the shelf edge and slope.

The Pacific sand lance, *Ammodytes hexapterus*, is a pelagic, schooling species common to coastal and shelf waters and it spawns demersal eggs. Its larvae have been found to be facultative members of the neuston along the U.S. west coast where the well-

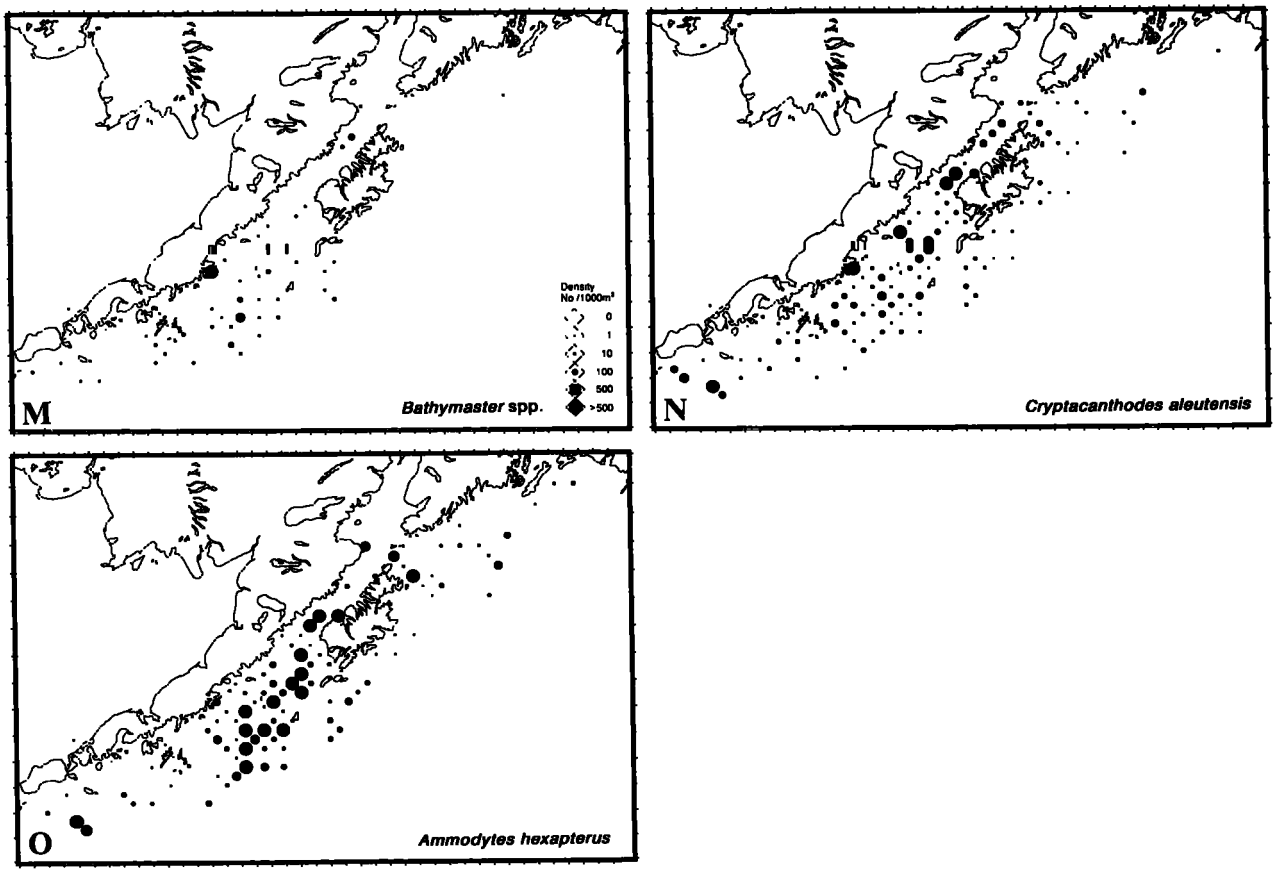

Figure 6 (continued)

developed larvae are abundant in the neuston mainly at night (Doyle, 1992). They are common in the neuston and subsurface zone in the western Gulf of Alaska from winter to summer (Kendall and Dunn, 1985; Rugen[3]). Mean larval lengths tended to be greater in the neuston, however, and densities were highest in the neuston during late spring and summer. As with many of the other species, *A. hexapterus* larvae were most abundant during spring in the mid-shelf area from southern Kodiak Island to the Shumagin Islands (Fig. 6O). They were scarce to the northeast and seaward of Kodiak Island and southwest of the Shumagin Islands. Kendall and Dunn (1985) and Rugen[3] found them to be more widely distributed in subsurface samples, including high numbers northeast and seaward of Kodiak Island, implying that spawning is widespread throughout the sampling area.

Multispecies spatial patterns

Three recurrent groups of larval fish taxa were identified by using Recurrent Group Analysis on data from all cruises (Fig. 7). Constituent members of these groups displayed affinity levels of ≥0.4 with each other. Individual species from these groups were also associated with individual species from other groups, or from outside the groups, at affinity levels of ≥0.3 or ≥0.4.

The largest group contained four taxa, *Cryptacanthodes aleutensis*, *Hemilepidotus hemilepidotus*, *Mallotus villotus*, and Stichaeidae, which frequently occurred together in the same samples. A second group comprising *Ammodytes hexapterus* and *Hexagrammos decagrammus*, the two most abundant larval species in the neuston, was connected to Group 1 via individual linkages among all taxa except Stichaeidae. The result, two groups and their associated weak linkages, suggested the existence of a loosely affiliated assemblage of larval species in the neuston for this region.

Pleurogrammus monopterygius and *Hemilepidotus* spp. belonged to a third recurrent group which did not display any linkages with other species or groups of species. This may reflect the unusual association

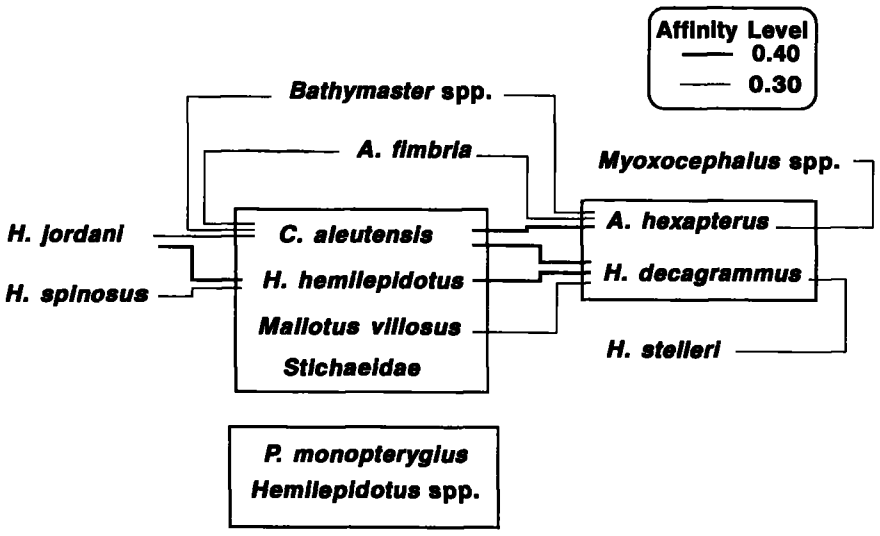

Figure 7

Results of recurrent group analysis on neuston data (larvae) for all cruises (1981–86). Boxes enclose members of recurrent groups that have affinity levels of 0.4 or higher with each other. Lines connect taxa with affinities outside their groups.

of *P. monopterygius* larvae with the outer shelf and slope particularly off Kodiak. *Hemilepidotus* spp. had a similar pattern of distribution.

Two species which were included in the analysis, but did not display significant affinities with any of the other taxa, were *Theragra chalcogramma* and *Zaprora silenus*. It seemed that at least in the neuston, *T. chalcogramma,* which is the dominant larval taxon in this region, had a unique pattern of occurrence, largely dissimilar to the other neustonic larvae. The lack of affinity of *Z. silenus* with other species was probably due to its infrequent occurrence in these samples.

Kendall and Dunn (1985) and Rugen[3] found a variety of recurrent groups and inter-species linkages among the neustonic fish larvae in the western Gulf of Alaska over four seasons. The species groups and affinities changed seasonally and were inconsistent among two-week sampling periods. Similar to the results presented here, *T. chalcogramma* did not occur among the recurrent groups or associated linkages of species identified in these studies.

Five species groups and eight sector groups (sectors= sampling sectors in Fig. 2) were identified from the agglomerative hierarchical classification of data combined for all the cruises (Table 5). The Bray-Curtis dissimilarity coefficient values at which these groups were formed were high (minimum value of 0.63), particularly among the sector groups. These indicated that the groupings were weak and that species were only loosely affiliated with each other in terms of density and distribution patterns.

The distribution of the eight sector groups seemed random (Fig. 8) but displayed certain geographical trends which reflected a variety of distribution pat-

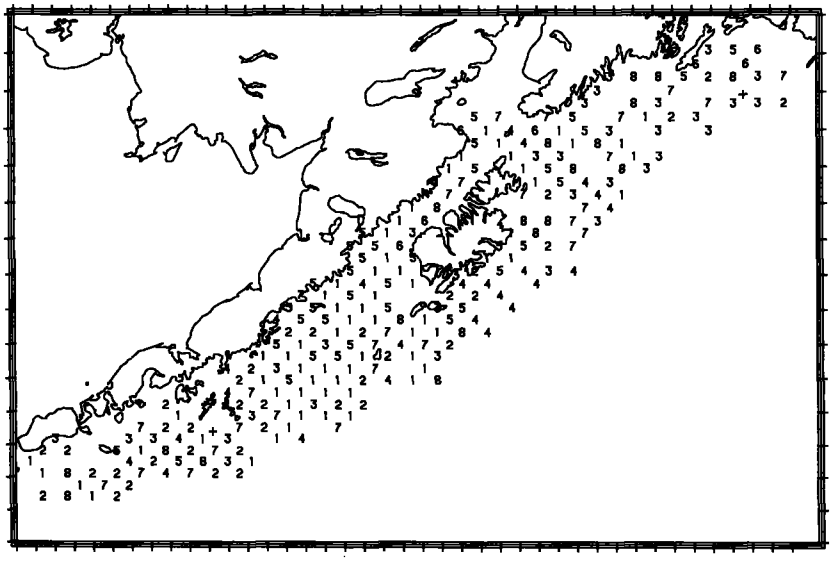

Figure 8

Distribution of sector groups resulting from numerical classification of density data for the dominant taxa of fish larvae in the neuston, based on all cruises (1981–86). A plus sign (+) indicates that no fish larvae were caught in that sector.

terns among the larval species. Groups 1 and 2 together were characterized by highest densities of most species (Table 5); these sectors were located primarily around Kodiak Island and particularly in the region between Kodiak Island and the Shumagin Islands to the southwest. Total larval abundance was very low in Group–3 sectors (Table 5) which were concentrated mainly to the northeast of Kodiak Island and to a lesser extent around the Shumagin Islands. Group–4 sectors displayed an offshore distributional trend, mainly seaward of Kodiak Island. Larval abundance was moderately high for this group, enhanced by highest mean density of *Hemilepidotus* spp. and *Pleurogrammus monopterygius* (Table 5). Most of the sectors in Group 5 were distributed close to Kodiak Island, and the coastal half of the region immediately southwest of Kodiak, along the Alaska Peninsula. Mean larval density was also moderately high for this group; *Theragra chalcogramma*, *Hexagrammos decagrammus*, and *Ammodytes hexapterus* were the predominant species. Group 6 included only eight sectors, five of which occurred close to Kodiak Island and three in the northeastern extremity of the sampling area. Mean densities of *T. chalcogramma* and *A. hexapterus* were highest for this group (Table 5) owing to their occurrence in extremely high numbers in one of the sectors (different one for each species) along the southern half of Kodiak Island (Fig. 5). *Hexagrammos decagrammus* was the only species to occur in sectors belonging to Groups 7 and 8 (Table 5) which were scattered randomly throughout the sampling area. This species was unusual in that its distribution was widespread in contrast with the other taxa that were confined primarily to two or three of the sector groups.

Discussion

Our results indicated that species diversity and density of fish eggs in shelf waters in the western Gulf of Alaska were essentially the same in the surface and subsurface zone. *Theragra chalcogramma* eggs were exceptionally abundant and, along with eggs of several pleuronectid species, accounted for >90% of all eggs taken in both bongo and neuston samples. Except for *T. chalcogramma*, pelagic eggs tended to be scarce in the neuston where the predominant mode of spawning among fish species is demersal (Kendall

Table 5

Two-way coincidence table showing mean density (no./1000 m^3) of dominant larval species among sector groups. Numbers in parentheses are dissimilarity coefficient values at which the groups were formed. Values are >1 in certain instances owing to use of the flexible sorting strategy in combining the entities into groups.

		Sector groups							
Species groups		1 (1.35)	2 (1.05)	3 (1.67)	4 (1.40)	5 (1.42)	6 (1.29)	7 (0.95)	8 (0.79)
1 (0.63)	*Hexagrammos stelleri*	2.9	0.8	1.8	4.1	0.8	1.4	0.0	0.0
	Hemilepidotus jordani	3.7	14.6	0.8	1.9	0.0	0.0	0.0	0.0
	Bathymaster spp.	65.4	0.1	0.0	0.6	0.0	1.4	0.0	0.0
	Cryptacanthodes aleutensis	171.2	18.6	1.7	0.3	2.0	45.6	0.0	0.0
2 (0.76)	*Anoplopoma fimbira*	85.4	1.3	3.6	0.1	0.0	0.0	0.0	0.0
	Hemilepidotus spp.	1.9	14.2	0.2	48.7	0.8	0.1	0.0	0.0
	Hemilepidotus spinosus	2.2	7.6	6.7	0.3	0.0	0.0	0.0	0.0
3 (0.79)	*Mallotus villosus*	18.6	15.0	0.0	6.3	1.0	0.0	0.0	0.0
	Pleurogrammus monopterygius	1.3	2.5	0.0	13.6	0.1	0.0	0.0	0.0
	Theragra chalcogramma	22.3	0.6	0.2	0.8	53.3	298.1	0.0	0.0
4 (0.98)	*Hexagrammos* spp.	2.9	0.7	4.1	0.2	0.3	0.0	0.0	0.0
	Hemilepidotus hemilepidotus	55.3	291.1	2.3	22.7	1.2	0.0	0.1	0.0
	Sebastes spp.	7.0	1.0	0.0	0.0	0.0	2.1	0.0	0.0
5 (0.90)	*Hexagrammos decagrammus*	233.3	303.8	32.6	105.7	91.4	0.0	93.0	6.5
	Ammodytes hexapterus	411.5	3.2	0.5	0.2	19.8	441.1	0.0	0.0
	Total (dominant taxa)	1084.9	675.1	54.5	206.5	170.7	789.8	93.1	6.5

and Dunn, 1985). In this region, fish eggs in the neuston could be considered strays because their accumulation at the surface may be attributed to their positive buoyancy rather than to the deposition of eggs in this zone. A similar conclusion has been made regarding the occurrence of fish eggs in the neuston of shelf and oceanic waters off Washington, Oregon, and northern California (Doyle, 1992).

In contrast, a unique group of larval fish appeared to be associated with the neuston in the western Gulf of Alaska, and most of the dominant taxa were scarce or absent in the subsurface zone. The dominance of hexagrammids, cottids, an osmerid, *Anoplopoma fimbria*, bathymasterids, *Cryptacanthodes aleutensis*, and *Ammodytes hexapterus* in this group has also been documented for the larval fish component of the neuston in the California Current region along the U.S. west coast (Brodeur et al., 1987; Shenker, 1988; Doyle, 1992). The occurrence of *T. chalcogramma* larvae in high numbers in the neuston of the western Gulf of Alaska, however, is unique to this region and reflects the overall dominance of this species in the plankton of the study area (Kendall and Dunn, 1985; Schumacher and Kendall, 1991; Rugen[3]).

Among the dominant taxa of fish larvae in the neuston, most were obligate tenants of the surface, despite the predominance of demersal spawning among these taxa. The most important taxa in this group included the hexagrammids, cottids, *Anoplopoma fimbria*, and *Cryptacanthodes aleutensis*, and, according to the general classification scheme for neustonic organisms (Zaitsev, 1970; Hempel and Weikert, 1972; Peres, 1982), they may be considered obligate members of the neuston. The same taxa of larvae have been identified as obligate neustonic organisms in the plankton off the U.S. west coast (Doyle, 1992). Because of their scarcity in bongonet samples, the dramatic daytime reduction in density of these larvae in the neuston samples may have been attributed primarily to light-aided avoidance of the sampling gear. The generally large sizes documented (predominantly >10 mm SL) for these neustonic larvae also contributed to their ability to avoid the neuston net.

Theragra chalcogramma, *Ammodytes hexapterus*, and *Bathymaster* spp. larvae were unusual among the dominant neustonic taxa in that they were extremely abundant in bongo net samples also; therefore, their association with the neuston was considered facultative. Their nighttime presence in the neuston suggested a pattern of diel vertical migration with movement upward at dusk and a return to deeper layers during the day. This pattern has been observed for many species of fish larvae and zooplankton in many different regions (Zaitsev, 1970; Hempel and Weikert, 1972; Neilson and Perry, 1990). *Mallotus villosus*, *Myoxocephalus* spp., and *Zaprora silenus* larvae, which were well represented in bongo net samples, but abundant in the neuston at night, may also exhibit this pattern of vertical migration. However, with the limited data presented here, it was difficult to verify this migration pattern. Daytime sampler avoidance, particularly by the larger larvae and early juveniles, is likely to have had a confounding influence on the observation of such a pattern. In addition, it is necessary to consider in more detail the diel variation in the vertical distribution pattern of the larvae over the entire range of the water column in which they occurred.

Kendall et al. (1987, 1994) observed that within the upper 50 m of the water column, *T. chalcogramma* larvae (size range approximately 7–10 mm SL) undergo limited vertical migration on a diel cycle. These larvae were found to be deepest during the day, shallowest in the evening, sink slightly at night, and sink more in the morning. Under controlled laboratory conditions, Olla and Davis (1990) also observed similar diel periodicity in vertical distribution of *T. chalcogramma* larvae; larvae moved downward with daytime light intensity, upward during evening twilight conditions, remained close to the surface at night, and moved downward again in the morning. The *T. chalcogramma* larvae caught in the neuston, mainly at night, during the present study were predominantly 5–14 mm SL unlike their counterparts in the bongo net samples that were mostly <6 mm SL. This diel pattern of neustonic occurrence for the larger-sized larvae was likely due to the pattern of diel vertical migration observed by the above authors.

Observations on the vertical distribution of *Ammodytes hexapterus* larvae have also been made in the western Gulf of Alaska (Rogers et al., 1979; Brodeur and Rugen, 1994). Unlike *T. chalcogramma* larvae, *A. hexapterus* larvae were found to be deepest in the water column at night and shallowest at dawn and during the day. This apparent migration pattern of nocturnal descent has also been observed for *A. personatus* larvae off Japan and has been interpreted as advantageous in terms of diurnal feeding and predator avoidance (Yamashita et al., 1985). If this is the normal diel pattern of vertical migration for *Ammodytes* larvae, the occurrence of high densities of *A. hexapterus* larvae in the neuston at night, documented during the present study, seems unusual. On examination of length-frequency distributions for these larvae, however, it appears that the pattern of nocturnal descent was prevalent among larvae <20 mm SL (Yamashita et al., 1985; Brodeur and Rugen, 1994), whereas the nocturnal concentration of larvae at the surface was restricted to larger larvae and early juveniles (Doyle, 1992; this study). Perhaps

these larger specimens undertake a nocturnal migration into the neuston as has been indicated by data collected off the U.S. west coast (Doyle, 1992). The length-frequency distributions documented for *A. hexapterus* larvae here, however, suggest that during spring in the western Gulf of Alaska, the well-developed larvae and early juveniles (>20 mm SL) almost exclusively occupied the neuston. Such specimens were rare in the bongo net samples where the predominant larval size range was 5–15 mm SL. The scarcity of the large *A. hexapterus* larvae in the daytime neuston samples in this instance could be attributed to light-enhanced sampler avoidance.

Brodeur and Rugen (1994) also found that *Bathymaster* spp. larvae (4–7 mm SL) were deepest in the water column at night in the western Gulf of Alaska and suggest a diel migration pattern of nocturnal descent similar to *A. hexapterus*. A similar pattern of downward migration at night has been observed for *Bathymaster* spp. larvae in the Bering Sea (Walline[6]). Their absence from daytime neuston samples during the present study seemed to contradict such a pattern of vertical migration. Whereas most of the young larvae may follow the above pattern, our data also suggest a facultative association with the neuston by some of these larvae and a nighttime occupation of the neuston as a result of migration upward to the surface. This seems feasible as it is apparent from observations by Kendall and Dunn (1985) and Rugen[3] in the Gulf of Alaska that *Bathymaster* spp. larvae become more neustonic with development. Most *Bathymaster* spp. larvae taken here, both in neuston net and bongo net samples, were <10 mm SL and would not be able to avoid the sampler as did the *A. hexapterus* larvae found in the neuston during the present study. The facultative nocturnal association with the neuston proposed here for *Mallotus villosus* larvae does not contradict what is already known concerning vertical distribution patterns for osmerids in the Gulf of Alaska. Haldorson et al. (1993) recorded that osmerid larvae in Auke Bay apparently spend most of their time in the mixed layer, rising to the surface at night and returning to relatively shallow depths during the day.

Recent investigations on the interaction between the early life history stages of *T. chalcogramma* and the oceanographic environment in the western Gulf of Alaska indicate that prevailing southwesterly currents transport larvae from the Shelikof Strait region to nursery grounds along the Alaska Peninsula (Kendall et al., 1987; Kim and Kendall, 1989; Hinckley et al., 1991; Schumacher and Kendall, 1991). Although the southwesterly flowing Alaska Coastal Current bifurcates southwest of Kodiak Island, most of this water remains on the shelf, thus potentially retaining the majority of fish larvae in the coastal region. Physical features such as plumes and eddies also serve to retain larvae on the continental shelf and transport them southwestward along the Alaska Peninsula (Vastano et al., 1992).

Given these current patterns, the distribution patterns observed for most taxa of fish larvae in the neuston during this study suggest that springtime spawning and emergence of larvae into the plankton (and subsequently the neuston) took place mainly around Kodiak Island (except along the seaward side) and along the Alaska Peninsula to the southwest. A high concentration of larvae over the shelf from Kodiak Island to the Shumagin Islands was the predominant pattern for most species. Despite their occurrence in the neuston, these larvae were likely retained over the shelf and in the coastal zone by the prevailing currents. In contrast, the more offshore distribution patterns observed for *A. fimbria*, *P. monopterygius*, and *H. hemilepidotus* indicate that a significant proportion of these larvae may have been entrained in the Alaskan Stream over the slope and in deep water.

Analysis of multispecies spatial patterns using recurrent group analysis and numerical classification did not reveal the existence of more than one neustonic assemblage of fish larvae in the study area. A unique and comparable assemblage of neustonic fish larvae has also been identified off the U.S. west coast and its geographical distribution is essentially confined to shelf and slope waters off Washington, Oregon, and northern California (Doyle, 1992; Doyle[7]). Apart from perhaps *P. monopterygius* larvae, which are known to occur throughout the Gulf of Alaska (Gorbunova, 1962), and to a lesser extent *A. fimbria* and *H. hemilepidotus*, members of the neustonic assemblage of fish larvae in the western Gulf of Alaska are likely to be scarce in the oceanic zone.

It has been postulated that the primary advantage of a neustonic existence as an early life history strategy for certain species of marine fish is the enhanced trophic conditions that prevail in this biotope (Moser, 1981; Tully and O'Ceidigh, 1989; Doyle, 1992). The suitability of the neuston as a feeding ground for larvae is, however, dependent on the ability of larvae to

[6] Walline, P. D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June-July 1979. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA 98115. Proc. Rep. 81-05, 22 p.

[7] Doyle, M. J. 1992. Patterns in distribution and abundance of ichthyoplankton off Washington, Oregon, and northern California (1980 to 1987). U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA, 98115. Proc. Rep. 92-14, 344 p.

seek and capture prey. Although surface aggregations of zooplankton are common at frontal and convergence zones, the neuston may in general have a reduced biota, at least during the daytime. The relatively large size and well-developed form that characterizes most fish larvae occurring in the neuston of the western Gulf of Alaska and elsewhere is possibly an adaptive advantage in terms of finding and consuming suitable quantities of food. The data of Kendall and Dunn (1985) and Rugen[3] indicate that hexagrammid and cottid larvae (obligate members of the neuston) are abundant in the study area during all seasons. Given that peak production of copepod nauplii, a dominant larval fish food, occurs during summer in this region (Cooney, 1986), the above larvae are likely to encounter a diminished biota in the neuston during fall and winter months in particular. Because of their relatively large size, however, a wide diversity of prey organisms are likely to be available to them in the neustonic layer and this diversity may compensate for the lower prey densities of copepod nauplii.

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Abstract.—Aerial surveys for sea turtles conducted in Core Sound and Pamlico Sound, North Carolina, 1989–91, indicated a spring immigration by the turtles into these sounds and a summertime dispersal followed by emigration in the late fall and early winter. Estimates of density in Core Sound were greater than estimates for Pamlico Sound. Core Sound density estimates were comparable to those reported for the lower Chesapeake Bay and those reported from offshore pelagic surveys in the region. The data were analysed by strip- and line-transect methods, and the choice of analysis did not influence the overall conclusions. The abundance of sea turtles in the inshore waters of the Atlantic Coast at densities at least as great as in the ocean indicates the importance of these estuarine habitats for the foraging and development of immature turtles.

Aerial surveys for sea turtles in North Carolina inshore waters

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Recent studies have demonstrated the importance of inshore waters as developmental and foraging habitats for threatened and endangered sea turtles along the Atlantic Coast of the United States (e.g. Medonça and Ehrhart, 1982; Ehrhart, 1983; Lutcavage and Musick, 1985; Keinath et al., 1987; Burke et al., 1992, 1993). A study of sea turtles in North Carolina waters used sightings reported by the public and documented the importance of Pamlico and Core Sounds for immature loggerhead, *Caretta caretta;* green, *Chelonia mydas;* and Kemp's ridley, *Lepidochelys kempii*, sea turtles (Epperly et al., in press, a). As part of the same study, aerial surveys were employed over a 3-yr period to provide independent quantitative verification of the importance of Pamlico and Core Sounds as sea turtle habitats.

We report the results of the aerial survey work in Pamlico and Core Sounds, part of the largest estuarine system in the southeast United States. Once aerial survey methodology was validated in inshore waters, our goals were 1) to obtain independent evidence for the seasonality and distribution patterns of turtles obtained from other sources, 2) to quantify the abundance of sea turtles in the sounds and compare those densities with other areas, and 3) to evaluate the consequences of the application of line vs. strip survey methodology to the data.

Materials and methods

Aerial surveys of Core and Pamlico Sounds

Pamlico and Core Sounds were divided into three areas (Fig. 1): Core Sound (34°41'N to 35°00'N), southern Pamlico Sound (35°00'N to 35°20'N), and northern Pamlico Sound (35°20'N to 35°48'N). Areas of each were 248 km^2, 2,501 km^2, and 1,951 km^2, respectively. The divisions were, in part, based on geography and on facilitating access to restricted airspace. In Core Sound, each flight surveyed approximately 26% of the total surface area of the sound (32, rarely 33 transects); for both southern and northern Pamlico Sound, approximately 6% of the total area was surveyed (8 transects in southern Pamlico Sound and 11 transects in northern Pamlico Sound). Surveys were taken from a Cessna 172 (from a side-viewing platform) at 128 km/h and at an altitude of 152 m. This altitude was chosen as a compromise between areal coverage and the ability to sight smaller turtles on the surface of inshore waters. Surveys were scheduled so that local apparent noon occurred approximately half-way through the survey. Surveys were undertaken only if winds were less than 28 km/h and seas were less than 0.6 m with no or few whitecaps (e.g. Beaufort Sea State ≤2). We attempted to perform

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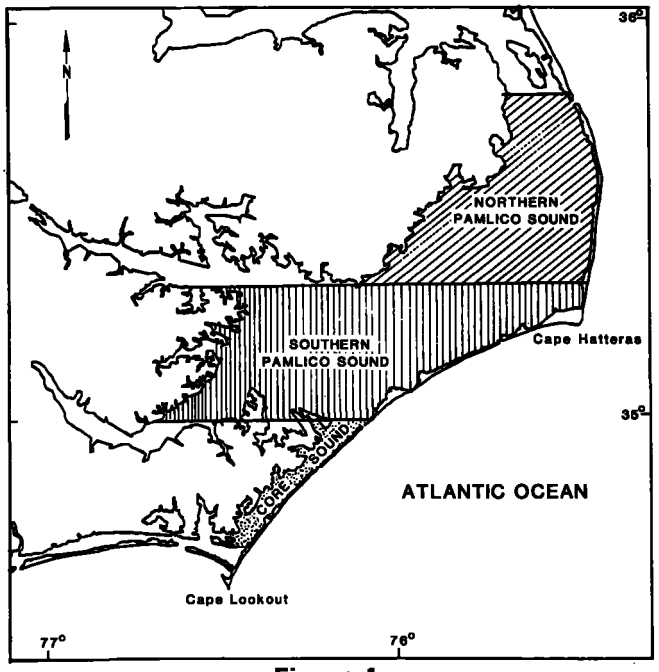

Figure 1

Core Sound and subareas of Pamlico Sound flown in aerial surveys for sea turtles in North Carolina inshore waters, 1989–91.

the surveys monthly beginning in spring 1989 and bimonthly May–November 1990 and 1991. Because it was difficult to obtain military airspace clearance over Pamlico Sound and because the results of the 1989–90 surveys indicated that our effort was best expended in Core Sound (greater sighting rates), the only area surveyed in 1991 was Core Sound.

We employed a systematic sampling design. The underlying assumption was that the systematic sample could be treated as a random sample. There was no reason to assume that the number of turtles sighted per transect would be autocorrelated (i.e. we assumed no areal trend in density or correlations between neighboring transect values). As recommended by Cochran (1977) and Eberhardt et al. (1979) in order to avoid potential selection biases of systematic sampling, the starting transect for each survey was chosen at random from all possible transects in the survey. Transect lines ran east-west and were spaced equi-distant from the starting transect. On the basis of the maximum known swimming speed of a loggerhead turtle (6 km/h, Keinath, 1993), transects were spaced far enough apart so that a turtle could not be sighted twice during any one survey. LORAN was used to maintain position on the prescribed transects. Beginning and ending longitudinal coordinates and time were recorded for each transect flown. Two observers on opposite sides of the plane scanned the waters, recording the time (with synchronized watches) and perpendicular angle to each turtle sighted (with handheld clinometers). On the assumption that groundspeed within a transect was constant, turtle positions were calculated by interpolating time and longitudinal coordinates and by converting sighting angle and survey altitude to perpendicular distance from the transect.

We used both strip- and line-transect theory to analyze the data. First, a histogram of all perpendicular sighting distances was constructed, one for Core Sound and one for Pamlico Sound (Fig. 2). From these histograms we empirically determined the strip width over which the probability of sighting a turtle was not reduced by nearness to the plane (acute viewing angle; turtles diving to avoid the plane) or by distance from the plane (reduced detection) to be 0.15–0.30 km from the flight line. Observations

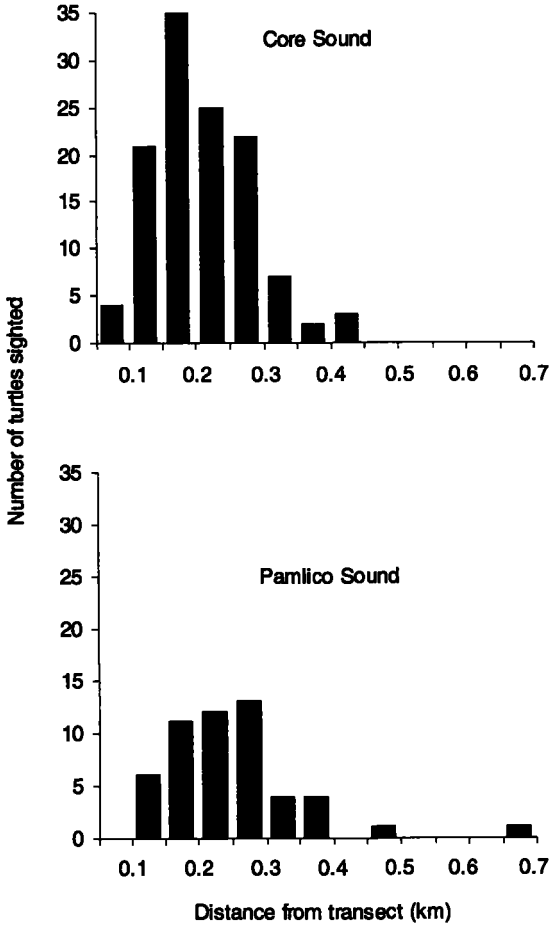

Figure 2

Histograms of distances at which turtles were sighted from the line of flight in Core and Pamlico Sound aerial surveys, 1989–91.

within this strip were then used to calculate ratio-to-size estimates of density ($\hat{D}_R$) for each survey by using a single-stage, sampling approach in which sampled transects were treated as clusters of unequal sizes (i.e. transect lengths varied; Cochran, 1977; Gates, 1979; Jolly and Watson, 1979):

$$\hat{D}_R = \frac{Y_R}{M_R},$$

the density of turtles on the surface of the sound; and

$$Y_R = \sum_{i=1}^{n} y_i,$$

the total number of turtles sighted during a survey,

where y_i = the number of turtles in the ith transect; and

$$M_R = \sum_{i=1}^{n} m_i, \text{ total area surveyed (km}^2\text{)},$$

where m_i = the area surveyed in the ith transect (km^2); and

n = the number of strip transects sampled.

Variances of the density estimates, $V(\hat{D}_R)$, were calculated as follows:

$$V(\hat{D}_R) = \frac{1-\frac{n}{N}}{n\overline{M}^2} \cdot \frac{\sum_{i=1}^{n} m_i^2 (D_i - \hat{D}_R)^2}{n-1},$$

where N = the total number of strip transects possible; and

$D_i = \frac{y_i}{m_i}$, the density of turtles in ith transect; and

$\overline{M} = \frac{M_R}{n}$, the average area of a single transect (km^2).

For line-transect analyses we used methods described by Burnham et al. (1980). The essential problem in line-transect analysis is to construct a probability density function (pdf) from the set of perpendicular distance observations of sighted organisms to estimate $f(0)$. The value of $f(0)$ is defined as the inverse of one-half the effective strip width (Burnham et al., 1980), mathematically equivalent to the value of the pdf exactly on the flight line (perpendicular distance=0). On the basis of the histograms of sighting distances, data were censored such that the probability of sighting a turtle was not reduced by proximity to the airplane. Distance data were rescaled such that x=0 at the point data were censored (0.15 km from flight line). Simple, generalized, and nonparametric models were examined with the program TRANSECT (Laake et al., 1979) to derive density estimators from the sighting distance data. Because only small numbers of turtles were seen during most sampling occasions, we could not conduct individual analyses for each survey. Instead, sighting information was combined for all Core Sound surveys and for all Pamlico Sound surveys, and an overall $f(0)_s$ was specified for each of the two water bodies (s). Density for each survey ($\hat{D}_R$) then was estimated as

$$\hat{D}_R = \frac{f(0)_s Y_R}{2L_R},$$

where $f(0)_s$ is the overall $f(0)$ for the water body, and is obtained from the TRANSECT program, and L_R (km) is the total length of all transects (l_i):

$$L_R = \sum_{i=1}^{n} l_i.$$

The estimated variance of the density estimate for each survey was computed as

$$V(\hat{D}_R) = \hat{D}_R^2 \left(\frac{V(Y_R)}{Y_R^2} + \frac{V(f(0)_s)}{f(0)_s^2} \right).$$

The variance of the number of turtles sighted during a survey $V(Y_R)$ is

$$V(Y_R) = \frac{L_R \sum_{i=1}^{n} l_i \left(\frac{y_i}{l_i} - \frac{Y_R}{L_R} \right)^2}{n-1},$$

and the variance of $f(0)_s$ is obtained from the pdf solution (Burnham et al., 1980).

Experiment to evaluate observer bias

Four observers participated in the study. An experiment was conducted on 29 August 1991 to evaluate the accuracy and comparability of observer sightings

and to validate methodology. Two planes, each carrying two observers positioned on the same side, conducted 12 flights over an area where painted plywood "turtles" were deployed. Turtle models representing loggerhead turtles of 30, 60, and 90 cm length, were attached to three anchored ground lines. Within an overflight pass, turtles of one size were grouped on a single line. All three lines could contain turtle models during any one pass. The number of turtle models of one size and the line on which they were placed during a single pass were chosen at random, but the experiment was constrained such that a total of six turtle models of each size were displayed within every three passes; the actual number of a given size displayed during a pass ranged from 0 to 4. The number, location, and size of the turtle models were unknown to the observers. Altitude and speed were identical to that used in the general survey (152 m and 128 km/h). The airplane flew on a line 0.10–0.30 km from the models. Analysis of variance techniques were used to examine the contribution of observers, turtle model size, and the interaction of observer and model size to the error in the counts.

Results and discussion

Under the ideal conditions under which the aerial survey experiment was performed, no significant differences were detected among observers (ANOVA, df=3, P=0.89). Within the range of sizes tested, turtle size was not a significant factor in the observers' ability to sight turtles (ANOVA, df=2, P=0.24). On average, 97.2% of the actual number of "turtles" were sighted during a pass (range 50–100%). We concluded that interobserver variability was not a major factor and that turtles could be sighted accurately in relatively turbid waters. The experiment did not test for the effect of fatigue on an observer's ability to sight turtles.

The inshore waters of temperate latitudes are seasonally repopulated with sea turtles. Nearly all sea turtles in Pamlico and Core Sounds, North Carolina, are immature individuals (Epperly et al., in press, a). Based on public reports, there is evidence that turtles immigrate into Core and Pamlico Sounds in the spring, disperse throughout the sounds in the summer, and emigrate from the sounds in the late fall and early winter (Epperly et al., in press, a). Results of the aerial surveys confirm this general

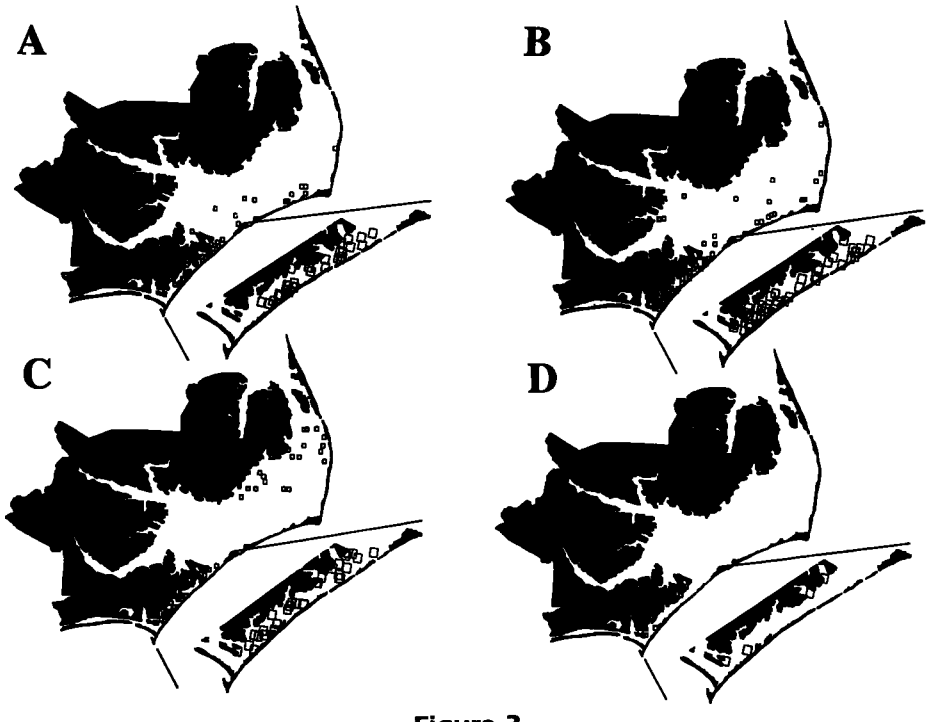

Figure 3

Seasonal sea turtle sightings in aerial surveys of Core and Pamlico Sounds, 1989–91. There were no fall surveys of southern Pamlico Sound, and Core Sound was the only area flown during the winter. The Core Sound area is enlarged to the right of each figure. (**A**) March–May; (**B**) June–August; (**C**) September–November; (**D**) December–February.

Table 1

Strip- and line-transect estimates of density for sea turtles, excluding leatherbacks, *Dermochelys coriacea*, on the surface of Core and Pamlico Sounds, North Carolina, 1989–91.

Survey	Number of turtles sighted within sound[1]	Total distance surveyed (km)	Strip-transect estimates of density: Turtles per 100 km²	Strip-transect estimates of density: SE of mean	Line-transect estimates of density: Turtles per 100 km²	Line-transect estimates of density: SE of mean
Core Sound						
1989						
22 May	30	197	30.48	7.62	37.19	11.63
12 Jul	22	203	22.95	5.75	36.00	9.67
16 Aug	10	227	7.35	2.96	12.55	4.85
12 Sep	15	224	19.34	3.69	25.41	7.09
13 Oct	6	217	1.54	1.20	3.75	2.41
6 Nov	5	231	5.78	2.07	7.05	2.91
14 Dec	5	219	6.08	2.85	9.28	4.49
1990						
4 Jan	0	216	0	—	0	—
15 Mar	0	219	0	—	0	—
24 Apr	3	212	3.15	1.69	5.76	3.16
3 May	2	204	3.27	1.81	3.99	2.70
6 Jun	2	228	2.93	1.64	3.57	2.73
7 Jul	0	219	0	—	0	—
2 Sep	0	234	0	—	0	—
4 Nov	0	228	0	—	0	—
1991						
25 May	2	222	1.50	1.19	1.83	1.59
7 Jul	1	228	1.46	1.17	1.78	1.75
31 Aug	16	212	17.30	5.48	21.11	9.28
3 Nov	6	217	6.15	2.32	11.26	4.97
Northern Pamlico Sound						
1989						
30 May	1	387	0.86	0.81	0.77	0.67
24 Jul	4	399	3.35	1.73	3.00	1.53
1 Sep	6	393	3.39	2.10	3.04	2.43
29 Sep	14	383	1.74	1.09	2.34	1.25
14 Oct	8	369	4.52	2.39	5.69	2.46
13 Nov	4	367	0.91	0.89	0.81	0.87
1990						
24 May	0	392	0	—	0	—
3 Jul	0	392	0	—	0	—
13 Sep	0	259	0	—	0	—
15 Nov	0	368	0	—	0	—
Southern Pamlico Sound						
1989						
29 May	14	523	4.46	1.33	6.30	1.39
15 Jul	14	510	6.53	2.15	7.63	2.59
1990						
19 May	1	504	0.66	0.62	0.59	0.54
4 Aug	2	534	0.62	0.58	0.56	0.49
3 Sep	0	512	0	—	0	—

[1] All turtles sighted, including those censored in calculations of density.

pattern (Table 1; Fig. 3). Volunteer commercial fishermen and the general public reported turtles in inshore waters April–December. Turtles were also sighted in the sounds during April–December aerial surveys. Spring aerial surveys (March–May) indicated that turtles were distributed mainly in Core Sound and along the eastern edge of southern Pamlico Sound. Summer (June–August) and fall (September–November) aerial surveys demonstrated that turtles were distributed throughout the sounds. No sea turtles were sighted during fall 1990 aerial surveys, but turtles were reported in the area by the public and by commercial fishermen (Epperly et al., in press, a). Turtles were still present in Core Sound in December 1989, but none was sighted during January or March 1990 aerial surveys.

Species were generally indistinguishable from the air because of their small size, except for leatherback sea turtles, *Dermochelys coriacea*, which were sighted only during the December 1989 survey (three individuals). The loggerhead turtle, with a reddish-brown carapace, was the species most often identified. Data from commercial fishermen indicated that the species composition in Pamlico and Core Sounds was 80% loggerhead, 15% green, and 5% Kemp's ridley sea turtles; leatherback turtles infrequently enter inshore waters, and hawksbills, *Eretmochelys imbricata*, are very rare (Epperly et al., in press, a). Nearly all of the turtles measured by fishermen were greater than 30 cm carapace length (measured over the curve)—the smallest model tested and successfully detected in the aerial survey experiment.

Density estimates from line- and strip-transect analysis are given in Table 1. The Fourier series estimator fit the sighting distance data from both sounds well (χ^2 goodness-of-fit test, $P>0.05$). Values of $f(0)$ differed substantially between the two sounds: $f(0)_{Core}=8.13$ (SE=0.75) and $f(0)_{Pamlico}=5.99$ (SE=0.52). Confidence intervals for the estimates of $f(0)_S$ overlapped at the 95% confidence level but not at the 90% confidence level. The cause of the difference in our ability to sight turtles between the two sounds was not obvious. Observer fatigue could have been a factor. Transects in Core Sound were short (2.7–14.9 km) and observers were able to take frequent breaks between them. Pamlico Sound transects were long (13.9–57.1 km in northern Pamlico Sound; 37.5–94.1 km in southern Pamlico Sound), and breaks occurred infrequently. Homogeneity of background could have been another factor. Core Sound waters were relatively clear, and bottom structures (channels, seagrass beds, etc.) were usually visible. This heterogeneous background served to attract observers and to intensify the observers' searches in order to detect turtles. Consequently, the visual sweep of the observers was confined to an area near the flight path. Conversely, the majority of Pamlico Sound waters usually were turbid and presented a homogeneous background, except for the easternmost portion of the sound which was very similar to Core Sound.

Line-transect estimates of density in Core Sound averaged 40% greater than estimates derived from strip-transect theory (Table 1). Line-transect estimates of density in Pamlico Sound were, on average, 14% greater than strip-transect estimates. Coefficients of variation of strip- and line-transect estimates of density were nearly identical within each sound (67% for strip- and 66% for line-transect estimates for Pamlico Sound; 47% and 54% for strip- and line-transect estimates, respectively, for Core Sound) (Table 1).

Application of line-transect and strip-transect analyses to the North Carolina aerial survey data requires several assumptions. Strip-transect analysis assumes that 1) transect lines are randomly located, 2) the strip over which all turtles are assumed to be seen and counted, 0.15–0.30 km, remains constant during a single survey and from survey to survey, i.e. sighting conditions (distance from plane, size of turtles, sun position and glare, sea state, weather, etc.) do not affect the ability to sight turtles, 3) no turtle is counted more than once in a given survey, and 4) sightings are independent events. In addition to the first, third, and fourth assumptions above, line-transect analysis requires that 1) all turtles on the line (defined as 0.15 km from the flight line) are seen with certainty, 2) turtles do not move prior to sighting or before distance measurements are made, 3) measurements are taken without error, and 4) the probability density function remains constant during a single survey and from survey to survey (i.e. the ability to sight turtles does not change).

The underlying assumptions of both methodologies are violated in important ways, primarily with respect to the ability to sight turtles. For strip-transect analysis, conditions are such that probabilities of sighting individual turtles within the strip are less than one. In addition, these probabilities vary within and among surveys. For line-transect theory, we do not know that all turtles on the line ($x=0$) are seen. The histogram of sighting distances (Fig. 2) indicates avoidance behavior in response to the aircraft in combination with poor downward visibility near the airplane, but we cannot be sure that locating the line ($x=0$) at 0.15 km from the flight line eliminated this effect entirely. In addition, the use of a pooled pdf may not be completely valid, because factors affecting the ability to sight turtles varied over the course of the study. As applied, strip-transect methods assuredly underestimate the density of turtles on the surface of the water. Line-transect methods, however, may over-

estimate or underestimate densities depending on the universality of the pdf. A criticism of strip-transect methods is that observations outside the strip are not included in the analysis and, in the study of rare animals, every observation is important (Eberhardt et al., 1979). In this study, however, only 22 of 171 turtles (13%) were sighted at distances greater than 0.30 km from the flight line. In the following comparative discussion, the results of strip-transect analysis are cited, but their use does not affect the overall conclusions.

Estimated densities of sea turtles on the surface of Core Sound were consistently higher than surface densities for Pamlico Sound (Table 1). Where comparative data exist, densities in southern Pamlico Sound were greater than in northern Pamlico Sound. Densities ranged from 0–30.5 turtles/100 km^2 in Core Sound to 0–4.5/100 km^2 in northern Pamlico Sound and to 0–6.5/100 km^2 in southern Pamlico Sound. Densities generally were highest during late spring through summer. Densities in northern Pamlico Sound tended to peak at least one month later than in southern Pamlico and Core Sounds. The estimated density of sea turtles on the surface of the sounds was quite different among the study years; turtles were more abundant in 1989.

The densities reported in this study are surface densities. Sea turtles are estimated to spend 3.8–41% of their time on the surface (Kemmerer et al., 1983; Keinath et al., 1987; Byles, 1989; Byles and Dodd, 1989; Musick et al.[1]). Thus, the estimated number of sea turtles on the surface represents a small fraction of those actually in the sounds. Because of the large range in proportion of time that monitored turtles spend on the surface, we did not try to extrapolate surface estimates to an estimate of the submerged population in the sounds. For comparison purposes, density estimates from studies that made the extrapolation were converted to surface densities.

Comparison of density estimates among aerial survey studies is confounded by differences in platforms and altitudes. Aerial surveys utilizing aircraft equipped with bubble observation windows (Fritts et al., 1983; Thompson et al., 1991; Shoop and Kenney, 1992; Thompson[2]; Lohoefener et al.[3]) afforded observers a direct and unobstructed view of the flight line, thus maximizing the area sampled and the number of sea turtles observed per transect. Conversely, our study and other studies utilizing side-viewing aircraft (Keinath et al., 1987; Lohoefener et al., 1988; Keinath, 1993; Epperly et al., in press, b) did not have downward visibility directly beneath the plane, thereby minimizing the area sampled and the number of sea turtles observed per transect. Likewise, differences in altitude could affect the number of sea turtles sighted. Smaller turtles have a decreased chance of being sighted at higher altitudes. The altitude used in this study, 152 m, is consistent with that of the 1982–84 study of the offshore waters between Cape Hatteras and Key West, Florida (Schroeder and Thompson, 1987; Thompson[2]), surveys of the Chesapeake Bay and adjacent waters (Keinath et al., 1987; Keinath, 1993) and surveys off the northern North Carolina coast (Epperly et al., in press, b). It differs from the 229 m altitude used in the 1983–86 and the 1988–89 surveys of offshore waters of the Gulf of Mexico (Thompson et al., 1991; Lohoefener et al., 1990) and the 1979–81 surveys of the offshore waters between Nova Scotia and Cape Hatteras (Shoop and Kenney, 1992). Lohoefener et al. (1988), collected turtle data during their 1987 red drum surveys of the Gulf of Mexico using altitudes of 305–457 m. Fritts et al. (1983) collected turtle data during marine mammal, bird, and turtle surveys of the Gulf of Mexico and eastern Florida using altitudes of 91 m and 228 m.

Another factor affecting comparability of density estimates is the proportion of suitable habitat surveyed in each study. Comparisons of density estimates can be made only for surveys with comparable ratios of suitable to unsuitable habitats surveyed. Suitable habitat presumably accounts for all the area surveyed in inshore studies. Offshore studies generally extended well seaward of suitable habitat and in winter included habitat rendered unsuitable by low temperatures nearshore. Because of methodological differences in aerial survey studies, the application of strip- versus line-transect theory, and our inability to reliably correct surface densities for the proportion of the population that was submerged, comparisons of density estimates among studies are nearly impossible. We compare the results of this study only with other studies with comparable methodologies.

Our density estimates for Pamlico and Core Sounds, respectively, were comparable to those for the mid- (0–8.5 turtles/100 km^2) and lower (0–57.4 turtles/100 km^2) Chesapeake Bay, Virginia (Keinath et al., 1987). Densities in Core Sound and the lower Chesapeake Bay were particularly high, comparable to density estimates of sea turtles in offshore waters

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(0–126.1, Keinath, 1993; 0–12.3 turtles/100 km^2, Epperly et al., in press, b). The abundance of sea turtles in the inshore waters of the Atlantic Coast (North Carolina and Virginia), at densities at least as great as in the ocean, indicates the importance of these estuarine habitats for the foraging and development of immature turtles.

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Assessing habitat use by nekton on the continental slope using archived videotapes from submersibles

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Abstract.—Videotapes of the sea floor were taken from a submersible during dives at two areas on the continental slope off Cape Hatteras and Cape Lookout, North Carolina, in September 1989. We counted demersal nekton, epifauna, and environmental features for 1-minute intervals from video transects. Common morphospecies of demersal nekton were identified, and multivariate analyses were performed to find environmental features that related to habitat use by these forms. In both areas, the ocean floor was extensively sculptured with holes and mounds, and both small and large sea anemones were commonly observed. Crinoids were seen in Cape Hatteras dives. Small sea anemones were much more abundant off Cape Hatteras, whereas holes and mounds were more densely distributed off Cape Lookout. Rattails, hake, and sergestid shrimp were common at both locations. Eels were extremely abundant at the Cape Lookout site, whereas eelpouts, flounder, and lizardfish were found only at the Cape Hatteras location. At both locations, analyses of nekton habitat choices showed that habitat selection was related to density of the holes and mounds made by infauna and to density of the epifauna, such as crinoids and the different types of anemones. Hake, squid, sergestid shrimp, and lizardfish showed the strongest evidence of habitat selection. Analysis of videotapes, originally recorded for other purposes, is a cost-effective means for preliminary examination of the problems that may only be addressed by in situ observations.

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Understanding of the ecology of the deep ocean floor has improved substantially since underwater cameras have begun recording life at depths beyond which divers may penetrate. Recently, nekton communities on the shelf and slope have been studied by means of underwater cameras carried by remotely operated vehicles (ROV's) and occupied submersibles. Such studies have included analyses of environmental features (Hecker, 1990b; Levin et al., 1991), spatial distribution of individual species (Vecchione and Gaston, 1986; Wenner and Barans, 1990; Schneider and Haedrich, 1991), and patterns of habitat use by species assemblages (Richards, 1986; Felley et al., 1989; Auster et al., 1991; Carey et al., 1990). Underwater cameras have allowed questions to be addressed that are intractable to conventional sampling methods (Haedrich and Gagnon, 1991). Though problems with accurate identification of species and habitat variables are inherent to these studies, such studies open an important window to poorly known ecosystems.

We used archived videotapes recorded by the submersible *Johnson Sea-Link* to investigate patterns of habitat use by demersal and benthopelagic nekton on the continental slope off Cape Hatteras and Cape Lookout, North Carolina. From the videotapes, we identified and counted nekton species, and quantified selected environmental variables discernible from video images. Using these environmental variables, we identified the habitat where each species was most likely to be found. We used factor analysis to identify patterns of habitat use among the species (Felley and Felley, 1987; Felley et al., 1989) and to determine which environmental variables seemed most important in structuring the nekton assemblage of the continental slope off North Carolina. We then compared distributional variances of environment and species occurrence to identify those species selecting subsets of available habitats.

Materials and methods

Video recording

Video transects were recorded during dives by the *Johnson Sea-Link II* submersible from the RV *Edwin Link*. Table 1 summarizes latitudes and longitudes, dates, and dive times. These data and videotapes are from NOAA's National Undersea Research Center at the University of North Carolina at Wilmington. Time starting and time ending are the beginning and ending points of the videotape section that we

Table 1

Information on dives at Cape Hatteras and Cape Lookout, North Carolina, from which videotapes were used for analysis of demersal nekton habitat use. "Dive no." is the identification number we used to request the tapes. "Start time" and "End time" are the beginning and ending points on the videotape section used in the analyses (not the launch and recovery times of the dives). Depths are in m.

Dive no.	Date 1989	Latitude °N	Longitude °W	Start time (HH:MM)	End time (HH:MM)	Start depth	End depth
Cape Hatteras							
2623	14 Oct	35°23'	74°50'	15:37	18:11	853	853
2627	16 Oct	35°38'	74°48'	8:52	10:01	782	573
2629	17 Oct	35°23'	74°51'	7:29	8:24	610	549
2630	17 Oct	35°29'	74°48'	13:16	13:43	511	420
Cape Lookout							
2619	12 Oct	34°15'	75°45'	13:40	14:47	903	853
2620	13 Oct	34°14'	75°45'	9:00	9:07	945	843
2621	13 Oct	34°14'	75°46'	16:31	18:28	793	843

used in the analyses (not the launch and recovery times of the dives). The videotapes were recorded as the submersible cruised along the bottom, generally at a speed of 0.5–1 knot (ca. 25–50 cm/sec). The camera faced forward and down and was not panned or moved during the recording of videotape sections used for analysis. At times the submersible stopped to deploy experiments or pick up samples and at other times moved away from the bottom. We recorded data from video images only during periods when the submersible was moving and the bottom was clearly visible. During these periods, we quantified environmental variables and counted individuals of nekton species during 1-minute intervals. If the submersible stopped or moved away from the bottom during an interval, that interval was discarded. We did not start measuring again until the submersible began moving steadily and the bottom was clearly visible. The bottom topography at the Cape Hatteras site was extremely complex, with gullies, walls, and flat expanses. Only videotapes of flat areas were used for the analysis. The videotapes of Cape Lookout dives included only broad expanses of flat slope.

Environmental variables recorded are listed in Table 2 and included holes, mounds, and tubes. Holes and mounds are indicators of infaunal activity. Holes were generally 1–3 cm in diameter and mounds generally >10 cm in diameter. Tubes were 5–10 cm in length and most often curved, sometimes with both ends touching the substrate. Objects classified as tubes were identified (Schaff[1]) as those of polychaetes and foraminifera (*Bathysiphon* spp.). Further characterization of sediment samples from these dives can be found in Levin (1991) and Gooday et al. (1992). Holes, mounds, and tubes were coded as follows: 0 = none visible during the whole interval; 1 = no more than a total of 1 or 2 visible during the whole interval; 2 = 1 or 2 visible at all times during the interval; 3 = several always visible at any time in the interval, but countable; 4 = too many to count in the interval. Category 4 coded those situations where the environmental feature was so densely distributed that individual features were obscured by others nearer the camera. Other coded variables were gastropod/echinoderm tracks (grooves in the substrate), sea grass detritus/*Hyalinoecia* tubes, and sargassum detritus. These were coded 1 or 0 for presence or absence in the interval; e.g. a value of 1 was assigned to the interval whenever one or more tracks were observed. Long thin dark objects that appeared to be bits of sea grass detritus might also include tubes of the polychaete *Hyalinoecia* (Schaff[2]). Such objects are referred to as "grass detritus" in this study. Finally, we counted raw numbers of small anemones, large anemones, gastropods, and crinoids. Small anemones probably represented *Actinauge verrilli* and large anemones may be *Bolocera* sp. (Levin[3]). Gage and Tyler (1991) give excellent descriptions of epifaunal and infaunal organisms and benthic features similar to those listed above.

[1] Schaff, T. Natl. Mar. Fish. Serv., Silver Spring, MD. Personal commun., 1992.

[2] Schaff, T. Natl. Mar. Fish. Serv., Silver Spring, MD. Personal commun., 1993.

[3] Levin, L. Scripps Institution of Oceanography, La Jolla, CA. Personal commun., 1992.

Numbers of individuals of selected demersal nekton species were also recorded for each 1-minute interval. This provided a consistent estimate of relative abundance. Nekton included fishes, cephalopods, and macrocrustacea. As no voucher specimens were collected, identifications were made visually with the assistance of specialists familiar with the groups (noted below in the Results section). Most of these forms could be confidently identified only to genus from the videotapes.

Data analysis

Data from dives at Cape Hatteras and at Cape Lookout were analyzed separately. Cape Hatteras dives spanned a depth range that included two faunal zones (upper and middle slope) identified by Haedrich et al. (1980) and Wenner and Boesch (1979). In general, these authors found differences between continental slope communities above 700 meters and those below. Thus, Cape Hatteras dives 2629 and 2630 (Table 1) were conducted on the upper slope, whereas dive 2623 was conducted on the middle slope. Dive 2627 crossed the boundary identified by Haedrich et al. (1980). All Cape Lookout dives were conducted on the middle slope. Depth was not included as a variable in the statistical analyses detailed below, because it was not recorded for each 1-minute videotape segment. Potential effects of biotic zonation were investigated separately by comparison of species distribution with dive depth.

Statistical analysis of habitat choice by the identified nekton followed Felley and Felley (1986, 1987) and Felley et al. (1989). All statistical analyses were conducted with the SAS program (SAS Institute, 1988). The steps in the analysis were as follows: 1) calculation of species' mean abundances for environmental variables; 2) calculation of a correlation matrix among species' mean abundances; 3) factor analysis of the correlation matrix; 4) comparison of variances of sampling units and of numbers of individuals of a species on the artificial variables (factors) generated by the factor analysis. These steps were accomplished as follows.

First, we calculated means of environmental variables for each species as each variable's mean over 1-minute intervals, weighted by the number of individuals of that species seen in each interval. Thus, a species' mean abundance for a variable represented the value of that environmental variable in intervals where the species was most likely to be found. The species' mean abundance was considered the species "preference" for the variable, assuming that these nektonic species select their habitat.

Second, species' mean abundances for the environmental variables were used to construct a correlation matrix among the variables. Note that this correlation matrix implies standardizing each variable using a "mean of means" and a "standard deviation of means." A high correlation between two variables is seen when species tend to occur in habitats with contrasting values for both of these variables. For example, an analysis might include some species found typically in shallow gravel areas and some preferring deep sandy areas. This analysis would generate a high correlation between such environmental variables as depth and substrate particle size. Thus, patterns of habitat use by species are reflected in patterns of interrelations among the variables. This is an analysis of species associations with particular environments, and the data contain no information about why a particular species is occurring more often in one habitat type than another.

Third, factor analysis (principal component analysis with Varimax rotation, Mulaik, 1972) was performed on the correlation matrix. Factor analysis resolves patterns of interrelationships among variables into a smaller set of composite variables (factors) to which observed variables (species mean abundances) are correlated. Sets of interrelated variables correlating highly with a factor are variables reflecting similar patterns of habitat use among the species. Each factor represents a particular trend in habitat use, an axis differentiating among sets of species that are likely to be found in habitats with contrasting conditions for the variables that define the factor. The example above might produce a factor defined by depth and substrate particle size.

Species' values, or scores, for a factor can be calculated by using a factor scoring function. Species with contrasting scores are those found most often in contrasting environments relative to that factor. To continue the example, species more likely to be found in deep water over sandy substrate would have factor scores that contrasted with those of species more often found in shallow water over coarse substrates (i.e. positive vs. negative scores on the factor). Species with intermediate scores may be characteristic of intermediate environments on that factor, or they may be found over the entire range of environments reflected by a factor (because the species' score is the weighted mean of scores of intervals where it was found).

Note that only a subset of the species analyzed in the example may in fact select habitat based on environmental variables related to depth and substrate. Though a trend in habitat use may be identified for a species assemblage, not all species in the assemblage may select habitat according to that trend. Further analysis is required to determine which species show evidence of active selection according to a particular habitat trend.

Fourth, we investigated habitat selection by individual species by comparing species' variances on each factor with variance of the environment. Environmental variance on a factor was determined by calculating factor scores for each 1-minute interval. First, the value for each environmental variable in a 1-minute interval was standardized by using the appropriate "mean of means" and "standard deviation of means" noted above. Then the scoring function was applied to each 1-minute sampling unit. Environmental variance was then determined as the variance of sampling unit scores. The score of a 1-minute interval was assigned to all individuals of all species seen in the interval. A species' variance was then calculated for each species as the variance of these scores. The procedure of investigating both species and locality scores on multivariate axes corresponds to Rotenberry and Wiens'[4] "synthetic approach" to the study of communities.

We compared a species' variance with environmental variance for each factor by using Levene's test (Levene, 1960; Van Valen, 1978). Bonferroni corrections for multiple statistical tests were made by using Rice's (1989) method for investigating tables of statistical test results. Rice's method is a correction for inflated type-I error in situations where several different tests of significance are made for a particular null hypothesis. Such a series of tests constitute a "table of statistical tests." In this study, a "table" was considered to be all significance tests made relative to a factor, the corresponding null hypothesis being "species variances are not significantly different from environmental variance with respect to this factor." Active habitat selection by a species was inferred when a species' variance was significantly smaller than the observed environmental variance (1-tailed test). This implies that the species was actively selecting a subset of the available environment with respect to that factor. See Felley and Felley (1987) and Felley et al. (1989) for more details.

[4] Rotenberry, J. T., and J. A. Wiens. 1981. A synthetic approach to principal component analysis of bird/habitat relationships. *In* D. E. Capen (ed.), The use of multivariate statistics in studies of wildlife habitat, p. 197–208. USDA Forest Serv. Gen. Tech. Rep. RM–87, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Results

Environments and biota

Cape Hatteras—Table 2 presents means of environmental variables for flat areas traversed by dives on the slope off Cape Hatteras. Holes and mounds were common environmental features: one to several holes and mounds were in view at almost all times. In general, intervals where holes were dense also had a large number of mounds. Tubes were variable in occurrence. Many were seen in dive 2627 but relatively few were seen in dives 2629 and 2630. Grass detritus was very common in dives 2627, 2629, and 2630, occurring in almost every interval. Sargassum detritus was infrequent in upper slope intervals (dives

Table 2

Environmental variables measured on each interval, with means and standard deviations (in parentheses) for each dive at Cape Hatteras and Cape Lookout, North Carolina. Holes, mounds, and tubes were coded as follows: 0=none in the interval; 1=no more than 1 or 2 seen in an interval; 2=always 1 or 2 visible throughout an interval; 3=several always visible, but countable; and 4=too many visible to count. Gastropod/echinoderm tracks, and grass and sargassum detritus were coded 1/0 for presence/absence in the interval (only percentages are reported for these variables). Number of individuals were counted for small anemones, large anemones, gastropods, and crinoids.

		Environmental variables									
	N	Holes	Mounds	Tubes	Tracks	Grass detritus	Sargassum detritus	Small anemones	Large anemones	Crinoids	Gastropods
Cape Hatteras											
2623	61	1.75 (0.830)	1.36 (0.484)	2.41 (1.321)	100.0	47.5	18.0	6.87 (6.711)	0.03 (0.180)	5.90 (15.367)	0.31 (0.564)
2627	35	2.63 (0.490)	1.66 (0.482)	2.23 (0.942)	45.7	88.6	8.6	25.80 (19.954)	0.17 (0.382)	0.00 (—)	0.40 (0.976)
2629	41	2.51 (0.506)	1.78 (0.571)	0.73 (0.633)	85.4	82.9	4.9	1.37 (1.577)	4.63 (3.006)	4.66 (13.190)	0.27 (0.449)
2630	7	2.29 (0.756)	1.14 (0.378)	0.57 (0.535)	14.3	100.0	0.0	0.00 (—)	0.00 (—)	0.00 (—)	0.00 (—)
Cape Lookout											
2619	36	3.36 (0.529)	2.22 (0.485)	0.25 (0.439)	16.7	69.4	38.9	0.33 (0.676)	0.53 (0.629)	0.00 (—)	0.03 (0.167)
2620	7	3.28 (0.488)	2.14 (0.378)	0.00 (—)	28.6	14.3	28.6	0.14 (0.378)	0.43 (0.534)	0.00 (—)	0.00 (—)
2621	32	3.25 (0.440)	2.25 (0.508)	0.25 (0.440)	53.1	62.5	40.6	0.41 (0.560)	0.44 (0.619)	0.00 (—)	0.00 (—)

2627, 2629, 2630), but was more common at the middle slope site (dive 2623).

Anemones, echinoderms, gastropods, and invertebrate tracks were common. Epifaunal forms tended to occur in patches. Coefficients of dispersion (CD, Sokal and Rohlf, 1981) were calculated for small anemones, large anemones, crinoids, and gastropods (data in Table 2). Coefficients of dispersion much greater than 1 (indicating clumped distribution patterns) were found for small anemones in all Cape Hatteras dives where they were observed. Small anemones were very abundant in dive 2627. For 15 minutes, the submersible traversed a dense aggregation where numbers ranged from 30 to 80 individuals per interval. Small anemones were also common (though not as densely distributed) in dive 2629. Large anemones were seen regularly and were relatively dense in dive 2629 (up to 12 in an interval). Large anemones had a clumped distribution in this dive, indicated by a high CD value. Coefficients of dispersion were very high for crinoids. A dense patch of crinoids appeared in dive 2629, with 4 to 62 individuals per interval for 6 consecutive intervals. Another area of dense crinoids appeared in dive 2623, with 7–70 individuals per interval in 10 consecutive intervals. In dive 2630, an extremely dense patch of ophiuroids appeared over 4 consecutive intervals (ophiuroids were not included in the statistical analysis as they were seen in so few intervals).

Cape Lookout—Holes and mounds were very dense; holes were, in fact, too dense to count during some portions of dives 2619 and 2621. As at Cape Hatteras, intervals with high numbers of holes also had large numbers of mounds. Tubes were rarely observed and were not seen in dive 2620. Grass detritus was commonly seen but was not as frequent as at Cape Hatteras. Conversely, sargassum detritus was quite frequent, occurring in 39–41% of Cape Lookout intervals. Epifaunal species were not abundant and were not patchily distributed. Small anemones were not common (fewer than one per interval) and were less abundant than large anemones. No crinoids were seen in the Cape Lookout dives.

Demersal nekton species

Many nektonic species were observed on the tapes, but only a few appeared in abundance. These were the species included in analysis of habitat preferences. As no voucher specimens were obtained, identifications were assigned on the basis of species known to be common in the area, after consultations with taxonomic experts (listed in the Acknowledgments section). Table 3 lists the species included in analyses of habitat choice and their mean numbers in particular dives.

The eel (*Synaphobranchus* sp.; Smith[5]), though rare at Cape Hatteras, was the most abundant form at Cape Lookout. This genus forms an important part of the middle-slope fauna (Markle and Musick, 1974; Haedrich et al., 1980; Sulak[6]). Eels were always ob-

[5] Smith, D. G. National Museum of Natural History, Washington, D.C. Personal commun., 1992.

[6] Sulak, K. Atlantic Reference Centre, Huntsman Marine Science Centre, New Brunswick, Canada. Personal commun., 1990.

Table 3

Common demersal nekton species identified in upper slope and middle slope dives, North Carolina, and average numbers of individuals per 1-minute interval seen in each dive (number of intervals are given in Table 2). See text for discussion of the probable identities of these forms and scientific names.

	Cape Hatteras dives				Cape Lookout dives		
Species	2627	2629	2630	2623	2619	2620	2621
Eel	—	0.02	—	0.10	2.17	2.71	1.75
Rattail	2.60	1.12	0.29	1.69	0.61	0.57	0.78
Longfin hake	0.43	0.66	0.57	0.54	0.22	0.14	0.25
Scorpaenid	4.26	0.07	0.57	1.20	—	—	0.03
Lizardfish	0.03	0.34	—	0.02	—	—	—
Eelpout	12.43	5.83	1.43	5.43	—	—	—
Flounder	2.14	1.90	0.86	1.25	—	—	—
Species A	—	0.15	—	—	—	—	—
Sergestid shrimp	0.17	0.59	0.86	0.25	0.11	0.29	0.72
Shrimp	0.09	0.02	—	0.07	0.03	—	0.03
Red deepsea crab	—	—	—	0.02	0.06	0.14	0.16
Cancroid crab	—	0.07	0.56	—	0.03	0.14	0.03
Shortfin squid	0.06	0.20	—	0.56	—	—	0.22
Octopod	0.03	0.05	—	0.03	—	—	0.06

served swimming slowly slightly above the bottom, maintaining position with low amplitude tail-beats.

Individuals identified as rattails represented either *Nezumia bairdi*, *N. aequalis* (Sulak[6]), or *Coryphaenoides rupestris*, the three species most commonly encountered in the depth range of these dives (Markle and Musick, 1974; Haedrich et al., 1980; Middleton and Musick, 1986). Rattails were common in all dives and were seen both lying on the bottom and maintaining position off the bottom by swimming slowly (with low amplitude tail-beats).

The hake commonly observed in the tapes was the longfin hake, *Urophycis chesteri*, a common species on the continental slope of the western North Atlantic (Markle and Musick, 1974; Haedrich et al., 1980; Wenner, 1983; Sulak[6]). Hakes were observed in every dive, normally lying on the bottom. Quite often they were found in depressions, their bodies in a circular or semicircular posture.

Scorpaenids were observed in all Cape Hatteras dives but only in dive 2621 at Cape Lookout. The species represented may be *Helicolenus dactylopterus* (Sulak[6]). At Cape Hatteras, they were abundant in both the upper slope (e.g. dive 2627) and the middle slope (dive 2623). When seen, they were always lying on the bottom, their bodies often in a semicircular posture.

Lizardfish were seen only on the upper slope, most notably in dive 2629, where 14 individuals were observed. These may represent *Saurida brasiliensis* or *S. normani* (Sulak[6]).

Several different eelpouts were likely present on these tapes, including *Lycenchelys verrillii* and *Lycodes atlanticus* (Sulak[6]). *Lycenchelys paxillus* is a more northerly species (Markle and Musick, 1974) but may occur on the North Carolina slope. Eelpouts were the most abundant fish at Cape Hatteras, in all dives, but were not seen at Cape Lookout. Individuals tended to be small (<15 cm), with dark blotches, and lay in sinusoidal posture, usually near objects on the bottom (most often small anemones).

Small flounders were seen in all dives at Cape Hatteras but were not found at Cape Lookout. There were most likely several species represented, including *Glyptocephalus cynoglossus*. This species is an important component of the slope fauna (Markle and Musick, 1974; Haedrich et al., 1980; Sulak[6]).

A fish occurring commonly only in dive 2629 was designated as Species A. This may have been the offshore hake, *Merluccius albidus* (Sulak[6]). It was light-colored with dark dorsal blotches, of moderate size (<20 cm), had a terete shape, and a relatively large head. It was always observed lying on the bottom, its body straight. Most individuals swam away before the submersible got close enough for adequate observation. The eel and the shortfin squid, *Illex illecebrosus* (see below), also tended to move away from the submersible.

Several decapod crustaceans were also observed. Sergestid shrimp were seen in every dive, always off the bottom. Another decapod seen regularly at both Cape Hatteras and Cape Lookout may have been the shrimp *Glyphocrangon* sp. (Williams[7]). Wenner and Boesch (1979) found *G. sculpta* and *G. longirostris* at depths greater than 1,000 m. These shrimp were most abundant in dives 2623 and 2627. Individuals were seen walking on the open bottom, where their dark coloration and highly reflective eyes made sighting these easy.

The red deepsea crab, *Geryon quinquedens*, was not seen in the upper slope dives but was observed in all middle slope dives, walking on the open bottom. It was included in analysis of Cape Lookout species but was too rare to be included in the analysis of Cape Hatteras species. Wenner and Boesch (1979) found this species throughout the depth range included here.

Cancroid crabs were seen at Cape Hatteras and Cape Lookout, in both upper and middle slope dives and likely represent two species. Wenner and Boesch (1979) found *Cancer borealis* and *C. irroratus* on the slope of the Middle Atlantic Bight and *C. borealis* farther downslope than *C. irroratus*. Several cancroid crabs were seen in dive 2630, where they occurred in association with an extremely dense patch of ophiuroids.

The shortfin squid was observed at both Cape Hatteras and Cape Lookout, in both upper and middle slope dives. Individuals were usually lying on the bottom but rose off the bottom when disturbed by the submersible. Occasionally schools were seen off the bottom.

Small octopods were seen at both Cape Hatteras and Cape Lookout in both upper and middle slope dives. Individuals were small and most often associated with objects on the bottom, including sea anemones, crinoids, and gastropod shells. The species had short arms and was probably *Bathypolypus arcticus*.

Galatheid crabs were very common on the bottom, especially in areas where holes were dense. We did not include them in the analysis, because we found that estimates of their numbers were biased depending on whether the submersible travelled up or down the slope. When travelling upslope, only individuals walking on the bottom were seen. When travelling downslope, the camera was able to look down into holes. Viewed in this way, many (if not most) of the holes were occupied by galatheid crabs.

[7] Williams, A. Natl. Mar. Fish. Serv. Systematics Laboratory, Washington, D.C. Personal commun., 1992.

Analysis of habitat preferences

Cape Hatteras—Analysis of species' habitat preferences produced three factors (Table 4). Factor 1 was related to species preferences for different types of epifaunal assemblages. Factor 2 was related to different amounts of mounds and crinoids and presence or absence of sargassum detritus. Factor 3 was related to density of holes and presence of grass detritus.

Factor 1 had high positive loadings for numbers of small anemones, tubes, and gastropods, and a negative loading for numbers of large anemones. This factor differentiated nekton species found more often in intervals with large numbers of small anemones, gastropods, and tubes, from forms more common in areas with few small anemones, tubes, and gastropods (but where large anemones might be found). Species' scores showed that the scorpaenid, rattail, and shrimp were characteristic of areas with large numbers of small anemones and tubes, whereas cancroid crabs, lizardfish, and Species A were not usually found in such areas (Fig. 1).

Factor 2 had high positive loadings for density of mounds and number of crinoids. Sargassum detritus had a high negative loading on this factor. This factor differentiated between forms found in association with crinoids and mounds, and forms found away from such areas, more in association with sargassum detritus. Species found more in areas with crinoids and mounds included the eel and lizardfish. Forms found in areas with few crinoids and mounds (but with sargassum detritus) included Species A, squid, octopod, and scorpaenid (Fig. 1).

Factor 3 had high loadings for density of holes and presence of grass detritus. Gastropods and crinoids also contributed positively to this factor. Species found more in areas where holes were dense included the lizardfish, flounder, and scorpaenid, while species not characteristic of such areas included the squid, cancroid crab, and shrimp (Fig. 1).

We compared species' and location variances on each of the three factors to determine which species appeared to be selecting subsets of the environment represented by each factor. Figure 2 illustrates the distributions on factor 1 of location scores, squids (a significant variance comparison), and scorpaenids (variance comparison not significant).

Habitat selection according to type of epifaunal assemblage (factor 1) was shown for the squid, which preferred areas where neither small anemones nor large anemones were found (Fig. 2). Habitat selection related to mounds and crinoids (factor 2) was demonstrated for the hake. Hakes tended to be found in areas with many mounds and crinoids. Habitat selection with respect to density of holes and grass detritus (factor 3) was demonstrated for the hake, sergestid shrimp, and lizardfish. These three forms all tended to be seen in areas with intermediate numbers of holes.

Cape Lookout—Only five species were observed in enough intervals to include in a factor analysis of their means. These included the rattail, eel, hake, sergestid shrimp, and red deepsea crab. Factor analysis of these species produced two factors (Table 4). Factor 1 related to density of holes and mounds, and factor 2 related to types of epifaunal assemblages.

Factor 1 had high positive loadings for density of holes, mounds, and tubes. Numbers of gastropods, presence of invertebrate tracks, and presence of sargassum debris contributed negatively to this factor. This factor differentiated between species found more often in areas with many holes and mounds and species not usually found in such areas. The hake and the red deepsea crab were characteristic of areas with many holes, whereas the sergestid shrimp tended to be found where holes, mounds, and tubes were less densely distributed. None of the comparisons between environmental and species variances were significant.

Factor 2 had high positive loadings for number of small anemones and number of large anemones, and for presence of detritus (both grass and sargassum). The hake was the species most characteristic of areas with many anemones and much detritus, whereas the red deepsea crab was most characteristic of areas devoid of epifauna and detritus. None of the comparisons between environmental and species variances was significant.

Discussion

Mobile species respond to environmental variables, seeking certain conditions and avoiding others. The assumption that individuals select their environment is central to this analysis, as it is to multivariate analyses of habitat selection in general (James and McCulloch, 1990). Environmental variables affecting an individual's habitat choice may include abiotic variables, the presence and density of other species, and the presence and density of members of its own species. The individual's response to a variable of importance may be negative (avoidance) or positive (attraction). Together, the habitat choices of all individuals in an area produce the distributional patterns observed by the investigator.

We used patterns of species distribution and associations between species and environmental variables as a guide to understanding the structure of a

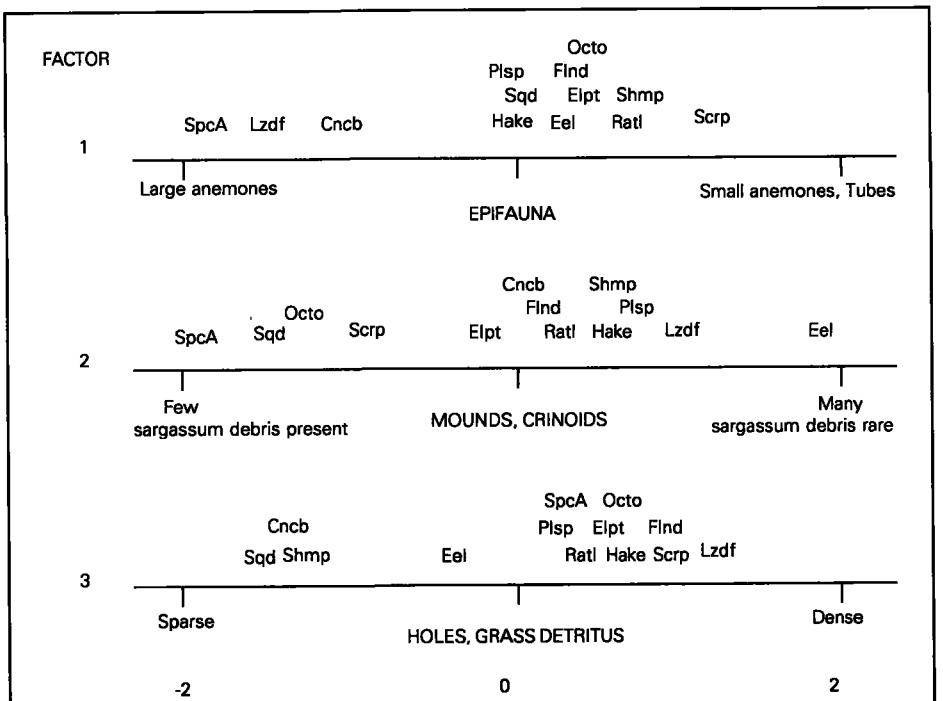

Figure 1

Distribution of species scores on axes representing habitat use by nekton species at Cape Hatteras. Factor 1 represented habitat use according to different epifaunal assemblages, factor 2 according to density of mounds and crinoids, and factor 3 according to density of holes and presence or absence of grass detritus. Species abbreviations are as follows: Cncb=cancroid crab, Elpt=eelpout, Flnd=flounder, Lzdf=lizardfish, Octo=octopod, Plsp=sergestid shrimp, Ratl=rattail, Scrp=scorpaenid, Shmp=shrimp, SpcA=Species A (possibly offshore hake), Sqd=shortfin squid.

poorly known deep-ocean nekton assemblage. Accepting the assumption discussed above, we confronted the following methodological questions: 1) which species to analyze, 2) which environmental variables to measure, and 3) at what scale to sample. Our answers to these questions were pragmatic. We quantified those forms we felt could be recognized easily and consistently and were consistently visible on the videotape. We measured as many variables as we could quantify visually in an accurate and repeatable fashion and also included those variables that seemed to be dominant in the environment (e.g. small anemones, holes). We sampled at a spatial scale assumed to approximate the area monitored by species of the assemblage. Although the area viewed in one minute of submersible cruising (a distance of ca. 15–30 m) is doubtless greater than the area monitored by an individual at any particular moment, we felt this to be the smallest manageable sampling unit. Shorter intervals (e.g. 30 seconds) required an inordinate amount of videotape stopping and starting. Preliminary analyses suggested that increasing the size of sampling units would create problems, including 1) a much smaller number of samples for the analysis, 2) loss of information in 1/0 coded variables, as these tended to become 1 (environmental attribute present) in all intervals, and 3) loss of information in variables whose scale of change was smaller than the sampling unit. In each case, increasing the size of sampling units tended to decrease the measurable association between a species and particular environmental variables (see also Schneider et al., 1987).

Correlations between species occurrence and particular environmental variables were subjected to multivariate analysis to find the patterns of habitat use in this species assemblage. In accordance with James and McCulloch's (1990) caveats, we recognize and stress the correlational aspect of this study. Our analysis produced artificial axes that only reflect real trends. These artificial axes provided the data for all further statistical tests. However, our interpretations are strictly tied to the real variables represented by the artificial axes. When a factor had high loadings for holes and small anemones, we inferred that one of these variables, or some other variable strongly related to them, was in fact affecting distri-

bution of some species in the assemblage. In this way, we attempted to move from our view of the environment to a view more concordant with that of the species that live there.

Our view was molded by the environmental variables we measured and the species distributions we observed. These highlighted differences between the Cape Hatteras and Cape Lookout sites, as well as differences between dives at a site. In all dives, the benthic environments included in this analysis had soft substrate, with visible epifauna and evidence of infauna (holes, mounds). Differences between the two dive sites were seen in the species composition and in the spatial distribution of these species. There were some depth-related patterns in species occurrence at the Cape Hatteras location (Cape Lookout dives were all at similar depths).

Density of organisms differed greatly between Cape Hatteras and Cape Lookout. Biota was much more dense at Cape Hatteras. Summing all demersal nekton, anemones, gastropods, and crinoids in each interval, we found that Cape Hatteras dives had a mean of 29.0 organisms per interval, whereas Cape Lookout dives had a mean of 4.6 organisms per interval. At Cape Hatteras, dives 2623, 2627, 2629, and 2630 averaged 24.3, 48.7, 23.0, and 5.1 organisms per interval, respectively. At Cape Lookout, dives 2619, 2620, and 2621 averaged 4.2, 4.9, and 5.0 organisms per interval, respectively. Schaff et al. (1992) found density of biota at the Cape Hatteras site to be much higher than at other slope localities, including the Cape Lookout site. They related the high density of biota at Cape Hatteras to nutrient enrichment due to an interaction between the complex topography of the area and upwelling currents.

Distribution patterns of sessile epifauna differed at the two sites. At Cape Hatteras, ophiuroids, crinoids, and small anemones showed evidence of clumped distributions. Large anemones showed a clumped distribution in dive 2629. There was no evidence of clumped distributions for any sessile organisms at Cape Lookout.

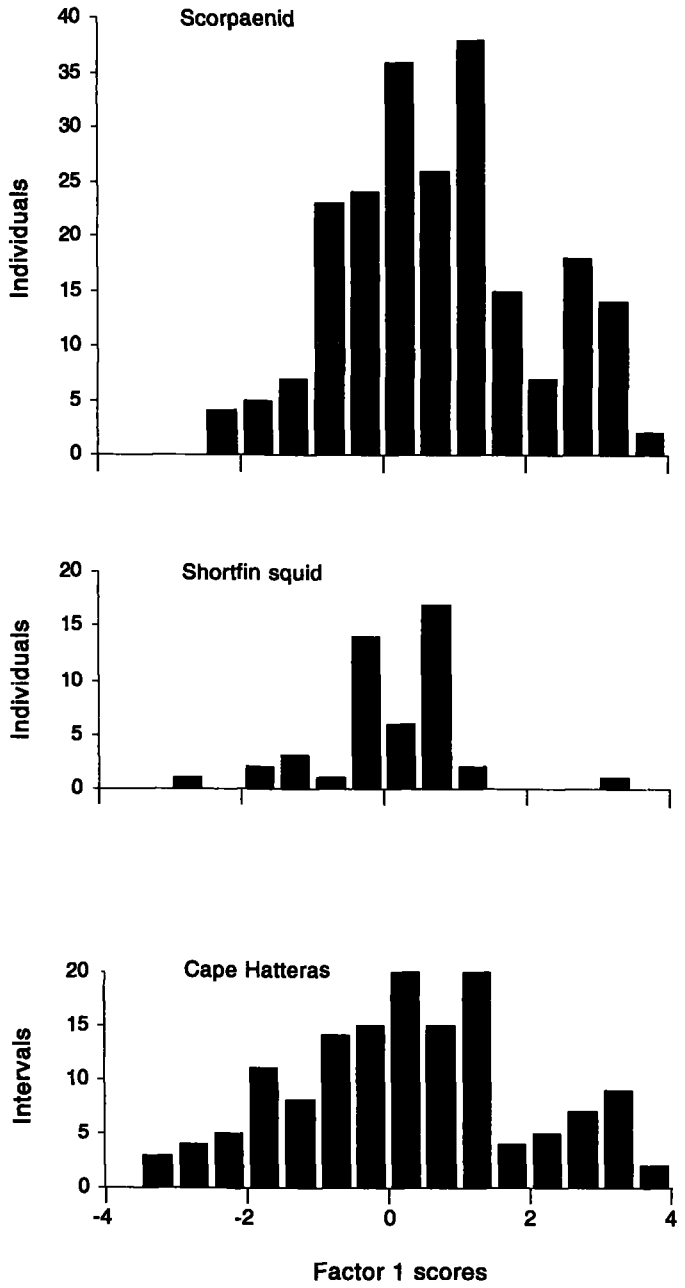

Figure 2

Distribution of intervals, shortfin squid, and scorpaenids on an axis representing epifaunal assemblages at Cape Hatteras. Variance of shortfin squid scores was significantly smaller than that of intervals, whereas variance of scorpaenid scores was not significantly different. This axis is the same as that labeled factor 1 in Figure 1.

At Cape Hatteras, some species were restricted to particular depths. Zonation by depth has been documented for slope megafauna (Gardiner and Haedrich, 1978; Rowe and Haedrich, 1979; Hecker, 1990a). The eel and the red deepsea crab were found almost exclusively at middle slope dives (2623 and 2627, Table 3), whereas the lizardfish and Species A were found mostly in the upper slope dives. Most species included in the analysis were found in a range of depths.

Table 4

Factor loadings of environmental means for benthic megafauna from the slope at Cape Hatteras and Cape Lookout, North Carolina. The representations below are of principal components rotated to simple structure. Only factor loadings >0.50 are shown.

	Factors					
Analysis	1		2		3	
Cape Hatteras	Large anemones	−0.91	Mounds	0.94	Holes	0.94
	Small anemones	0.83	Crinoids	0.73	Grass detritus	0.65
	Tubes	0.88	Sargassum detritus	−0.88	Gastropods	0.54
	Gastropods	0.54			Crinoids	0.50
Cape Lookout	Holes	0.92	Grass detritus	0.89		
	Mounds	0.93	Large anemones	0.88		
	Tracks	−0.72	Small anemones	0.91		
	Tubes	0.93	Sargassum detritus	0.82		
	Gastropods	−0.96				
	Sargassum detritus	−0.52				

Although the various areas appeared qualitatively different, analyses of species' habitat preferences showed us that species in both areas were distributed in relation to similar types of benthic features. Some forms were typically seen in areas with dense aggregations of holes and mounds; others were seen in areas with fewer holes and mounds. Thus, at both localities, nekton distributions were related to particular types of infaunal assemblages. Associations with particular epifaunal assemblages were demonstrated by those species found most often in dense patches of small anemones and (at Cape Hatteras) in areas with dense patches of large anemones or crinoids. Analysis of species preferences suggested that in different areas on the continental slope, nekton species respond to similar sets of environmental variables.

While analysis of species preferences identified broad patterns of habitat selection for a group of species, analysis of species variances allowed identification of habitat selection by individual species. Active habitat selection (occurrence of a species in a subset of available environments) was demonstrated for 4 of the 13 species included in the Cape Hatteras analysis. While habitat selection according to factors 1 and 2 was shown for only one species each, habitat selection according to density of mounds and grass detritus (factor 3) was shown for three species (hake, lizardfish, sergestid shrimp). Note that sergestid shrimp distribution was related to benthic features, although shrimp were always seen hovering 1 to 2 m above the bottom. Such a seemingly counterintuitive result (a species selecting habitat according to a variable that it does not seem to monitor) suggests the need for more study in this environment.

For most species at Cape Lookout and for several at Cape Hatteras, small sample sizes made tests of variance equality quite weak. An uncommon species restricted to a particular habitat might be sampled in numbers too low to allow a statistically significant test. Examples abound in this study. Our analyses identified various environmental gradients. Locations with scores at the extremes of the gradients were sampled in low numbers (e.g. Fig. 2). Forms characteristic of these extreme environments were sampled in correspondingly low numbers, unless they happened to be extremely abundant in a few intervals. Thus, we found it most difficult to show statistically significant habitat selection for those species that were tightly clustered in specific habitat types.

Some examples of uncommon forms found in specific habitat types came from dive 2629 (Table 3). The lizardfish was most abundant in this dive, and Species A and the only eels observed on the upper slope were visible during this dive. The dive area had a high diversity of habitats. The submersible passed over areas with many holes and few anemones or other epifauna, areas dense with small anemones, a dense patch of crinoids (from 5 to 50 individuals per interval over 8 intervals), and an aggregation of large anemones (from 4 to 12 individuals over 18 intervals). The extreme scores of Species A, cancroid crab, and lizardfish were strongly affected by their high densities in particular habitats seen in dive 2629. Detailed studies of such heterogeneous areas could clarify the environmental variables used by slope species to select their habitats.

In this study, we saw patterns of habitat choice by nekton at different scales, from differences along the slope, to species preferences for different habitats

within a dive. Most species were found across the range of habitat types identified by the analysis, though they might be most abundant in one specific habitat. Active habitat selection (species variances smaller than environmental variance) was not seen for such species. Other species were found in numbers too small to allow a powerful test of active habitat selection. Despite these qualifications, this study demonstrated trends in habitat selection by slope nekton and suggested hypotheses for further work.

At both sites, habitat selection by demersal nekton was related to numbers and types of sessile invertebrates and to infaunal organisms that created holes and mounds. These are also two of the trends seen by Felley et al. (1989). They found that habitat selection by demersal nekton of a sandy-bottom shelf environment of the Gulf of Mexico was related to presence or absence of large sessile invertebrates (sponges, cnidarians, and small corals) and to presence or absence of holes and mounds. Habitat selection in that study was also related to amount of algal cover.

Both this study and that of Felley et al. (1989) were based on analysis of videotapes originally recorded for other purposes. There may be problems with using such videotapes. The submersible tracks were not arranged as transects; therefore, we had to remain aware of potential sampling problems (e.g. the submersible crossing and recrossing a particular area, which did not occur on these videotapes). Sampling bias might result from the conditions under which we collected data. We had to stop collecting data when the submersible stopped, when it moved away from the substrate, or when it traversed areas of gullies or ridges. Thus our results can be generalized to only the habitat we did sample—flat areas. Despite such qualifications, archived videotapes are an inexpensive source of data for exploration of questions relating to distribution patterns in deep-sea organisms. Such patterns are difficult to study in the deep sea (Gage and Tyler, 1991). By using archived videotapes, hypotheses can be developed, utility of specific sampling systems assessed, and improvements in methods recommended. We feel that consistent collection and archiving of video transects is important for extending the usefulness of submersible missions.

Acknowledgments

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Abstract.—Little is known of the early ocean life of juvenile chinook salmon, *Oncorynchus tshawytscha*. During the summers of 1981 through 1985 we collected juvenile chinook salmon with fine-mesh purse seines in shelf waters off the Oregon and Washington coasts. Most coded-wire tagged (CWT) fish caught in the ocean were yearlings from Columbia River basin hatcheries. Catch per unit of effort of CWT yearling fish was much higher in the May–June period than in the August–September period, probably, for the most part, because of the migration of these fish out of the sampling area by late summer. CWT subyearling fish were more abundant in late summer than in spring and early summer. A few fish from the Columbia River Upriver Bright stock of fall chinook salmon were recovered many months after release near where they entered the ocean, indicating that northward migration of some smolts from this highly migratory stock may be delayed for several months following release, or that some individuals of the stock undertake less extensive migrations than others. Subyearling smolts were rare in our catches, despite the larger spawning populations producing these smolts than those producing the yearling smolts in this area. Subyearling fish may have been mainly distributed in shallow water inshore of our sampling. Our largest catches of small chinook salmon (≤130 mm FL) were taken in the low salinity, high-temperature waters of the Columbia River plume. CWT fished were usually recovered north of where they entered the ocean, except in May 1982 when southward currents were strong. Average net rate of migration of yearling smolts between the head of the Columbia River estuary and ocean capture was 4.1 km·d^{-1}. Average growth rate of CWT yearling fish downstream of river km 75 in the Columbia River was 1.05 mm·d^{-1}. Average instantaneous rate of growth in weight of yearling CWT Columbia River fish between hatchery release and capture in the ocean was 0.92% body wt·d^{-1}.

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Distribution, migration, and growth of juvenile chinook salmon, *Oncorhynchus tshawytscha*, off Oregon and Washington

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The Columbia River once produced the largest runs of chinook salmon (*Oncorhynchus tshawytscha)* in the world (Van Hyning, 1973). Today, runs are only a fraction of the size they were in the late 19th and early 20th century (Chapman, 1986), and a large fraction of the present population is produced in hatcheries. Although the runs of Columbia River chinook salmon are affected by many factors (e.g. dams, freshwater habitat depredation, ocean fisheries, etc.), environmental conditions during early ocean life also may be important determinants of year-class success for these fish.

Little is known of the early ocean distribution, migration, and growth of chinook salmon during their first year in the ocean prior to becoming vulnerable to ocean fisheries. Hartt and Dell (1986) collected juvenile salmon with purse seines over a wide area of the Gulf of Alaska and the Bering Sea in the late 1950's through the early 1970's. Although relatively few juvenile chinook salmon were caught during their sampling (358 fish in 505 sets between 1964 and 1968; their Appendix Table A1), subsequent recoveries of juvenile fish tagged at sea provided information on early ocean migrations of these fish. Four juvenile fish tagged in the northern Gulf of Alaska in July and August of the fish's first summer in the ocean were recovered in later years in the spring in the Columbia River, indicating that some Columbia River spring chinook salmon migrate rapidly to the north into the Gulf of Alaska during the first three or four months of ocean life (Hartt and Dell, 1986).

Miller et al. (1983) caught juvenile chinook salmon with purse seines in the ocean off southern Washington and northern Oregon during three periods in 1980: late May through early June; July; and late August through early September. They sampled in water where the bottom depth was ≥30 m near the mouth of the Columbia River, a major source of chinook salmon smolts. Marked Columbia River spring chinook salmon (yearling smolts) were caught only during their spring cruise, and only in gillnet sets that opened to the south, suggesting that this stock group migrates rapidly to the north soon after entering the ocean (Miller et al., 1983). Very few fish <130 mm FL were found over water greater than 30 m bottom depth, in contrast to the great numbers of small fish caught in shallow marine waters near the surf zone by Dawley et al.[1]

[1] Dawley, E. M., C. W. Sims, R. D. Ledgerwood, D. R. Miller, and J. G. Williams. 1981. A study to define the migrational characteristics of chinook and coho salmon in the Columbia River estuary and associated marine waters. Coast. Zone and Estuarine Studies Div., Northwest Fish. Sci. Cent., NMFS, Seattle WA 98112.

Hence, they concluded that offshore movement of chinook salmon is size dependent, beginning when the fish are about 130 mm FL (Miller et al., 1983).

Healey (1980, 1991) studied juvenile chinook salmon in Georgia Strait, British Columbia. He found that "stream-type" chinook salmon (those spending a year in streams before entering the ocean) were only abundant in marine sampling from about late April to late May, suggesting that these fish migrated out of the protected waters of Georgia Strait soon after leaving fresh water. Conversely, "ocean-type" fish (those entering salt water as small subyearling fish) were abundant in the protected marine waters of Georgia Strait throughout the summer and early fall.

In this study we describe the abundance, distribution, migration, and growth of juvenile chinook salmon collected by purse seine during the spring and summer of 1981–85 in coastal marine waters from northern Washington to southern Oregon. This study extends the temporal and spatial scope of available information on the early ocean life of juvenile chinook salmon off Oregon and Washington. The following paragraphs include a short review of life histories, spatial and temporal patterns of hatchery releases, and seaward migrations of different stocks of chinook salmon smolts in the area from northern Washington to northern California to aid the reader in the interpretation of the distribution and movement of juvenile chinook salmon in the ocean as presented in this paper.

The majority of stocks of chinook salmon found along the coast of North America from northern Washington to northern California return to rivers to spawn in the fall (i.e. are fall-run fish), and their offspring migrate to the ocean as subyearling smolts (ocean-type) in the summer or fall of the same year during which they emerge from the gravel (Nicholas and Hankin, 1988; Healey, 1991). Although stocks that enter the ocean as yearling smolts (stream-type) are also found in this region, mainly in large river systems (e.g. the Columbia River), they are not as abundant as the ocean-type stocks (Healey, 1983, 1991; Nicholas and Hankin, 1988; Table 1, this paper). Most stream-type fish begin their upstream spawning migration in the spring (i.e. are spring-run fish), and the downstream migration of their offspring to the ocean as smolts begins earlier than that of the ocean-type fish (Healey, 1982; Dawley et al., 1985, a and b).

Total releases of yearling and subyearling fall and spring chinook salmon from coastal Washington, Columbia River, and coastal Oregon hatcheries averaged 138 million fish per year in the two-year period 1982–83 (Table 1[2]). Of these releases, about 75% were subyearling fall chinook salmon, 14% were subyearling spring chinook salmon, and 11% were yearling spring chinook salmon (Table 1). (A much smaller number of summer, winter, and late fall chinook salmon, not included in Table 1, were also released in these two years).

Fish from the Columbia River accounted for over 89% of all hatchery releases of chinook salmon in this area; Columbia River subyearling fall, subyearling spring, and yearling spring chinook salmon represented 66%, 12%, and 11% of the total, respectively. Subyearling fall chinook salmon from coastal Washington and coastal Oregon hatcheries represented 6% and 2% of the total release, respectively. Subyearling spring chinook salmon from coastal Oregon hatcheries represented 2% of the total release.

Most subyearling fall chinook salmon from the Columbia River and coastal Washington hatcheries were released from April through June at a small size (about 4 or 5 g body wt; Table 1). A smaller proportion of subyearling fall chinook salmon from these two areas was also released later in the year at a much larger size (Table 1). In contrast, most subyearling fall and subyearling spring chinook salmon from coastal Oregon hatcheries were released in late summer or fall at a large size (averaging roughly 30–60 g; Table 1). Releases of yearling Columbia River spring chinook salmon were concentrated in the April–June period, whereas releases of subyearling Columbia River spring chinook salmon were spread throughout the year.

Some of the fish released from hatcheries were marked with coded-wire tags (CWT) from which the release history of the fish could be obtained. In the two years examined, an average of 2.9% of the subyearling, and 6.5 % of the yearling fish released from January through June in the Columbia River drainage were marked with CWT's.

Releases of chinook salmon smolts from California hatcheries averaged about 30 million fish per year in 1982 and 1983, most of which were fall chinook salmon.[3] Of the California releases about 25 million were small subyearling fish in the spring and about 5 million were large subyearling fish in the fall.

Extensive sampling of juvenile salmon in the lower Columbia River (rkm 75) between 1977 and 1983 determined that yearling chinook salmon smolts entered the Columbia River estuary (at rkm 75) mainly from April through June and that peak migration

[2] This table was compiled from data received in 1994 from the salmonid release data files of the Regional Mark Information System of the Pacific States Marine Fisheries Commission, 45 SE 82nd Drive, Suite 100, Gladstone, OR 97027-2522.

[3] Calculated from data supplied in 1994 by Frank Fisher, Calif. Dep. Fish. and Game (CDFG), 2440 North Main St., Red Bluff, CA; Gary Ramsden, CDFG, Trinity River Hatchery, Lewiston, CA; and Kim Rushton, Iron Gate Hatchery, 8638 Lakeview Rd. Hornbrook, CA.

Table 1

Total number, percent coded-wire tagged fish, and average fish size for hatchery releases of different age and run groups of chinook salmon, *Oncorhynchus tshawytscha,* for the Columbia River drainage, coastal Oregon, and coastal Washington areas by quarter (average of releases in 1982 and 1983).

Total	Jan–Mar	Apr–Jun	Jul–Sept	Oct–Dec
Columbia River				
Fall run (subyearlings)	3,595,917	77,520,135	8,366,243	1,567,369
91,049,664	2.1%	3.2%	7.1%	23.5%
	1.9 g	5.9 g	5.8 g	24.5 g
Fall run (yearlings)	694,978	622,582		
1,317,560	17.1%	8.0%	0	0
	63.0 g	53.9 g		
Spring run (subyearlings)	2,476,963	6,248,487	3,606,772	3,478,973
15,811,195	0%	1.3%	1.5%	8.2%
	1.0 g	3.4 g	12.1 g	57.6 g
Spring run (yearlings)	2,988,851	11,820,322		76,310
14,885,483	14.9%	3.7%	0	0%
	40.8 g	26.2 g		6.6 g
Coastal Oregon				
Fall run (subyearlings)	180,984	40,032	1,312,591	1,478,026
3,011,633	0%	0%	14.8%	23.7%
	0.6 g	2.5 g	34.0 g	48.1 g
Spring run (subyearlings)	177,518	25,134	1,055,342	1,500,590
2,758,584	14.5%	0%	13.9%	22.5%
	2.9 g	2.1 g	40.3 g	58.7 g
Spring run (yearlings)	118,731			
118,731	41.7%	0	0	0
	89.4 g			
Coastal Washington				
Fall run (subyearlings)		7,659,325	869,200	
8,528,525	0	3.0%	22.7%	0
		5.3 g	11.7 g	
Fall run (yearlings)		27,625		
27,625	0	49.9%	0	0
		64.9 g		
Spring run (subyearlings)			43,987	
43,987	0	0	0%	0
			10.1 g	
Spring run (yearlings)		120,575		
120,575	0	15.6%	0	0
		71.2 g		

was in May (Dawley et al., 1985a, Dawley et al.[4]). Downstream migration of subyearling chinook salmon smolts into the Columbia River estuary took place somewhat later, mainly from May through July, with a peak in late June or early July (Dawley et al.[4]). The average length of subyearling chinook

[4] Dawley, E. M., R. D. Ledgerwood, T. H. Blahm, C. W. Sims, J. T. Durkin, R. A. Kirn, A. E. Rankis, G. E. Monan, and F. J. Ossiander. 1986. Migrational characteristics, biological observations,

[4] (continued) and relative survival of juvenile salmonids entering the Columbia River estuary 1966–1983. Final Res. Rep., Bonneville Power Admin., Div. Fish Wildl., Portland, OR 97208.

salmon at the time they entered the Columbia River estuary was usually under 100 mm FL, whereas that of yearling chinook salmon was about 130–150 mm FL (Dawley et al., 1985a). Between January and July 1981–83 about eight times as many subyearling fish as yearling fish were caught at rkm 75 (purse and beach seines combined, Dawley et al., 1985a). During the same period an average of 2.3% of subyearling fish and 2.5% of yearling fish caught at rkm 75 were CWT'd (calculated from data in Dawley et al., 1985, a and b). Large numbers of subyearling chinook salmon, the mean lengths of which ranged from 91 mm in May to 135 mm in September, were caught in shallow (<4 m water depth) marine waters outside of the river mouth in some years (Dawley et al.[1]).

Most naturally reared chinook salmon from coastal Oregon river systems also enter the ocean as subyearling smolts (Nicholas and Hankin, 1988). Peak abundance of subyearling chinook salmon in Oregon estuaries generally occurs from late June through August (Reimers, 1973; Nicholas and Hankin, 1988). Although peak abundance in estuaries is earlier, juvenile chinook salmon are often caught in estuaries in the late fall (Myers and Horton, 1982; Nicholas and Hankin, 1988). By September, subyearling chinook salmon smolts caught in beach seines in the lower estuaries were generally from 100 to 130 mm mean FL (Nicholas and Hankin, 1988).

Ocean migrations of stocks originating in northern California and in Oregon south of Cape Blanco are limited in extent, and few maturing fish of these stocks are caught outside of the California and Oregon ocean or freshwater fisheries (Nicholas and Hankin, 1988; Garrison[5]). However, some northern coastal Oregon and Columbia River stocks (both spring and fall runs) undertake very extensive migrations and are caught in large numbers in the ocean fisheries of Alaska and northern British Columbia (Nicholas and Hankin, 1988; Garrison[5]; Hansen and Johnson[6]; Howell et al.[7]; Vreeland[8]).

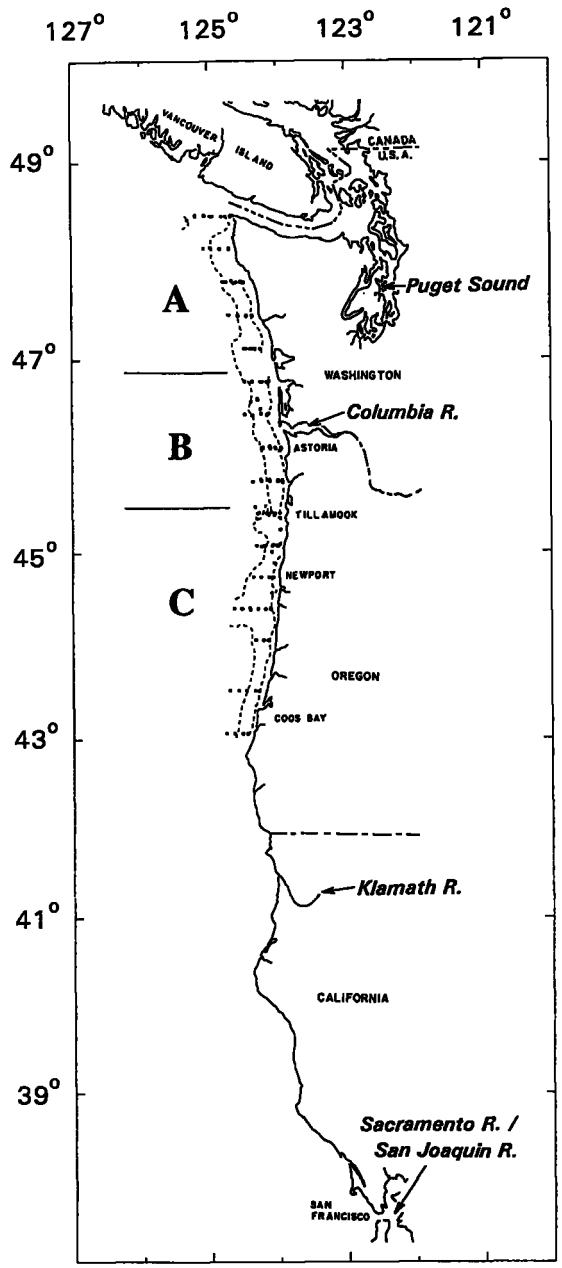

Figure 1

Sampling areas (**A**, **B**, **C**) where juvenile chinook salmon, *Oncorhynchus tshawytscha*, were collected in purse seines, 1981–85. Sampling sites occupied in 1983 are shown (dots) along with the 40 and 120 m depth contours (dashed lines). Basins which are major sources of chinook salmon in this region are indicated by arrows. Latitudinal extent of sampling varied in the different months and years (see Fig. 5).

Methods

Chinook salmon were collected with a fine-mesh purse seine between May and September, 1981–85, along a series of east-west transects off Oregon and

[5] Garrison, R. L. 1986. Stock assessment of anadromous salmonids. Oregon Dep. Fish Wildl., Annual Prog. Rep., Portland, OR 97207, 47 p.

[6] Hansen, H. L., and R. L. Johnson. 1987. An evaluation of fishery contribution from fall chinook salmon reared in Oregon hatcheries on the Columbia River, coded-wire-tag recovery program. Oregon Dep. Fish Wildl., Annual Prog. Rep., Portland, OR 97207, 47 p.

[7] Howell, P., K. Jones, D. Scarnecchia, L. LaVoy, W. Kendra, and D. Ortmann. 1985. Stock assessment of Columbia River anadromous salmonids. Vol. 1: chinook, coho, chum and sockeye salmon stock summaries. Final Rep., U.S. DOE, Bonneville Power Admin., Div. Fish Wildl., Portland, OR 97208.

[8] Vreeland, R. R. 1986. Evaluation of the contribution of chinook salmon reared at Columbia River hatcheries to the Pacific salmon fisheries. Annual Rep., U.S. DOE, Bonneville Power Admin., Div. Fish Wildl., Portland, OR 97208.

Washington (Fig. 1; Pearcy and Fisher, 1988, 1990). The sampling area was divided latitudinally into three sections (A, B, and C in Fig. 1). Additional sampling in July 1984 occurred off northern California as far south as 40°32'N and off the west coast of Vancouver Island as far north as 50°26'N, and in May 1985 in a concentrated area off the mouth of the Columbia River. The months sampled in each year are shown in Table 2. The latitudinal range of sampling varied among years and months (Pearcy and Fisher, 1988; see also Fig. 5, this paper). Transects were generally 37 km apart and collecting stations along each transect were 9.3 km apart starting at about the 37 m depth contour and continuing out to 37 or 46 km offshore. Occasionally stations farther offshore were sampled.

For this study we considered all chinook salmon less than 401 mm fork length (FL) to be juvenile fish. This was based on the sizes of known age coded-wire tagged (CWT) fish in our catches. This length range included those fish that entered the ocean as yearlings or subyearlings in the same year in which they were caught in the ocean (age 1.0 or age 0.0, respectively[9]) and those that entered the ocean as subyearlings in the year prior to capture in the ocean (age 0.1[9]).

[9] The number before the period indicates winters spent in freshwater after hatching and before migration to the sea, and the number following the period indicates winters spent at sea (Koo, 1962).

Fork length (FL) of most fish was measured at sea to the nearest mm. CWT fish were measured at sea, then frozen, and later weighed in the laboratory. Tags were decoded by personnel at the Oregon Department of Fish and Wildlife laboratory in Clackamas, Oregon.

Growth rates of CWT chinook salmon between release from hatcheries and capture in the ocean were estimated by $(FL_1 - FL_0)/d$; where FL_0 = mean length of fish in the tag group at release, FL_1 = length of the individual fish when caught in the ocean, and d = the number of days between release and capture ($d \geq 10$). Often only mean weight at release was readily available for a tag group. For these groups we converted mean weight at release to mean FL by using the geometric mean functional relationship (Ricker, 1973) between average weight (g) and average FL (mm) for CWT groups released in California and the Columbia River for which both mean weight and mean length at release were measured: $\ln(FL) = 0.3122(\ln(wt))+3.8233$, n=311, r^2=0.94. Average instantaneous rates of growth in weight (% body wt/d) between release and ocean capture were estimated by $(\ln(Wt_1)-\ln(Wt_0))/d$; where Wt_1 = weight at capture in the ocean, Wt_0 = average weight at release, and d = the number of days (≥10) between release from the hatchery and capture in the ocean (Ricker, 1975).

Growth rates of chinook salmon in the Columbia River estuary and in the ocean prior to capture in

Table 2

Catch (n), mean catch per set (CPUE, in parentheses), and percentage of coded-wire tagged fish in the catch of juvenile chinook salmon, *Oncorhynchus tshawytscha*, for different months and years.

	May		June		July		Aug		Sept	
Year	n (CPUE)	% CWT	n (CPUE)	% CWT	n (CPUE)	% CWT	n (CPUE)	% CWT	n (CPUE)	% CWT
1981	68 (1.08)	5.9%	37 (0.55)	2.7%	73 (1.09)	4.1%	51 (0.77)	2.0%	— —	—
1982	217 (3.50)	7.8%	228 (4.07)	7.0%	— —	—	— —	—	15 (0.39)	6.7%
1983	128 (2.32)	5.5%	52 (0.90)	3.8%	— —	—	— —	—	213 (4.18)	0.0%
1984	— —	—	104 (1.58)	12.5%	72 (1.20)	2.8%	— —	—	59 (0.93)	10.2%
1985	533* (19.04)	15.6%	282 (3.52)	10.3%	— —	—	— —	—	— —	—

[1] Late May and early June sampling off the mouth of the Columbia River.

1981, 1982, and 1983 for individuals from groups of CWT fish sampled 75 km upstream from the ocean (rkm 75) during their downstream migration were estimated by $(FL_1 - FL_0)/d$; where FL_0 = mean FL of the tag group when sampled in the river (from Dawley et al., 1985b), FL_1 = length of the individual fish when caught at sea, and d = days (≥10) between the date when half the fish in the tag group had passed rkm 75 and the date of capture in the ocean. (See Dawley et al., 1985, a and b; Dawley et al.[4] for detailed information on in-river sampling.)

Net migration speed of individual CWT smolts in the lower Columbia River estuary, downstream of rkm 75, and in the ocean prior to capture was estimated by dividing the distance between rkm 75 and the point of capture in the ocean (straight line segments) by the number of days (≥10) between the date when half the fish in the CWT group had passed rkm 75 during downstream migration (Dawley et al., 1985b), and the date when the individual CWT fish was caught in the ocean.

In September 1983 we caught a large number of juvenile chinook salmon, none of which were CWT'd. We examined scales from 128 of these fish in order to estimate their size at time of ocean entry and the length of time they had been in the ocean. Scale radii were measured from the focus to what we interpreted to be the ocean entrance mark (the last abrupt change in circulus spacing, often accompanied by a few narrowly spaced circuli). Fork length of fish at ocean entry was backcalculated by using a geometric mean regression (Ricker, 1973) of FL and scale radius for juvenile chinook salmon (length range approximately 100–350 mm FL) caught by us in the ocean (1981–84) and in four Oregon estuaries by the Oregon Department of Fish and Wildlife ($FL_{(mm)} = 2.3772 \times Scale\ radius_{(mm\ at\ 88\times)} + 0.08, n=202, r^2=0.88$). We roughly estimated the length of time these fish had been in the ocean by dividing their ocean growth (FL at capture minus back-calculated FL at time of ocean entry) by an assumed ocean growth rate of 1.5 $mm \cdot d^{-1}$; a growth rate common for juvenile coho salmon during their first summer in the ocean (Fisher and Pearcy, 1988) and similar to the estimated mean growth rate downstream of rkm 75 of five CWT Columbia River chinook salmon in the same year (this study).

Results

Catch per unit of effort

A total of 2,132 juvenile chinook salmon were caught in 880 purse-seine sets during our ocean sampling 1981–85. A consistent seasonal trend among years in mean CPUE (all sampling areas combined) of juvenile chinook salmon was lacking (Table 2). In 1982, CPUE was considerably higher in May and June than in September, but in 1983, CPUE in September was higher than it was earlier in May and June. In 1981 and 1984 little change occurred in CPUE between early and late summer. By far the largest CPUE was during latitudinally restricted sampling off the Columbia River mouth in May 1985 (Table 2).

Origin and age of CWT fish

CWT fish represented 8.7% (185) of juvenile chinook salmon caught in purse seines 1981–85. The percentage of CWT fish during the different cruises ranged from 0.0% in September 1983 to 15.6% in late May 1985 off the mouth of the Columbia River (Table 2).

Most CWT fish caught in the ocean originated in the Columbia River basin (Table 3). CWT Columbia River fish represented 92% (170) of all CWT fish caught in the ocean 1981–85. CWT fish from coastal Oregon hatcheries and from coastal Washington hatcheries represented 6.4% (12) and 1.1% (2) of the total catch of CWT fish, respectively. No CWT fish that originated in British Columbia or Puget Sound, Washington, and only one CWT fish that originated in a California hatchery (Klamath R. system) was caught.

Most of the CWT fish that we caught in the ocean were released from hatcheries as yearling fish the same year we recovered them in the ocean (age 1.0, Table 3). In addition, two CWT fish caught in the ocean were released from hatcheries as subyearling fish, but overwintered in freshwater before entering the ocean (based on their size and scale characteristics at time of capture). Age-1.0 fish represented 90.8% (168) of the catch of CWT fish 1981–85. Subyearling fish released from hatcheries in the spring or summer, a few months or less prior to capture in the ocean (age 0.0 at ocean capture), accounted for only 3.7% (7) of the catch of CWT fish between 1981 and 1985. Fish that overwintered in the ocean after being released as subyearlings in the summer, fall, or winter of the year prior to capture in the ocean (age 0.1 at ocean capture) accounted for only 5.4% (10) of the catch of CWT fish 1981–85 (Table 3).

Yearling (age-1.0) chinook salmon smolts from the Columbia River basin were the predominant group of CWT fish in the May and June samples in most years. Most of these were spring run fish, but fall run yearling fish were also abundant in May and June 1985, and fall, summer, and mixed stock yearlings were also present in some years (Table 3).

Age-1.0 CWT fish from the Columbia River basin (all runs combined) accounted for 4.4%, 5.1%, 5.5%, and 15.5% of the total ocean catch in May 1981, 1982,

Table 3

Number of coded-wire tagged (CWT) fish of different stock groups and ages and their percentage of the total catch (in parentheses) of chinook salmon, *Oncorhynchus tshawytscha*, caught during ocean sampling in different months and years, 1981–85. Absence of sampling is indicated by —. No CWT fish were caught in September 1983.

				Month				
Year	Release area	Age	Run	May	June	July	August	Sept
1981	Columbia River	1.0	spring	3 (4.4%)		2 (2.7%)		
1981	Columbia River	0.0	mixed				1 (2.0%)	
1981	Columbia River	0.0	fall			1 (1.4%)		—
1981	Coast of Oregon	1.0	spring		1 (2.7%)			
1981	Klamath River	0.1	fall	1 (1.5%)				
1982	Columbia River	1.0	spring	11 (5.1%)	9 (3.9%)			1 (6.7%)
1982	Columbia River	1.0	fall		2 (0.9%)			
1982	Columbia River	1.0	summer	1 (0.5%)	2 (0.9%)			
1982	Columbia River	0.1	fall	2 (0.9%)		—	—	
1982	Columbia River	0.1	mixed		1 (0.4%)			
1982	Coast of Oregon	1.0	spring	1 (0.5%)				
1982	Coast of Oregon	0.1	fall	2 (0.9%)	1 (0.4%)			
1982	Coast of Washington	1.0	spring	1 (0.5%)				
1983	Columbia River	1.0	spring	5 (3.9%)				
1983	Columbia River	1.0	fall	1 (0.8%)				
1983	Columbia River	1.0	summer	1 (0.8%)		—	—	
1983	Columbia River	0.0	spring		1 (1.9%)			
1983	Coast of Washington	1.0	fall		1 (1.9%)			
1984	Columbia River	1.0	spring		9 (8.7%)			
1984	Columbia River	1.0	fall		2 (1.9%)	1 (1.4%)		
1984	Columbia River	1.0	summer	—	2 (1.9%)		—	2 (3.4%)
1984	Columbia River	0.0	spring			1 (1.4%)		
1984	Coast of Oregon	0.1	fall					1 (1.7%)
1984	Coast of Oregon	0.0	spring					3 (5.1%)
1985	Columbia River	1.0	spring	50 (9.4%)	5 (1.8%)			
1985	Columbia River	1.0	fall	23 (4.3%)	17 (6.0%)			
1985	Columbia River	1.0	summer	6 (1.1%)				
1985	Columbia River	1.0	mixed	4 (0.8%)	3 (1.1%)	—	—	—
1985	Columbia River	0.1	fall		2 (0.7%)			
1985	Coast of Oregon	1.0	spring		2 (0.7%)			

1983, and 1985, respectively, and 5.7%, 12.5%, and 7.8% of the total ocean catch in June 1982, 1984, and 1985, respectively (Table 3). These percentages of CWT fish were much higher than those of downstream migrant yearling chinook salmon entering the Columbia River estuary, which averaged 2.3% CWT fish during the period January–June, 1981–83 (calculated from Dawley et al., 1985, a and b), and were comparable to the CWT percentages of hatchery yearling Columbia River spring and fall chinook salmon released during the period April–June 1982–83 (3.7 and 8.0%, respectively, Table 1). The high proportion of CWT yearling (age 1.0) chinook salmon from the Columbia River basin in the May and June ocean catches indicates that most unmarked fish caught in the ocean during these months probably were also yearling hatchery fish from the Columbia River basin.

Five stocks from the Columbia River basin dominated our catch of age-1.0 smolts: Snake River summer, Upriver Bright (URB) and Snake River fall chinook salmon, and Cowlitz River and Willamette River spring chinook salmon (Table 4). These stocks are caught in ocean fisheries as maturing fish mainly to the north of Oregon (Howell et al.[7]).

Catch per unit of effort of CWT Fish

Some distinct seasonal trends were apparent in the abundance of the different age classes of CWT fish. Age-1.0 fish were most abundant in catches in May

Table 4

Coded-wire tagged chinook salmon, *Oncorhynchus tshawytscha*, stocks caught during ocean purse-seine sampling, 1981–85.

Stock group	Recovery age	Number recovered	Mean FL (mm)
Columbia River Fall Chinook Salmon			
Lower river hatchery	0.0	1	91
	1.0	1	147
Upriver Bright	1.0	20	202
	0.1	4	292
Snake River	1.0	26	208
Columbia River Summer Chinook			
Salmon River (Snake R.)	1.0	13	163
Upper Columbia River	1.0	1	189
Columbia River Spring Chinook			
Cowlitz River	1.0	29	214
Carson NFH	1.0	16	169
Deschutes River	1.0	6	242
	0.0	1	124
Willamette River	1.0	34	190
Upper Columbia River	1.0	7	161
	0.0	1	138
Rapid River (Snake R.)	1.0	2	152
Mid-Columbia River Mixed	0.0	1	137
	0.1	1	355
	1.0	7	158
Coastal Oregon Fall Chinook			
Domsea Inc. (Siuslaw R.)	0.1	2	290
Elk River	0.1	1	316
Rogue River	0.1	1	389
Coastal Oregon Spring Chinook			
Anadromous Inc.	0.0	3	214
Umpqua River	1.0	4	279
Coastal Washington			
Fall Chinook	1.0	1	238
Spring Chinook	1.0	1	203
Klamath River			
Fall Chinook	0.1	1	290

and June, when they dominated the catch of CWT fish. They were much less abundant in July, August, and September. (Table 5). The few age-0.1 fish were also more common in the May–June period than in the July–September period. Conversely, recoveries of CWT subyearling (age 0.0) fish were mainly in the July–September period (Table 5).

Size-frequency distributions

Mean FL of age-1.0 CWT fish was 183 mm, 215 mm, 214 mm, and 281 mm in May, June, July, and September, respectively, for all years combined (Table 5). Age-0.1 fish were generally larger than the age-1.0 fish, averaging 294 mm, 310 mm, and 389 mm FL in May, June, and September, respectively (Table 5). Except for three fish caught in September, age-0.0 fish were considerably smaller than the other two age classes, averaging 124 mm, 115 mm, and 137 mm FL in June, July, and August, respectively (Table 5).

Length-frequency distributions (on a catch/set basis) of juvenile chinook salmon are shown for the three standard sampling areas (A, B, and C) for all years combined (Fig. 2, top), for sampling in July 1984 off northern California (CA) and Vancouver Island (BC) and for sampling off the mouth of the Co-

Table 5

Number, catch per unit of effort (CPUE) and fork length (FL) of coded-wire tagged age-1.0, age-0.0 and age-0.1 chinook salmon, *Oncorhynchus tshawytscha*, by cruise for all years combined, 1981–85.

			Age 1.0				Age 0.0				Age 0.1			
Cruise	Years	Sets	*n*	CPUE	Mean FL	FL Range	*n*	CPUE	Mean FL	FL Range	*n*	CPUE	Mean FL	FL Range
May	81–83	180	23	0.13	200	139–302	0	0.00	—	—	5	0.03	294	270–316
May	85[1]	28	83	2.96	178	118–261	0	0.00	—	—	0	0.00	—	—
June	81–85	327	56	0.17	215	140–295	1	<0.01	124	—	4	0.01	310	220–355
July	81, 84	107	3	0.03	214	206–223	2	0.02	115	91–138	0	0.00	—	—
Aug.	81	66	0	0.00	—	—	1	0.01	137	—	0	0.00	—	—
Sep.	82–84	152	3	0.02	281	236–340	3	0.02	214	211–217	1	0.01	389	—

[1] Sampling restricted to an area immediately off the Columbia River.

lumbia River (CO) in May 1985 (Fig. 2, bottom). For each month and area the effort (number of purse-seine sets) and total CPUE are also shown. The length-frequency distributions of CWT age-1.0 Columbia River fish are shown in black, and lengths of other CWT fish are indicated by letters (Fig. 2).

In the May and June samples, most CWT age-1.0 fish from the Columbia River were between 130 mm FL and 250 mm FL. As discussed earlier, from the percentages of CWT fish in the catches, most unmarked fish in this size range were probably also age-1.0 hatchery fish from the Columbia River. On the basis of CWT's and scale characteristics, we concluded that larger fish (about 220–400 mm FL) in May and June were a mixture of age-1.0 and age-0.1 fish. CPUE of fish in May was greatest in Area B, which straddles the mouth of the Columbia River, and was about half as great in areas to the south (C) and to the north (A). Relative to May, CPUE in June decreased in Area C, remained about the same in Area B, and increased in Area A. CPUE in June was much higher in the two northern areas than in Area C.

Age-1.0 Columbia River fish were much rarer in all areas in the July–September period than in the May–June period, based both on the catches of CWT fish and the length-frequency distributions of unmarked fish. Generally, CPUE of fish between 150 mm FL and 330 mm FL was low in July and August in all areas. In September only a few age-1.0 and age-0.1 fish were caught in Area A. Only one CWT age-1.0 fish (340 mm FL) was caught in Area C in September.

The most abundant fish in July and August were less than 150 mm FL (Fig. 2). Catches of these small fish were highest off northern California (CA), the Columbia River (B), and the Washington coast (A). The few CWT fish caught in July and August in this size range were age-0.0 fish from the Columbia River (Fig. 2). The catches in the ocean in July and August of these small fish coincided with the time of peak abundance of subyearling chinook salmon in Oregon estuaries (Nicholas and Hankin, 1988) and with the later half of the peak migration of subyearling chinook salmon in the Columbia River estuary (Dawley et al.[4]) and was well after the time when most yearling chinook salmon enter the ocean (in May, Dawley et al.[4]). Therefore, it is most likely that the unmarked fish <150 mm FL caught in the ocean in July and August were age-0.0 fish.

Catches of chinook salmon in September in Areas B and C occurred mainly in 1983 and 1984. In September 1984, 32 moderately large (range 160–260 mm FL) fish were caught off Oregon (Area C). These were mainly age-0.0 fish released in August from the Anadromous Inc. release facility on Coos Bay (this conclusion was based on associated CWT fish and their percentage of the catch).

During September 1983 we caught 207 unmarked juvenile chinook salmon in areas B and C off Oregon. Fish caught in area B were smaller (mean FL=185, n=35) than those caught to the south in area C (mean FL=227 mm, n=172; Fig. 2). Estimated mean FL at time of ocean entry backcalculated from scales was 138 mm and 173 mm for fish caught in areas B and C, respectively. Growth while in the ocean averaged 48.5 mm for fish caught in area B and 52.2 mm for fish caught to the south in area C. Dividing by a growth rate of 1.5 mm/d, we estimated time since ocean entry to be just over one month for both these groups.

The estimated date of ocean entry of these fish (sometime in mid or late August) indicates that these were subyearling rather than yearling chinook salmon, since both naturally and hatchery produced yearling fish generally enter the ocean in the spring or early summer (see the introduction to this study).

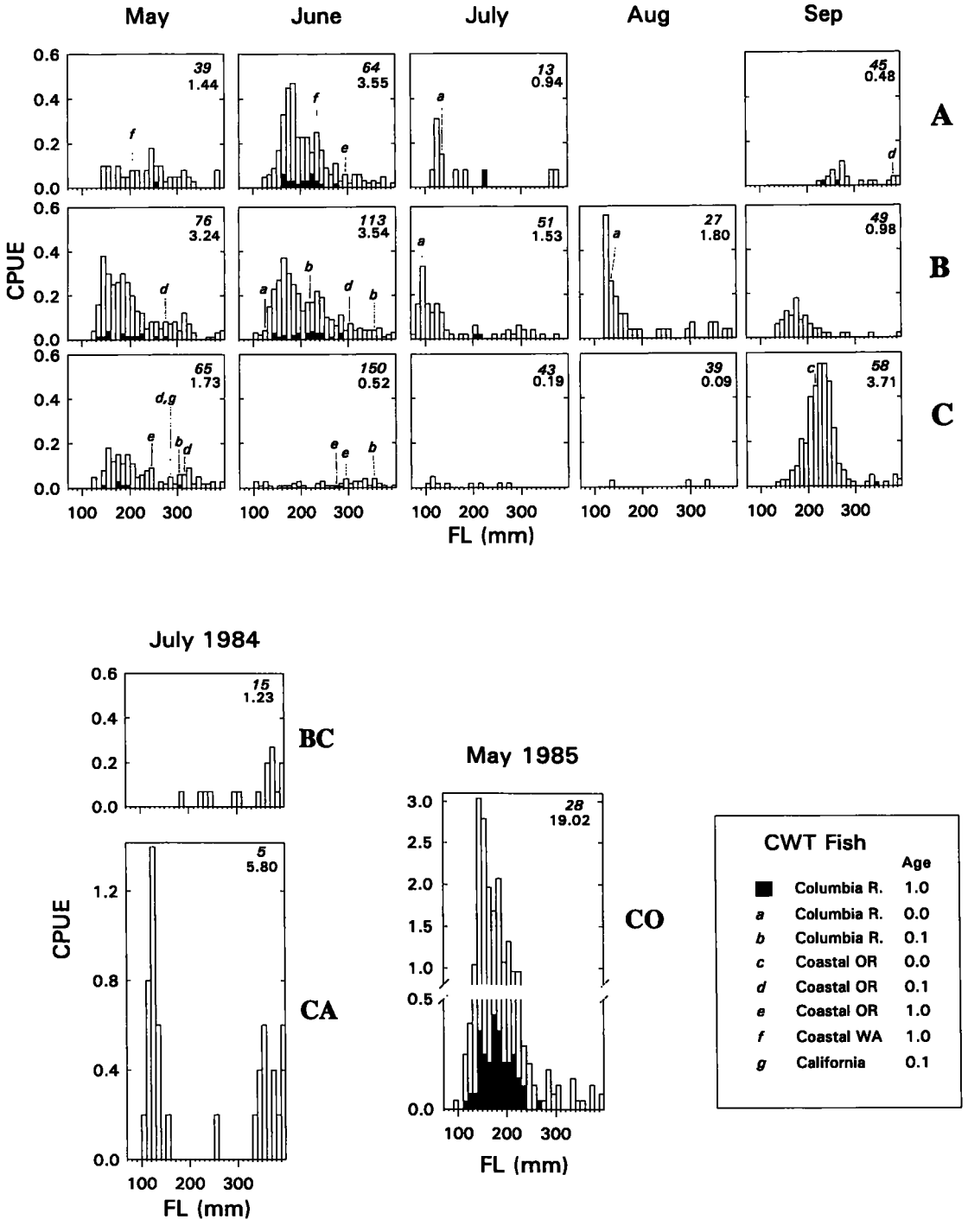

Figure 2

Length-frequency distributions of juvenile chinook salmon, *Oncorhynchus tshawytscha*, by month and area (**A**, **B**, and **C** in Fig. 1) for all years combined, for July 1984 off northern California (CA) and the west coast of Vancouver Island (BC) and for May 1985 off the mouth of the Columbia River (CO). Total effort (number of sets, in italics) and total catch per unit of effort (CPUE) are indicated for each month and area. The size-frequency distributions of coded-wire tagged (CWT) age-1.0 Columbia River fish are indicated in black, lengths of other CWT fish are indicated by letters.

However, the mean size at ocean entry backcalculated from scales (173 mm FL) of the fish caught in Area C was much larger than the mean sizes of naturally produced fall chinook salmon reported by Nicholas and Hankin (1988) in Oregon estuaries in the late summer (100–140 mm FL by mid-September, depending on the river system).

Since the estimated average size at time of ocean entry of the fish caught in Area C in September (173 mm FL) was much larger than the average size at which age-0.0 wild smolts enter the ocean (Nicholas and Hankin, 1988; Dawley et al.[1]; Dawley et al.[4]), it is probable that these fish were released from a hatchery. The only releases in the study area (excluding California) of large smolts in groups not represented by CWT's during the July–August period were from the Oregon Aqua Foods (OAF) saltwater rearing and release facility on Yaquina Bay, Oregon, which is located within 5 km of the ocean. Almost 800,000 unmarked subyearling fall chinook and 55,000 unmarked subyearling spring chinook salmon were released from this facility between 28 August and 5 September 1983[10], about three weeks before our sampling in the ocean (22–24 September). The mean weight at time of release for these groups ranged from 47 to 57 g for the fall chinook salmon and was 100 g for the spring chinook salmon. From a regression of FL and body weight (this study) we estimated that the mean lengths of these OAF-released fall chinook salmon at time of release ranged from 152 to 162 mm, close to the mean size at ocean entrance (backcalculated from scales) of the fish we caught in Area C in September 1983 (173 mm). If these OAF-released fish were the source of the unmarked fish caught in the ocean in September 1983, then they were in the ocean about three weeks before capture. If fish size at ocean entrance that we backcalculated from scales was accurate, then their growth rate since entering the ocean was slightly over 2 $mm \cdot d^{-1}$, considerably higher than the mean growth rate (1.05 $mm \cdot d^{-1}$) estimated for age-1.0 Columbia River fish downstream of rkm 75 (see below), and about one and a third times that estimated for juvenile coho salmon, *Oncorhynchus kisutch*, caught in the ocean in late summer (Fisher and Pearcy, 1988).

Inshore-offshore distributions

The inshore-offshore distributions of very small fish (≤130 mm FL), which were mainly age-0.0 fish, and of larger fish (>130 mm FL) were similar; the median offshore distance of the catch of each size category was about 13 km (Fig. 3A). However, small fish were strongly associated with warm, brackish waters (mainly the Columbia River plume), whereas larger fish were not (Fig. 3, B and C). Fully 38% of the small fish, but only 2% of the large fish, were caught in waters ≤17‰ (Fig. 3B). Over 40% of small fish, but only 4% of large fish were caught where sea-surface temperature was ≥15°C (Fig. 3C). These data indicate that, at least over the depths sampled (mainly >37m), the smallest chinook salmon juveniles were much more likely to be found in the warm, low salinity waters of the Columbia River plume than in the colder, more saline adjacent waters.

Our largest catches of juvenile chinook salmon in late summer were taken in September 1983. On the basis of their scale characteristics we concluded that these were hatchery subyearling chinook salmon that had been in the ocean about a month (see section on Size-Frequency Distributions). Almost all of these fish were captured within 4 km of the shoreline, in depths of <40 m (Fig. 4). This is a much more restricted inshore-offshore distribution than was found in general for the juvenile chinook salmon (mainly age-1.0 fish) caught during all months and years of our sampling combined (Fig. 3A). Since daily upwelling indices during September 1983 at both 42°N and 45°N were almost all positive (Mason and Bakun, 1986), the restricted inshore distribution of juvenile chinook salmon in this month does not appear to have been caused by onshore transport of water. The difference in offshore distribution between this group of large age-0.0 hatchery chinook salmon and the mainly age-1.0 fish caught in early summer may be due to behavioral differences between these groups of fish; the age-0.0 fish appear to prefer shallower, more nearshore areas.

Migration

Several trends are apparent in the migrations of CWT juvenile chinook salmon between ocean entry and capture in purse seines (Fig. 5). In 1983, 1984, and 1985 most fish originating in the Columbia River basin were caught north of where they entered the ocean. In May 1982, however, all Columbia River fish were caught south of the river mouth, but by the following month most were caught to the north. All but one of the ten tagged chinook salmon originating from coastal Oregon hatcheries were caught north of where they entered the ocean.

Thirteen fish were caught more than 190 km north of where they entered the ocean. Seven of these were age-1.0 fish from the Columbia River drainage (three Snake River fall, two Snake River summer, one URB fall, one Deschutes River spring), one was an age-1.0 fish from a coastal Oregon River system (Umpqua

[10] Information obtained from the Pacific States Marine Fishery Commission's salmon release data base.

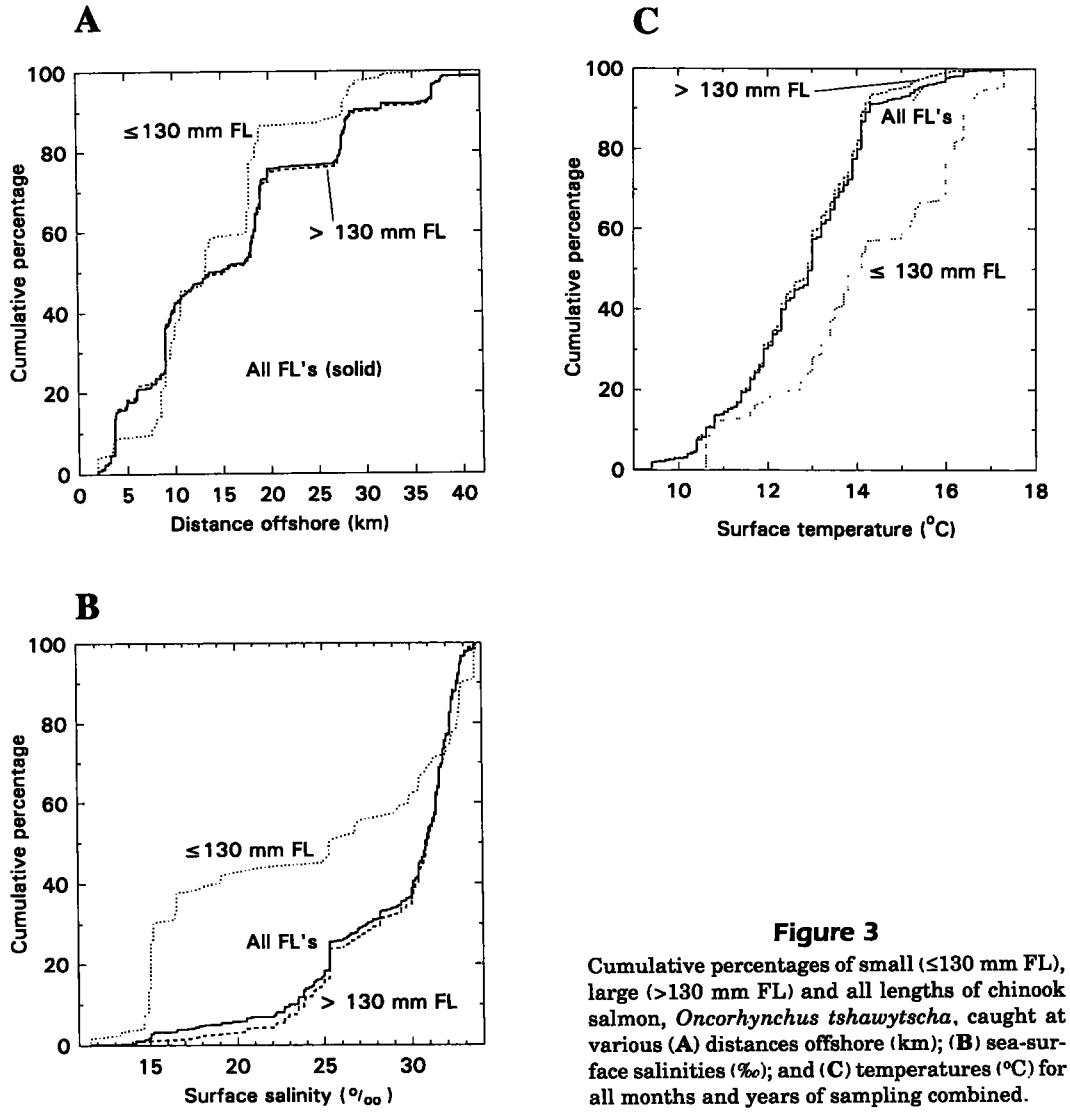

Figure 3

Cumulative percentages of small (≤130 mm FL), large (>130 mm FL) and all lengths of chinook salmon, *Oncorhynchus tshawytscha*, caught at various (**A**) distances offshore (km); (**B**) sea-surface salinities (‰); and (**C**) temperatures (°C) for all months and years of sampling combined.

R. spring chinook salmon), and five were age-0.1 fish from coastal Oregon and California hatcheries (two Siuslaw R. fall, one Elk R. fall, one Rogue R. fall, and one Trinity R. (Klamath R. system) fall chinook salmon). The two farthest northward migrations were made by an age-1.0 spring chinook salmon from the Umpqua River, Oregon, caught 481 km to the north off northern Washington in June 1985, and by an age-0.1 fall chinook salmon from the Trinity River, California, caught 317 km to the north in May 1981.

Speed of migration

Average net migration rate of CWT age-1.0 Columbia River juvenile chinook salmon between rkm 75 and their ocean capture locations was 4.1 km·d^{-1} (range 1.1–14.2 km·d^{-1}, n=31; 1981, 1982, and 1983 data combined). This net migration rate was equivalent to 0.3 body lengths·sec^{-1} (where body length is the average between the mean length of the CWT group at rkm 75 and the length of the individual fish at capture in the ocean).

Growth of juvenile chinook salmon

Estimated mean growth rates of age-1.0 CWT Columbia River juvenile chinook salmon between hatchery release and capture in the ocean and between

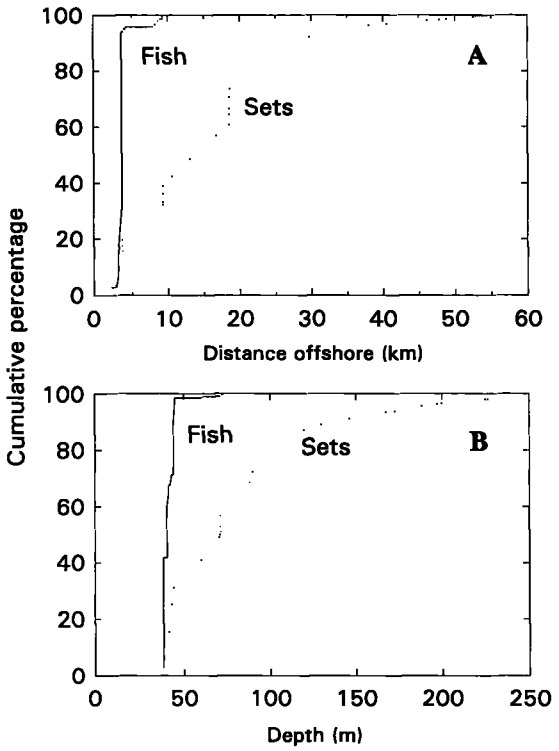

Figure 4

Cumulative percentages of number of sets (effort) and number of chinook salmon, *Oncorhynchus tshawytscha*, caught at various (**A**) distances offshore (km) and (**B**) bottom depths (m), in September 1983.

rkm 75 and capture in the ocean were 0.75 mm·d^{-1} (n=152) and 1.05 mm·d^{-1} (n=31), respectively, for all years combined. The higher estimated growth rates for fish downstream of rkm 75 suggest that growth rates of fish in the Columbia River Estuary and ocean were higher than growth rates in the areas upstream in the Columbia River. Growth rates between rkm 75 and ocean capture were 0.98 (n=5), 0.98 (n=21), and 1.41 mm·d^{-1} (n=5) in 1981, 1982, and 1983, respectively. Average instantaneous rate of growth in weight of age-1.0 CWT Columbia River juvenile chinook salmon between hatchery release and ocean capture was 0.92% body wt·d^{-1} (n=152), for all years combined.

Discussion

Age-1.0 chinook salmon smolts from the Columbia River basin migrate rapidly to the north after entering the ocean in the spring. Evidence for this rapid northward migration is found in the sharp decrease between early and late summer in CPUE of CWT age-1.0 fish in the area off Oregon and Washington (Table 5); in the much higher CPUE of age-1.0 fish in the area north of the Columbia River than south of the Columbia River in June (Fig. 2); in the low CPUE of age-1.0 fish in late summer (Fig. 2); and in the predominantly northward migrations of CWT Columbia River fish (Fig. 5). These results are consistent with those of Miller et al. (1983), who found CWT age-1.0 fish only in their late spring sampling in 1980 off southern Washington and northern Oregon, and who caught CWT age-1.0 fish only in purse-seine sets that were open to the south (sets that catch northward swimming fish). Our results are also consistent with those of Hartt and Dell (1986) who caught juvenile Columbia River spring chinook salmon in the northern Gulf of Alaska in August of their first year in the ocean. Only in May 1982 were many CWT age-1.0 Columbia River fish found to the south of the Columbia River (Fig. 5). This was a period of strong northerly winds and southward flowing surface currents which may have transported the juvenile salmon to the south by advection (Pearcy and Fisher, 1988).

Unlike age-1.0 chinook salmon, age-1.0 coho salmon were fairly abundant in late summer off the Columbia River mouth and off Washington (Pearcy and Fisher, 1988). The Columbia River is the major source for both of these species in the study area, and yearlings of both enter the ocean at about the same time (April through June). The continued presence in late summer of age-1.0 coho salmon off the Columbia River and Washington coast suggests that they are less migratory than yearling Columbia River chinook salmon during their first summer in the ocean. As maturing fish, these two species of salmon generally also have different ocean distributions. A major part of the ocean catch of several stocks of Columbia River spring chinook salmon occurs far to the north in British Columbia and Alaska ocean fisheries (e.g. Willamette R. and Klickitat R. stocks); conversely, Columbia River and coastal Oregon coho salmon stocks are mainly caught in Washington, Oregon, and California ocean fisheries (Garrison[5]; Howell et al.[7]). This divergence in the ocean distributions of these two species is already apparent in the first few months of their ocean life.

On the basis of estimated growth rates of CWT fish, we concluded that both age-1.0 coho and chinook salmon appear to grow at fairly similar rates during the first few months they are in the ocean. Estimated mean growth rates of CWT age-1.0 Columbia River chinook salmon between release and capture in the ocean (0.75 mm·d^{-1}) and between rkm 75 and capture in the ocean (1.05 mm·d^{-1}) were similar to the estimated mean growth rate of juvenile coho salmon

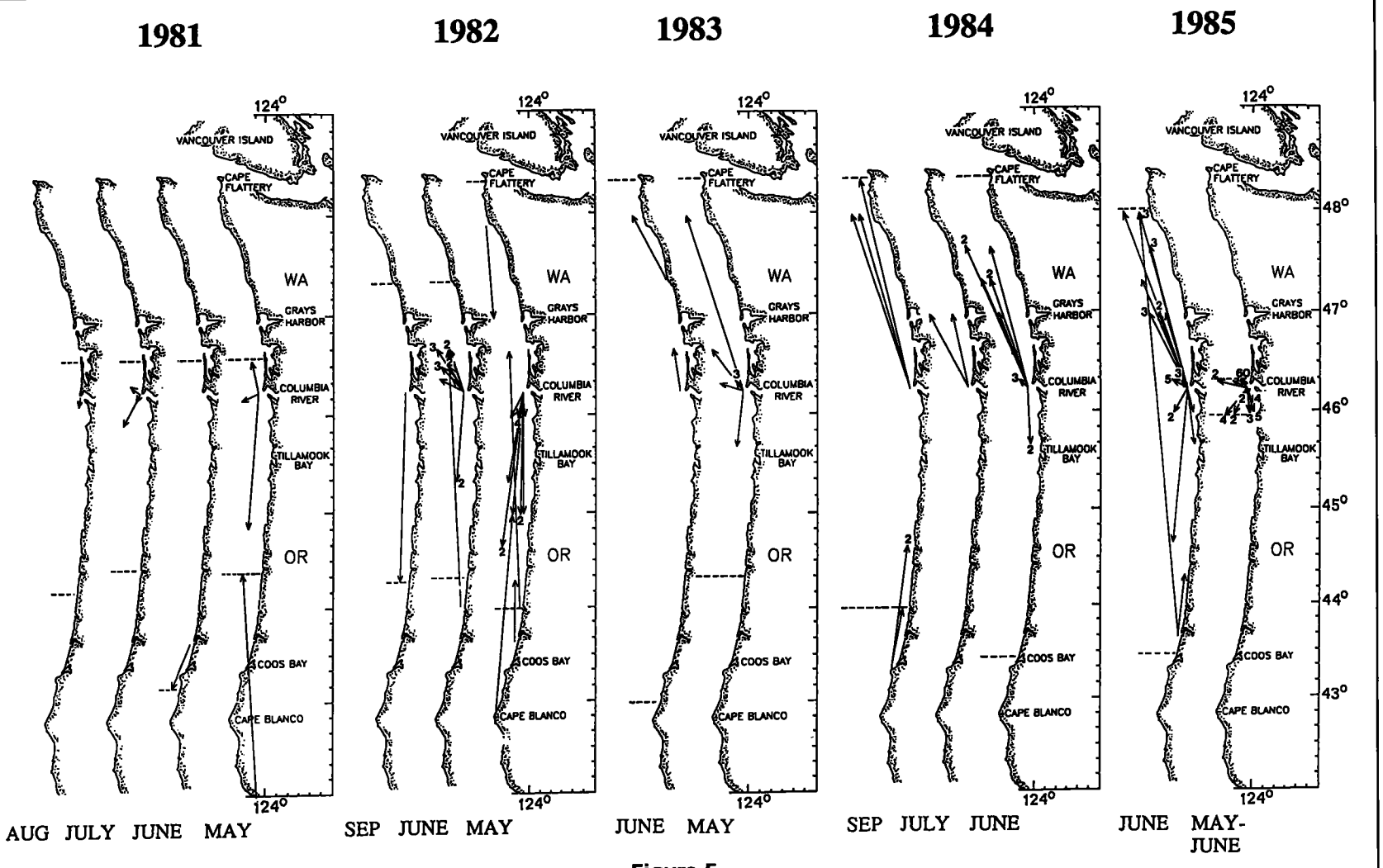

Figure 5

Net migration of coded-wire tagged juvenile chinook salmon, *Oncorhynchus tshawytscha*, from point of ocean entry to capture in purse seines. When more than one fish followed a particular net migration path, the number of fish is indicated at the head of the arrow. Dashed lines indicate the latitudinal extent of purse-seine sampling in each month in each year

caught in the ocean in May and June (0.93 mm·d^{-1}, n=142; Fisher and Pearcy, 1988). Mean growth rates of CWT juvenile coho salmon caught in the ocean in the July–September period were higher (1.43 mm·d^{-1}, n=69) than growth rates in early summer. Unfortunately, we caught too few CWT age-1.0 chinook salmon in late summer to compare their growth rates with those of coho salmon in late summer. Our estimates of growth rates of CWT age-1.0 Columbia River chinook salmon based on mean size of fish in the CWT group at time of release or during downstream migration may be biased by size-related differences in mortality rates or migration rates out of the sampling area.

The ratio of age-1.0 to age-0.1 chinook salmon in our ocean purse-seine samples was disproportionately high compared with the relative numbers of these two age classes entering the ocean. Although subyearling chinook salmon were much more numerous than yearling chinook salmon among downstream migrating smolts in the Columbia River (Dawley et al., 1985a), and many more subyearling than yearling chinook salmon were released from hatcheries (Table 1), yearling fish predominated in our catches in the ocean. The high catches in the ocean in May and June of age-1.0 fish coincided with the period of peak downstream migration and ocean entry of these yearling fish. However, no similarly large catches of the more numerous age-0.0 fish occurred in the June, July, and August ocean samples, following their peak period of downstream migration in the Columbia River. In fact, CPUE of age-0.0 fish during July and August in Areas A and B, was not nearly as great as the CPUE of age-1.0 fish earlier in May and June (Fig. 2).

The relatively low numbers of small age-0.0 chinook salmon caught in water >37 m bottom depth support the hypothesis of Miller et al. (1983) that offshore movement of subyearling chinook salmon is size dependent; few fish move offshore until they reach a size of around 130 mm FL. Many of the small age-0.0 fish caught over deep water in July and August appeared to have been carried offshore in the Columbia River plume, since they were found in waters of high temperature and low salinity (Fig. 3). During June, July, and August large numbers of small age-0.0 chinook salmon may have been present in shallow nearshore waters inshore of our sampling. Subyearling smolts of those stocks caught in ocean fisheries far to the north as maturing fish (e.g. Columbia River Upriver Bright Fall chinook, Howell et al.[7]) may migrate to the north while they are still in shallow waters near the surf zone and thus may not be available to sampling over deeper water. Even large age-0.0 fish may prefer shallow water habitats. In late summer, when many age-0.0 fish should be quite large, this age class was rare in our samples. Our only large catches of age-0.0 fish (in September 1983) were inshore of 4 km (Fig. 4).

The apparent difference in inshore-offshore distribution between age-0.0 and age-1.0 chinook salmon suggests that these two age groups are exposed to different environmental conditions in the ocean and that different factors may be critical in determining their survival in the ocean. Small subyearling chinook salmon may be more susceptible than yearling chinook salmon to processes affecting the nearshore environment, such as storms that cause heavy surf conditions, concentrations of nearshore predators, or nearshore dredging and other habitat modifications. On the other hand, by staying in shallow nearshore waters, where southward currents in the summer tend to be slower than 15–20 km farther offshore (Kundu and Allen, 1976; Huyer, 1983), the northward movement of the small subyearling fish may be facilitated.

In contrast to stream-type age-1.0 chinook salmon from the Columbia River, some ocean-type fish may overwinter in areas near where they enter the ocean. We found four age-0.1 CWT fish of the Columbia River URB fall chinook salmon stock, which is harvested mainly in Alaska and British Columbia ocean fisheries (Howell et al.[7]), near or south of the Columbia River many months following their release from hatcheries. Apparently, some individuals of this highly migratory ocean-type stock may delay their northward migration for a long period of time. Alternatively, the extent of the migrations of individuals of this stock may vary. Those that mature at younger ages (jacks for example) may undertake less extensive migrations than those that spawn at older age.[5]

Acknowledgments

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Providing quantitative management advice from stock abundance indices based on research surveys

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Abstract.—Index-based assessments, in which research survey indices serve as the primary source of abundance information, are used for many commercially harvested stocks in the Northeast region. Such assessments generally provide advice only on trends in the relative size of the stock, lack a biological reference point or level, and lack a decision framework for drawing statistical inferences about the state of the resource. We present a stochastic simulation technique for inferring population status relative to an index-based reference point. We applied an integrated moving average model to trawl data on Atlantic wolffish, *Anarhichas lupus*, to derive fitted indices and propose using the lower quartile (25th percentile) of the fitted indices as a reference point. From bootstrapping techniques applied to model residual errors we empirically characterized the variance and shape of the parent distributions of both a fitted abundance index at any point in time and the lower quartile. Treating these distributions as jointly continuous random variates, we generated the cumulative density function for the condition $Pr(index < lower\ quartile)$. Thus, for any value of the lower quartile, we can determine the probability that the fitted index at any point in time lies below that value of the biological reference point. An examination of the joint cumulative probability satisfying this condition is important because it allows us to ascertain quantitatively the likelihood of correctly deciding whether such a stock is below a prescribed threshold level.

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Fishery Bulletin 93:290–298 (1995).

Standardized multispecies bottom trawl surveys conducted annually in the spring and autumn by the Northeast Fisheries Science Center (NEFSC, 1993) have been integral to the scientific advice for managers of the northwest Atlantic fishery resources. Not only do the surveys provide an efficient means of collecting biological and ecological information on a suite of finfish and invertebrates in the Northwest Atlantic, but they also provide the principal means of monitoring changes in population abundance. The trawl surveys use a stratified random sampling design in which stations are allocated to strata roughly in proportion to stratum area and are randomly assigned to specific locations within strata. Generally, the stratified mean number or weight per tow is used as an index of relative abundance (Grosslein, 1969; Clark, 1979). Such indices of abundance can be quite variable because of heterogenous spatial distributions (Byrne et al., 1981), year to year changes in catchability (Byrne et al., 1981; Collie and Sissenwine, 1983), and natural changes in population abundance. As such, the observed time series of abundance indices reflects two sources of random variation: 1) measurement error arising from within and between year survey sampling variability; and 2) true or "process" error arising from actual changes in population abundance. Measurement error in the survey estimates can be filtered from process variability by using autoregressive-integrated-moving-average (ARIMA) models (Box and Jenkins, 1976). However, the estimation of the parameters of a full ARIMA model for fisheries research surveys is often problematic because of the relative shortness of the time series (Pennington, 1985). Pennington (1985) described an approach based on an a priori specification of an integrated moving average model in which change in population size follows a simple random walk. Pennington (1986) and Fogarty et al. (1986) have applied this approach to a number of northwest Atlantic species or stocks, such as yellowtail flounder, *Pleuronectes ferrugineus*. This approach has become the standard method for deriving "fitted" abundance indices used in the Northeast region (NEFSC, 1993).

While over 400 species of finfish and invertebrates have been caught in NEFSC's bottom trawl survey during 1963–92, 62 species are caught consistently nearly every year (Fig. 1). Roughly half of these 62 species have some economic importance and are therefore assessed by various means (NEFSC, 1993; Fig. 2). For the traditionally important groundfish species, such as Atlantic cod, *Gadus morhua*, haddock, *Melanogrammus aeglefinus*, and yellowtail flounder, adequate data are available to perform a size or age-structured assessment (yield per recruit or Virtual Population Analysis [VPA]). These types of assessments are usually accompanied by biological reference points based on fishing mortality rates, absolute stock abundance levels, or both, as indicators for stock sizes below which long-term yield or productivity may be jeopardized. While survey abundance indices are important to "calibrate" results of analytical models for these species and stocks, they serve as the only source of abundance information to assess the status of the majority of stocks in the Northeast region (Fig. 2). Research survey index-based assessments generally provide only qualitative advice on the relative size of the stock and typically do not generate reference points commonly used by fishery managers.

In this paper, we extend the present procedures of deriving fitted survey abundance indices to inferring population status relative to an index-based reference point in a probabilistic framework through simulation. We use Pennington's (1985) a priori integrated moving average approach to derive fitted survey time series and then characterize trends in population abundance relative to an index-based reference point defined to be the lower quartile (25th percentile) of the fitted time series. Our choice of the lower quartile for a reference point was rather arbitrary. However, the use of an interquartile (such as the 25th percentile) computed from the data series over a range of years with reasonably high (as well as low) population sizes probably provides a reasonable reference point and would serve as such even as the time series lengthens. We then used a bootstrap procedure to characterize the uncertainty in both the fitted index and the reference

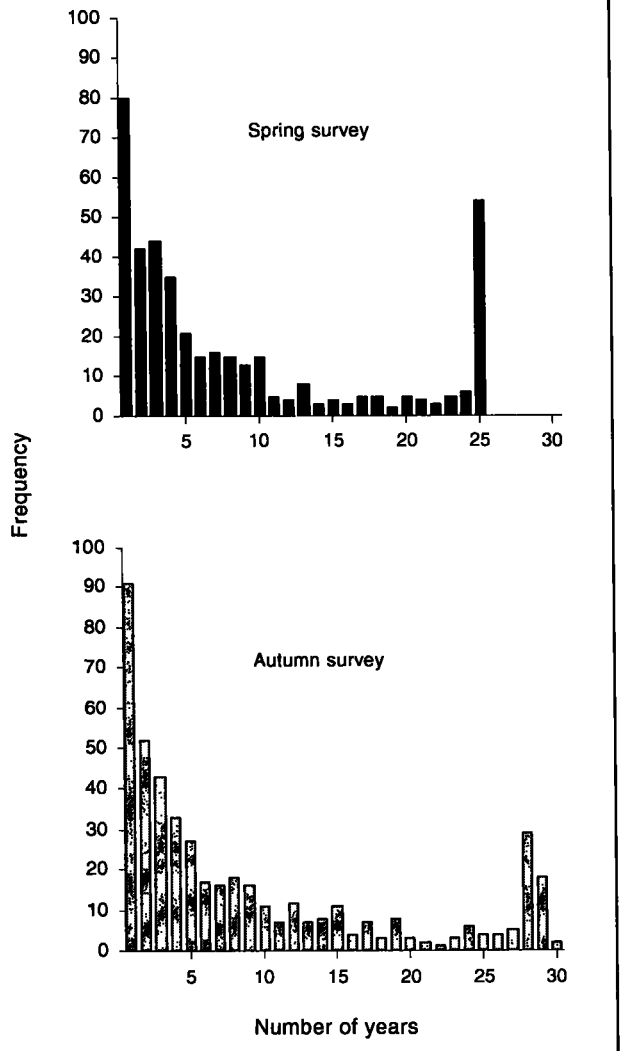

Figure 1

Frequency of the number of years various species (includes over 400 fish and invertebrates) occurring in the Northeast Fisheries Science Center's autumn bottom trawl survey since 1963 and spring bottom trawl survey since 1968. Data included up to 1992.

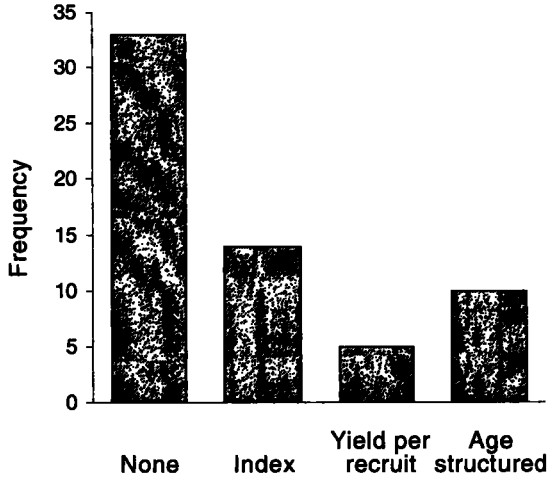

Figure 2

Frequency of assessment types performed on 62 species of fish consistly caught each year in the Northeast Fisheries Science Center's autumn and spring bottom trawl survey.

point and provide a probabilistic framework within which management decisions may be based.

Statistical methods

Estimation of abundance indices

Bottom trawl surveys have been conducted in the autumn since 1963 and in the spring since 1968 by the Northeast Fisheries Science Center. The surveys are based on a stratified random sampling design and are used to develop time series of abundance indices that are not subject to biases inherent in fishery-dependent data. A detailed review of the survey sampling design, methodology, and application has been provided by Grosslein (1969), Clark (1979), and Almeida et al. (1986). Following Cochran (1977), the stratified mean catch per tow is expressed as

$$\bar{y}_t = \sum_{h=1}^{l} \frac{N_h \bar{y}_h}{N}, \tag{1}$$

where N = total area of all strata; N_h = area of stratum h; $\bar{y}_h$ = sample mean in stratum h. The true abundance of a fish stock can be modeled as a population process with a linear stochastic difference equation of the form

$$\begin{aligned} z_t &= \phi_1 z_{t-1} + \phi_2 z_{t-2} \ldots \phi_p z_{t-p} \\ &\quad -\theta_1 a_{t-1} - \theta_2 a_{t-2} \ldots \theta_q a_{t-q}, \end{aligned} \tag{2}$$

where z_t is the population abundance at equally spaced points in time, ϕi and θi are autoregressive and moving average parameters, respectively, and a_t's are independent identically distributed (*iid*) normal random $N(0, \sigma^2)$ errors. The autoregressive component represents "memory," while the moving average component represents past "shocks" or perturbations in the system. A principal objective of time-series analysis is to filter the effects of measurement error in the raw survey abundance indices from "true" or process variability resulting from changing population levels. Box and Jenkins (1976) described a general class of models that estimate the parameters in Equation 2 that represent the autoregressive integrated moving average process. The model can be expressed in more compact form as

$$\phi(B) z_t = \theta(B) a_t, \tag{3}$$

where B is the backward shift operator, and all other parameters are defined as above in Equation 2. If a time series of survey abundance estimates, y_t, are assumed to be directly proportional to the true population size, z_t, and it is further assumed that the survey index is measured with error, that is $y_t = z_t + e_t$ (where the e_t's are *iid* $N(0, \sigma_e^2)$), then the survey time series may be represented by

$$\phi(B) y_t = \eta(B) c_t, \tag{4}$$

where y_t is the survey abundance estimates, B is the backshift operator, and c_t's are *iid* $N(0, \sigma_c^2)$. The autoregressive parameter, ϕ, remains unchanged in Equation 4 while η is the new integrated moving average parameter that reflects error in the survey abundance estimates. Appropriate model specification is determined by examining the autocorrelation and partial autocorrelation functions, by estimating appropriate parameters, and by checking for model adequacy (Box and Jenkins, 1976). However, this formal procedure of specifying and adequately estimating parameters is typically hampered by short time series of data such as those from fishery-independent surveys. Pennington (1985, 1986) has proposed an approach based on a priori specification of the model which addresses: 1) the limitation in the length of the survey time series; and 2) changes in the population availability or catchability. Following Pennington (1986), the true population can be represented as

$$z_t = z_{t-1} e^{a_t} \text{ or } (1-B) \ln z_t = a_t. \tag{5}$$

Here the a_t's represent the process variability or those factors which cause changes in the population from year $t-1$ to year t (such as recruitment, fishing mortality, migrations, etc.). Pennington (1985) demonstrated that if the model (Eq. 5) and the ratio of variances, σ_e^2/σ_c^2, are known, then z_t and the variance of the estimator can be estimated. If we again assume the survey index, y_t, to be an estimate of the true population abundance, z_t, and that the measurement errors of the index are multiplicative, then

$$\ln y_t = \ln z_t + e_t. \tag{6}$$

Assuming the e_t's are *iid* $N(0, \sigma_e^2)$ and independent of the a_t's, then y_t can be represented by the integrated-moving average model:

$$(1-B) \ln y_t = (1-\theta B) c_t, \tag{7}$$

where the c_t's are *iid* $N(0, \sigma_c^2)$ and represent the residuals generated by fitting the model to the observed data. For the model (Eq. 7)

$$\theta = \frac{\sigma_e^2}{\sigma_c^2} \text{ and } (1-\theta)^2 = \frac{\sigma_a^2}{\sigma_c^2}. \quad (8)$$

Therefore, fitting the model (Eq. 7) to the observed survey abundance indices provides an estimate of θ and from Equation 8, an estimate of σ^2_e/σ^2_c. Pennington (1986) notes that this approach has several advantages over using the raw indices in that: 1) the resulting model variance is more precisely estimated, as survey variance is affected by varying catchability from year to year; and 2) relevant information contained in the other years of the survey is used in estimates for a particular year. Further, the fitted survey series is considered to be more precise than the original series (Pennington, 1985, 1986; Fogarty et al., 1986). At this point the fitted index, with sufficient length of time, may be used to characterize trends in abundance relative to a chosen reference point. An estimate of the forecast variance of the fitted time series can be calculated (Box and Jenkins, 1976), although the reference point (i.e. interquartile) is deterministic. Further, if the time series is short, a correct specification and estimation of the model parameters will be difficult and parametric estimation of the variance uncertain. To overcome these constraints, nonparametric methods with bootstrapping techniques (Efron, 1982) were used to estimate the variances of the fitted index and the reference point as well as to determine the shape of their parent distributions. This approach is particularly useful in making inferences between the observed population level as estimated by the fitted index and the reference point, within a probablistic framework.

Bootstrap procedure

Once a maximum likelihood estimate of the integrated moving average parameter, θ, has been obtained from Equation 7, "fitted" estimates of the survey population abundance, y_t, with known residual errors are available at equally spaced points in time, such that

$$(1-B)\ln \hat{y}_t = (1-\hat{\theta})c_t = a_t, \quad (9)$$

where $Var(a_t) = Var[(1-\theta)c_t] = (1-\theta)^2\sigma_e^2 = \sigma_a^2$ (see Eq. 8). The variance of $\hat{y}_t$ is given by

$$V(\hat{y}_t) = \sigma_e^2\left(1 - \frac{\sigma_e^2}{\sigma_c^2}\right). \quad (10)$$

We applied bootstrapping procedures (Efron, 1982) to the vector of residual errors generated by the integrated moving average model (Eq. 7) applied to log-transformed survey abundance estimates. For the *ith* bootstrap replicate, n values of the model residuals were randomly selected with replacement (redefined as c'_t) and added to the predicted abundance estimates (y_t) to obtain n new pseudo-values y_t^*. Thus, a particular realization with the same underlying process was generated, where

$$y_t^* = \hat{y}_t + \sqrt{\hat{\theta}C_t^*}. \quad (11)$$

Assuming that Equation 7 provides an adequate representation of the actual population levels of the time series, it can be shown from Equations 8–11 that the bootstrap generated realizations take on the random component because of measurement error, since (from Eq. 8)

$$V\left(\sqrt{\hat{\theta}C_t^*}\right) = \theta\sigma_c^2 = \sigma_e^2. \quad (12)$$

Conceptually, this random resampling of the residuals mimicked a hypothetical resampling of the entire time series of abundance estimates with random variation generated from measurement error superimposed on the underlying process variation (i.e. variation in population levels). Random sampling of residuals and generation of n new time-series pseudo-values were repeated m times (i.e. m bootstrap replicates were performed). For each ith bootstrap replicate, the prespecified integrated moving average model in Equation 7 was again fitted to the n new pseudo-values of the time series by using the same moving average parameter estimate, $\hat{\theta}$. The n new pseudo-values of the times series and the new fitted values for the m bootstrap replicates are given as

$$\left[y_{t_1}^*, y_{t_2}^*, y_{t_3}^*, \ldots, y_{t_m}^*\right], \quad (13)$$

and

$$\left[\hat{y}_{t_1}^*, \hat{y}_{t_2}^*, \hat{y}_{t_3}^*, \ldots, \hat{y}_{t_m}^*\right], \quad (14)$$

respectively. The lower quartile corresponding to each of the n new pseudo-values of the m bootstrap replicated time series as

$$\left[\hat{q}_1^*, \hat{q}_2^*, \hat{q}_3^*, \ldots, \hat{q}_m^*\right]. \quad (15)$$

Rather than obtaining new estimates of θ for the model fitting to each bootstrap replicate, we followed Pennington's (1985) suggestion that, given the large variability inherent in marine trawl surveys, a preliminary estimate of $\hat{\theta}$ between 0.3 and 0.4 appears to be an appropriate value for estimating an abundance index, and we set the value of $\hat{\theta}$ to that origi-

nally obtained from Equation 7. Finally, to complete the bootstrap replication procedures we made two final calculations; the mean of the lower quartile obtained from the n-fitted pseudo-values of the m bootstrap replicates, and the mean-fitted survey abundance index for each year. These are given as

$$\bar{\hat{y}}_t = \frac{1}{m}\sum_{i=1}^{m} \hat{y}_t^* \quad (16)$$

and

$$\bar{\hat{q}} = \frac{1}{m}\sum_{i=1}^{m} \hat{q}^*. \quad (17)$$

This resampling process is conditioned on the set of residuals from a fitted model to the observed data, and no distributional assumption is made concerning the structure of the error. The sample size of residuals for the example given here (25 to 30) should be adequate to characterize the tails of the underlying error distribution, and bootstrap estimates of the mean and lower quartile should have converged sufficiently as the number of resampled replicates m was performed 1,000 times. As such, the mean and variances generated by these new realizations of the time series for both the fitted index and the reference point, as well as the shape of their parent distributions, provide the necessary information for making inferences about the population. Further, this approach to generating variances and confidence intervals is particularly useful because explicit solutions to the "normal equations" cannot be derived because of the nonlinear nature of the equations representing the underlying population process (Rawlings, 1988).

Making inferences

Decisions made by fishery managers are often based on the state of the resource relative to a chosen management target or reference point. One question that forms the basis of management action is the following: Given the uncertainty in both the index of abundance and the value of the chosen reference point, what is the probability that the index in year t is less than or equal to the reference point? Statements of probability and inferences regarding the state of the resource can be formulated by using the bootstrap generated data in the following manner: Let the fitted index for any particular year ($\hat{y}_t^*$) and the lower quartile ($\hat{q}^*$) generated from m bootstrap replications be random variates Y_1 and Y_2, respectively. In addition, assume that Y_1 and Y_2 are jointly continuous random variates with the density function $f(y_1,y_2)$. In practice, we want to determine the $P(Y_1<Y_2)$, that is, the probability that Y_1, which takes of the value of y_1, is less than Y_2, taking on the value of y_2. This probability is computed as

$$P(Y_1 < Y_2) = \int_{-\infty}^{\infty}\left[\int_{-\infty}^{y_2} f(y_1,y_2)dy_1\right]dy_2. \quad (18)$$

Further, we may wish to determine the probability of Y_1 being less than Y_2 for each possible value of y_2 in its domain and sum the resulting probabilities giving the cumulative probability distribution function. Thus, for any possible value of the reference point, $\hat{q}^*$, we can determine the probability that the fitted index, $\hat{y}_t^*$, lies below the value of the lower quartile for all possible values. By analogy, this can be extended to consider the joint probability that two consecutive years of the fitted survey abundance indices lie below the reference point. This approach takes into account the uncertainty in both the value of the fitted survey index for any given year (or two consecutive years) and the reference point to which the population level is compared.

An example

The Atlantic wolffish, *Anarhichas lupus*, is a cold water, bottom-dwelling species distributed from the Newfoundland banks to Nantucket (Bigelow and Schroeder, 1953). Little is known about the biology of wolffish in the western Gulf of Maine and Georges Bank region. Catches of wolffish in research surveys are low owing to its rather sedentary behavior and small, localized populations.

In U.S. waters, wolffish are taken primarily as bycatch in a mixed groundfish fishery and in other large mesh otter trawl fisheries. Commercial landings of wolffish in the Gulf of Maine-Georges Bank region averaged only about 220 metric tons (t) before 1970, after which they increased by nearly a factor of six; from 200 t in 1970 to 1,300 t in 1984 (Fig. 3). After peaking in 1984, commercial landings have steadily declined by about 100 to 200 t per year and reached 500 t in 1990, the lowest in nearly a decade. NEFSC spring survey abundance indices have shown a consistent downward trend, particularly since the early 1980's (Fig. 3).

Although no formal definition of overfishing presently exists for wolffish, this resource is presently considered overexploited and depleted on the basis of declining trends in commercial landings and survey indices (NEFSC, 1993). While this may intuitively be the correct conclusion regarding the status of the resource, there is little guidance in terms of its present level relative to its long-term abundance or to an appropriate reference point for fisheries

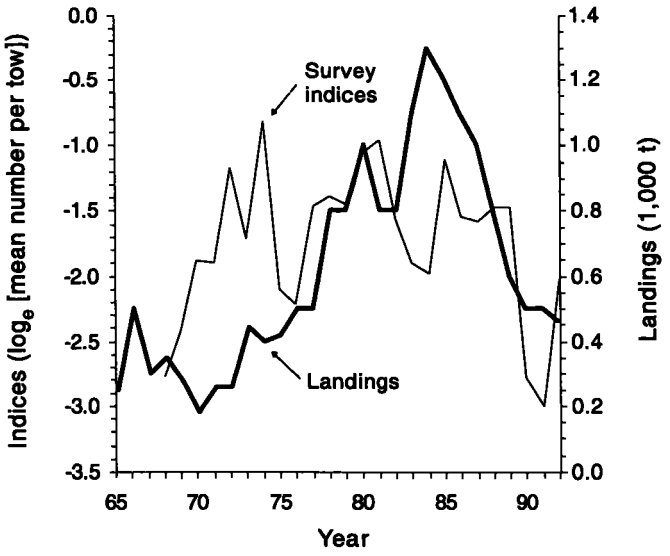

Figure 3

Atlantic wolffish, *Anarhichas lupus*, landings (thousands of metric tons) and spring bottom trawl survey indices ($\log_e$[stratified mean number per tow]) from 1968 to 1992.

management, or both. Given the data limitations for wolffish, what value will serve as a reasonable reference point or proxy for a level of stock abundance below which the stock may be in jeopardy? For our example we chose the lower quartile of the fitted survey abundance indices for wolffish as a reference point. Admittedly the choice of a computed statistic and the period of years of the survey indices used are rather arbitrary; the situation for each species should be carefully considered and a suitable reference point agreed upon by fishery managers. However, no matter which reference point is used, a simple comparison of a survey index in any given year with a survey-based reference point fails to consider the variability in each of these quantities.

Results and discussion

Estimates of the stratified mean number per tow (transformed by natural logarithms) clearly show declining trends in abundance, and the fitted index derived from time-series analysis appeared to provide a good, and less variable, representation of the observed data (Fig. 4). The maximum likelihood estimate of the integrated moving average parameter (θ) was 0.50 [SE(θ)=0.20], although it is probably not reliably estimated as indicated by the relatively flat maximum likelihood surface between 0 and 0.6.

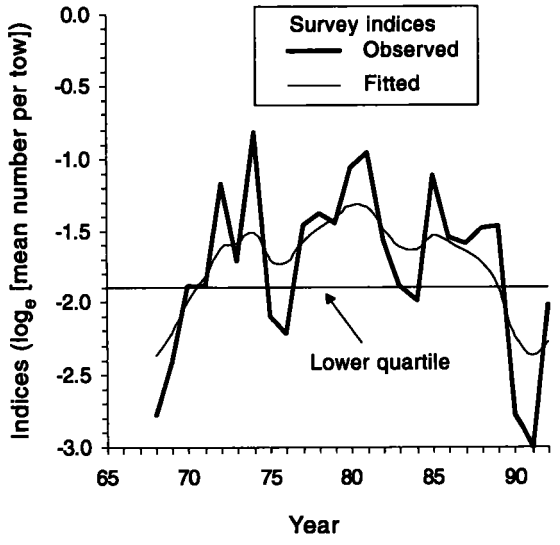

Figure 4

Predicted indices derived from an integrated moving average model fitted to observed Atlantic wolffish, *Anarhichas lupus*, spring bottom trawl survey indices ($\log_e$[stratified mean number per tow]) from 1968 to 1992. Predicted indices are compared to the lower quartile (25th percentile) of 1968–92 fitted indices as an arbitrary chosen reference point.

Pennington (1985, 1986) noted similar problems and concluded that the relative shortness of the time series of trawl data makes reliable estimation of the moving average parameter difficult. Although Pennington suggested using a value ranging from 0.3 to 0.4 appropriate for many stocks, we used the value of 0.50 because an analysis of the residuals from the model indicated that they were normally distributed ($P>0.10$).

The fitted estimates of abundance over the entire time series produce an index whose variance is considerably less than the variance of the observed series (Pennington, 1986). A comparison of a fitted index to the reference level (i.e. the lower quartile or 25th percentile) derived from the fitted indices should provide a reasonable evaluation of the stock's status because these reflect "true" trends in population abundance from only process variability (the effect of survey variance has been reduced). The fitted indices indicate that wolffish abundance has declined since the early 1980's and that by 1990 the index had fallen below the reference point (lower quartile= −1.90) to −2.2 (Fig. 4). In a hypothetical sense, if managers of this resource considered the lower quartile of the fitted indices a reasonable reference point, the 1990 index might have triggered some action, although it could be argued that the downward trend itself might be cause for concern. However, given the relative closeness of the fitted value of the 1990 index (−2.2) to the reference point (−1.9), as well as the uncertainty in both values, a logical question to ask is: What is the probability that the fitted 1990 index lies below the reference point?

Probability statements addressing this question can be derived from the parent distributions of both the fitted indices and reference points from the 1,000 bootstrap replications (Fig. 5). For the wolffish example, each of these distributions appear log-normally distributed, the 1990 fitted index exhibiting slightly more dispersion about its mean (as would be expected) compared with the reference point (Fig. 5). Both the fitted index and lower quartile means are nearly identical to the expected values (computed from the initial integrated moving average model fit), indicating little or no bias and uncorrelated model residual errors. Thus, for the time series on wolffish, an a priori integrated moving average model specification appears appropriate to describe the underlying population process.

For any value of the lower quartile we can state the probability that the fitted 1990 index lies below that value of the reference point using a discrete approximation of Equation 18. This simply represents the area integrated under the joint density

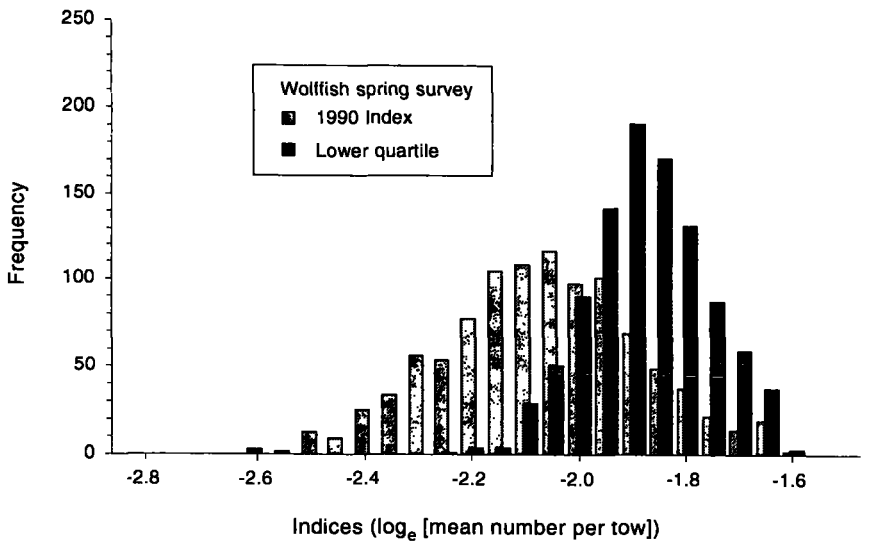

Figure 5

Comparison of empirical distributions of the 1990 spring survey index predicted by an integrated moving average (IMA) model fitted to 1,000 bootstrapped generated realizations of the survey time series 1968–92 and the lower quartile (25th percentile) of those predicted indices. The 1,000 realizations of the time series were generated by sampling with replacement the IMA model residual errors and randomly adding these to the predicted survey indices.

where the value of the fitted index is less than the value of the lower quartile (Fig. 6). The probability that the fitted 1990 index lies below the estimated value of the lower quartile (−1.9) is approximately 60% (Fig. 6). Further, because of the shape of the parent distribution of the lower quartile, the probability that the 1990 index lies below the reference point increases rapidly for higher and higher values of the reference point. For example, the probability that the 1990 index lies below a value of −1.85, which is nearly as likely as the bootstrapped mean (Fig. 5), increases to almost 75% and reaches nearly 85% at a value of −1.8 (Fig. 6). As an alternative to making inferences about the level of the population at only one point in time, fishery managers may wish to consider the likelihood of two (or more) consecutive years jointly falling below the value of the reference point. To address this question, we computed the joint probability of the 1990–91 and the 1990–92 fitted survey indices falling below our chosen reference point. The fitted survey indices over the 1990–92 period were as likely as those over the 1990–91 period to be below the reference point: approximately a 57% probability that the indices jointly fell below the reference point. This indicates that current population levels (as indexed by the fitted abundance indices) are considerably below the prescribed threshold level if the lower quartile of the fitted time series were adopted as the acceptable reference point. It should be emphasized that an "acceptable" reference point in this example refers more to choice of the range of years used for computation of the reference than to the choice of the interquartile, specified in this case to be the 25th percentile. We advise using a range of years for the abundance index which represents reasonably high population sizes and then using that fixed set of years for computation of the reference point even as the time series lengthens. This would prevent a ratcheting effect where the reference point declines as the abundance index declines, while allowing a characterization of the uncertainty in the reference point.

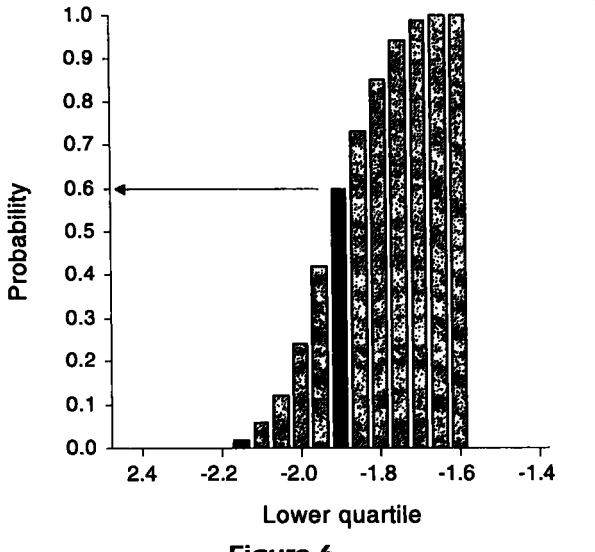

Figure 6

Probability that the value of the 1990 spring survey index predicted by an integrated moving average (IMA) model fitted to 1,000 bootstrapped generated realizations of the survey time series 1968–92 lies below the value of the lower quartile (25th percentile) derived from the predicted bootstrapped indices 1968–92.

In conclusion, this technique represents an advancement for index-based assessments in the provision of quantitative advice for the management of fish populations surveyed by research vessels that are otherwise lacking in data sources. This approach provides an examination of the joint cumulative probability for the condition *Pr*(*index in year t, t*+1, ... , *t*+*m* < lower quartile) and is important because it allows the likelihood of correctly deciding whether or not a stock is below a prescribed threshold abundance or reference point to be ascertained quantitatively. We emphasize that the computation of a reference point from the time-series data is arbitrary and should be based on a series of observations representing reasonably high as well as low stock abundances. Finally, we illustrated these procedures with trawl survey data for wolffish in the natural log scale, which when the data are differenced, produces homogeneity of variance and stationarity of the time series (Nelson, 1973). It should be noted that retransformation back to the linear scale is likely to result in some bias. We did not examine the effects of transformation bias in this study but suggest that these effects be investigated in the future.

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Nutritional dynamics of reproduction in viviparous yellowtail rockfish, *Sebastes flavidus*

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Abstract.—Nutritional dynamics of yellowtail rockfish, *Sebastes flavidus*, were analyzed from the perspective of temporal changes in tissue composition of liver, muscle, mesentery, and gonad to determine aspects specific to female reproduction. Monthly tissue composition data over an annual reproductive cycle indicated that females accumulated greater somatic tissue energy reserves than did males during the summer and fall months. Maternal lipid and protein reserves were depleted in a reciprocal relation with ovarian growth during the winter. The greatest declines of lipid and protein occurred in mesenteries and muscle, respectively. Females lost approximately 40% more somatic tissue than males during the time interval from ovarian development to parturition. Lipid was the primary energy source, contributing 74% of the energy lost from somatic tissues for female-specific reproductive purposes. Two-thirds of lipid depleted from maternal soma was for adult metabolic maintenance. Of the other one-third, 43% was gained in ovary tissue during development, leaving 57% for reproductive metabolic costs. Protein increased 220% in ovaries relative to female-specific somatic protein loss, indicating de novo ovarian synthesis. This study is the first report of comprehensive tissue composition dynamics and allocation to reproduction in a viviparous marine teleost. The analytical design used demonstrated the significance of each tissue component and the temporal pattern of allocation to reproductive development.

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Maternal nutritional status and the allocation of nutrients into developing young are important factors contributing to reproductive success in fish. Previous investigations have shown that nutritional status can influence fecundity and the vitality of offspring (Anokhina, 1959; Rijnsdorp, 1990; DeMartini, 1991; Kjesbu et al., 1991). By determining the temporal patterns of somatic and gonadal tissue components involved in fish nutritional dynamics, we can improve our understanding of energy and nutritional needs for successful reproduction.

Several studies of nutrient dynamics in fish have used chemical composition analyses of primary body constituents, including lipid, protein, glycogen, water, and ash components, to assess physiological status and the level of available nutritional reserves (Love, 1970; Caulton and Bursell, 1977; Cui and Wootton, 1988). These reserves have been shown to vary by species and interannually in location, quantity, and the sequence of allocation into reproductive development (Sargent, 1976; Medford and Mackay, 1978; Henderson et al., 1984; MacFarlane et al., 1993). Generally, the principal source of nutritional energy reserve in fish is lipid (Sargent, 1976; Sargent et al., 1989). Protein, primarily used in structural development and enzyme synthesis, may also be an additional source of energy when lipid reserves are depleted (Mommsen et al., 1980; Walton and Cowey, 1982).

Many temperate fish species follow a similar seasonal pattern of nutrient dynamics, where energy reserves are accumulated in the summer and depleted during the winter reproductive period (Shul'man, 1974). The transfer of nutrients from somatic reserves into ovarian growth has been indicated by the reciprocal relationship between the depletion of somatic stores and ovarian development (MacKinnon, 1972; Dawson and Grimm, 1980; Dygert, 1990). While this general pattern has been documented in oviparous species, little data on nutritional dynamics are available for viviparous teleosts (Wourms et al., 1988). For the marine viviparous genus *Sebastes*, only changes in tissue lipids have been measured in relation to reproduction (Guillemot et al., 1985; Larson, 1991; MacFarlane et al., 1993).

The yellowtail rockfish, *Sebastes flavidus*, range from San Diego, California, to Kodiak Island, Alaska (Eschmeyer et al., 1983), and are important both commercially and recreationally (Reilly et al.[1]; Pacific

[1] Reilly, P. N., D. Wilson-Vandenberg, D. Watters, J. E. Hardwick, and D. Short. 1993. On board sampling of the rockfish and lingcod commercial passenger fishing vessel industry in northern and central California, May 1987–December 1991. Calif. Dept. Fish Game Admin. Report. 93-4, 242 p.

Fisheries Management Council[2]). Distinctive characteristics of the reproductive strategy of yellowtail rockfish (e.g. small testes, copulation months before fertilization, quiescent testes during period of ovarian development [Eldridge et al., 1991], and nonmigratory behavior [Pearcy, 1992]) allow male nutrient dynamics to serve as adult metabolic controls. Consequently, nutritional energy expenditures specific to female reproduction can be estimated by the difference between female and male dynamics.

Knowledge of the nutritional dynamics specific to female reproduction may contribute understanding to the causes of interannual variability of larval production and health (Moser and Boehlert, 1991). The typical nutrient dynamic pattern may be altered by episodic environmental perturbations that impact reproductive output. Phenomena such as El Niños modulate the duration and intensity of upwelling, thus lowering oceanic productivity and subsequent energy flow (Boje and Tomczak, 1978; Ainley, 1990). In fact, Lenarz and Wyllie Echeverria (1986) suggested that the 1983 El Niño adversely influenced fat accumulation and reproduction in yellowtail rockfish.

The purpose of the present study was to determine the temporal dynamics of tissue components in somatic and ovarian tissues in relation to the annual reproductive cycle for yellowtail rockfish. Our objective was to determine the allocation of tissue components for nutrition and energy committed to female reproductive development. This report presents the first comprehensive nutritional dynamics study on a marine viviparous species.

Materials and methods

Adult yellowtail rockfish were collected by hook-and-line at depths of 50 to 150 m from Cordell Bank, a marine bank located approximately 20 nautical miles west of Point Reyes, California (38°01'N, 123°25'W). Specimens were obtained monthly during one reproductive cycle from May 1987 to April 1988. Fish were immediately placed on ice and returned to the laboratory for analyses.

Within 24 hours of capture, ovarian or testicular stage and morphometrics were recorded and tissues were excised for proximate and chemical analysis. Tissues removed included liver, gonad, and a section of muscle from the epaxial portion of the fish just below the spinous dorsal fin. In addition, mesenteric fat deposits attached to the viscera were dissected and weighed.

Muscle mass for individual fish was estimated by a regression equation. We regressed muscle weight on body weight minus gonad weight from representative fish spanning the typical total body weight range (800 to 1600 g) for yellowtail rockfish from Cordell Bank. Muscle mass was determined by

$$\text{muscle (g)} = 24.51 + 0.433\ [\text{body weight (g)} - \text{gonad weight (g)}]. \quad (r=0.994, P<0.0005)$$

Determinations of water, ash, and protein content were performed on fresh tissues. Samples analyzed for water content were dried at 80°C to a constant weight and cooled in a desiccator prior to weighing. Dried tissues were incinerated for 4 hours at 550°C to measure ash content. Protein concentration was assayed by the Lowrey method (Lowrey et al., 1951) with bovine serum albumin (Sigma Chemical Co., St. Louis, MO) as a standard.

Tissue samples for lipid and glycogen determinations were stored at –70°C and analyzed within one month of collection. Lipid was extracted in duplicate from 1 to 2 g of liver, gonad, and muscle by the biphasic method of Bligh and Dyer (1959) following homogenization with a Polytron homogenizer (Brinkman Inc., Westbury, NY). Total lipid was quantified by automated thin layer chromatography/flame ionization detection (TLC/FID), by using an Iatroscan TH–10 Mark III (Iatron Laboratories Inc., Tokyo, Japan) with T Datascan software (RSS Inc., Bemis, TN). Triplicates of 1 µl were spotted on Chromarods S-III, dried, and scanned by the FID at 3.1 mm/sec, 0.95 kg/cm^2 hydrogen pressure and air flow of 2000 mL/min. Peak areas were converted to total lipid weight by using external standards prepared gravimetrically from lipid extracts of *S. flavidus* livers. Standard concentrations were attained by evaporating the organic layer to dryness and reconstituting with chloroform to known concentrations ranging from 2 to 70 µg lipid/µL. Chromarods were cleaned with 9N sulfuric acid, rinsed in Milli-Q water and stored in a desiccator between analytical runs.

Glycogen content was measured by the anthrone method (Carroll et al., 1956). Values were standardized with glycogen from rabbit liver (Sigma Chemical Co., St. Louis, MO).

To evaluate variation in tissues and their components over the reproductive cycle, tissue component concentrations were converted to component masses by determining the product of tissue mass and component concentration. Since tissue and component masses are a function of fish size, we adjusted the

[2] Pacific Fishery Management Council. 1992. Status of the Pacific coast groundfish fishery through 1990 and recommended acceptable biological catches for 1993: stock assessment and fishery evaluation. Document prepared for the council and its advisory entities. Pacific Fishery Management Council, Portland, OR.

data to compensate for size variation. Tissue and component masses were converted to natural logarithms [ln(X + 0.01)] and subjected to the general linear model analysis of covariance (ANCOVA) by using the natural log of standard length (ln SL) to adjust for individual size differences among monthly samples. The adjusted means and standard errors of tissue and component masses were backtransformed by taking their antilogs. ANCOVA also determined the statistical significance of tissue and component variation across the reproductive cycle within each sex. We determined differences among specific monthly means by Duncan's multiple contrast test with $\alpha = 0.05$. Differences in monthly means between sexes were assessed by t-tests. All analyses were performed within the Number Cruncher Statistical Software package (NCSS, Provo, UT).

We estimated the contribution of somatic nutritional components to female reproduction by determining changes in tissue component masses between the onset of rapid ovarian growth and parturition. The decrease in somatic component quantities from maximal values before December to minimal levels in March was calculated for each tissue for each sex. Likewise, ovarian accumulation of nutritional components was calculated as the gain in mass from November to maximal values in December or January. Since male yellowtail rockfish are sexually quiescent during this interval (Eldridge et al., 1991), declines in their somatic nutritional components reflect utilization for adult metabolic maintenance. Differences in net losses of somatic components between males and females were considered estimates of allocations specific to female reproduction.

Results

Size variation

Monthly mean standard lengths (±SE) for females and males were 36.5 ±0.7 cm and 35.3 ±0.4 cm, respectively (Table 1). Differences in length between sexes and among males over the entire study interval were not significant (P>0.05). Because there were differences among monthly mean lengths of females (P<0.01), analysis of covariance eliminated tissue or component mass variation due to size.

Temporal dynamics

Ovarian development was largely synchronous within the yellowtail rockfish population from the onset of recrudescence in May through late vitellogenesis in November, as documented histologically by Bowers (1992) and MacFarlane et al. (1993) (Fig. 1). During December, females were in late vitellogenesis and migratory nucleus stages. Since fertilization occurred in January, both late oocyte and early embryonic stages were represented. In February, all females were in mid to late gestation. Parturition, or larval release, was completed in March when ovaries returned to a small, spent condition.

In males, testicular development was evident in August and September; in all other months testes were regressed and quiescent (Fig. 1). Copulation appeared to have occurred in September and October; sperm were stored in ovaries prior to fertilization.

During the annual reproductive cycle, ovarian mass increased 11-fold from September through December (Fig. 1). The most significant increase occurred during late vitellogenesis between November and December. Ovaries reached maximum size by January and retained mass through February. In comparison, testes reached maximum size in September and were less than 5% of ovarian mass between December and February.

The masses of liver, muscle, and mesenteric fat varied significantly (P<0.01) across the annual repro-

Table 1

Monthly mean standard length (SL) ± standard error (SE) for female and male yellowtail rockfish, *Sebastes flavidus*. Female mean lengths with same superscript were not significantly different (P > 0.05). Mean SL for males did not vary significantly among months, and did not differ significantly from females (P>0.05). n = sample size.

	Females			Males		
Month	n	SL	SE	n	SL	SE
May	6	33.0^{a}	0.9	4	37.2	0.6
June	5	37.0^{abc}	2.2	5	35.9	0.7
July	6	40.5^{c}	1.2	4	37.4	1.7
Aug	5	40.3^{c}	0.8	5	35.0	0.8
Sept	9	35.7^{abc}	1.3	1	32.0	—
Oct	5	36.7^{abc}	1.5	5	34.6	0.8
Nov	6	37.4^{abc}	1.7	4	37.1	0.9
Dec	5	35.1^{ab}	1.6	5	34.7	1.0
Jan	6	37.0^{abc}	2.3	5	35.6	0.8
Feb	5	32.7^{a}	1.7	5	34.0	0.4
Mar	5	38.2^{bc}	1.1	5	34.5	1.5
Apr	5	34.8^{ab}	1.5	5	36.0	0.8
Monthly mean		36.5	0.7		35.3	0.4

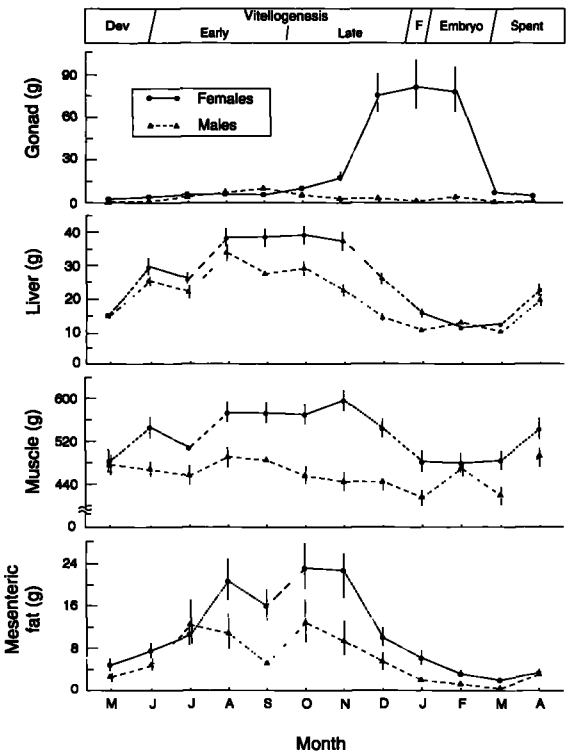

Figure 1

Annual ovarian reproductive cycle and monthly tissue wet weights for gonad, liver, muscle, and mesenteric fat of yellowtail rockfish, *Sebastes flavidus*. Values are means ±SE in grams adjusted by ANCOVA for variations in fish size. Temporal sequence of ovarian maturation stages are shown in bar across the top; recrudescence or early development (Dev), early and late vitellogenesis, fertilization (F), embryogenesis (Embryo), and spent.

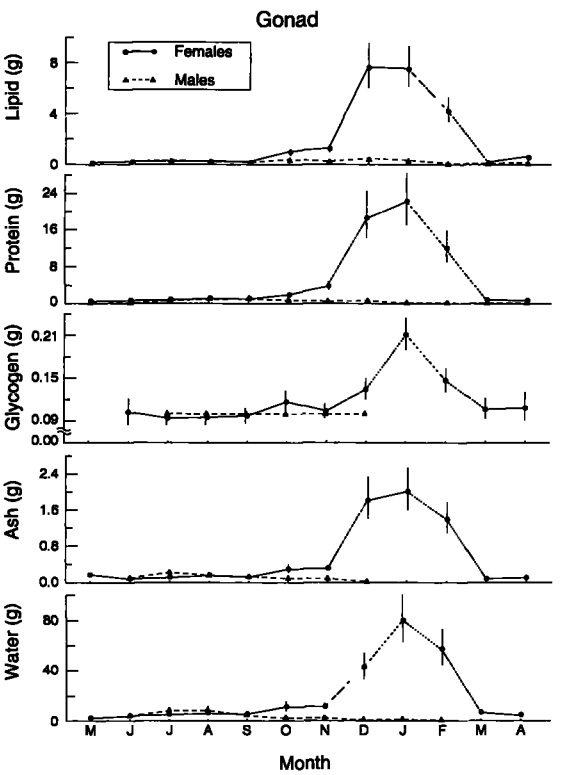

Figure 2

Monthly lipid, protein, glycogen, ash, and water content in gonad tissues of yellowtail rockfish, *Sebastes flavidus*, during one reproductive cycle. Values are means ±SE in grams on a wet weight basis. Missing male values are due to small testes size.

ductive cycle in both sexes (Fig. 1). These somatic tissues increased in mass during the summer and remained elevated into fall. Females accumulated significantly more mesenteric fat, liver, and muscle than did males ($P<0.001$). Declines in female somatic tissues in the fall and winter, during late vitellogenesis and embryogenesis, were inversely related to the accretion of ovarian tissue.

Temporal changes of ovarian tissue components followed a pattern similar to ovarian mass (Fig. 2). Protein and lipid increased 22-fold and 7-fold, respectively, from vitellogenesis in October to early gestation in January. Although glycogen showed a significant increase ($P<0.001$), quantities were always small, representing less than 1% of ovarian mass. Ash and water profiles reflected increased ovarian mass. At maximal size, water accounted for about 70% of ovary mass. Fluctuation in the masses of testicular components were insignificant compared with ovarian changes. In many cases, testicular quantities were insufficient to perform analyses of all constituents.

Dynamics of liver components were dissimilar across the reproductive cycle and between sexes (Fig. 3). Lipid and protein increased from late spring into summer in both sexes; the greatest net gain in female lipid was between July and August. In August, lipid was about 40% of liver mass, whereas protein contributed 10–15%. After August, female liver lipid decreased, but protein remained elevated during vitellogenesis until January. Significantly more liver protein was retained in females than in males from October to January ($P<0.001$). Both female and male liver glycogen followed a temporal pattern of a bimodal increase in the spring and summer with a decrease in the winter. The quantity of glycogen was only a small portion of total liver weight. Water in female liver accounted for a large portion of retained liver mass relative to males during late summer and fall (September through December).

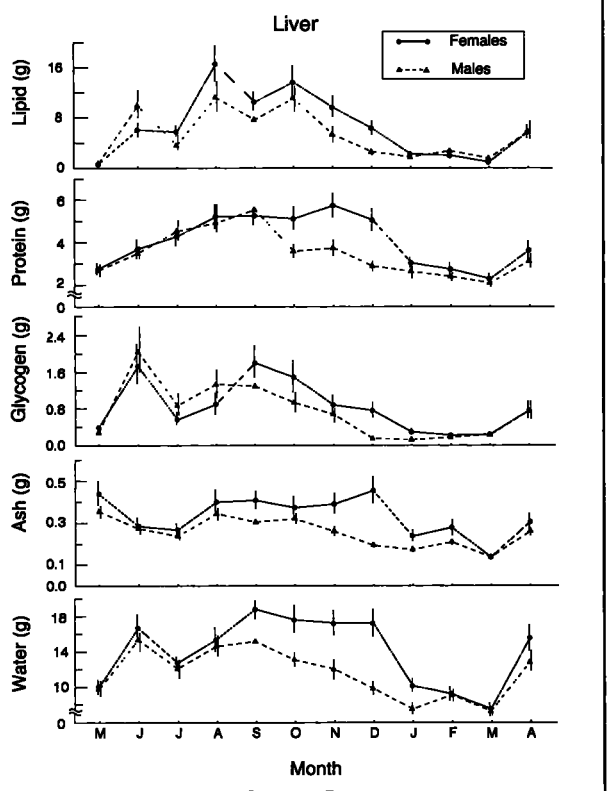

Figure 3

Monthly lipid, protein, glycogen, ash, and water content in liver tissues of yellowtail rockfish, *Sebastes flavidus*, during one reproductive cycle. Values are means ±SE in grams on a wet weight basis.

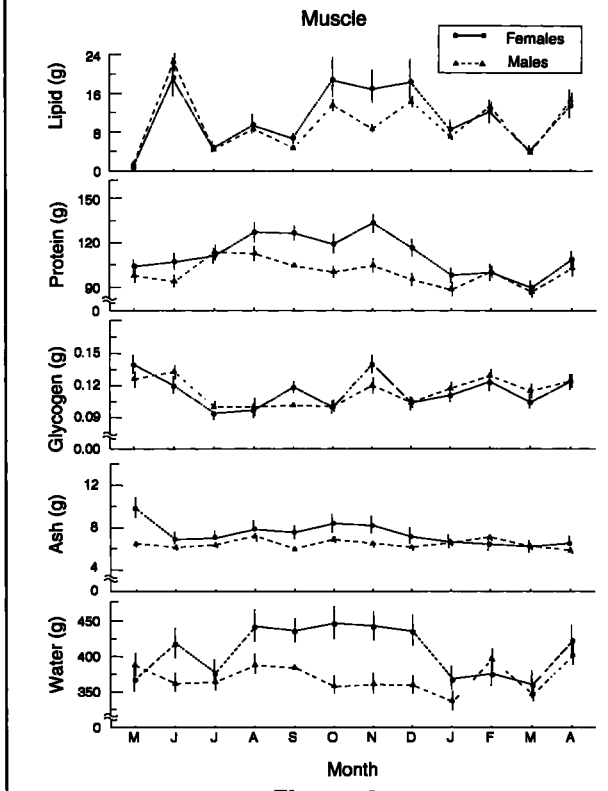

Figure 4

Monthly lipid, protein, glycogen, ash, and water content changes in muscle tissues of yellowtail rockfish, *Sebastes flavidus*, during one reproductive cycle. Values are means ±SE in grams on a wet weight basis.

In terms of quantity, protein content and water content were largely responsible for variation in muscle mass (Fig. 4). Protein content in female muscle increased 30% from July through November and was significantly greater than that in males ($P<0.005$). Muscle protein declined significantly in vitellogenic females after November ($P<0.01$). Males experienced a gradual decline in muscle protein from July to January. Lipid accounted for less than 5% of muscle mass in both sexes. In the fall, females had greater muscle lipid than males ($P\leq0.05$); lipid levels were similar during the other periods.

Muscle glycogen and ash content in females and males changed little across the reproductive cycle and did not appear to coincide with other component dynamics. Also, muscle glycogen content was an order of magnitude lower than liver glycogen.

Nutritional energy dynamics

By calculating changes in quantities of somatic and gonadal components from the onset of ovarian development to parturition, a mass balance of nutritional energy dynamics relative to the female annual reproductive cycle was constructed (Table 2).

Females lost 94 g of somatic tissue from the start of ovarian development through parturition. Virtually all of this loss was lipid (51 g) and protein (41 g). Females lost 27 g, or about 40% more somatic reserves than did males.

Lipid was mobilized from all somatic tissues. From the total lipid loss of 51 g in females, mesenteric fat contributed the most, 21 g, followed by liver and muscle. Mesenteric fat was also the greatest source of lipid loss in males; however, females used approximately 8 g more lipid from mesenteries than did males during the annual cycle. Overall, females lost 17 g more lipid from soma than did males, suggesting that about two-thirds of lipid depleted from somatic stores was used for adult maintenance.

Both females and males lost protein, primarily from muscle, during the time interval of ovarian maturation. Females mobilized 37 g of protein from muscle tissue, which was about 10 grams more than

Table 2

Mean net change in tissue components during annual reproductive cycle of yellowtail rockfish, *Sebastes flavidus*. All values in grams or kilocalories adjusted by ANCOVA for fish size variation. Differences (diff) are changes from start of ovarian development to parturition with male data as baseline. Net gain(+) and loss(–) indicated.

Tissue	Sex	Lipid	Protein	Glycogen	Total
Liver	♀	–15.5	–3.4	–1.6	–20.5
	♂	–10.1	–3.6	–1.2	–14.9
	diff	–5.4	+0.2	–0.4	–5.6
Muscle	♀	–14.6	–37.4	–0.04	–52.0
	♂	–11.1	–27.6	+0.01	–38.7
	diff	–3.5	–9.8	–0.05	–13.3
Mesentery	♀	–21.3			–21.3
	♂	–13.1			–13.1
	diff	–8.2			–8.2
Σ soma	♀	–51.4	–40.8	–1.6	–93.8
	♂	–34.3	–31.2	–1.2	–66.7
	diff (g)	–17.1	–9.6	–0.4	–27.1
	(kcal)	–161.6	–54.2	–1.6	–217.4
Ovary	(g)	+7.4	+21.2	+0.1	+28.7
	(kcal)	+69.9	+119.8	+0.4	+190.1
Ovary	(g)	0.43	2.2	0.25	1.06
Σ soma (diff)	(kcal)				0.87

that mobilized by males. Depletion of liver protein was similar in both sexes and accounted for only about 10% of the total protein loss. Mesenteric fat deposits are almost exclusively lipid.

Glycogen dynamics in both female and male somatic tissues were insignificant to the mass balance. Data are included here to complete the nutritional energy budget for reproduction.

Somatic component losses in females in excess of those in males showed 63% was lipid and 35% protein. By converting to energy equivalents (lipid, 9.45 kcal/g; protein, 5.65 kcal/g; carbohydrate, 4.10 kcal/g), we determined that 74% of female-specific energy depletion was lipid, whereas only 25% was from protein.

Lipid, protein, and glycogen accumulated in the ovaries during vitellogenesis and gestation with a net gain of 29 g (Table 2). Protein accounted for 21 g and lipid 7 g of the net accumulation. The lipid gained in ovaries represented 43% of the lipid depleted from female soma in excess of male losses. The 21-g gain in ovary protein during ovarian development was a 220% net increase relative to female-specific somatic protein loss. Unlike somatic tissue depletion where lipid accounted for the greatest energy loss, protein accretion contributed the greatest amount of energy to the fully developed ovaries (63%). Summing all components, the ratio of ovarian tissue generated to somatic organic matter depleted was balanced (i.e. 1.06).

Discussion

Yellowtail rockfish follow a viviparous mode of reproductive development with significant maternal investment (MacFarlane et al., 1993). Their reproductive strategy provided a model to determine nutritional energy dynamics of female viviparous reproduction. Males could be used to estimate adult metabolic maintenance because testicular development and other reproductive functions are quiescent during the period of ovarian growth and somatic reserve depletion. Moreover, the depletion of somatic reserves was directly reciprocal to ovarian growth, allowing a more accurate estimation of nutrient mobilization for ovarian development. Consequently, differences between female and male somatic losses reflect costs for female reproduction. Since this species does not migrate (Carlson and Haight, 1972; Carlson and Barr, 1977; Pearcy, 1992), there is no energy utilization for increased locomotion, as found with anadromous or catadromous fishes.

In yellowtail rockfish, somatic energy reserves were accumulated in both sexes during the summer and fall and depleted over winter when food availability decreased greatly (Hobson and Chess, 1988; Ainley, 1990). Although female soma gained greater mass than males during the summer, tissue masses were about the same in both sexes at the end of winter. Approximately 40% more somatic reserves were depleted from females than from males between October or November (maximal somatic mass) and March, or during the period spanning vitellogenesis to parturition. This difference was attributed to utilization of these reserves for ovarian development and related reproductive costs.

The location and quantitative importance of somatic reserves varies interspecifically in teleosts (Love, 1970; Weatherley and Gill, 1987). Interestingly, in yellowtail rockfish, a largely inactive fish,

somatic depletions were greatest in muscle. Muscle loss occurs in other fish (e.g. capelin and sockeye salmon) as well, but unlike yellowtail rockfish, these species often have high metabolic demands for migration in addition to reproduction (Idler and Bitners, 1960; Henderson et al., 1984).

Although muscle was the site of greatest net depletion of somatic tissue, mesenteric fat contributed more energy than muscle for female-specific costs of reproduction. Previous studies have demonstrated the importance of mesenteric fat as an energy source in yellowtail rockfish (Guillemot et al., 1985; MacFarlane et al., 1993). Lipid stored in mesenteries seems to be readily mobilized for reproduction in this live-bearing species as well as other oviparous fishes (Idler and Bitners, 1960; Ince and Thorpe, 1976; Jezierska et al., 1982).

In yellowtail rockfish, lipid was the main source of energy for female reproduction. About one-third of total lipid depleted from female soma was available for reproduction. Lipid lost from all the major reserve tissues equalled 74% of the total somatic energy mobilized for female-specific reproductive development. Lipid is typically the primary source of energy for reproduction in oviparous teleosts (Sargent, 1976; Sargent et al., 1989). Data from yellowtail rockfish suggest the importance of lipid for reproduction extends to marine viviparous fishes.

Female-specific protein loss from yellowtail rockfish somatic tissues was approximately half that of lipid. The utilization of protein from muscle as a supplemental source of energy for reproduction has been reported in some oviparous fishes (Niimi, 1972; Medford and Mackay, 1978; Jobling, 1980). But this contrasts with herring, where Iles (1984) and Bradford (1993) suggested that somatic protein was the primary fuel for gonad development whereas storage lipid supported nonreproductive metabolic processes.

Determining the partitioning of somatic reserves between reproduction and adult metabolism is very difficult in most teleosts. Reproductive strategies involving factors such as sex differences in activity, simultaneous development of testes and ovaries, migration, and somatic energy accumulation concurrent with gonadal development obscure fractional distribution. Because the yellowtail rockfish reproductive strategy, including physiological processes and behavior, does not include these factors (Carlson and Barr, 1977; Eldridge et al., 1991; Pearcy, 1992), we were able to estimate the nutritional energetic costs directed toward oocyte and embryo development. Forty-three percent (43%) of female-specific somatic lipid depletion was incorporated into ovaries, leaving 57% for reproductive metabolism.

Henderson et al. (1984) employed an analytical design well-suited to determining somatic lipid partitioning among adult maintenance, reproductive metabolism, and ovarian accretion in capelin, *Mallotus villosus*. Although ovaries accumulated 38% of mobilized somatic lipid and testes gained none, both sexes mobilized essentially the same quantity of somatic lipids. The absence of a difference between sexes in lipid mobilization precluded estimation of allocations between gonadal metabolism and adult maintenance.

Significant increase in ovarian protein during maturation was expected because de novo synthesis is required for oocyte and embryonic proliferation. However, the net increase in ovarian protein was 220% of female-specific somatic loss and indicated a dietary source during late vitellogenesis and gestation. Although there is a general paucity of prey in the California Current ecosystem during the winter (Hobson and Chess, 1988; Ainley, 1990) and stomach contents of yellowtail rockfish samples were minimal at this time (Whipple[3]), feeding remains the most likely source for the excess protein accumulated in the ovary. Data from yellowtail rockfish off the Washington and Oregon coast showed that they may feed over winter (Brodeur and Pearcy, 1984). Since we observed frequent regurgitation during capture, it is possible that expulsion of stomach contents contributed to imprecise estimation of feeding intensity in the yellowtail rockfish of the present study.

There are limited data on female-specific nutritional dynamics in other species. Thus, it may be beneficial to compare allocations from soma to gonadal tissue, uncorrected for sex differences, for yellowtail rockfish to those of other fishes. Such comparisons do not provide information on the partitioning of nutrients for various female metabolic and reproductive processes, only the net transfer to ovaries. For yellowtail rockfish, the gain of lipid and protein in ovaries during reproductive development was 14% and 52% of somatic depletions, respectively. This net transfer of lipids into ovaries was mid-range in comparison with values in oviparous species. Net lipid transfers of 38% in capelin (Henderson et al., 1984), 22% in plaice, *Pleuronectes platessa* (Dawson and Grimm, 1980), 8% in sockeye salmon, *Oncorhynchus nerka* (Idler and Bitners, 1960), and 5% in English sole, *Pleuronectes vetulus* (Dygert, 1990) have been reported. Protein transfers in yellowtail rockfish are comparable to English sole, 55% (Dygert, 1990). In plaice 48% more protein accumulated in ovaries than was lost from soma during oocyte

[3] Whipple, J. A. 1988. National Marine Fisheries Service, Southwest Fisheries Science Center, Tiburon Laboratory, 3150 Paradise Drive, Tiburon, CA 94920. Unpubl. data.

development, but plaice are known to feed during this time (Dawson and Grimm, 1980).

The efficiency of net transfer between somatic tissues and ovaries, or the ratio of ovary tissue gained during development to the total somatic tissue lost, was about 30% in yellowtail rockfish. This compares with 33% in English sole (Dygert, 1990), 43% in plaice (Dawson and Grimm, 1980), and 23% in American plaice, *Hippoglossoides platessoides* (MacKinnon, 1972), suggesting that although the temporal sequence of nutritional dynamics may differ between oviparous and viviparous teleosts, the quantitative budgets are similar.

The present study documents the first comprehensive analysis of the nutritional energetics of reproduction in a viviparous marine teleost. Although there are many similarities to oviparous species, the reproductive nutritional energetics of this viviparous species are likely adaptive to environmental constraints of the upwelling-dominated productivity pattern of the California Current ecosystem. Energy reserves, mainly lipid, were accumulated in intestinal mesenteries and other somatic tissues in both sexes through the summer upwelling (feeding) season. Females acquired greater amounts of lipid and protein than did males. These reserves were depleted to a greater extent in females for ovarian development, as well as in adult metabolism and survival over winter when ecosystem productivity is low. This strategy results in the release of larvae at the onset of improved feeding conditions when upwelling renews. Because lipid is the most important energy source allocated to ovarian development, inadequate accumulation of lipid reserves in females during the typically productive period of the year may alter the maternal energy balance. Thus, periodic perturbations, such as El Niños, may result in reduced nutritional input to developing larvae and consequently lower reproductive success or pelagic larvae survival.

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Abstract.—Virtual population and cohort analyses are sometimes conducted with an age category known as the "plus group." This category is used to keep track of the abundance and catches of older fish that cannot be assigned individual ages accurately. In this study we present a procedure for solving the catch equation backwards in time when it involves a plus group. The procedure consists of an initial analytical approximation, followed by a correction function based on an empirical analysis, followed by the application of Newton's Method. The results indicate that the procedure works well for a wide range of natural and fishing mortality values. For comparison, we also applied the same procedure to the basic catch equation (without a plus group) and found that adequate approximation to the true fishing mortality value is achieved even before application of Newton's Method.

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Approximations for solving the catch equation when it involves a "plus group"*

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A solution to $F_{a,t}$ in the catch equation

$$N_{a+1,t+1} = \frac{C_{a,t} Z_{a,t}}{F_{a,t} (e^{Z_{a,t}} - 1)}; \qquad (1)$$

where a denotes the age, t denotes the time period, $C_{a,t}$ is the catch in numbers, $N_{a+1,\,t+1}$ is the cohort size at the start of the following time period, $F_{a,t}$ is the fishing mortality rate and $Z_{a,t}$ is the total (fishing + natural) mortality rate ($Z_{a,t} = F_{a,t} + M_{a,t}$), is required in many stock assessment problems that track the exploitation history of a cohort (cohort and virtual population analyses). Here, Equation 1 is expressed in a form known as "backward in time," meaning that a solution to F for age a during time period t is to be obtained given known values of $C_{a,t}$, $N_{a+1,t+1}$, and $M_{a,t}$.

An analytical solution to $F_{a,t}$ is not possible and this prompted several authors to develop useful approximations (see Pope, 1972; Sims, 1982; MacCall, 1986; Allen and Hearn, 1989). Most current computer implementations of age-structured models use numerical algorithms to solve the catch equation; therefore approximations are seldom used in stock assessment applications. However, approximations provide initial estimates that may improve the efficiency of the numerical algorithms, an important consideration when the algorithm is used repeatedly. More important, as with analytical solutions, simple approximations enable scientists to explore relationships between variables easily.

The objective of this study is to present a simple procedure for solving a catch equation that involves a "plus group." A plus group lumps together a number of the oldest age classes in a population into a single age category. For example, a plus group may be used when large (old) fish in the catches cannot be aged with a desired degree of accuracy or precision as can smaller fish (Restrepo and Powers, 1991). We are not aware of definitive analyses that have been conducted to evaluate the general merits of data aggregation into a plus group. Using simulated data with ageng errors in an age-structured model, Fournier and Archibald (1982) found that using a plus group gave better results than did ignoring the ageing errors and extending the analyses to a last "true" age. Deriso et al. (1989), also using simulated data in an age-structured model, found that aggregation of older fish into a plus group produced comparable estimates to those obtained from disaggregated data. However, Hiramatsu (1992) warned that use of a plus group in virtual population analyses could cause large biases under certain cir-

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cumstances. It seems that the decision of whether or not a plus group should be used in an assessment depends on the ageing errors and characteristics of the population being assessed (Restrepo and Powers, 1991).

The basic plus group dynamics can be presented as follows. Assume that M is the same for the plus group and the previous age (we will drop age and year subscripts for M) and let p denote the plus group age category. The number of fish alive at the beginning of time period $t+1$ is given by

$$N_{p,t+1} = N_{p,t}\, e^{-Z_{p,t}} + N_{p-1,t}\, e^{-Z_{p-1,t}}, \qquad (2)$$

and the corresponding catch equation is

$$N_{p,t+1} = \frac{C_{p,t} Z_{p,t}}{F_{p,t}(e^{Z_{p,t}} - 1)} + \frac{C_{p-1,t} Z_{p-1,t}}{F_{p-1,t}(e^{Z_{p-1,t}} - 1)}. \qquad (3)$$

Given known values of $C_{p,t}$, $C_{p-1,t}$, $N_{p,t+1}$, and M, no unique joint solution exists for the two unknowns, $F_{p,t}$ and $F_{p-1,t}$ in Equation 3. In this study, we use the simplifying assumption that the value of α in

$$\alpha = \frac{F_{p,t}}{F_{p-1,t}} \qquad (4)$$

is known so that $F_{p,t}$ in Equation 3 can be replaced by $\alpha F_{p-1,t}$. Now the solution consists of a single fishing mortality rate, $F_{p-1,t}$. Theoretically, one or more α values can be estimated as parameters in an age-structured model. However, estimation of several α values is difficult, particularly for the last years for which catch data are available (Powers and Restrepo, 1992). Thus, in many assessment applications, α values are assumed from a knowledge of the population and the fishery being examined (Powers and Restrepo, 1992). For example, selectivity studies of the fishing gear may indicate that fish of ages $p-1$ and older are equally vulnerable, giving $\alpha = 1$.

Approach

The approach we follow is similar to that used by Sims (1982). We first provide simple approximations to $F_{p-1,t}$, similar to those developed by Pope (1972). On the basis of simulated parameter values, we then empirically estimate correction factors that can be used to improve upon the initial approximations. Finally, we use the corrected approximations as starting guesses for Newton's Method (see Sims, 1982), which can be used to obtain a more accurate numerical solution to the catch equation. For comparative purposes, we also use the same approach for catch equations not involving a plus group.

Range of values examined

In order to evaluate the accuracy of the approximations and to develop empirical corrections, we generated 1,000 uniform random values of each parameter in the following ranges: $N_{p,t}$ [500, 1,500], $N_{p-1,t}$ [500, 1,500], M [0.05, 1.0], $F_{p-1,t}$ [0.05, 3.0], α [0.5, 2.0]. These ranges are arbitrary but we felt that they represent realistic extremes: the stock size of the plus group and the preceding age can differ by a factor of 3; the range in M is representative of a wide range in lifespans; the fishing mortality range is extremely wide because our purpose was to find reasonable approximations for a wide range of F's; and the range in α allows the fishing mortalities of the plus group and the previous age to differ by a factor of 2.

Initial approximations

Pope's (1972) approximation to $F_{a,t}$ in Equation 1 can be explained as follows. Consider the equations (from Appendices A and B in Pope, 1972)

$$N_{a,t} = N_{a+1,t+1}\, e^{Z_t} \qquad (5)$$

and

$$N_{a+1,t+1}\, e^{M} = N_{a,t} - C_{a,t}\, \frac{Z_{a,t}(1 - e^{-F_{a,t}})}{F_{a,t}(1 - e^{-Z_{a,t}})}. \qquad (6)$$

Pope (1972) demonstrated that, over a range of fishing and natural mortality values, the function multiplying $C_{a,t}$ in Equation 6 can be reasonably approximated by $e^{(M/2)}$. Making use of this approximation and substituting Equation 5 into Equation 6 gives

$$N_{a+1,t+1}\, e^{M} = N_{a+1,t+1}\, e^{Z_{a,t}} - C_{a,t}\, e^{M/2},$$

which can be solved for $F_{a,t}$ as

$$F_{a,t} = \ln\left[\frac{C_{a,t}}{N_{a+1,t+1}} e^{-M/2} + 1\right]. \qquad (7)$$

We followed a similar approach for the purpose of obtaining an initial analytical approximation to $F_{p-1,t}$ in Equation 3. Consider the special case when the fishing mortalities of the plus group and the preceding age are the same (i.e. α=1 in Eq. 4, giving $F_{p,t} = F_{p-1,t}$). Then, the equation analogous to Equation 5 is obtained from Equation 2:

$$[N_{p,t} + N_{p-1,t}] = N_{p,t+1} e^{Z_{p-1,t}}, \quad (8)$$

and the equation analogous to Equation 6 is

$$N_{p,t+1} e^{M} = N_{p,t} - C_{p,t} \frac{Z_{p-1,t}(1 - e^{-F_{p-1,t}})}{F_{p-1,t}(1 - e^{-Z_{p-1,t}})} + N_{p-1,t}$$

$$- C_{p-1,t} \frac{Z_{p-1,t}(1 - e^{-F_{p-1,t}})}{F_{p-1,t}(1 - e^{-Z_{p-1,t}})}, \quad (9)$$

which, using the same approximation given by Pope (1972), becomes

$$N_{p,t+1} e^{M} = [N_{p,t} + N_{p-1,t}] - [C_{p,t} + C_{p-1,t}] e^{M/2}.$$

Substituting Equation 8 into the last equation results in

$$N_{p,t+1} e^{M} = N_{p,t+1} e^{Z_{p-1,t}} - [C_{p,t} + C_{p-1,t}] e^{-M/2},$$

which can be solved for the fishing mortality rate as

$$F_{p-1,t} = \ln\left[\frac{(C_{p,t} + C_{p-1,t})}{N_{p,t+1}} e^{-M/2} + 1\right]. \quad (10)$$

We found that Equation 10 is often a poor approximation for values of $\alpha \neq 1$ (see Results section). A much better approximation can be obtained by introducing α into the equation as

$$F_{p-1,t} = \ln\left[\frac{(C_{p,t}/\alpha + C_{p-1,t})}{N_{p,t+1}} e^{-M/2} + 1\right]. \quad (11)$$

Empirical correction factors

In many cases, given the widespread availability of computers, the approximation given by Equation 11 can be used as an adequate starting guess for an iterative procedure to get a more accurate solution (e.g. see the next section). In some cases, however, it is desirable to improve upon this approximation in order to obtain either a better starting guess, or to obtain as close as possible to an accurate solution because iterative computations are expensive. The latter is the case of solving multiple catch equations while conducting a cohort analysis on a computer spreadsheet and is the motivation for this study.

The empirical approach we used was simple. Denote the approximation in Equation 11 by ${}^{A}F$ and the true fishing mortality by ${}^{T}F$. Our approach was 1) to generate a large number of plausible combinations of parameter values; 2) to plot values of the ratio ${}^{A}F/{}^{T}F$ against α and M (parameters usually assumed to be known a priori) and to identify types of functions that can adequately describe the observed relationship, if any; and 3) to estimate the coefficients of such functions and use them to correct ${}^{A}F$ so it becomes closer to ${}^{T}F$. This empirical approach is similar to the multiple regression approximations suggested by Allen and Hearn (1989). For comparative purposes, we also followed the same approach using the approximation given by Equation 7 for a case without a plus group.

Newton's Method

Sims (1982) suggested the use of Newton's Method for solving F in the catch equation with a desired degree of precision. For Equation 1, the functional equation of interest is

$$f(F_{a,t}) = \frac{C_{a,t} Z_{a,t}}{F_{a,t}(e^{Z_{a,t}} - 1)} - N_{a+1,t+1},$$

and a solution to $F_{a,t}$ is obtained when $f(F_{a,t}) = 0$. Sims (1982) showed that all requirements for convergence were met in order for Newton's Method to converge to that solution. One iteration of Newton's Method (denoted by i) changes the estimate of $F_{a,t}$ as follows:

$$F_{a,t}(i+1) = F_{a,t}(i) - \frac{f\left(F_{a,t}(i)\right)}{f'\left(F_{a,t}(i)\right)} \quad (12)$$

with

$$f'(F_{a,t}) = -\frac{C_{a,t}\left(e^{Z_{a,t}}(F_{a,t}^2 + F_{a,t} M + M) - M\right)}{F_{a,t}^2 (e^{Z_{a,t}} - 1)^2}.$$

For the application of Newton's Method to the solution to the catch equation involving a plus group, the functional equation of interest is (from Equation 3)

$$f(F_{p-1,t}) = \frac{C_{p,t}(\alpha F_{p-1,t} + M)}{\alpha F_{p-1,t}(e^{\alpha F_{p-1,t} + M} - 1)}$$

$$+ \frac{C_{p-1,t}(F_{p-1,t} + M)}{F_{p-1,t}(e^{F_{p-1,t} + M} - 1)} - N_{p,t+1}$$

and its derivative with respect to $F_{p-1,t}$ is

$$f'(F_{p-1,t}) =$$

$$-\frac{C_{p,t}\left(e^{\alpha F_{p-1,t}+M}(\alpha^2 F_{p-1,t}^2+\alpha F_{p-1,t}M+M)-M\right)}{\alpha F_{p-1,t}^2(e^{\alpha F_{p-1,t}+M}-1)^2}$$

$$-\frac{C_{p-1,t}\left(e^{F_{p-1,t}+M}(F_{p-1,t}^2+F_{p-1,t}M+M)-M\right)}{F_{p-1,t}^2(e^{F_{p-1,t}+M}-1)^2}.$$

One iteration of Newton's Method proceeds in the same manner as explained above in Equation 12, if the empirically corrected estimates of fishing mortality (see previous section) as initial values are used. Although we did not carry out a rigorous analysis of conditions for convergence, as Sims (1982) did, we did not encounter any cases where an iteration did not result in an improvement.

Results

Table 1 provides some statistics of the ratio ${}^{A}F/{}^{T}F$ for the 1,000 random combinations of inputs, with and without a plus group. In each case, the first column provides these statistics for the initial approximation (${}^{A}F$ from Equation 7 for the case without a plus group and ${}^{A}F$ from Equations 10 and 11 for the plus group approximation). The next column provides the statistics for the ratios after an empirical correction function is applied (the coefficients of these correction factors are presented in the following subsections). The last two columns give the statistics after one and two iterations of Newton's Method. Implications of these results are explained in more detail below.

Case I: without a plus group

The initial approximation provided by Equation 7 (from Pope, 1972) was reasonable, as expected (See Table 1 and Fig. 1, top panel). The mean ${}^{A}F/{}^{T}F$ ratio indicated an overall 3% bias and the largest error was slightly greater than 8%.

Visual inspection of a plot of ${}^{A}F/{}^{T}F$ against M indicated that a linear relationship would improve the approximation. We fitted the model ${}^{A}F/{}^{T}F = a + b\,M$ by minimizing the sum of absolute deviations between the observed ratios and those predicted by the model. The parameter estimates were

$$a = 0.9970, \text{ and } b = 0.0808.$$

Thus the empirical correction to the initial approximation to F was

$${}^{emp.A}F = {}^{init.A}F/(a+bM). \quad (13)$$

Much improvement in the approximation was obtained by use of this simple correction function (Table 1, second column, and Fig. 1, middle panel). The largest observed error was now 3%, which compares favorably with the errors reported by Pope (1972) over a much narrower range of fishing and natural mortality rates. Application of a single iteration of Newton's Method resulted in virtual conver-

Table 1

Summary statistics for 1,000 ratios of the approximated fishing mortality rate to the true fishing mortality rate (${}^{A}F/{}^{T}F$, see text for a description of how the 1,000 realizations were made). Case I represents analyses not using a plus group. Case II represents analyses with a plus group. Each column corresponds to a different step in the analyses, progressing from an initial approximation (two initial approximations are given for Case II), to an empirically corrected approximation, to the first two iterations of Newton's Method. CV = coefficient of variation.

	Case I: no plus group			
	Initial approx. (Eq. 7)	Empirical correction (Eq. 13)	Newton iter. 1 (Eq. 12)	Newton iter. 2 (Eq. 12)
Mean	1.0350	0.9969	1.0000	1.0000
Median	1.0318	1.0000	1.0000	1.0000
CV	0.0217	0.0069	0.0000	0.0000
Min.	1.0007	0.9700	1.0000	1.0000
Max.	1.0826	1.0046	1.0001	1.0000

	Case II: plus group			
	Initial approx. (Eqs. 10, 11)		Empirical correction (Eq. 14)	Newton iter. 1 (Eq. 12)	Newton iter. 2 (Eq. 12)
Mean	1.1193	1.0663	0.9976	0.9983	1.0000
Median	1.1418	1.0660	1.0000	0.9995	1.0000
CV	0.1805	0.0876	0.0368	0.0028	0.0000
Min.	0.6315	0.7654	0.8778	0.9814	0.9994
Max.	1.6757	1.3493	1.1204	1.0000	1.0000

gence to the true F values (Table 1 and Fig. 1, bottom panel).

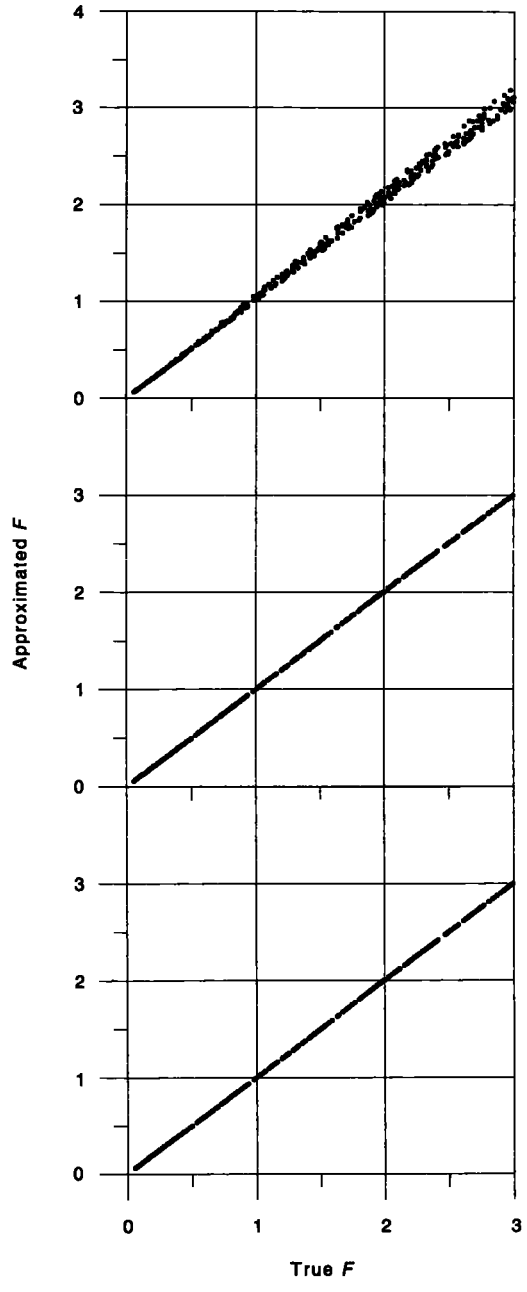

Figure 1

Progression in the approximation to the fishing mortality rate for a catch equation not involving a plus group (400 of the 1,000 pairs of approximated and true F are shown). (**Top**) Initial approximation (Eq. 7); (**Middle**) approximation after application of empirical correction function (Eq. 13); (**Bottom**) approximation after one iteration of Newton's Method (Eq. 12).

Case II: with a plus group

The initial approximations obtained for the plus group problem were rather poor compared with those of the catch equation without a plus group (Table 1, Fig. 2, top panel). This was not unexpected, because the plus group catch equation is not amenable to algebraic manipulations that lead to analytical approximations. However, note that the initial approximation from Equation 11 was much better than that from Equation 10: the observed ${}^{A}F/{}^{T}F$ ratios indicated smaller biases and a tighter approximation overall (see Table 1). (Note: Subsequent statistics and data reported in Table 1 and Figure 2 are based on the approximation given by Equation 11.)

In order to find empirical correction factors, we plotted the observed ${}^{A}F/{}^{T}F$ ratios against M (for different α values) and against α (for different M values) (see Fig. 3). Visual inspection of these figures indicated that 1) the relationship between ${}^{A}F/{}^{T}F$ and M could be approximated by a linear model; 2) the relationship between ${}^{A}F/{}^{T}F$ and α could be approximated by a logarithmic model; and 3) there was an interaction between M and α in terms of explaining variability in ${}^{A}F/{}^{T}F$. Therefore, we fitted the model

$$ {}^{A}F/{}^{T}F = a_0 + b_1 \ln(\alpha) + b_2 M + b_3 \alpha M $$

to the observed ratios, again by minimizing the sum of absolute residuals. The empirical correction factor used was then

$$ {}^{emp.A}F = {}^{init.A}F/(a_0 + b_1 \ln(\alpha) + b_2 M + b_3 \alpha M) \quad (14) $$

with

$a_0 = 0.9951$,
$b_1 = 0.2053$,
$b_2 = 0.0636$, and
$b_3 = 0.0161$.

This empirical correction function provided a substantial improvement in the approximations (Table 1, Fig. 2, middle panel). However, solution errors on the order of 12% were still obtained after the correction. One iteration of Newton's Method was sufficient to reduce the errors to within 2% (Table 1 and Fig. 2, bottom panel) and the second iteration resulted in virtual convergence (Table 1).

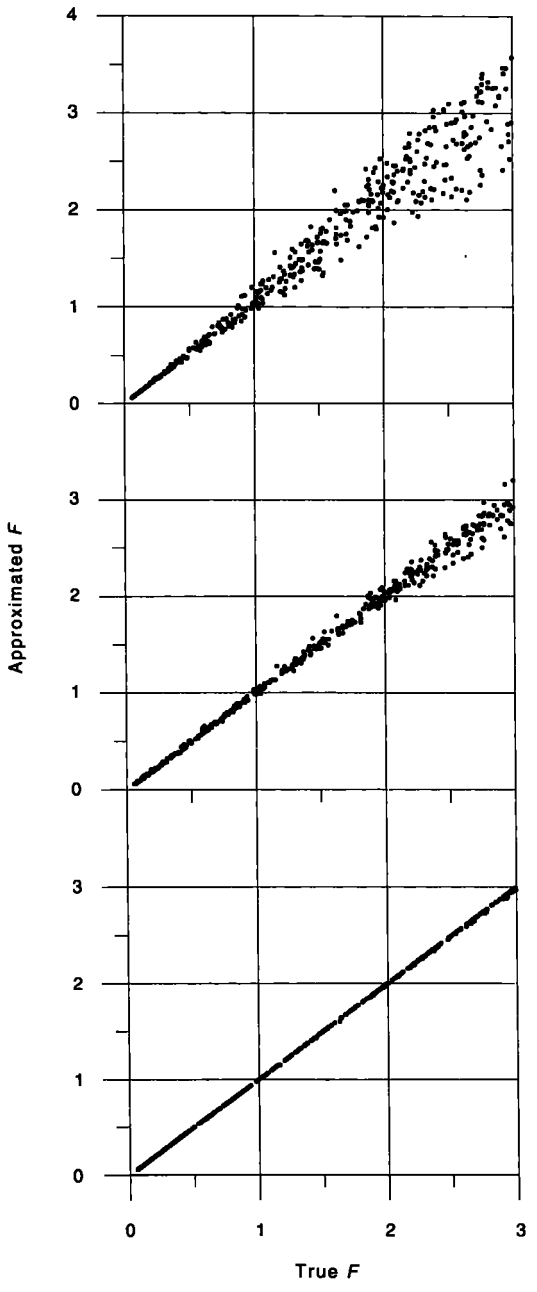

Figure 2

Progression in the approximation to the fishing mortality rate for a catch equation involving a plus group (400 of the 1,000 pairs of approximated and true F are shown). (**Top**) Initial approximation (Eq. 11); (**Middle**) approximation after application of empirical correction function (Eq. 14); (**Bottom**) approximation after one iteration of Newton's Method (Eq. 12).

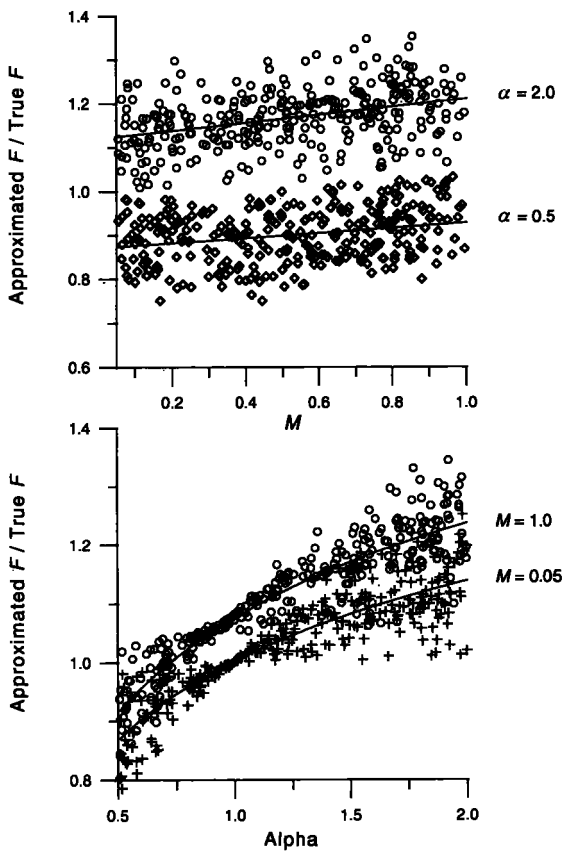

Figure 3

Example of visual analysis to determine the shape of reasonable empirical correction functions. (**Top**) Values of the ratio of initial approximated F to the true F ($^{A}F/^{T}F$) as a function of M for two levels of α, with a linear fit; (**Bottom**) $^{A}F/^{T}F$ values as a function of α for two levels of M, with a logarithmic fit. See text for definition of parameters.

Summary

The results of our study indicate that the empirical correction in Equation 13 applied to Pope's (1972) approximation (Eq. 7) provides an accurate solution to the catch equation that does not involve a plus group (Table 1, Case I). Over a wide range of plausible fishing and natural mortality values, Equation 7 gives errors of up to 8% whereas the empirical correction gives errors of up to 3%. These errors are practically eliminated after one iteration of Newton's Method following the empirical correction.

For the catch equation that involves a plus group, the initial approximations analogous to Pope's (1972) approximation may not be very accurate. For a wide range of plausible mortality values, errors of up to 68% and 35% are obtained from the use of Equations 10 and 11, respectively (Table 1, Case II). The empirical correction in Equation 14 applied to the approximation in Equation 11 reduces the errors to within 12% of the exact solution. One iteration of Newton's Method following the empirical correction

reduces the errors to under 2%, and a second iteration practically eliminates the errors.

The computational requirements of our approach for obtaining a solution to the catch equation that includes a plus group are small. If errors up to 12% can be tolerated, the initial approximation (Equation 11) and the subsequent empirical correction (Equation 14) can be incorporated into a single formula. One or two additional computations from the application of Newton's Method substantially reduce or eliminate the biases altogether.

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Abstract.—Factors that affect survival and growth of larvae and influence recruitment variability of striped bass, *Morone saxatilis*, were investigated in the Potomac River and Upper Chesapeake Bay from 1987 to 1989. Ages and growth rates of larvae hatched within 3-day periods (cohorts) were estimated from otolith daily increments. Cohort-specific mortality rates were estimated from declines in cohort abundances over time. Temperature strongly affected larval cohort dynamics and potential to recruit. Storm fronts caused water temperature to drop near to or below 12°C, resulting in episodic mortalities of eggs and newly hatched larvae. Cohort-specific growth rates of larvae were variable, ranging from 0.11 to 0.46 mm·d^{-1} in the Potomac and from 0.18 to 0.36 mm d^{-1} in the Upper Bay, and were positively correlated with mean water temperatures. Cohort instantaneous mortalities (d^{-1}) also ranged widely, from Z = 0.05 to 0.92 in the Potomac and from Z = 0.02 to 0.28 in the Upper Bay, but were not correlated with temperature, growth rate, or other measured variables. The medians of cohort G/Z ratios (ratios of weight-specific growth rate to instantaneous mortality rate) and productions of 8.0-mm standard length larvae in each year were positively correlated with juvenile recruitment indices. Larval productions at 8.0 mm also were positively correlated with mean water temperatures because temperature strongly affected larval growth and because of the strong selection for survival of cohorts hatched later in the spawning seasons when water temperatures were consistently >17°C.

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The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay

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Landings of anadromous striped bass, *Morone saxatilis*, along the Atlantic Coast of the United States declined sharply in the 1970's and 1980's owing to overfishing and a series of poor recruitments (Boreman and Austin, 1985). Indices of striped bass recruitments in the Chesapeake Bay vary more than 100-fold (Schaefer et al.[1]). Recruitment levels are established by the juvenile stage, when seine-survey indices correlate with subsequent commercial catches of adults (Goodyear, 1985).

Striped bass spawn in Chesapeake Bay tributaries from April to June, when frequent storms and heavy rainfall cause temperature, river flow, and pH levels to fluctuate. Temperatures experienced by eggs and larvae during the two-month spawning season may range from 10 to 29°C and may have dramatic effects on production, survival, and growth of cohorts. Initiation of spawning in Chesapeake Bay tributaries occurs at 12–18°C when temperatures are increasing rapidly (Olney et al., 1991; Setzler-Hamilton and Hall, 1991; Setzler Hamilton et al.[2]). Rapid drops in temperature to below 12°C are lethal to striped bass eggs and larvae (Bar-

[1] Schaefer, R. K., R. H. Bradford, J. L. Markham, and H. T. Hornick. 1991. Characterization of striped bass stocks in Maryland, p.1–74. *In* H. T. Hornick (project leader), Investigation of striped bass in Chesapeake Bay. US Fish and Wildlife Serv. Fed. Aid Proj. F-42-R-3, MD Dep. Natl. Resour., Tidewater Admin., Annapolis, MD. Available: Maryland Department of Natural Resources, Tidewater Administration, Tawes State Office Bldg., Taylor Ave., Annapolis, MD 20688.

[2] Setzler-Hamilton, E. M., J. A. Mihursky, K. V. Wood, W. R. Boynton, D. Shelton, M. Homer, S. King, and W. Caplins. 1980. Potomac estuary fisheries program, ichthyoplankton and juvenile investigations. 1977 Final Rep. to Maryland Dep. Natl. Resour., Power Plant Siting Program. Univ. of Maryland. Ref. No. [UMCEES]CBL 79-202. Available: University of Maryland Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, 1 Williams St., Solomons, MD 20688.

kuloo, 1967; Doroshev, 1970; Davies, 1973; Morgan et al., 1981). Temperature also strongly influences the development of striped bass eggs and larvae (Polgar et al., 1976; Rogers et al., 1977; Rogers and Westin, 1981), the generation times and turnover rates of zooplankton prey (Heinle, 1969), and probably the consumption rates of predators.

Previous studies on striped bass recruitment variability averaged larval growth and mortality rates over multiple daily cohorts (Polgar, 1977; Dey, 1981; Kernehan et al., 1981; Uphoff, 1989; Setzler-Hamilton et al.[2]; Low[3]), thereby obscuring relationships with environmental factors. The presence of daily increments on otoliths allows accurate estimates of larval hatchdates, growth, and survival (Methot, 1983; Crecco and Savoy, 1985; Essig and Cole, 1986; Leak and Houde, 1987; Rice et al., 1987, a and b) and can provide valuable information about processes and factors affecting recruitment. Otolith-based estimates of larval growth histories have the potential to detect the subtle changes in growth rate that could cause order-of-magnitude variability in recruitment (Houde, 1987, 1989).

We hypothesize that variable striped bass recruitments are generated by variable growth and survival rates of cohorts of larvae produced during a two-month period of highly variable environmental conditions. In a related paper (Rutherford et al.[4]), results of a 3-year study of striped bass larval dynamics in the Potomac River and Upper Chesapeake Bay indicated that, on an annual basis, mean larval abundances and ratios of weight-specific growth to instantaneous mortality rate (G/Z) are correlated with juvenile recruitment indices, indicating that recruitment level is fixed during the larval stage. In this study, an analysis of daily cohort abundances and vital rates (growth and mortality) of larvae is presented to describe the process of year-class formation in striped bass and to illustrate how a primary variable, temperature, affects cohort-specific growth, survival, and recruitment potential in Chesapeake Bay.

Methods

Striped bass eggs and larvae were sampled every 3 to 7 days from April to June in the Potomac River (1987–89) and in the Upper Bay (1988 and 1989; Rutherford et al.[4]; Fig.1). Methods of collecting ichthyoplankton and environmental data are described briefly below and in more detail by Houde and Rutherford[5] and Rutherford et al.[4]

Eggs and larvae were collected in duplicated oblique tows of a paired 60-cm bongo sampler, with 333- and 505-μm mesh nets. Larval abundances based upon the 505-μm mesh size, 60-cm bongo net samples were adjusted for extrusion of some small larvae by comparing catches with those in a paired, 333-μm mesh net. Adjustments for gear avoidance by large larvae were made by comparing 60-cm net catches during daylight with a series of night catches made on the same dates, and by comparing the 60-cm net catches with those in a 2-m^2 Tucker trawl at the same stations and dates. The 2-m^2 Tucker trawl (700-μm mesh) also provided collections of large larvae in late-season surveys. Riverwide abundances of eggs and larvae were estimated by multiplying mean station densities by the river volume which those stations represented. Egg abundances also were estimated and are reported in Houde and Rutherford (1992).

Densities of zooplankton that were potential prey for striped bass larvae were estimated from pumped water samples taken near-bottom, mid-depth, and at surface and filtered onto a 53-μm screen, or taken by vertical lifts of a 20-cm, 53-μm mesh plankton net. Temperature, pH, and salinity were measured at all stations on each survey. Conductivity was measured in 1988 and 1989, and turbidity and light were measured in 1987 and 1988. In addition, gauges at dams upstream of the spawning grounds provided continuous temperature measurements.

Larval ages, hatch dates, and age-frequency distributions were estimated from an analysis of sagittal otolith increments, which are deposited daily in striped bass (Jones and Brothers, 1987; Secor and Dean, 1989). Otolith increments were counted at least three times and the mean of the last two counts was used to estimate age. Aged larvae were grouped into 3-day periods (cohorts) based upon their hatch dates. Three-day cohorts were designated because 95% confidence intervals around mean ages indicated a 3-day range. Otolith-aged larvae from represented length classes were used to estimate the proportions of unaged larvae in each 0.5-mm length class that fell within each one-day age class. These 'age-length

[3] Low, A. F. 1986. Striped bass egg and larva survey in the Sacramento-San Joaquin estuary. California Dep. Fish and Game. Unreferenced report, November 1986. Available: California Department of Fish and Game, Stockton, CA 95205.

[4] Rutherford, E. S., E. D. Houde, and R. M. Nyman. Relation of larval stage growth and mortality to recruitment of striped bass, *Morone saxatilis*, in the Chesapeake Bay. Unpubl. manuscr.

[5] Houde, E. D., and E. S. Rutherford. 1992. Egg production, spawning biomass and factors influencing recruitment of striped bass in the Potomac River and Upper Chesapeake Bay. Rep. to Maryland Dep. Natl. Resour., Contract No. CB89-C01-003. Univ. Maryland, Center for Environmental and Estuarine Studies, Ref. No. [UMCEES]CBL 92-017, 313 p. Available: University of Maryland Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, 1 Williams St., Solomons, MD 20688.

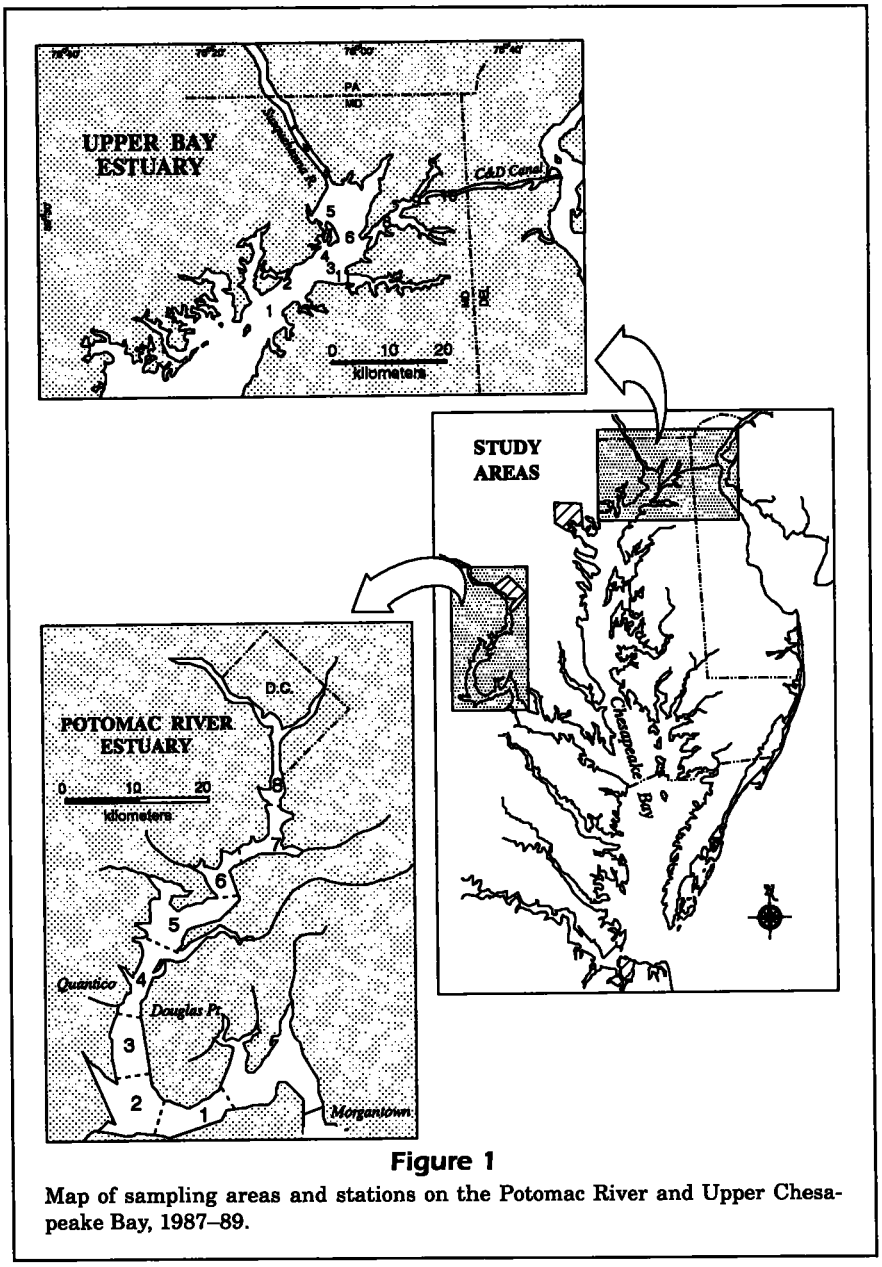

Figure 1

Map of sampling areas and stations on the Potomac River and Upper Chesapeake Bay, 1987–89.

keys' were developed separately for the Potomac River and the Upper Bay in each year, except 1988, from regressions of otolith-derived ages on larval lengths. In 1988, otoliths of the few larvae collected in the Upper Bay were unreadable because of poor preservation; consequently the age-length key for 1988 Potomac River larvae was also applied to Upper Bay larval catches.

Larval growth rates were estimated by using both an "aggregate sample" method and a back-calculation method. In the aggregate sample method, standard lengths and otolith-derived ages of the entire sample of otolith-aged larvae were analyzed for each cohort in each of the areas. Growth rates of larvae were derived from exponential regressions of larval lengths on ages. Exponential models also were fit to the mean back-calculated length at age of larvae to estimate back-calculated, cohort-specific growth rates.

We backcalculated fish lengths at age by using the "biological intercept" method (Campana, 1990). This method does not assume that larvae from all cohorts or populations have the same body length and otolith-radius relationship; thus it allows reconstruction of individual growth histories, which was desirable for our analysis. This method, and other back-calculation methods that assume a constant proportional-

ity between otolith growth and fish growth (Fraser-Lee, simple regression), will accurately estimate fish length if somatic growth is relatively fast (Secor and Dean, 1989, 1992; Campana, 1990). If somatic growth is slow, otoliths of slow-growing fish may grow relatively fast, causing the relationship between fish and otolith growth to be nonlinear and thus bias back-calculated growth-rates (Geffen, 1982; Reznick et al., 1989; Secor and Dean, 1989, 1992; Campana, 1990). To minimize biased estimates of back-calculated lengths at age for 1988 Potomac River larvae, when growth effects were significant and body size and otolith-size relationships were nonlinear, we followed the recommendation of Campana and Jones (1992) and $\log_e$-transformed fish lengths and otolith radii before applying the biological intercept method.

Larval cohort mortality rates were estimated from the exponential declines in cohort abundances at age obtained from 60-cm sampler catches. In 1989, larval mortality rates in the Potomac River and Upper Bay may have been overestimated when only larvae collected in the 60-cm sampler were considered. Striped bass spawned later in 1989 than in 1987 or 1988, and abundances of cohorts hatched in late May probably were under-represented in 60-cm sampler collections that were completed by 1 June. Better estimates of cohort mortality rates in 1989 were obtained by combining larval collections from the 60-cm sampler with those from the 2-m^2 Tucker trawl made from late May to mid-June.

A "Pareto" model, which assumes that mortality rate declines in relation to age (Lo, 1986), was compared with the linear model, and the model with the lowest residual sum of squares was selected to estimate each cohort's mortality rate. The ratio of instantaneous growth-in-weight rate to instantaneous mortality rate (G/Z), an index of larval production (biomass), was estimated for each cohort. Instantaneous growth-in-weight rates were derived from back-calculated growth-in-length rates by using a length-weight relationship (Houde and Lubbers, 1986) for striped bass larvae. Abundances of cohorts at 8 mm standard length (SL) were estimated to index their potential contributions to recruitment. At 8–10 mm, striped bass larvae reach the postfinfold larval stage (Fritsche and Johnson, 1980; Olney et al., 1983), when development of fins and increased swimming ability facilitates feeding as well as ability to avoid predators and can result in a decline in mortality rate. Abundances, and growth and mortality rates of larval cohorts were analyzed in relation to environmental variables by using stepwise multiple regression analysis (SAS, 1988) to identify factors associated with variable recruitments.

Results

Spawning, egg and larval abundances, and zooplankton densities

Striped bass spawned during April and May, generally during periods of rising temperatures (Figs. 2 and 3). The major spawning peak in the Potomac

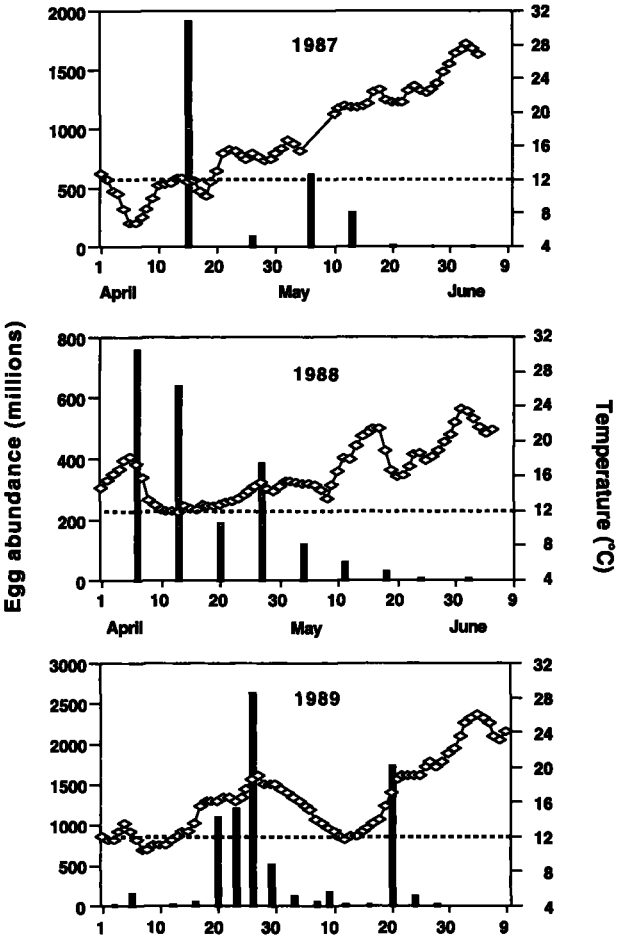

Figure 2

Riverwide egg abundances (millions) of striped bass, *Morone saxatilis*, estimated on each survey date (bars) during the three years of sampling effort in the Potomac River, 1987–89. Water temperatures recorded at Wilson Bridge during the spawning season also are given (open diamonds). The 12°C critical low temperature, at which 100% egg and larval mortality may occur, is indicated by the dotted line. Note that the Y-axis scales change among years.

River occurred in April in each year when temperatures rose to ≥12°C. A secondary spawning peak was evident in mid-May of 1989 (Fig. 2). Peak spawning in the Upper Bay occurred in mid to late May when water temperatures rose to ≥14°C (Fig. 3). Striped bass egg abundances were highest in 1989 and lowest in 1988 (Rutherford et al.[4]). Egg abundances were nearly an order of magnitude higher in the Upper Bay in 1989 (77.9 eggs·m^{-2}) than in 1988 (8.2 eggs·m^{-2}) but did not differ significantly (P>0.05) among years in the Potomac (25.1 to 73.5 eggs·m^{-2}).

Episodic mortalities of striped bass eggs and larvae occurred in the Potomac River in each year after spring storms, which caused flood conditions and sharp declines in river temperatures to or below the 12°C lethal limit. In 1987, a storm on 16–17 April and a subsequent temperature drop caused complete mortality of all striped bass eggs and larvae, effectively eliminating >50% of the season's egg production (Rutherford et al.[4]). Although no larvae survived that event, relatively minor spawning (Fig. 2) that occurred later, combined with favorable conditions for larval growth and survival, resulted in higher mean larval abundances than those in 1988 or 1989 (Rutherford et al.[4]). After 20 April 1987, Potomac River temperatures increased steadily and were both warmer and less variable than in 1988 or 1989. Temperature profiles in the Upper Bay were similar in both 1988 and 1989 (Fig. 3). In the Upper Bay, the initial order of magnitude difference between years in egg abundance was maintained through the larval stage (Rutherford et al.[4]).

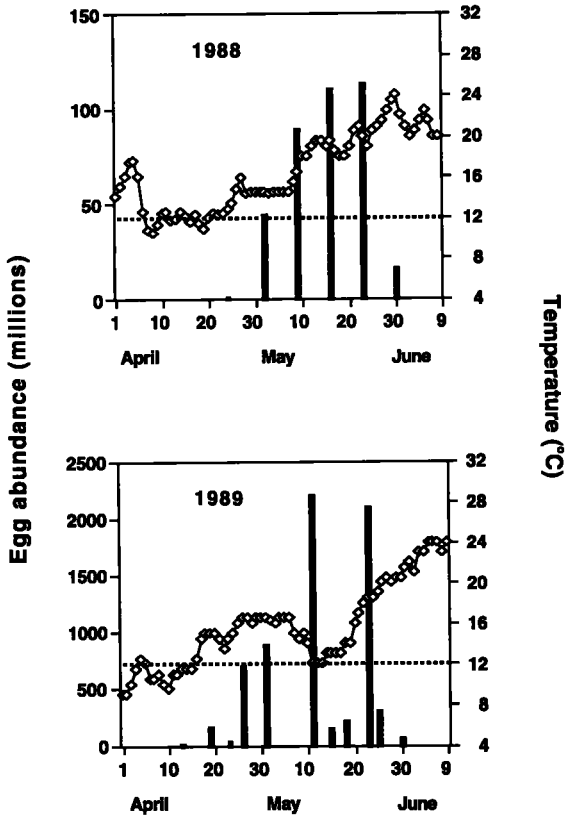

Figure 3

Areawide egg abundances (millions) of striped bass, *Morone saxatilis*, estimated on each survey date (bars) during the two years of sampling effort in the Upper Bay, 1988–89. Water temperatures recorded at Conowingo Dam during the spawning season also are given (open diamonds). The 12°C critical low temperature, at which 100% egg and larval mortality may occur, is indicated by the dotted line. Note that the Y-axis scales change between years.

Mean densities of zooplankton that were potential prey for larval striped bass cohorts during the first 5–20 days posthatch were highest in the Potomac River in 1987 and in the Upper Bay in 1989 (Fig. 4). Densities of copepod nauplii, *Eurytemora affinis*, and rotifers (including *Brachionus*, *Asplanchna*, *Synchaeta*, *Polyarthra*), in particular, which are initial prey of striped bass larvae (Takacs, 1992; Beaven and Mihursky[6]), were higher in the Potomac River in mid to late May 1987 than in 1988 or 1989.

Growth

Body length and otolith-radius relationships Larval length was strongly correlated with otolith size in each year (Table 1). The best regression relationships were linear for most cohorts with adequate sample sizes (n>4) and ranges in body length. Exponential models provided better fits for some Potomac River cohorts, and age was a significant covariate of otolith size for two cohorts in 1989 (Table 1).

With few exceptions, cohorts hatched early in the season, experienced mean temperatures <17°C during the first 20 days posthatch, and had relatively larger otoliths per unit body length than did cohorts hatched when temperatures were warmer. Differences in body length-otolith radius relationships among Potomac River striped bass cohorts were significant in 1989 (ANCOVA; P<0.001), but not in 1987 (ANCOVA; P>0.10) or 1988 (ANCOVA; P>0.20).

Growth rates Growth rates of striped bass larval cohorts, estimated by both aggregate and back-calculated methods, indicated that growth varied sea-

[6] Beaven, M. S., and J. A. Mihursky. 1979. Food and feeding habits of larval striped bass: an analysis of larval striped bass stomachs from 1976 Potomac estuary collections. Ref. No. [UMCEES]CBL 79-045, Chesapeake Biological Laboratory. Available: University of Maryland Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, 1 Williams St., Solomons, MD 20688.

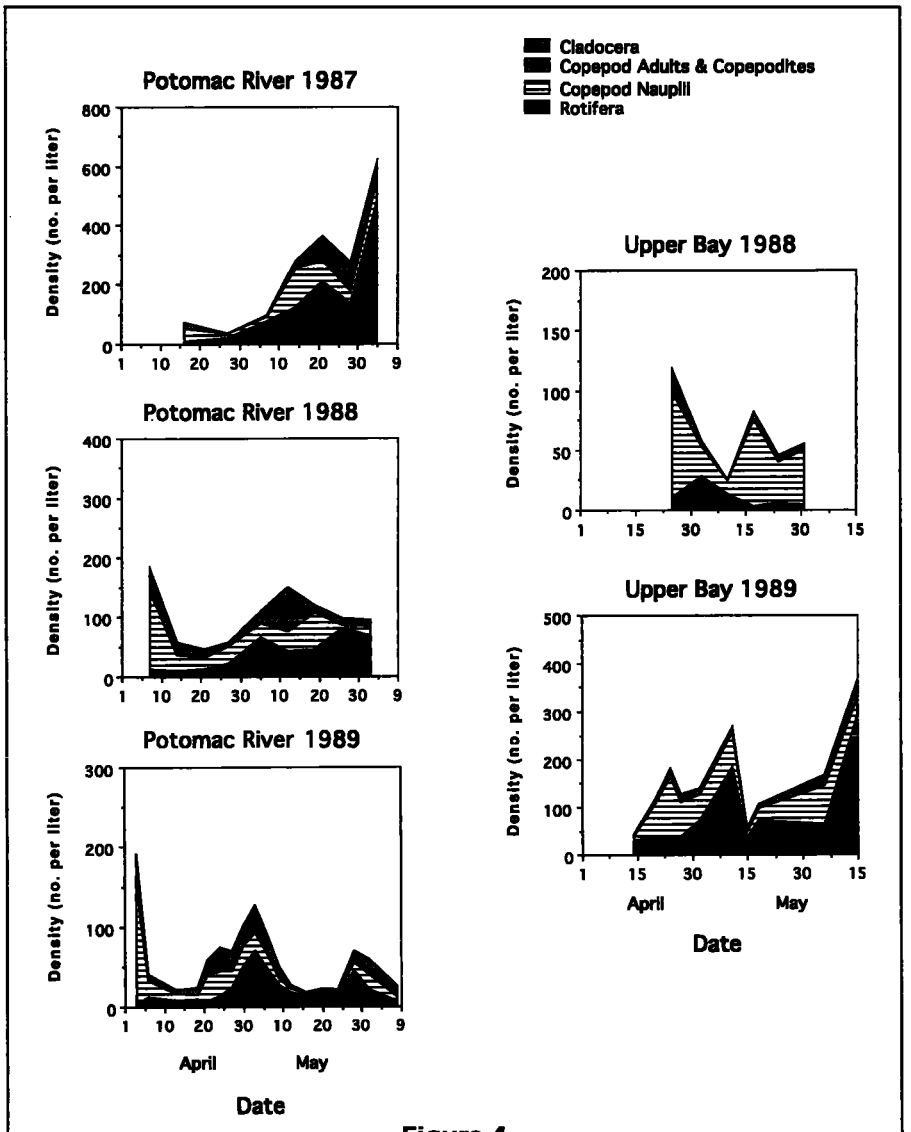

Figure 4

Densities of zooplankton taxa estimated on each survey date in the Potomac River, 1987–89 and Upper Bay, 1988–89. Note that Y-axis scales change among years and areas.

sonally in each year. Cohorts that hatched late in the season grew relatively fast, had shorter stage durations (Fig. 5), and reached larger sizes by 20 days posthatch than did cohorts hatched earlier, which grew in cooler water. Both methods of estimating growth produced similar rates, although estimates from the aggregate method were much less precise (Figs. 5 and 6).

Aggregate-sample growth rates of Potomac River larvae differed significantly among 3-day cohorts in 1987 and 1989. Cohort growth rates, after adjusting for age by analysis of covariance, tended to increase as the season progressed (Fig. 5). They ranged from 0.19 to 0.44 $mm \cdot d^{-1}$ (mean ±95% CI=0.26 ±0.06 $mm \cdot d^{-1}$) in 1987, from 0.11 to 0.22 $mm \cdot d^{-1}$ (mean=0.18 ±0.04 $mm \cdot d^{-1}$) in 1988, and from 0.12 to 0.53 $mm \cdot d^{-1}$ (mean=0.24 ±0.07 $mm \cdot d^{-1}$) in 1989. The regression fits of growth data were poor for some Potomac River cohorts in 1988. The predicted mean lengths at 20 days posthatch of larval cohorts were variable, ranging from 7.7 to 11.7 mm SL in 1987, from 6.9 to 9.0 mm SL in 1988, and from 4.8 to 11.1 mm SL in 1989. Predicted ages at 8.0 mm SL also varied, ranging from 13.2 to 21.2 days in 1987, from 14.2 to 23.8 days in 1988, and from 14.6 to 31.6 days in 1989 (Fig. 5).

Table 1

Body length (SL mm)-otolith radius (R, μm) regressions for larval cohorts of striped bass, *Morone saxatilis*, larvae, collected from the Potomac River, 1987–89 and the Upper Bay, 1989. "A" = Age (days posthatch); SE = standard error, n = sample size.

Cohort Hatch Date	Regression	SE (slope)	r^2	n	$P <$
Potomac River 1987					
22 April	SL = 6.220 + 0.029R			2	
25 April	Ln(SL) = 1.907 + 0.003R	<0.001	0.99	7	0.001
28 April	SL = 6.025 + 0.022R	0.004	0.99	3	0.010
1 May	SL = 5.160 + 0.033R	0.001	1.00	5	0.001
4 May	SL = 5.922 + 0.024R	0.004	0.95	4	0.050
7 May	SL = 5.221 + 0.024R	0.002	0.98	8	0.001
10 May	SL = 5.235 + 0.033R	0.003	0.96	9	0.001
13 May	SL = 5.057 + 0.032R	0.002	0.95	25	0.001
16 May	SL = 4.900 + 0.031R	0.002	0.94	21	0.001
19 May	SL = 4.856 + 0.036R	0.002	0.97	20	0.001
Potomac River, 1988					
12 April – 3 May	SL = 4.491 + 0.035R	0.002	0.92	32	0.001
6 May	SL = 3.233 + 0.045R	0.003	0.94	9	0.001
9 May	SL = 5.919 + 0.026R	0.004	0.88	10	0.001
12 May	SL = 4.658 + 0.036R	0.005	0.86	11	0.001
15 May	SL = 5.683 + 0.029R	0.012	0.37	12	0.050
18 May	SL = 5.693 + 0.030R	0.008	0.51	16	0.001
Potomac River, 1989					
17–26 April	SL = 6.068 + 0.021R	0.002	0.97	9	0.001
29–April	SL = 5.976 + 0.024R	0.002	0.94	10	0.001
2 May	SL = 6.531 + 0.021R	0.006	0.76	11	0.001
5 MayS	SL = 3.13 + 0.18A + 0.01R	0.058, 0.004	0.78	27	0.001
8 May	SL = 3.69 + 0.02A + 0.13R	0.002, 0.034	0.97	19	0.001
11 May	SL = 5.331 + 0.031R	0.003	0.90	19	0.001
14 May	Ln(SL) = 1.914 + 0.003(R)	<0.001	0.80	14	0.001
17 May	SL = 4.513 + 0.034R	0.003	0.83	25	0.001
20 May	SL = 5.027 + 0.029R	0.003	0.77	28	0.001
23–26 May	SL = 6.606 + 0.015R	0.005	0.44	14	0.01
Upper Bay, 1989					
8 May	SL = 3.890 + 0.037R	0.002	0.97	6	0.001
11 May	SL = 4.400 + 0.035R	0.001	0.99	6	0.001
14 May	SL = 5.058 + 0.031R	0.003	0.95	11	0.001
17 May	SL = 5.058 + 0.032R	0.000	0.97	34	0.001
20 May	SL = 5.402 + 0.027R	0.002	0.92	50	0.001
23 May	SL = 5.146 + 0.028R	0.003	0.91	47	0.001
26 May	SL = 4.507 + 0.032R	0.003	0.90	17	0.001
29 May	SL = 4.750 + 0.029R	0.003	0.93	14	0.001
1 June	SL = 4.211 + 0.038R	0.005	0.97	4	0.050
4 June	SL = 3.393 + 0.056R			2	

The larval growth rate estimates of Upper Bay cohorts in 1989 did not differ significantly ($P>0.25$) and ranged from 0.21 mm·d^{-1} for larvae hatched on 8 May to 0.32 mm·d^{-1} for larvae hatched on 1 June (Fig. 5). The mean cohort growth rate was 0.25 ±0.03 mm·d^{-1}. Predicted mean lengths at 20 days posthatch of the 9 cohorts ranged from 7.4 to 10.0 mm. Predicted ages at 8.0 mm SL ranged from 14.8 to 22.1 days (Fig. 5).

Back-calculated growth rates of 5–20 days posthatch larval cohorts from the Potomac River ranged from 0.19 to 0.46 mm·d^{-1} in 1987 (mean=0.27 ±0.05 mm·d^{-1}), from 0.18 to 0.34 mm·d^{-1} in 1988 (mean=0.23 ±0.04 mm·d^{-1}), and from 0.11 to 0.36 mm·d^{-1} in 1989 (mean=0.23 ±0.04 mm·d^{-1}) (Fig. 6). Back-calculated growth rates of Upper Bay larvae, available only for 1989, ranged from 0.18 to 0.36 mm·d^{-1} (mean=0.26 ±0.03 mm·d^{-1}) (Fig. 6).

The differences in back-calculated growth rates among cohorts in each year resulted in different predicted lengths at 20 days posthatch. There were

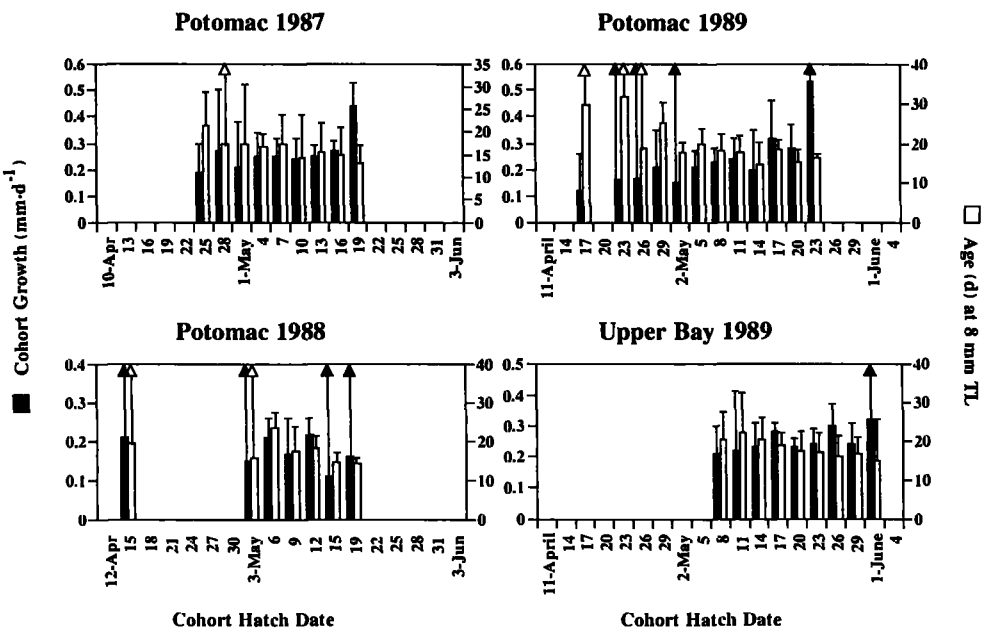

Figure 5

Cohort-specific, mean growth rates (closed bars, mm·d^{-1}) and stage durations (open bars, age (d)) of 8-mm-total-length striped bass, *Morone saxatilis*, larvae by hatch date in the Potomac River, 1987–89, and Upper Bay, 1989. Growth rates determined by the aggregate-sample method. Error bars indicate 95% confidence intervals.

among-cohort differences of up to 4.8 mm, 3.0 mm, and 4.6 mm in the Potomac in 1987, 1988, and 1989, respectively, and differences of 3.4 mm in the Upper Bay. Maximum among-cohort differences in predicted ages at 8.0 mm were 11, 9, and 21 days in the Potomac River in 1987, 1988, and 1989, respectively, and 10 days in the Upper Bay (Fig. 6).

Back-calculated (r^2=0.67; Fig. 7) and aggregate-sample (r^2=0.62) cohort growth rates were strongly and positively related to the mean water temperatures in which larvae grew. A stepwise multiple regression analysis indicated that densities of copepod nauplii, a probable prey of first-feeding striped bass larvae, were negatively correlated with larval growth rate, presumably because nauplii densities were higher near the beginning of the spawning season (Fig. 4) when growth rates were lowest. No other environmental variable, including densities of other zooplankton taxa or densities of striped bass eggs, larvae, or *Morone* spp. larvae (striped bass plus white perch, *M. americana*), explained a significant proportion of the variance in larval growth rates.

Individual growth rate variability Growth histories of larvae *within* each cohort that presumably had experienced the same suite of environmental conditions indicated that some individuals grew much faster than average. Within a cohort, individual larvae differed by as much as 5.0 mm in length at 20 days posthatch (Upper Bay 1989, cohort hatched 23 May), and by up to 0.33 mm·d^{-1} in growth rate (Upper Bay 1989, cohort hatched 23 May). The maximum individual growth rate of a 3-day cohort was 68% higher than the mean. Variance (%CV) in larval growth rate or lengths at 20 days posthatch within-cohorts did not differ significantly (Kruskal-Wallis; P>0.10) among years. There was no significant relationship between variance in growth rate within-cohorts and the mean (P>0.20) or variance (P>0.50) in daily temperatures experienced by cohorts.

Evidence for size-selective mortality operating on larger individuals was detected in back-calculated growth histories of striped bass larval cohorts examined from the Potomac River, 1987 and 1989, and Upper Bay, 1989. To detect evidence of size-selective mortality, lengths at capture of larval cohorts collected early in the spawning season were compared with back-calculated lengths at age of older larvae in the same cohort collected later in the season. For 10 of the 11 cohorts examined from the Potomac River 1987 (n=5), 1989 (n=4), and the Upper Bay 1989 (n=2), mean back-calculated lengths at 10 and 20

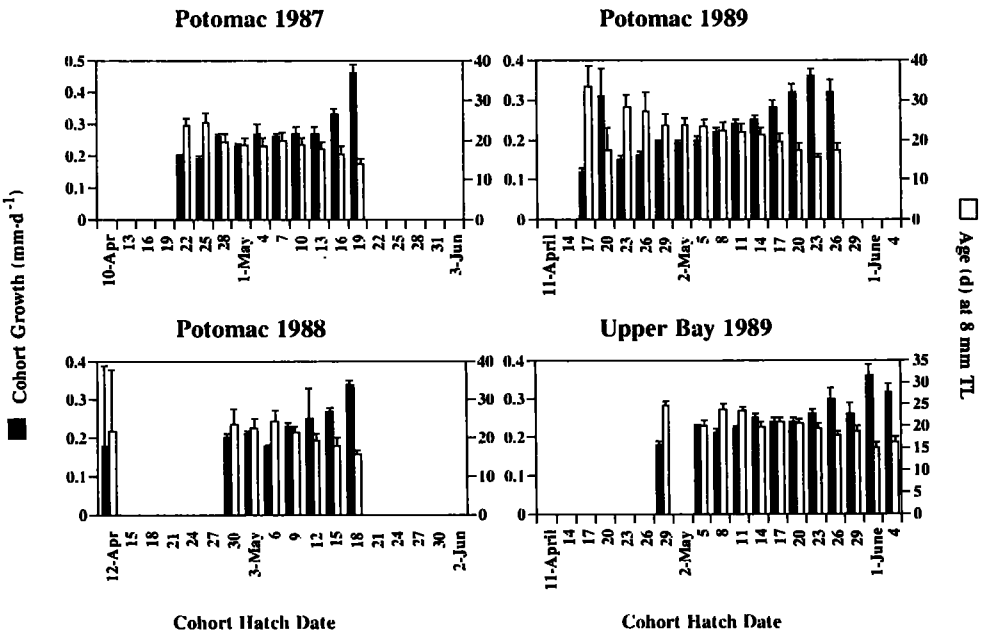

Figure 6

Cohort-specific, mean growth rates (closed bars, mm·d^{-1}) and stage durations (open bars, age (d)) of 8-mm-total-length striped bass, *Morone saxatilis*, larvae by hatch date in the Potomac River, 1987–89, and Upper Bay 1989. Growth rates determined by the back-calculation method. Error bars indicate 95% confidence intervals.

days posthatch of surviving larvae collected late in the season were significantly smaller (t-test; $P<0.001$) than lengths at capture of larvae collected earlier, suggesting that within-cohort mortality had acted selectively against larger individuals. There was no significant difference ($P>0.50$) in mean lengths at age between early and late-captured larvae in the eleventh cohort.

Analysis of back-calculated larval growth histories suggested that in most Potomac River and Upper Bay cohorts in each year, small larvae are able to compensate for slow initial growth and obtain the same length at >20 days posthatch as larvae with large initial lengths. Lengths at capture were compared with back-calculated growth rates in the period 5–20 days posthatch and with calculated lengths at 5, 10, 15, and 20 days posthatch. For all cohorts (n=38) in all years, there either was no significant relationship between length at capture and their back-calculated lengths at 5 and 10 days posthatch, or the relationship was negative, i.e. within a cohort, some of the smallest-sized larvae at capture had relatively large back-calculated lengths at 5 and 10 days posthatch.

For individuals hatched early in the spawning season (in 14 of 15 cohorts), there also was no relationship between lengths at capture and back-calculated lengths at 15 and 20 days posthatch. However, larvae that hatched later in the season (in 20 of 23

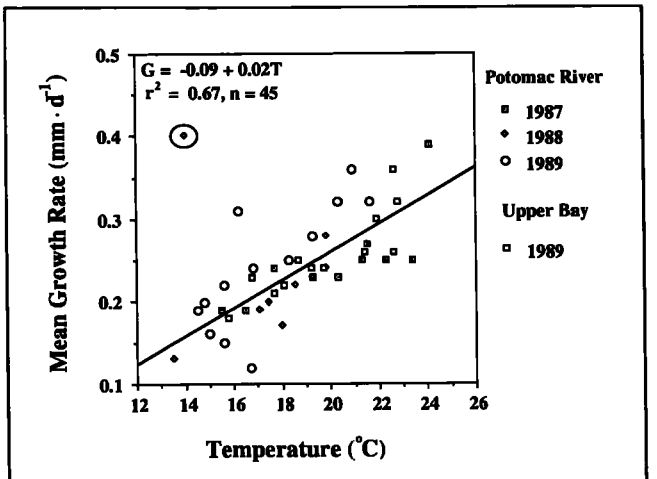

Figure 7

Back-calculated growth rates (G, mm·d^{-1}) of striped bass, *Morone saxatilis*, larval cohorts, in relation to river temperatures (T, °C) averaged over the first 20 days posthatch in the Potomac River, 1987–89, and Upper Bay, 1989. Circled data point is an outlier and was not included in the regression.

cohorts), when mean water temperatures were relatively warm, had within-cohort growth rates and back-calculated lengths at 15 and 20 days posthatch that were positively related to lengths at capture. For example, individual growth rates of Upper Bay larvae hatched on 14 May 1989 were not correlated with their lengths at capture, suggesting that there had been compensation for slow (or fast) growth at earlier ages (Fig. 8). Growth rates of Upper Bay larvae hatched on 23 May were positively related to their lengths at capture, indicating that initial growth rate differences had been maintained (Fig. 8).

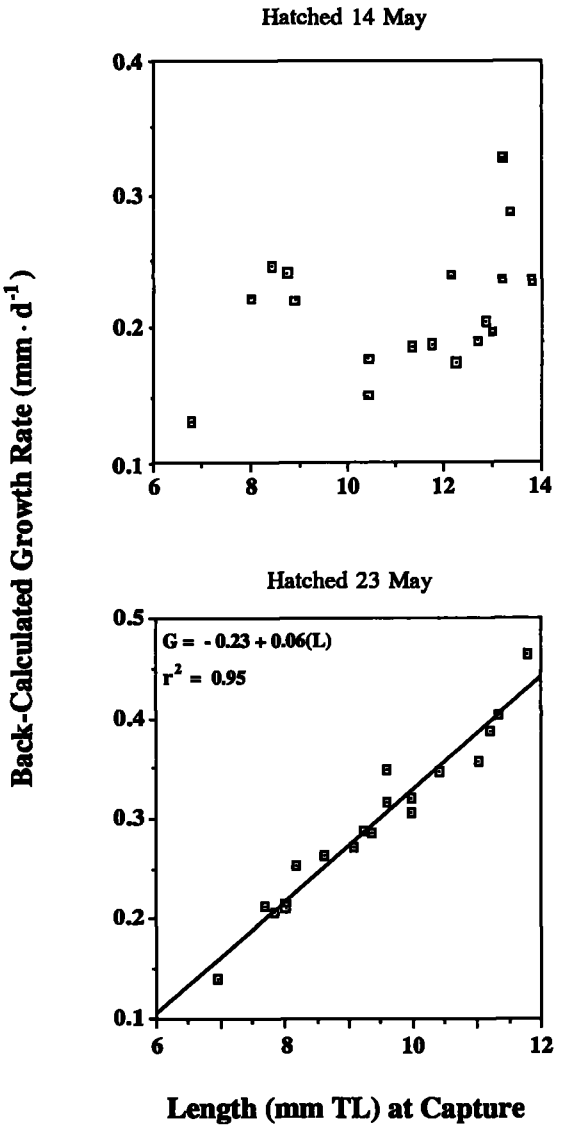

Figure 8

Back-calculated growth rates (G, mm·d^{-1}) of individual striped bass, *Morone saxatilis*, larvae in relation to total lengths (TL) at capture for Upper Bay larvae hatched on 14 May and on 23 May 1989.

Mortality rates

Mortality rates of larval cohorts, which were highly variable, were not correlated with initial cohort abundance, growth rate, growth rate variability, stage duration, or with any measured environmental factor. Mean mortalities of cohorts from the Potomac River ranged from 21.9 to 23.9% d^{-1} in 1987–89. Cohort-specific mortality rates of Potomac River larvae ranged from Z = 0.05 to 0.92·d^{-1} in 1987, from Z = 0.05 to 0.46·d^{-1} in 1988, and from Z = 0.07 to 0.60·d^{-1} in 1989 (Fig. 9). Temporal trends indicated that mortality rates of Potomac River larvae were high in April, lowest in early May, and apparently highest in late May (Fig. 9). Larval cohort mortality rates in the Upper Bay during 1989 ranged from Z = 0.02 to 0.28·d^{-1}, averaging 11% d^{-1}. There was no obvious temporal trend in Upper Bay larval mortality rates (Fig. 9).

G/Z ratio

The cohort-specific G/Z ratios were variable, but the median values in each year were positively related to apparent year-class strength in the Potomac River. The median ratios were 1.03 in 1987, 0.41 in 1988, and 0.94 in 1989 (Fig. 9). The Upper Bay median G/Z ratio in 1989 was 1.70, a value higher than the Potomac River median ratios because cohort mortality rates generally were lower in the Upper Bay. In the Potomac River, the cohort-specific G/Z ratios in each year were generally highest for cohorts hatched during the last week of April and the first 10 days of May, when growth rates were increasing and mortality rates were lowest (Fig. 9).

Productions of late-stage larvae

Summed cohort productions of 8-mm-SL larvae were correlated with juvenile recruitment indices in the Potomac River, suggesting that recruitment is essentially fixed during the larval stage. Summed cohort productions were 190 million in 1987, 23 million in 1988, and 109 million in 1989. Potomac River indices of juvenile recruitment for those years were 6.4, 0.4, and 2.2, respectively (Schaefer et al.[1]). Summed production of Upper Bay larval cohorts at 8 mm SL was 47 million in 1989. The Upper Bay's juvenile recruitment index in 1989 was 19.4, a value 1.6 times higher than the long-term mean (Schaefer et al[1]).

Most cohorts with larvae surviving to 8 mm SL were hatched late in the spawning season when egg production was low or declining (Fig. 10). In the Potomac River, cohort productions of 8-mm-SL larvae were positively

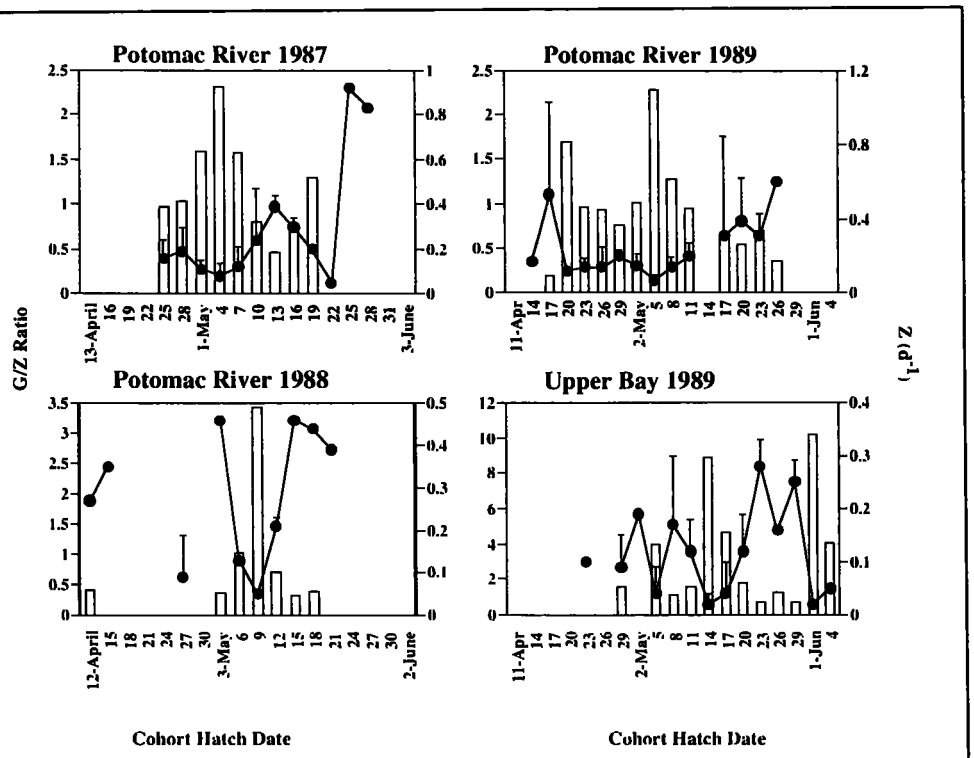

Figure 9

Cohort-specific, instantaneous daily mortality rates (Z, •) and G/Z ratios (bars) of striped bass, *Morone saxatilis*, larvae by hatch date from the Potomac River, 1987–89, and Upper Bay, 1989. Error bars on mortality rates indicate 1 standard error of mean. Scale on Y-axis varies among panels.

related to cohort growth rates, and in the Upper Bay to water temperature. The relationships are

for the Potomac River,

$$\text{Ln}(N_8) = 6.43 + 31.43\ (G);\ (r^2=0.22,\ P<0.01,\ n=28)$$

for the Upper Bay,

$$\text{Ln}(N_8) = -36.65 + 4.75\ (T) - 0.11\ (T^2);\ (r^2=0.91,\ P<.001,\ n=12)$$

where $\ln(N_8)$ is the $\log_e$-transformed cohort production of 8-mm-SL larvae, G=cohort growth rate (mm·d^{-1}) and T=mean temperature experienced by the cohort from 5–20 days posthatch. In the Potomac River, cohort larval productions at 8 mm SL also tended to be positively correlated with water temperature, but the correlation was not significant ($P>0.10$). In the Upper Bay, cohort production at 8 mm SL was not correlated with cohort growth rate ($P>0.50$).

The relative cohort abundances of larvae collected in the 2-m^2 Tucker trawl on the last day of the sampling season, standardized to 8-mm-SL productions from cohort-specific stage durations and survival rates, provided another indicator of larval survival and potential recruitment. Tucker trawl catches in the Potomac River on 4–5 June 1987 indicated that surviving cohorts, which potentially contributed to recruitment, were hatched from 22 April to 19 May and that most survivors hatched in the 22–25 April and 4–10 May periods (Fig. 11A). In 1988, Tucker trawl catches on 2–3 June indicated that surviving 8-mm larvae were hatched from 3 May to 30 May and that most hatched during the 18–24 May period (Fig. 11B). The 1989 Tucker trawl index of 8-mm larvae on 8–9 June suggested that, while some potential recruits were hatched in every 3-day period from 20 April to 23 May (Fig. 11C), cohorts hatched on 20 April and 14 and 17 May accounted for >80% of the total numbers represented on 8 June.

Relative cohort abundances of 8-mm larvae in the Upper Bay on the last sampling day in 1989 (14 June) indicated that potential recruits were hatched from 5 May to 4 June (Fig. 11D). More than 80% of these larvae were hatched between 14 May and 1 June.

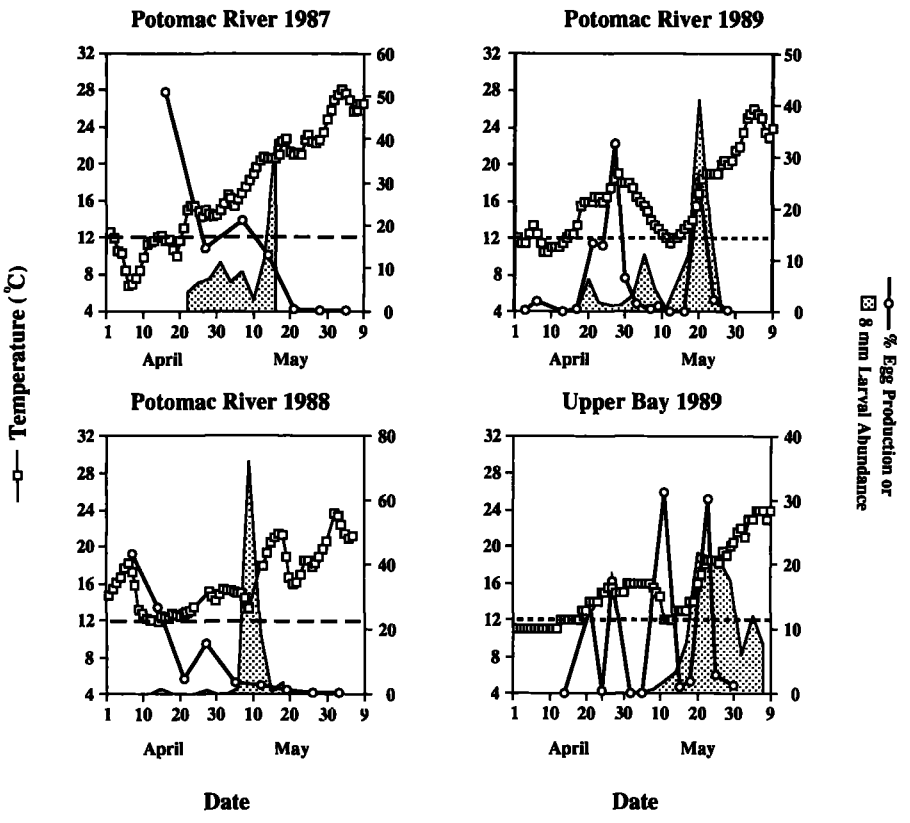

Figure 10

River temperatures at Wilson Bridge (Potomac River) or Conowingo Dam (Susquahanna River, Upper Bay), percent egg production, and percent estimated abundances by hatch dates of striped bass, *Morone saxatilis*, larvae at 8.0 mm TL in 3-day cohorts from the Potomac River, 1987–89, and Upper Bay, 1989. Larval abundances at 8.0 mm were estimated from 60-cm net samples in the Potomac River, 1987–88, and from 60-cm net and 2-m^2 Tucker trawl catches in the Potomac and Upper Bay, 1989. The dashed line indicates the 12°C critical low temperature at which 100% mortality of egg and yolk-sac larvae may occur.

Discussion

Temperature, larval survival, and growth

Estuarine nurseries of anadromous fishes are dynamic environments, subject to fluctuating and sometimes unpredictable conditions for survival and growth. Striped bass spawn in the freshwater, tidal regions of mid-Atlantic estuaries during the spring months, a transitional season when average temperatures are increasing rapidly, but erratically, from 10 to 25°C. Frequent storms and flood conditions can cause temperatures to drop quickly to lethal or near-lethal levels. The unusually wide range of temperatures to which striped bass eggs and larvae may be exposed suggest that temperature may be a factor controlling growth rate, stage duration, and survival rate.

Our results confirmed that temperature affects larval growth rates and stage durations. Except for observed episodic mortalities associated with temperature drops to or below the 12°C lethal limit, more subtle, direct effects of temperature on mortality rates could not be demonstrated. Despite episodic mortalities which impacted early-spawned cohorts, favorable temperatures during the latter half of spawning seasons resulted in significant potential recruitment from small cohorts of late-spawned eggs. The relatively good potential recruitments in the Potomac River, 1987, and Upper Bay, 1989, were derived from modest, late-season spawning that produced fast-growing larvae in environments where water temperatures were steadily increasing.

The application of otolith-ageing to identify 3-day cohorts and to derive cohort-specific growth and

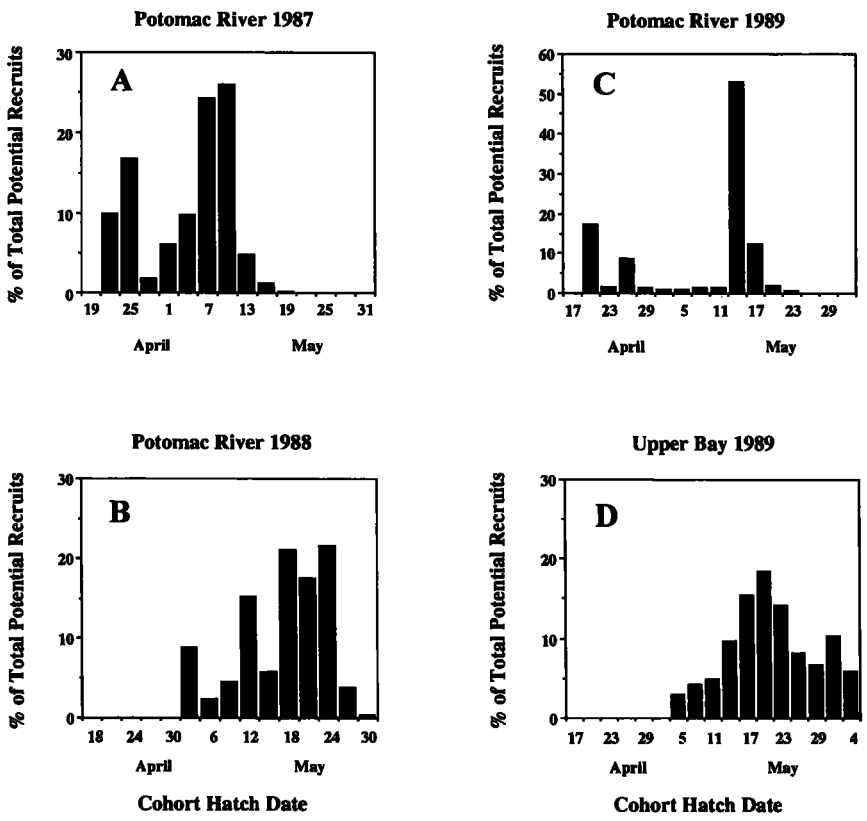

Figure 11

Relative abundance of striped bass, *Morone saxatilis*, larval cohorts by hatch date, collected in the $2m^2$ Tucker trawl from the Potomac River, 1987–89, and Upper Bay, 1989: (**A**) 4–5 June, 1987; (**B**) 2–3 June, 1988; (**C**) 8–9 June, 1989; (**D**) 14–15 June, 1989. Relative abundance estimates were adjusted for age-specific survival differences among cohorts.

mortality rates of striped bass larvae allowed us to examine the larval stage dynamics of a species that develops over a broad temperature range. Past research on survival and growth of striped bass larvae has depended upon modal-length analyses, assumed hatch dates, and assumptions about developmental stages and stage-durations to make inferences about early-life dynamics and recruitment potential (Polgar, 1977; Dey, 1981; Uphoff, 1989; Low[3]). Our otolith microstructure analysis demonstrated that in 1987–89, only a few cohorts contributed significantly to Potomac River and Upper Bay recruitments and that successful cohorts were hatched late in the season, grew relatively fast, and had short larval-stage durations.

The critical role of temperature, particularly its potential to cause episodic mortalities and its effect on growth, has been identified in previous research on striped bass. For example, Dey (1981) and Kernehan et al. (1981) argued that year-class failures in the Hudson River and Upper Chesapeake Bay, respectively, were caused by low-temperature events. Positive relationships between mean growth rates of larval striped bass year classes and temperatures have been reported for the Potomac River (Setzler-Hamilton et al., 1980; Martin and Setzler-Hamilton[7]), the Choptank River (Uphoff, 1989), the Hudson River (Dey, 1981), and the Sacramento-San Joaquin Rivers (Low[3]).

In our study, it was clear that estimated productions of cohorts at 8 mm SL were positively correlated with cohort-specific growth rates. Growth rates, in turn, were strongly and positively correlated with

[7] Martin, F. D., and E. M. Setzler-Hamilton. 1983. Assessment of larval striped bass stock in the Potomac estuary. Final report to U.S. National Marine Fisheries Service. Ref. No. [UMCEES]CBL83-55, 37 p. Available: University of Maryland Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, 1 Williams St., Solomons, MD 20688.

temperature, supporting the conclusion that late-hatched cohorts, which grew faster than average, were the principal contributors to striped bass recruitments in 1987–89. Although cohort-specific mortality rates were not significantly related to cohort growth rates or to any measured variable, the annual median *G/Z* ratios (i.e. for combined cohorts) were positively correlated with the juvenile recruitment index (Rutherford et al.[4]). This result indicated that, while the relationships between growth and survival of individual cohorts are complex and difficult to demonstrate, the effect of reduced stage duration on larval production and on potential recruitment did occur and could be discerned when cohorts were aggregated. Chesney's (1993) simulation model of Potomac River striped bass larval dynamics in 1987 predicted good growth and survival of cohorts hatched late in the season when temperatures and prey densities were high. Research on other species of temperate estuarine and freshwater fishes also has demonstrated that survival and recruitment are highest for fast-growing cohorts (Rice et al., 1987a; Crecco and Savoy, 1985; Jennings et al., 1991), supporting Cushing's (1973) "single-process" concept, in which fast larval-stage growth enhances recruitment success through shortened stage durations.

Differences in mean temperatures between 1987, 1988, and 1989 in the Potomac River may have led to significant differences in production of 8.0-mm-SL larvae, owing solely to effects on stage duration. Egg productions in the Potomac River were approximately 10 billion in 1987 and 1989, and 6.7 billion in 1988 (Houde and Rutherford, 1992). If larval mortality rate had been equal in all years (e.g. Z=0.25), then the mean effect on larval growth and stage duration of the observed 4.0°C higher mean temperature in 1987, compared with 1988 or 1989, could have accounted for a 3.7-fold greater production of 8.0-mm-SL larvae in 1987 than in 1988, and a 2.6-fold greater production in 1987 than in 1989. Our estimated production of 8.0-mm-SL larvae in 1987 was 7.8 and 1.7 times higher, while the juvenile recruitment index (Schaefer et al.[1]) was 16.0 and 2.9 times higher in 1987 than in 1988 or 1989, respectively. Although our results point to temperature as a critical factor and Chesney's (1993) simulation supports this view, other simulation models of major factors thought to influence year-class strengths of Potomac River striped bass suggest that temperature may be less important than maternal size or zooplankton prey abundance (Cowan et al., 1993), or, under special circumstances, than contaminant levels (Rose et al., 1993).

Previous studies of striped bass larval growth have suggested that growth rates are correlated with temperatures in the spawning areas (Dey, 1981; Uphoff, 1989; Low[3]). However, most growth estimates were based upon modal analysis of larval lengths and, consequently, may have been inaccurate. Without benefit of otolith-increment analysis, among-cohort variability in growth rates was unevaluated. In the Choptank River of the Chesapeake Bay, Uphoff (1989) estimated annual mean growth rates of striped bass larvae to be 0.37–0.56 mm·d^{-1} from 1981 to 1986, on the basis of length-frequency distributions. These rates were higher than our mean estimates in the Potomac and Upper Bay and were higher than growth rates of all except 4 of the 46 cohorts that we analyzed, although temperature ranges and prey densities are similar in these Chesapeake Bay tributaries. Larval cohort growth rates that were backcalculated from otolith-aged, juvenile striped bass from South Carolina also were higher (0.35 to 0.68 mm·d^{-1}; Secor, 1990) than most of our estimates. However, larvae from South Carolina experience mean temperatures during spawning and larval development that are 3–5°C higher than temperatures encountered by Chesapeake Bay striped bass (Secor, 1990). Growth rates of Hudson River larvae in 1973–76, estimated from the weekly seasonal increases in larval mean lengths from a designated, arbitrary hatch date until 15 July, were 0.10 to 0.20 mm·d^{-1} (Dey, 1981). Those rates were lower than our mean rates and generally lower than our individual cohort growth rates, even though mean temperatures encountered by larvae in the Hudson and Chesapeake estuaries are similar. Mean annual growth rates of larvae in the Sacramento-San Joaquin River system, estimated for the 1968–86 period from modes in length-frequency distributions, ranged from 0.29 to 0.46 mm·d^{-1} (Low[3]). These rates are higher, on average, than our mean rates, although many cohorts of Chesapeake Bay larvae grew at rates in this range.

Individual growth rate variability

Our analysis of individual larval growth histories to detect evidence of growth compensation and size-selective mortality may have been compromised somewhat by the back-calculation method. Campana's (1990) biological intercept method will provide accurate estimates of mean back-calculated growth rate even in the presence of a "growth effect" but will tend to linearize individual growth rates and mask growth inflections (Campana, 1990; Secor and Dean, 1992). Campana (1990) demonstrated through simulation analysis that time-varying changes in the body length-otolith radius relationship caused by increasing somatic growth rate could result in underestimated lengths at earlier ages and overestimated lengths of older larvae, giving the appearance of com-

pensatory growth by slow-growing individuals and selective mortality against larger individuals within cohorts.

If our analysis of size-selective mortality against larger individuals is correct, it may be that larger individuals experienced higher mortality because their faster swimming speeds increased contact rates with predators. Recent experimental studies (Litvak and Leggett, 1992; Monteleone and Houde, 1992; Pepin et al., 1992; Cowan and Houde, 1993) indicate that as larvae grow and encounter different predator fields, their probability of being encountered and eaten by some predators may increase, resulting in a higher mortality rate for larger individuals than for smaller individuals. Effects of selective mortality against smaller individuals may not become apparent until later in the larval stage (e.g. Post and Prankevicius, 1987), because it takes time for differences in growth rate to result in significant differences in size that would lower vulnerability to predation (Rice et al., 1993).

We had hypothesized that mortality would select against smaller individuals within cohorts, and that cohorts with higher mean growth rates and highly variable growth rates would contribute more potential recruits than cohorts with lower and less variable growth rates (Pepin, 1989; DeAngelis et al., 1991; Rice et al., 1993). In our study, although mortality rates may have been highest for the largest or fastest-growing individuals, cohorts contributing most to recruitment in each year were those hatched near the end of the spawning season and which had higher but not more variable growth rates than those hatched earlier. For example, in the Potomac River, 1989, late-hatched cohorts grew, on average, nearly twice as fast from 5–20 days posthatch as did early-hatched cohorts. The high productions of late-hatched, fast-growing cohorts suggest that stage duration, by reducing the time that larvae experience high mortalities, is more important than body size alone in determining potential recruitment of striped bass.

Prey densities and growth

The failure to detect any significant influence of prey density on cohort-specific growth, survival, or abundance at 8.0 mm SL was surprising, because mean zooplankton densities were highest in the Potomac River and Upper Bay in years when mean growth rates, *G/Z* ratios and recruitment indices were highest (Rutherford et al.[4]). Laboratory, pond, and model-simulation studies have demonstrated repeatedly that growth and survival of striped bass larvae increase as prey density increases (Miller, 1976; Eldridge et al., 1981; Rogers and Westin, 1981; Houde and Lubbers, 1986; Tsai, 1991; Chesney, 1989, 1993; Daniel[8]). The strong and dominant effect of temperature upon larval growth rate may have obscured effects of prey density at the cohort-specific level. In the Potomac River, 1987, and in the Upper Bay, 1989, when highest growth rates were observed, zooplankton densities were highest, increased as the season progressed, and were correlated positively with temperature. In the Potomac River, 1988 and 1989, zooplankton densities were lower and not significantly correlated with temperature, yet growth rates of striped bass cohorts at similar temperatures did not differ significantly from the cohort rates in 1987, indicating that the temperature effect dominated.

It is possible that the failure to demonstrate a relationship between temperature-adjusted, cohort-specific growth rates and prey densities was an artifact that resulted from backcalculating growth rates from mostly older larval survivors. Growth rates of these larvae conceivably may have been higher than growth rates of larvae that died (Miller et al, 1988; Pepin, 1989) and may have obscured impacts of low prey densities on growth. Although for most cohorts, back-calculated growth rates and lengths at age of larvae collected early in the season were not significantly lower than rates and lengths at age of larvae caught later, this result might be artifactual, because of the potential bias on back-calculated growth histories caused by nonlinear changes in the otolith-body size relationship.

We believe that recruitment level of striped bass in Chesapeake Bay is essentially set by the abundances of cohorts that survive to 8.0 mm SL. Relative productions at 8.0 mm SL and abundances in the juvenile surveys conducted 50 to 100 days later were strongly correlated in the Potomac River and Upper Bay (Rutherford et al.[4]). Other evidence that striped bass recruitment is fixed during the early postlarval stage (8.0–10.0 mm TL) has resulted from research on striped bass in the Choptank River (Uphoff, 1989) and from the Sacramento-San Joaquin system (Low[3]). Our results demonstrate that not only is recruitment potential fixed by 8.0 m SL but that relatively few daily cohorts contribute significantly to recruitment in most years. The success of particular cohorts is strongly dependent upon the temperature regime that larvae experience between hatch and 8.0 mm SL. Examination of intraseasonal differences in cohort-specific growth, survival, and pro-

[8] Daniel, D. A. 1976. A laboratory study to define the relationship between survival of young striped bass (*Morone saxatilis*) and their food supply. Calif. Dep. Fish and Game, Anadromous Fisheries Branch, Admin. Rep. 76-1, Sacramento, CA, 13 p. Available: California Department of Fish and Game, Anadromous Fisheries Branch, Sacramento, CA.

duction has provided a clearer picture of the processes influencing striped bass recruitment than could have been obtained solely from analysis of interannual differences in larval vital rates and abundances.

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Abstract.—Condition of field-caught walleye pollock, *Theragra chalcogramma*, larvae was assessed by using a measurement of midgut cell height that reliably diagnosed the nutritional status of laboratory-reared walleye pollock. The midgut cell height was simple to measure on histological sections. Several correction factors were developed for applying the midgut measurement to a field study. These included regressions to characterize change in larval length associated with net collections of various elapsed times and with fixation in several types of preservatives. The response of midgut cell height to field collection procedures also was tested. The field study indicated larval walleye pollock were starving in the Shelikof Strait, Gulf of Alaska, in 1991. At some stations up to 40% of the larvae were in poor condition. Larvae were most vulnerable to starvation for 2 weeks following the day of first-feeding.

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Condition of larval walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska assessed with histological and shrinkage indices*

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In 1986 the Fisheries-Oceanography Coordinated Investigations (FOCI) program of the Alaska Fisheries Science Center and the Pacific Marine Environmental Laboratory began studying the biological and physical processes controlling variability in recruitment of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska. Each year, large concentrations of adult walleye pollock aggregate in the Strait and spawn in late March and early April, producing dense patches of eggs at a depth of about 200 m; there is little variation in the timing or location of the spawning (Kim and Kendall, 1989; Kendall and Picquelle, 1990; Schumacher and Kendall, 1991). After hatching, larvae rise to the upper waters where they may be transported along the Alaska Peninsula, off the shelf to the southeast, or be retained in eddies (Vastano et al., 1992). It is believed that the area young pollock occupy during the larval stage is important for their survival (Schumacher and Kendall, 1991). Assessing the nutritional condition of larval pollock collected from different areas in Shelikof Strait should aid in determining whether food availability is one of the factors influencing survival and recruitment.

A variety of indices have been applied to examine the nutritional condition of larval fish. However, for most of the indices, the response rate of the variable to changes in feeding is unknown. Thus, it is difficult to apply the index to estimate mortality rates in the field and subsequent recruitment variability. Histological analyses have yielded valuable information on larval nutritional condition (O'Connell, 1976; Theilacker, 1978; O'Connell and Paloma, 1981; Sieg, 1992). Furthermore, starvation-induced mortality rates for histological studies have been estimated by combining the results from histological condition assessments with information on growth and starvation rates (Theilacker, 1986; Theilacker and Watanabe, 1989). Using the estimate of starvation-induced mortality rates, attempts have been made to calculate the proportion of natural mortality due to starvation mortality (Hewitt et al., 1985; Owen et al., 1989).

Preliminary studies on larval walleye pollock have revealed that the height of the midgut mucosal cells are sensitive to starvation, decreasing in height measurably over time

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as food is withheld. A decrease in the thickness of the intestine during starvation has been noted for other fishes (Kostomarova, 1962; Nakai et al., 1969; Umeda and Ochiai, 1975; Ehrlich et al., 1976; O'Connell, 1976; Theilacker, 1978, 1986; Kashuba and Matthews, 1984; Boulhic and Gabaudan, 1989; Oozeki et al., 1989; Theilacker and Watanabe, 1989; McFadzen et al., 1994), including the Altantic cod, *Gadus morhua* L. (Yin and Blaxter, 1987), which is closely related to walleye pollock. In this study we describe a midgut cell height index for laboratory-reared walleye pollock.

Shrinkage of larval fish captured in a net and preserved aboard ship differs from that observed in the laboratory (Blaxter, 1971; Theilacker, 1980, 1986; Hay, 1981; McGurk, 1985; Jennings, 1991). The amount a larva shrinks may be dependent on size, the duration of handling (time in the net and how soon after death it is preserved), and the type of preservative used. Preservative and gear-related (net) shrinkage have been examined for larvae of a variety of fish species (Theilacker, 1980, 1986; Hay, 1981, 1982; Fowler and Smith, 1983; Tucker and Chester, 1984; McGurk, 1985; Radtke, 1989; Kruse and Dalley, 1990; Jennings, 1991; Hjorleifsson and Klein-MacPhee, 1992). Jennings (1991) found that the magnitude of shrinkage differed among species and concluded that a correction factor for each species must be determined. To relate our laboratory observations to the field, we derived shrinkage indices for larval walleye pollock subject to net treatment and several preservatives. To determine the utility of the midgut cell height index in the field, larval walleye pollock were collected in Shelikof Strait, and their nutritional condition was assessed from experimental results.

Methods

Laboratory rearing

Adult walleye pollock were collected from Shelikof Strait, Gulf of Alaska, in April of 1990 to 1993. The fish were spawned aboard ship and the fertilized eggs flown to Friday Harbor Laboratories, University of Washington, in 1991 and to the Alaska Fisheries Science Center in 1990, 1992, and 1993. We raised the larvae in 120-L black fiberglass circular tanks with clear plastic covers and used a 16-h daylight cycle. Seawater temperatures were maintained at 6°C which are typical in May in Shelikof Strait when larvae initiate feeding (Kendall et al., 1987). Each year there were two treatments: one tank contained larvae into which prey were added (fed tank), the second contained larvae that were never offered prey (starved tank). Prey consisted of rotifers, *Brachionus plicatilis*, at 10/mL and copepod nauplii, *Acartia* sp., at a minimum of 1–2/mL. Rotifers were raised on algal diets of *Isochrysis galbana* and *Pavlova lutheri*, which are high in unsaturated fatty acids (Nichols et al., 1989). The dinoflagellate, *Katodinium rotundatum*, was also added as prey for the rotifers and copepods. Ammonia levels were low for both treatments (<0.4 ppm). We sampled larvae from both the fed and starved tanks every day or every other day.

Calibration of midgut cell height

For the histological analysis, walleye pollock larvae were preserved in either Bouin's solution which was replaced with 70% ethanol 24 to 48 h later or in Z-Fix (solution of 10% formalin with zinc and buffers added[1]). Larvae were processed with standard histological procedures; they were dehydrated in a butyl alcohol series, embedded in paraffin wax, serially sectioned at 6 μm in the sagittal plane, and stained with hematoxylin and eosin. We measured the mucosal cell height of the anterior dorsal portion of the midgut at 400× magnification (Fig. 1). This area was chosen because it exhibits little gut folding which can make the midgut cell height measurement too variable to be useful. We measured three to six neighboring cells (with clearly defined nuclei, basement membrane, and microvilli) from the top of the basement membrane to the top of the microvilli and recorded the average height.

Fixative effects on larval length

To determine the shrinkage of larvae placed directly into preservative (laboratory shrinkage), we measured the standard length (SL, tip of upper jaw to end of notochord, to nearest 0.08 mm) of live larvae sampled from the fed tank and placed them individually into Bouin's solution, 5% formalin, Z-Fix, or 95% ethanol. Bouin's solution was changed to 70% ethanol 24 to 48 h later. Final size of larvae was determined one year after preservation. Final size of ethanol-fixed larvae was measured in distilled water; larvae preserved in the other fixatives were measured in the fixative.

Net-treatment and subsequent fixative effects on larval length

To examine the effect of net treatment on larval length, a larva was sampled from the fed tank and its standard length was measured. It was then placed in a small net and submerged in a tank of 6°C seawater that recirculated through the net to simulate a towed sam-

[1] Anatech, Ltd., Battle Creek, MI.

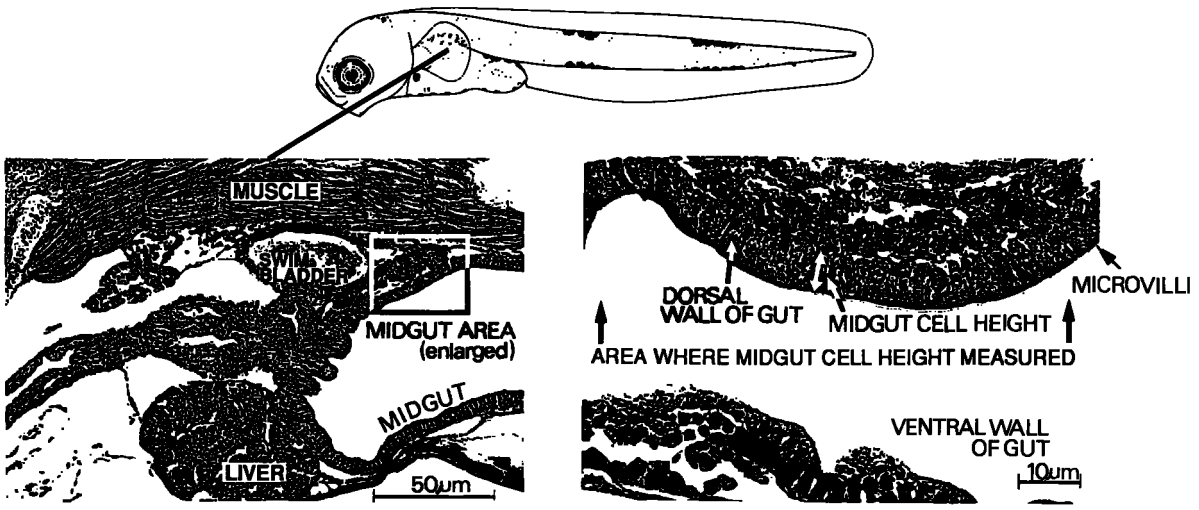

Figure 1

The location where the midgut cell height measurement was taken in larval walleye pollock, *Theragra chalcogramma*. The left photomicrograph shows a sagittal section of the midgut and surrounding organs (larva 8 d after hatch, 4.88 mm SL in Bouin's fixative); the right photomicrograph shows the area where midgut cell height was measured (larva 12 d after hatch, 5.68 mm SL in Bouin's fixative).

pling net (Theilacker, 1980). The larva was remeasured after 5 minutes. The final measurement was taken at 10, 15, or 20 min, and then the larva was placed into Bouin's, Z-Fix, or 5% formalin. For additional shrinkage due to preservation, larvae were remeasured from 1 month to 1 year after they were preserved.

Change in midgut cell height due to fixative and net treatment

Two fixatives used to preserve field-collected larvae were compared to determine their effect on the height of the midgut cells. The effect of Bouin's solution and Z-Fix was compared by sampling 10 fish daily from the fed tank and preserving 5 in Bouin's solution and 5 in Z-Fix. To determine whether the height of the midgut cells changed as larval length decreased during the net shrinkage experiment, one group of 20 larvae was measured and placed directly into Z-Fix while a second group of 20 was measured, net-treated, and then preserved in Z-Fix.

Data analysis

Data were analyzed by using SAS (SAS, Inc. 1988), SYSTAT (Wilkinson, 1988), and Minitab (Ryan et al., 1985) computer software. Simple linear regression analysis was used to derive equations to adjust larval size for shrinkage. ANOVA was used to compare the midgut cell height of starved and fed larvae of the same size. Midgut cell height of starved larvae reared in 1991 and 1993 was compared with midgut cell height of fed larvae reared in 1991 and 1992 (in 1992, no starved larvae were sampled for midgut measurement, and in 1993, midgut was not measured for fed larvae). Years were used as independent treatments to avoid pseudoreplication (Hurlbert, 1984).

Field collections

Larval walleye pollock were collected for histology from stations located throughout the Shelikof Strait, Gulf of Alaska, during two cruises in the spring of 1991 (Fig. 2). The area sampled covered the entire spawning area in the Strait (Kendall and Picquelle, 1990). Collections were made with a 60-cm bongo net equipped with a 333-µm mesh and solid cod end, which were retrieved vertically from 70 m in about 7 minutes. Because larval fish tissues deteriorate quickly owing to autolysis (Theilacker, 1978), the net was not washed following a tow, and larvae were quickly sorted on sea water ice and preserved in Bouin's fixative. Earlier laboratory studies conducted with larval walleye pollock indicated they must be preserved within 12 min at 6°C in order to retain cellular integrity.[2]

[2] Theilacker, G. H., S. M. Porter. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115. Unpubl. data.

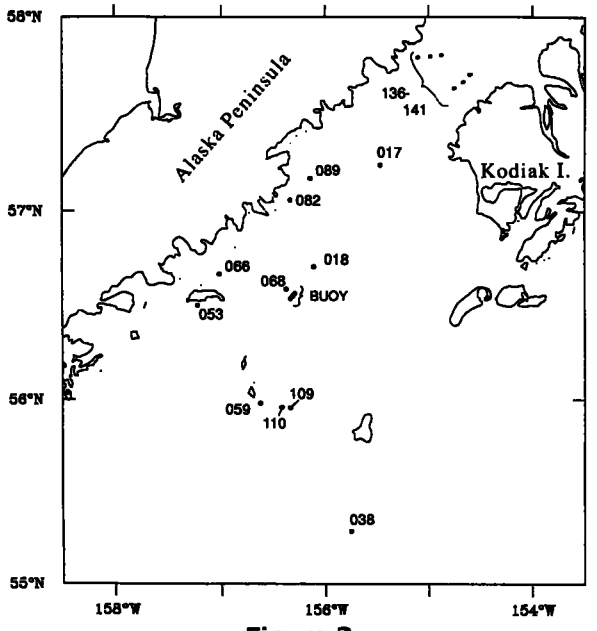

Figure 2

Stations in the Shelikof Strait, Alaska, where walleye pollock, *Theragra chalcogramma*, were collected for histological analysis in April and May 1991.

Table 1

Size of fed and starved treatments of 1991 laboratory-reared larval walleye pollock, *Theragra chalcogramma*. Larvae were reared at 6°C and preserved in Bouin's fixative. Means and standard deviations (SD) are for 5–10 larvae.

	Laboratory-preserved standard length (mm)			
	Fed		Starved	
Days after hatching	mean	SD	mean	SD
8[1]	5.01	0.18	5.01	0.07
9	5.12	0.16	4.93	0.12
10	5.10	0.16	4.98	0.12
11	5.22	0.16	4.93	0.09
12	5.32	0.29	4.91	0.17
13	5.40	0.20	4.90	0.07
14	5.31	0.23	4.93	0.18
15	5.30	0.30	4.80	0.11
16	5.34	0.20	4.91	0.07
17	5.44	0.34	4.82	0.14
19			4.66	0.13
20			4.67	0.09

[1] Day of first feeding.

The standard length of all field larvae was measured before processing for histology. We processed all larvae from each field sample that were preserved within 12 minutes. Larvae were processed in the same manner as the laboratory-raised pollock, and midgut cell height was measured in the same area to determine their past feeding history.

The vertical depth inhabited by most walleye pollock larvae less than 10 mm is between 25 and 37 m (Kendall et al., 1994). Thus we estimated that the elapsed handling time from capture to placement into fixative for the average larva was from 6 to 9 min (3 to 4 min in the net retrieved at 10 m/min plus 3 to 5 min to sort and preserve), or an average of 7.5 minutes. We used 7.5 min as the average handling time to calculate field-collected size.

Results

Laboratory rearing 1991

Walleye pollock hatched at a mean SL of 3.5 mm (laboratory-preserved size), grew at an average rate of 0.12 mm/d, and at 17 d after hatching averaged 5.4 mm SL (Table 1). Larvae started feeding on average ($\bar{x}$±SD) 8 d after hatching (range 7–9 d) at 5.01 ±0.15 mm SL (range 4.56–5.20 mm SL, n=15), and the yolk was completely absorbed about 5 d later. The growth rate from first-feeding on day 8 to 13 d after hatching averaged 0.078 mm/day.

Starved larvae decreased in size as food was withheld for 11 d after first feeding (Table 1). The length of starved larvae began to decrease slowly on day 9 after food was withheld for only 1 day. After 8 d of starvation (16 d after hatching), larvae rapidly decreased in size.

Calibration of midgut cell height

The height of the midgut cells of larvae sampled from the starved and fed tanks and preserved in Bouin's solution ranged from 5 to 34 µm (Figs. 3 and 4). Cells were largest in prefeeding yolk-sac larvae before midgut differentiation was complete and the lumen fully formed. Starving the larvae caused the midgut cells to decrease slowly in height from about 13 µm at first feeding to about 9 µm after starving for 4 days; the average height remained at about 8 µm as food was withheld for an additional 5 days (Fig. 3). We arbitrarily set 11 µm to delimit the fed and starved groups because it gave the best division; this cutoff separated 87.2% of the fed larvae and 80.4% of the starved larvae.

The height of the mucosal cells of the anterior dorsal portion of the midgut increased slightly as fed

larvae grew (Fig. 4). Midgut cell heights of fed larvae were significantly larger (ANOVA, P=0.006, df=1) than those of starved larvae of equal length (4.50–5.49 mm SL), and the same treatment was not significantly different between years (ANOVA, P=0.533, df=2; Table 2). Moreover, the difference in midgut cell heights was attained after food was withheld for 1 day (t-test; P<0.01, df=8; mean fed midgut cell height after 1 d of feeding=12.96 ±1.31 µm, n=5; mean starved midgut cell height after 1 d of starvation = 9.12 ±0.99 µm, n=5; 1991 rearing data).

Midgut cell height was not affected by a net treatment of 7.5 min, the estimated time a larva is handled during field collection. The cell height of fish that were net-treated before being placed into preservative was not significantly different from those placed directly into preservative (t-test; P=0.12; df=30). Additionally, midgut cell height was not influenced by preservative type when Bouin's solution was compared with Z-Fix (t-test; P=0.17; df=80).

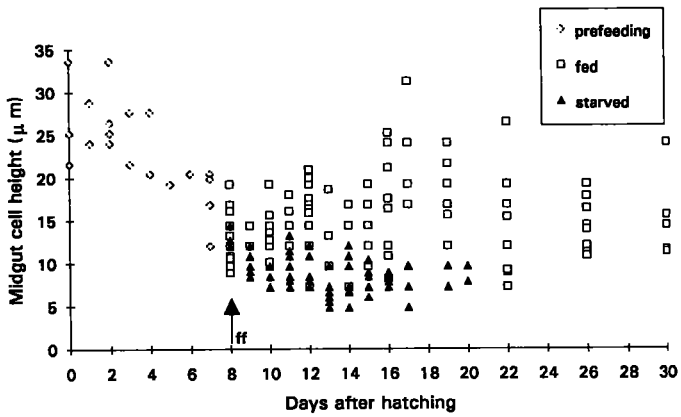

Figure 3

Midgut cell height of laboratory-reared prefeeding, fed, and starved larval walleye pollock, *Theragra chalcogramma*, from hatching to 20 d after hatching. Arrow shows day of first feeding (ff).

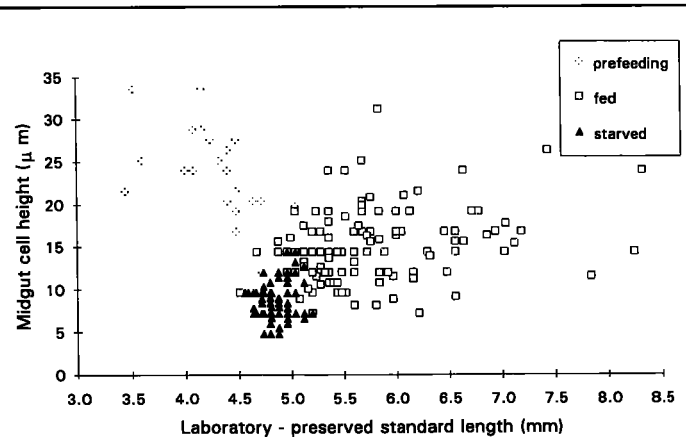

Figure 4

Midgut cell height of laboratory-reared prefeeding, fed, and starved larval walleye pollock, *Theragra chalcogramma*, related to laboratory-preserved standard length in Bouin's fixative.

Fixative effects

Larval walleye pollock shrank an average of 4.7% in Z-Fix, 13% in Bouin's, and 8% in 5% formalin. There was no measurable shrinkage in 95% ethanol. For live larvae placed directly in Z-Fix, shrinkage was a constant proportion of size (Table 3). Laboratory shrinkage in Bouin's and 5% formalin was not a constant proportion of size; in each case the y-intercept of the regression differed significantly from zero (P=0.04 for Bouin's, and P=0.001 for 5% formalin). Smaller larvae shrank proportionately more than larger larvae in both preservatives (Fig. 5A; Table 3). For example, in using the regression equations in Table 3, the decrease in size of 5-mm-SL larvae preserved in Bouin's was 15% and in 5% formalin was 9%, whereas the decrease in size of 7-mm-SL larvae in Bouin's was 12% and in formalin was 7%. However, there was no observed shrinkage of larvae preserved in 95% ethanol. In fact, the average larva increased slightly in size, about 1% for 5-mm-SL larvae and 3% for 7-mm-SL larvae (Table 3).

Net-shrinkage effects

Larvae shrank an average of 7% after a 5-min net treatment, 14% after 10 min, 17% after 15 min, and 22% after 20 min; initial sizes ranged from 4.48 to 9.90 mm SL (Table 3), and sizes after net treatment ranged from 3.76 to 9.48 mm SL. Length after net treatment was linearly related to initial standard length (net time=0) for each treatment period (Fig. 5B; Table 3). Analysis of covariance (ANCOVA) showed that it was possible to interpolate a 7.5-min regression (needed for field procedures; see Field Collections in Methods section; Table 3) between the 5- and 10-min net-shrinkage regressions; the slopes of the two regressions were not significantly different (P=0.785) and the lines were not coincident (P<0.01).

Table 2

Midgut cell height of fed and starved laboratory-reared larval walleye pollock, *Theragra chalcogramma*, at 6°C.

		Midgut cell height (μm)				
		Fed		Starved		
Size class (mm)[1]	year	*n*	mean (SD)	*n*	mean (SD)	*P*
4.50–5.49	1991	34	14.06 (3.62)	57	8.89 (2.23)	0.006
	1992	31	14.53 (4.01)			
	1993			20	8.16 (1.76)	
5.50–5.99	1991	13	18.78 (5.68)			

[1] Adjusted to equal Bouin's laboratory preserved size.

Table 3

Regression equations for adjusting the size of larval walleye pollock, *Theragra chalcogramma*, exposed to various conditions that cause shrinkage.

Shrinkage type	Live SL range (mm)	*n*	Regression equation	r^2
1a) Laboratory shrinkage in Bouin's[1]	5.27–7.06	47	live SL = 0.617+1.033(laboratory preserved SL)	0.88
1b) Laboratory shrinkage in Z-Fix[2,3]	5.20–7.60	56	live SL = 1.047(laboratory preserved SL)	0.99
1c) Laboratory shrinkage in 5% formalin[4]	4.20–20.00	42	live SL = 0.344+1.021(laboratory preserved SL)	0.98
1d) Laboratory shrinkage in ethanol (95%)[4]	5.80–18.90	42	live SL = 0.296+0.929(laboratory preserved SL)	0.99
2) Net treatment, 5 min	4.48–9.90	135	live SL=0.509+0.994(NL SL[5])	0.93
3) Net treatment, 7.5 min (interpolated)			live SL=0.703+0.988(NL SL)	
4) Net treatment, 10 min	4.48–9.90	134	live SL=0.974+0.983(NL SL)	0.90
5) Net treatment, 15 min	4.48–9.90	97	live SL=1.26+0.961(NL SL)	0.87
6) Net treatment, 20 min	4.96–9.90	71	live SL=2.26+0.841(NL SL)	0.84
7a) Shrinkage in Bouin's after net treatment[3]	5.52–8.24	18	NL SL = 1.118(preserved SL)	0.99
7b) Shrinkage in Z-Fix after net treatment[3]	5.36–7.84	35	NL SL= 1.036(preserved SL)	0.99
7c) Shrinkage in 5% formalin after net treatment[3]	4.48–8.40	50	NL SL = 1.097(preserved SL)	0.99

[1] Laboratory shrinkage = live larva placed directly into preservative.
[2] Z-Fix histological preservative, 10% formalin with aqueous zinc and buffers (see text).
[3] In some cases the constant was not significant and was removed from the regression.
[4] Data provided by K. M. Bailey, Alaska Fisheries Science Center.
[5] NL SL = net live standard length (size after net treatment before preservation).

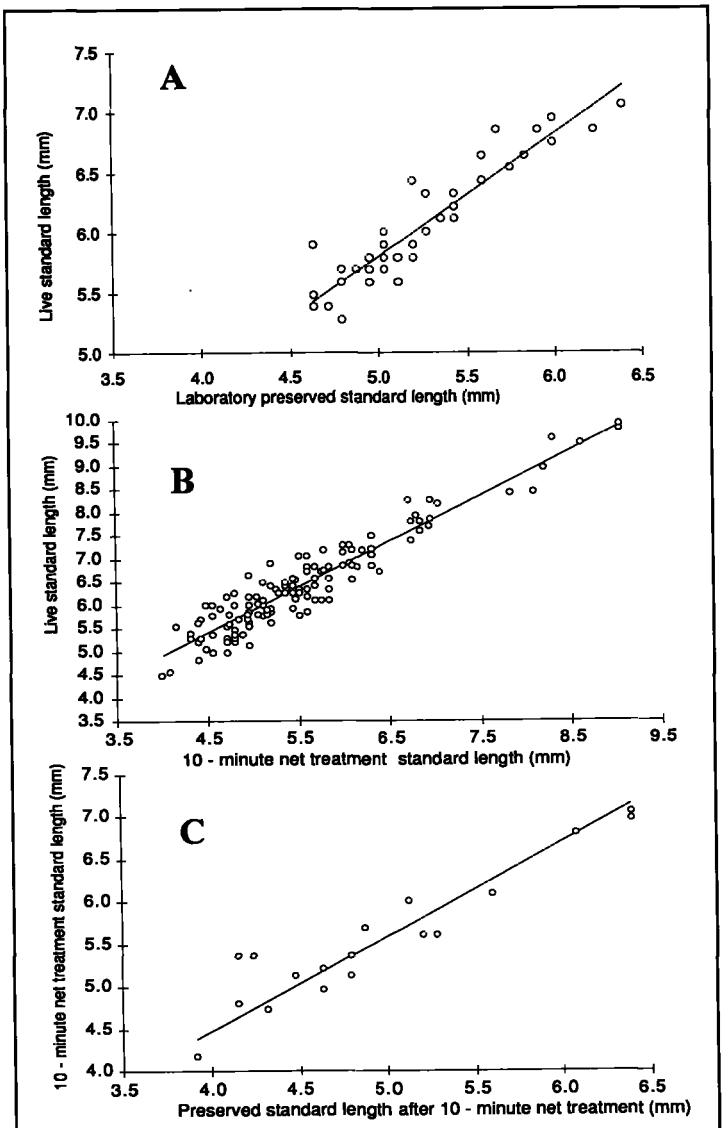

Figure 5

Size of fed walleye pollock, *Theragra chalcogramma*, measured live in the laboratory related to (**A**) their size after preservation in Bouin's fixative, to (**B**) their live size after a 10-min treatment in a net, and to (**C**) the size of live larval walleye pollock treated in a net for 10-min (NL SL [see explanation in Footnote 5 of Table 3]) related to their preserved size in Bouin's fixative after the net treatment. Regression equations are found in Table 3.

Shrinkage in preservative after net treatment

Net-treated larvae shrank an additional 11.8% after being preserved in Bouin's preservative (Table 3). Shrinkage was constant over the size range treated (5.52–8.24 mm SL, n=18; Fig. 5C). Additional shrinkage of net-treated larvae in Z-Fix was 3.6% (5.36–7.84 mm SL, n=35; Table 3) and in 5% formalin was 9.7% (4.48–8.40 mm SL, n=50; Table 3).

Correction for field-captured size

The elapsed time from larval collection to preservation and the preservative type determine which two equations in Table 3 are needed to adjust field-collected and preserved size to the equivalent live size. To examine the accuracy of the regression equations for estimating the live length of field-collected larvae (Table 3), we measured the live size of 20 larvae,

net-treated them for 7.5 min to simulate field collection, preserved them in Z-Fix, and remeasured them several months later. The mean net-treated and preserved SL (4.58 mm ±0.25) was estimated to be 5.39 mm live size from Equations 3 and 7b in Table 3. The observed mean live standard length of the same 20 larvae was 5.46 mm (± 0.21), a difference of 1%.

Field distribution of larvae

Yolk-sac and first-feeding walleye pollock larvae were collected in the eastern Shelikof Strait in April 1991 (Fig. 2; stations 136–141). The abundance of first-feeding larvae increased from April to May. In May, larvae ranging in size from first-feeding to 7 mm were fairly evenly distributed along the coast, within the Strait, and out the sea valley.[3] Some yolk-sac larvae were also found near the Alaska Peninsula and at the exit of Shelikof Strait.

Condition of field-captured walleye pollock

Larvae were sampled from six stations in late April and from 15 stations in early May (Table 4). The level of starvation ranged from 10 to 17% at 3 of the 6 stations in April and at 7 of the 15 stations in May. However, in May, at 3 stations along the sea valley (018, 059, and 068), the percent starvation ranged from 30 to 40% (Fig. 2; Table 4).

Thirty-two percent (n=17/54) of larvae <5.00 mm SL were classified as starving in the combined April and May samples (Table 5). This category included larvae that were smaller than average at first feeding and those that had shrunk from starvation. The percent starving in the first-feeding size category (5.0 to <5.5 mm SL) was 27% (n=12/45), and the number decreased to 12% (n=5/41) for 5.5 to <6.0 mm SL group and finally to zero for larvae >6.0 mm (Table 5).

Discussion

The histological analysis showed that the height of the midgut mucosal cells of laboratory-reared walleye pollock corresponded to their feeding condition and that significant changes in cell height could be detected after food was withheld for one day. Thus, a simple measurement of midgut cell height discerned larval nutritional condition. To confirm the usefulness of the measurement for assessing the nutritional condition of field-collected larvae, it was necessary to determine the effects of field collection procedures on the midgut measurement. Although one might expect some compression of the fish body and perhaps a change in gut morphology as a larva shrinks, our experiments with walleye pollock showed no change in size of the midgut cells during the net shrinkage experiments. Thus, we felt confident in applying the laboratory calibration to assess the condition of sea-caught larvae. Theilacker and Watanabe (1989) also demonstrated that there was no change in the midgut cell height for northern anchovy, *Engraulis mordax*, held for periods up to 25 min in the net. Additionally, although preservative type affected the final size of pollock larvae, the midgut cell height did not differ between two preservative types tested, Bouin's and Z-Fix. Therefore field-collected larval pollock that are to be analyzed for condition may be preserved in either Bouin's or Z-Fix.

Since Farris (1963) first noted that larval sardine, *Sardinops sagax*, shrink when preserved in formalin, and Ryland (1966) observed that larval plaice, *Pleuronectes platessa*, collected in the field were smaller at comparable stages of development than were their laboratory-raised counterparts, information has accumulated on shrinkage of larval fish placed directly into preservatives and during the process of field collection and preservation (Blaxter, 1971; Theilacker, 1980, 1986; Hay, 1981; Tucker and Chester, 1984; Fowler and Smith, 1983; McGurk, 1985; Radke, 1989). The cause of larvae shrinkage is related to the loss of osmoregulatory ability when they die (Parker, 1963). Fish larvae also shrink while they are alive, and this shrinkage may be due to damage by the net to the integument, the main osmoregulatory system in larvae before the gills develop (Holliday and Blaxter, 1960). The amount of shrinkage is directly related to the interval that larvae remain in a collecting net. Shrinkage differs among fixatives within species because of the ionic strengths of the preserving fluids (Parker, 1963; Hay, 1982; Tucker and Chester, 1984). Why shrinkage is species specific may be related to differences in osmolarity (Theilacker, 1980; Jennings, 1991) or to thickness of the integument and mucous layer.

The shrinkage values found for walleye pollock larvae placed directly into preservative are similar to those in previous studies (reviewed by Jennings, 1991). Shrinkage of walleye pollock in 5% formalin was greater (as a percentage of length) for smaller larvae (9% for 5 mm SL) than for larger larvae (7% for 7 mm SL). These values are within the range of shrinkage values (3–15%) for other fish larvae summarized by Hjorleifsson and Klein-MacPhee (1992).

[3] Bailey, K. M., M. F. Canino, J. M. Napp, S. M. Spring, and A. L. Brown. Two contrasting years of prey levels, feeding condition and mortality of larval walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115. Manuscr. in review.

Table 4

Number of starving walleye pollock, *Theragra chalcogramma*, larvae assayed for midgut cell height (MGCH) and prey concentrations in Shelikof Strait, Alaska, in April and May 1991. *n* = number larvae assayed or number starving (STV).

Station	Date 1991	Time PST[1]	Temp °C[2]	MGCH (*n*)	SL (mm)[3]	STV (*n*)	STV (%)[4]	Prey[5]
April 1991								
136	26 April	0428	3.93	2	4.70	2	—	—
137	26 April	1535	3.81	9	4.53–5.30	2	22	—
138	26 April	1706	4.08	8	4.27–5.22	1	13	—
139	26 April	2342	3.92	4	4.10–5.22	0	—	—
140	27 April	0047	3.96	7	4.10–5.47	1	14	—
141	27 April	0157	3.71	6	4.10–5.04	1	17	—
May 1991								
017	2 May	1417	—	14	4.70–5.47	2	14	—
018	2 May	1839	4.15	27	3.93–6.76	8	30	5.00
038	4 May	1309	3.45	6	4.45–5.81	1	17	1.97
053	5 May	1230	—	1	4.19	0	—	—
059	5 May	2153	3.78	5	4.70–5.64	2	40	—
066	6 May	1547	—	2	5.30–5.81	1	—	—
068	6 May	2006	3.86	10	4.62–5.90	4	40	3.93
082	7 May	1835	4.12	3	4.87–5.04	2	—	3.07
089	8 May	0507	4.21	3	5.73–6.07	0	—	3.67
109	10 May	1349	4.26	14	5.13–6.93	2	14	—
110	10 May	1525	4.28	14	4.36–6.76	2	14	—
Buoy 3	12 May	1045	4.14	15	4.79–6.58	0	0	—
Buoy 4	12 May	1147	4.15	9	4.96–6.67	1	11	8.53
Buoy 5	12 May	1256	4.10	10	5.56–6.76	1	10	10.54
Buoy 8	12 May	1555	4.27	7	5.22–6.33	1	14	—

[1] Pacific standard time.
[2] Average temperature between 21 and 40 m depth where a majority of walleye pollock larvae are found (Kendall et al., 1994) (— = no measurements taken).
[3] Preserved standard length (SL) of larvae assayed (SL adjusted to equal Bouin's laboratory preserved size, Table 3).
[4] Percent of larvae starving at stations where at least 5 larvae were assayed.
[5] Number of copepod eggs and nauplii > 150 µm/L averaged over 60 m depth (Bailey et al.[3]).

Walleye pollock preserved in 95% ethanol and measured in water showed a slight increase in size, between 1 and 3%. Values in the literature for ethanol shrinkage vary greatly from 0% (Theilacker, 1980) to 14% (Radtke and Waiwood, 1980), possibly because of concentration differences or because fish are often transferred from ethanol into water for measurement. The transfer permits rehydration which usually negates the original shrinkage.[4]

[4] Theilacker, G. H. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, Wa 98115. Unpubl. data.

Table 5

Histological condition of walleye pollock, *Theragra chalcogramma*, larvae collected in the Shelikof Strait, Alaska in April and May 1991.

Size class SL (mm)[1]	Midgut cell height: Starving ≤11 µm *n*	Midgut cell height: Healthy >11 µm *n*	No. of larvae	Percent starving
April 1991				
<5.00	6	20	26	23
5.00–5.49	1	9	10	10
May 1991				
<5.00	11	17	28	39
5.00–5.49	11	24	35	31
5.50–5.99	5	36	41	12
6.00–6.49	0	19	19	0
6.50–6.99	0	17	17	0
		Total	176	

[1] Standard length (SL) adjusted to equal Bouin's laboratory preserved size.

It is not clear why the amount of shrinkage is related to larval size for some fixatives and not for others. In this study for example, shrinkage was a constant proportion of size for larvae preserved in Z-Fix. However, in Bouin's solution and 5% formalin, smaller larvae shrank more than larger ones.

The net-treatment experiment showed that shrinkage increased with elapsed time in the net, as in other studies addressing net-capture shrinkage of larval fish (Theilacker, 1980; Hay, 1981; McGurk, 1985). Although our field collections averaged 7.5 min, we included net shrinkage values for up to 20 min in a net for adjusting the size of larvae collected in standard bongo net hauls and MOCNESS tows.

The histological criteria demonstrated that a significant number of larval walleye pollock were starving in the Shelikof Strait, Alaska, in April and May, 1991. These results agree with the 1991 field study of Bailey et al.[3] who used biochemical criteria to determine condition of walleye pollock collected in the same area of Shelikof Strait. They found that more walleye pollock were in poor condition in 1991 than in 1990. Subsequent larval mortality, determined independently by ageing larvae from sequential cruises spanning 2 to 3 weeks, was also higher in 1991 than in 1990.[3] Concentrations of copepod nauplii and invertebrate eggs, the main prey eaten by walleye pollock (Canino et al., 1991), were anomalously low throughout Shelikof Strait in 1991, averaging 6 prey/L, as compared with 38 prey/L in 1990[3] and >20 prey/L in earlier years (Incze et al., 1990; Canino et al., 1991). Others have shown that condition of wild larvae is associated with food availability. In particular, Canino et al. (1991) using a biochemical index showed that larval walleye pollock in Shelikof Strait inhabiting areas of sparse prey were in poorer condition and had fewer prey in their guts than their counterparts inhabiting areas of high prey density. Likewise, larval haddock, *Melanogrammus aeglefinus*, and cod, *Gadus morhua*, a close relative of walleye pollock, were shown to be in poorer condition in well-mixed areas on Georges Bank than in stratified sites where prey levels were higher (Buckley and Lough, 1987). Kashuba and Mathews (1984) showed that poor histological condition of larval shad, *Dorosoma* spp., correlated with low prey levels and with a subsequent abrupt decline in the population.

Our results for walleye pollock indicate that the youngest larvae are most vulnerable to starvation. While 29% of the first-feeding walleye pollock (combined <5.50 mm SL groups; n=29/99; Table 5) were classified as starving, one week later the number was reduced to 12%, and 2 weeks later it was zero (Table 5). Others also have found that starvation of larval fishes in the sea decreases quickly, usually within 1 or 2 weeks, as fish larvae mature (O'Connell, 1980; Theilacker, 1986; Robinson and Ware, 1988). Resistance to starvation increases after larval fish first feed (Hunter, 1972; Blaxter and Staines, 1971), acquire the ability to eat more varied prey (Hunter, 1972; Arthur, 1976) and are able to store energy reserves (Ehrlich, 1974; Fraser, 1989; Hakanson, 1989). We also found patchy areas along the Shelikof Strait sea valley in early May 1991 with large numbers of starving larvae, two to three times the background level. Whether small areas of high mortality affect total recruitment is unknown.

Despite arguments to the contrary (Sissenwine, 1984; Peterman et al., 1988) and a general belief that starvation is not a widespread occurrence in the sea (Heath, 1992), evidence from this study shows that starvation does occur and that it is the young stages of walleye pollock that are vulnerable. The advantages of the midgut histological assay, rather than one requiring grading of several tissues, is that it takes less time than does an extensive histological background and is a quantitative rather than a qualitative measure (Theilacker and Watanabe, 1989). Additionally, rates of starvation-induced mortality may be estimated by using the assay and employing laboratory-determined growth rates to determine size and stage durations. Currently, studies are underway to correlate changes in the physical environment

with larval histological condition, feeding, growth, prey availability, and independently determined mortality.

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Revised estimates of incidental kill of dolphins (Delphinidae) by the purse-seine tuna fishery in the eastern tropical Pacific, 1959–1972

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Abstract.—Dolphins (Delphinidae) have been killed incidentally by the purse-seine fishery for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific since at least 1959. Annual estimates of the number of dolphins killed from each stock are used by the National Marine Fisheries Service in making management decisions about the population status of affected stocks. Mortality estimates from the period with the greatest kill of dolphins, 1959–72, are important for estimates of the level of depletion of these stocks from their unexploited population sizes. A redefinition of the geographical boundaries of offshore stocks of pantropical spotted dolphins, *Stenella attenuata*, makes it necessary to estimate annual kill for these newly defined stocks for 1959–72. I estimated the number of dolphins killed annually from 1959 to 1972 for the northeastern and western/southern stocks of spotted dolphins, using the methods of Lo and Smith (1986). I also revised the estimates of annual kill for the eastern and whitebelly stocks of spinner dolphins, *S. longirostris*, by correcting minor problems in previous data and analyses. Additionally, I estimated a coefficient of variation (CV) for each stock-specific estimate of incidental kill, which had not previously been done. Estimates of total kill were similar to previous estimates: 4.9 million dolphins are estimated to have been killed by the purse-seine fishery over the fourteen year period considered here, an average of 347,082 per year. Nearly all of the fisheries kill of pantropical spotted dolphins was of the northeastern stock, totaling 3.0 million (211,612 per year). Estimates of kill for the eastern stock of spinner dolphins were similar to previous estimates, totaling 1.3 million (91,739 per year). As expected, CV's of the kill for each stock were higher than those previously reported for the total kill.

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Dolphins (Delphinidae) have been killed incidentally by the purse-seine fishery for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific (McNeely, 1961) since at least 1959 (Perrin, 1969). Purse seiners catch tuna by locating and capturing dolphin schools, taking advantage of an association between these species (Au, 1991). In spite of attempts to release dolphins alive using a procedure called the backdown (Barham et al., 1977), dolphins are killed when they become entangled in the net. Dolphins from several species are killed; the majority represent either pantropical spotted dolphins, *Stenella attenuata*, or spinner dolphins, *Stenella longirostris*. Several stocks of each species are impacted.

Annual estimates of the number of dolphins killed from each stock are used by the National Marine Fisheries Service (NMFS) in making management decisions about the population status of affected stocks. For example, Wade (1993) used annual estimates of mortality and variance in mortality to conclude that eastern spinner dolphins, *Stenella longirostris orientalis*, were likely below 60% of their unexploited population size in 1959. This led to the listing of eastern spinner dolphins as a depleted species under the U.S. Marine Mammal Protection Act.[1] During the period of greatest dolphin mortality, 1959–72, the kill of spotted dolphins was estimated to be twice that of spinner dolphins (Smith, 1983). Therefore, it is also important to investigate the management status of stocks of spotted dolphins. Wade (1993) showed that the estimated decline of the eastern spinner dolphin was mostly due to the early period of high mortality. Thus, estimates of incidental kill from 1959 to 1972, along with a measure of their uncertainty, are crucial for assessing whether spotted dolphin stocks are also depleted.

Recently, Dizon et al. (1994) established new geographical boundaries for the offshore stocks of pantropical spotted dolphins (Fig. 1) on the basis of a reexamination of cranial morphology (Perrin et al., 1994). Estimates of the number of spotted dolphins killed from each stock must be revised to reflect this stock structure. Therefore, my first objective was to estimate annual kill of the northeastern and west-

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ern/southern stocks of offshore spotted dolphins for 1959–72, by using the methods of Lo and Smith (1986). My second objective was to revise estimates of annual kill for the eastern and whitebelly stocks of spinner dolphin by correcting minor problems in previous data and analyses. My final objective was to estimate variances for these stock-specific mortality estimates, which has not previously been done.

Background

The number of purse-seine sets capturing dolphins ("dolphin sets" or "sets") is known from fishing vessel logbooks for every year since 1959 (Punsley, 1983). Data on mortality per set (MPS) of dolphins have been collected by scientists on tuna purse seiners since 1964 (Smith and Lo, 1983). A formal observer program to collect MPS data was started by NMFS in 1971 (Edwards, 1989). Estimates of incidental dolphin mortality were first presented during workshops[2,3] to assess the status of impacted dolphin stocks and were first published by Smith (1983). The most recent estimates of dolphin mortality for 1959–72 are from Lo and Smith (1986).

Since 1979, the Inter-American Tropical Tuna Commission (IATTC) has been responsible for estimating the number of dolphins killed from each stock (IATTC, 1989). At the request of NMFS, IATTC provided revised estimates of kill for the northeastern stock of spotted dolphin for the years 1979 to 1992.[4] Additionally, they revised the estimates for 1973 to 1978, last calculated by Wahlen (1986).

IATTC chose not to revise estimates for 1959 to 1972, citing the scarcity of observer data on MPS, the lack of a formal observer program prior to 1971, and potential biases in the data.[5] However, the numbers of sets made during that period are known with high precision (Punsley, 1983). Lo and Smith (1986) presented a method of analysis that should provide accurate estimates of kill for 1959–72, given certain important but reasonable assumptions. Therefore, I used that method to estimate the number of dolphins killed in each stock annually for the years 1959 to 1972.

[2] Anonymous, 1976. Report of the Workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. NOAA, Natl. Mar. Fish. Serv., SWFC Admin. Rep. LJ-76-29.

[3] Smith, T. (ed.). 1979. Report of the status of porpoise stocks workshop (August 27–31, 1979, La Jolla, Ca.). NOAA, Natl. Mar. Fish. Serv., SWFC Admin. Rep. LJ-79-41, 120 p.

[4] Estimates provided to National Marine Fisheries Service by J. Joseph, Director, IATTC, La Jolla, CA, 18 May 1993.

[5] Joseph, J., director, IATTC, La Jolla, CA, 17 February 1993, in a letter addressed to Michael Payne at the NMFS Office of Protected Resources, Silver Spring, MD.

Lo and Smith (1986) estimated the variance of the total kill of dolphins in each year, but uncertainty in prorating that total to individual stocks has not previously been accounted for. In this study, I include uncertainty of the species and stock proportions by bootstrapping the variance estimates (Efron, 1982) instead of using the analytical estimates of Lo and Smith (1986). This procedure allows this source of variance to be correctly included for the first time in assessments of the status of these dolphin stocks.

Methods

Lo and Smith (1986) formulated a model of total dolphin kill, $\hat{T}_t$, as:

$$\hat{T}_t = \sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{k=1}^{2} \hat{R}_{tijk} X_{tijk}, \quad (1)$$

where

$\hat{R}_{tijk}$ = estimated mortality-per-set of dolphins in year t and stratum ijk;

X_{tijk} = the number of dolphin sets in year t and stratum ijk,

and where strata were defined as

i = 1 for large vessels (capacity >600 tons), 2 for small (capacity ≤600 tons);

j = 1 for successful yellowfin tuna catch (≥1/4 ton); 2 for unsuccessful catch (<1/4 ton);

k = 1 if the backdown procedure was used to release dolphins; 2 if the backdown was not used.

Lo and Smith (1986) chose these strata because they accounted for significant differences in dolphin kill: MPS was higher for small vessels with successful tuna catches and with sets without backdown (Lo et al., 1982). Lo and Smith (1986) modified Equation 1 to estimate total dolphin kill as:

$$\hat{T}_t = \sum_{i=1}^{2}\left[\hat{R}_{\bullet i11} X_{ti1\bullet}\left[\hat{P}_t + C(1-\hat{P}_t)\right] + \hat{R}_{\bullet i2\bullet} X_{ti2\bullet}\right], \quad (2)$$

where

• = data were pooled across that stratum;

$\hat{P}_t$ = the proportion of successful sets using the backdown procedure to release dolphins,

C = $\hat{R}_{\bullet\bullet 12}/\hat{R}_{\bullet\bullet 11}$, the ratio during successful sets of MPS without backdown to MPS with backdown, pooled across large and small vessels.

Lo and Smith (1986) solved for Equation 2 from Equation 1 for the following reasons:

- MPS was assumed to be constant within a stratum during this period because they found no significant differences in MPS by year, and some years had no data on MPS available.
- The vessel logbooks did not show use or not of the backdown procedure, so the number of sets could not be stratified on this variable. Instead, the proportion of use of backdown procedure, $\hat{P}_t$, was estimated from the MPS data where it was assumed that backdown 1) increased linearly between the known use of 0.0 in 1959 and the observed proportion of 0.79 in 1964–65; 2) equaled the proportion of 0.89 observed in 1966–71; and 3) equaled the proportion of 0.93 observed in 1972.
- Unsuccessful sets were not frequent and usually captured few or no dolphins. Backdown was thus not often used during these sets, which killed relatively few dolphins. Therefore, MPS was pooled across stratum k, the use or not of backdown, for unsuccessful sets.
- The use or not of the backdown procedure was assumed to have the same magnitude of effect on small and large vessels. Therefore, the ratio of MPS with no backdown to MPS with backdown, C, was pooled across vessel stratum to increase the sample size.

To confirm that I was correctly duplicating Lo and Smith's (1986) method, I recalculated their kill estimates using my calculations of MPS and the number of sets reported in their Table 3.

I modified their method in the following ways. The first modification was to account for the revised stocks of offshore spotted dolphin. IATTC provided the number of sets by year previously reported by Punsley (1983) but stratified geographically into separate totals for the northeastern and western/southern areas (Fig. 1).[6]

[6] Data provided by M. G. Hinton, Senior Scientist, Inter-Am. Trop. Tuna Comm. % Scripps Inst. Oceanogr., La Jolla, CA 92093, 24 June 1993. A typographical error in Punsley (1983) led to the inadvertent use of an incorrect value for the total number of dolphin sets in 1959 in Lo and Smith (1986). The correct value of 391 has been used here in place of 591.

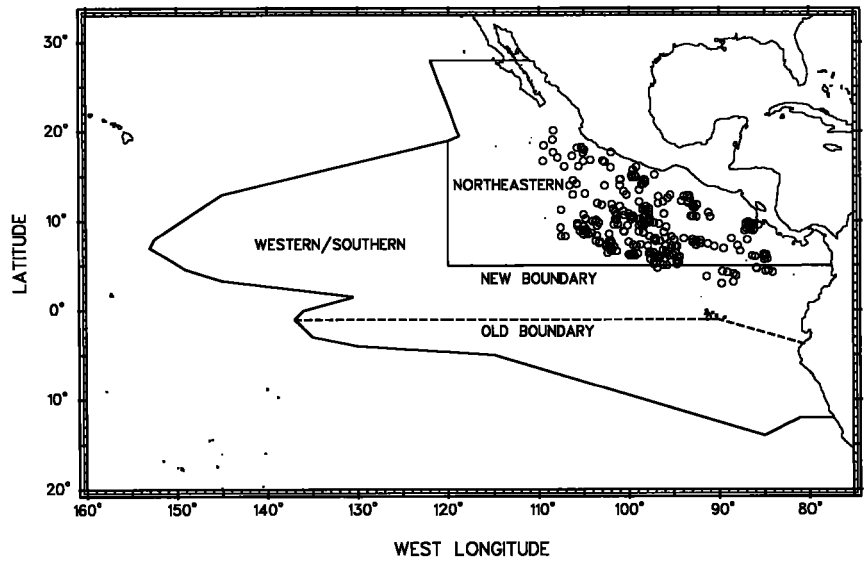

Figure 1

Newly defined areas for offshore stocks of pantropical spotted dolphins, *Stenella attenuata*. The outer line is the eastern tropical Pacific study area as defined by the National Marine Fisheries Service. The inside solid line represents the new boundary between the northeastern and western/southern stocks of spotted dolphins. Sightings of offshore spotted dolphins to the north of 5°N and to the east of 120°W are assigned to the northeastern stock, and sightings outside of that area are assigned to the western/southern stock. The dashed line represents the old boundary between the previously defined northern and southern stocks. The circles represent the location of observed dolphin sets used to estimate mortality per set in this paper, consisting of one fishing trip in 1968, five trips in 1971, and 12 trips in 1972. The exact location of sets from the 1964 and 1965 trips were not available, but the 1964 trip was stated to be 200 miles off the coast of Acapulco, Mexico.

The stocks of offshore spotted dolphins are not distinct in external morphology and therefore could not be noted as proportions in the observer data. Therefore, I estimated kill for each stock by using these stratified numbers of sets to estimate total dolphin kill in each stock area, then prorated the total kill by the observed proportion of offshore spotted dolphins in the kill. The same method as in Smith (1983) was used for prorating species proportions and will be explained in more detail below.

Because eastern spinner and whitebelly spinner dolphins are morphologically distinct, estimates of kill for those two stocks were prorated from the estimated total dolphin kill (summed across the two geographic areas) by observed proportions of the two stocks in the kill. Observed proportions of dolphins killed from species other than spotted and spinner were reported as "other dolphins." Therefore, estimates were made for this pooled category in the same way as for the stocks of spinner dolphins. Dolphins in this category were primarily common dolphins, *Delphinus delphis* (Smith, 1983).

A second modification was possible because IATTC provided the number of sets additionally stratified by tuna catch and vessel size (Table 1). Estimates of the number of sets in each stratum were made by multiplying Punsley's (1983) estimates of total dolphin sets by the proportions of known sets (from the IATTC logbook database) that were in each stock area, set type, and vessel size category.[6] This is likely a substantial improvement in accuracy over the proration method based on less data used by Lo and Smith (1986).

A third modification to the Lo and Smith (1986) method was a change in the way that the variance was calculated. They derived analytical equations for estimating the variance of total dolphin mortality in each year. More important for management is the variance of the estimate of dolphins killed in each stock in each year, which cannot be obtained from the equations in Lo and Smith (1986). Observations of stock and species proportions of the kill were not systematically collected until the observer program started in 1971 (Edwards, 1989). Therefore, Smith (1983) used the observed proportions from 1971 to 1972 for the entire 1959–72 time period, with the exception that all spinner dolphins killed before 1969 were assumed to be from the eastern stock and that no whitebelly spinner dolphins were killed until 1969. This was assumed because no dolphin sets occurred in the whitebelly stock area before 1968, and only a very small number occurred in 1968 (Punsley, 1983).

Table 1

Total dolphin sets for the years 1959–72 stratified by geographical area, by vessel capacity (large is >600 tons, small is ≤600 tons), and by catch of yellowfin tuna (successful is >1/4 ton, unsuccessful ≤1/4 ton). Areas are northeastern (north of 5°N and east of 120°W and western/southern (all areas outside of the northeastern area). Estimates are based on apportioning total dolphin sets estimated by Punsley (1983) to strata (data provided by the Inter-American Tropical Tuna Commission, La Jolla, CA).

	Northeastern				Western/southern			
	Large		Small		Large		Small	
Year	Successful	Unsuccessful	Successful	Unsuccessful	Successful	Unsuccessful	Successful	Unsuccessful
1959	0	0	125	259	0	0	3	5
1960	0	0	3117	2258	0	0	53	46
1961	59	79	3637	3652	17	7	212	187
1962	5	15	1583	1812	10	6	182	126
1963	7	13	2068	1876	7	19	222	204
1964	44	54	4238	2968	17	17	189	117
1965	21	10	5055	2226	78	75	223	131
1966	56	26	4385	1702	65	20	489	111
1967	3	1	3133	788	57	20	172	36
1968	152	50	2857	949	64	12	58	12
1969	1161	165	4424	1281	599	66	584	80
1970	2003	342	3097	769	1166	117	985	142
1971	1296	219	1430	646	1106	104	641	90
1972	2226	452	2364	935	2432	241	666	73

In this study, I duplicated the method of Smith (1983), using the observed proportions of dolphins killed in each stock from the 1971–72 MPS data, with the same assumption about whitebelly spinner kill. However, to calculate the variance of the estimate of the number of dolphins killed in each stock in each year, I used the bootstrap method (Efron, 1982): each fishing trip was a resampling unit and there were 1,000 iterations. Thus, on each bootstrap iteration, 20 fishing trips were resampled with replacement from the 1959–72 pooled observer data, and the MPS rates were recalculated and multiplied by the stratified set totals to estimate the total kill, which was then prorated to stock by the recalculated species proportions. The variance of the kill of each stock in each year was then estimated as the variance of the 1,000 bootstrap estimates of that stock. This method automatically incorporates into the variance uncertainty due to the observed proportions of each stock killed in the 1971–72 MPS observer data. Estimates of number of dolphin sets were precise, having coefficients of variation less than 1% in all years except 1959 and 1960 (Punsley, 1983) and were therefore treated as constants.

For comparative purposes, I made two additional calculations. First, I investigated the effect of the 1964, 1965, and 1968 trips by recalculating the kill of dolphins using only the MPS data collected during the observer program in 1971 and 1972. Second, I calculated stratified MPS rates from the 1973 observer data to compare to MPS rates used here from 1964 to 1972.

Results

Average MPS for each of the 20 observed trips between 1964 and 1972 showed that most of the trips had similar kill rates (Table 2). Calculated estimates of the MPS for each category of year, vessel size, and set type (Table 3) were, as expected, equivalent to the values reported by Lo and Smith (1986). The six R_{tijk} values used in Equation 4 are also shown in Table 2.

Estimating total dolphin mortality with my MPS rates (Tables 2 and 3) and the number of sets from Lo and Smith (1986, their Table 3) resulted in slightly different estimates of the total number of dolphins killed than those they reported in their Table 4. However, when I used the six MPS values reported in their Tables 1 and 2, I obtained their estimates. Of six MPS values in their Tables 1 and 2, two were not the same as the MPS values required by their Equation 4. Their Table 1 reports MPS for both large and small vessels by category of successful set, but pooled over backdown or no backdown ($R_{\bullet 11\bullet}$ and $R_{\bullet 21\bullet}$, respectively), whereas Equation 4 requires the MPS for both large and small vessels by category of successful set and by backdown status ($R_{\bullet 111}$ and $R_{\bullet 211}$, respectively). I duplicated the results of Lo and Smith (1986) exactly using $R_{\bullet 11\bullet}$ and $R_{\bullet 21\bullet}$ and conclude that they inadvertently used these values, versus $R_{\bullet 111}$ and $R_{\bullet 211}$ as they intended, because their equation is correct.[7] The estimates reported here (Table 4) were calculated by using Equation 4 and $R_{\bullet 111}$ and $R_{\bullet 211}$ of 29.9 and 65.8, respectively.

Lo and Smith (1986) did not prorate their estimates of total dolphin mortality to stocks. Using reported proportions from the 1971–72 MPS observer data, Smith (1983) prorated 0.70, 0.23, 0.03, and 0.04 of the total mortality to offshore spotted, eastern spinner, whitebelly spinner, and other dolphins, respectively. My results assign 0.694, 0.241, 0.034, and 0.029 of the mortality to the same categories.[8]

Annual estimates of incidental mortality of dolphins ranged from a low of 23,485 in 1959 to a high of 558,572 in 1961; CV's ranged from 0.13 to 0.48 (Table 4). Nearly 5 million dolphins were estimated to have been killed by the purse-seine fishery over the fourteen-year period considered here, an average of 347,082 per year. More northeastern spotted dolphins were killed than from any other stock; a total estimate for the period was 3.0 million (211,612 per year). Totals for other stocks were 0.4 million (29,361 per year) western/southern spotted dolphins, 1.3 million (91,739 per year) eastern spinner dolphins, 0.05 million whitebelly spinner dolphins, and 0.15 million dolphins from other species. CV's of the annual kill estimates ranged from 0.17 to 0.53 for the northeastern spotted, 0.19 to 0.54 for the western/southern spotted, 0.32 to 0.47 for the eastern spinner, 0.45 to 0.50 for the whitebelly spinner, and from 0.84 to 0.89 for other dolphins.

When I recalculated dolphin mortality using only MPS data from the 17 trips for 1971–72, total dolphin kill for 1959–72 was estimated to be 5.1 million. In all years except 1972 the estimates were slightly higher than those in Table 4 that were calculated by using all 20 1964–72 trips. The higher value in 1972 was due to a slightly higher value for the ratio of MPS without backdown to MPS with backdown (C in Eq. 3). Owing to the decrease in the

[7] Original records were not available to confirm which values were used (Lo, N. C. H., Southwest Fisheries Science Center, NMFS, La Jolla, CA, 92038, and T. D. Smith, Northeast Fisheries Science Center, NMFS, Woods Hole, MA, 02543. Pers. commun., 1993).

[8] Differences are likely due to round-off error. Additionally, they may be also due to revisions made to the NMFS observer database (Rasmussen, R. C., Southwest Fisheries Science Center, NMFS, La Jolla, 92038. Pers. commun., 1993).

Table 2

Average numbers of dolphins killed in purse-seine sets in the eastern tropical Pacific by trip, for the 20 observed trips between 1964 and 1972. n equals the total number of observed dolphin sets during the trip. Also given are the six mean mortality per sets ($R_{\bullet ijk}$) used in Equation 4, where i equals 1 for large vessels (>600 tons carrying capacity) and 2 for small vessels (≤600 tons carrying capacity), j equals 1 for successful set (≥1/4 ton yellowfin tuna) and 2 for unsuccessful set (≤1/4 ton yellowfin tuna), k equals 1 for when backdown was used and 2 for when backdown was not used, and where the subscript $\bullet$ indicates pooling across that variable. Sample sizes of number of observed sets in each stratum are in parentheses. The data used are from 1) Smith and Lo (1983) for the years 1964, 1965, and 1968, and 2) unpublished National Marine Fisheries Service tuna vessel observer data for the years 1971 and 1972.

Year	n	Successful set, backdown	Unsuccessful set, pooled	Successful set, no backdown
Small vessels				
1964	21	44.2 (16)	60.0 (1)	127.8 (4)
1965	19	48.0 (6)	2.6 (11)	24.0 (2)
1968	14	142.5 (11)	4.0 (2)	92.0 (1)
1971	11	89.1 (11)	.0 (0)	.0 (0)
1971	7	258.0 (3)	11.0 (2)	214.5 (2)
1971	3	33.0 (1)	16.0 (1)	.0 (1)
1972	24	57.9 (15)	0.0 (8)	1.0 (1)
1972	19	82.1 (15)	0.5 (4)	.0 (0)
1972	11	44.5 (11)	0.0 (0)	.0 (0)
1972	16	80.7 (14)	0.0 (1)	179.0 (1)
1972	23	45.8 (22)	0.0 (1)	.0 (0)
1972	23	23.6 (20)	28.5 (2)	7.0 (1)
Total	191	($R_{\bullet 211}$) 65.8 (145)	($R_{\bullet 22\bullet}$) 5.9 (33)	
Large vessels				
1971	14	49.2 (13)	0.0 (0)	14.0 (1)
1971	2	2.0 (2)	0.0 (0)	.0 (0)
1972	27	30.3 (24)	0.0 (1)	643.5 (2)
1972	36	25.7 (28)	0.0 (5)	16.0 (3)
1972	18	49.3 (17)	0.0 (1)	.0 (0)
1972	16	16.8 (15)	0.0 (0)	.0 (1)
1972	9	11.9 (8)	0.0 (1)	.0 (0)
1972	8	11.5 (4)	1.3 (4)	.0 (0)
Total	130	($R_{\bullet 111}$) 29.9 (111)	($R_{\bullet 12\bullet}$) 0.4 (12)	
Small and large vessels				
Total	321	($R_{\bullet\bullet 11}$) 50.3 (256)		($R_{\bullet\bullet 12}$) 130.8 (20)

quantity of data, the CV's using just 17 trips were somewhat higher.

The 1973 observer data include 668 observed dolphin sets from 25 trips. My calculations of MPS from those data resulted in values of 13.1, 7.9, 22.0, and 1.3 for the strata $R_{\bullet 211}$, $R_{\bullet 22\bullet}$, $R_{\bullet 111}$, and $R_{\bullet 12\bullet}$, respectively.

Discussion

Nearly all the mortality of spotted dolphins was observed in the northeastern stock (Table 4) because very few dolphin sets were located outside the northeastern area prior to 1969 (Punsley, 1983). The few sets that occurred outside this area prior to 1968 were sets that were not far offshore but were south of the southern boundary of the stock area at 5°N (Punsley, 1983). Consequently, there were few observations of MPS in western/southern area except in the area south of 5°N and north of the Galapagos (Fig. 1). Although this should have little effect on the estimates for the northeastern stock, estimates of mortality for the western/southern stock were not based on many actual observations of MPS of spotted dolphins in the western/southern area. There was complete knowledge of the number of dolphin sets within the western/southern area, but the estimates of mortality for that stock are based on the assumption that MPS was the same in both stock areas. Annual mortality estimates for the western/southern stock, though relatively small, may therefore be biased. In

areas corresponding to the western/southern area, MPS rates were as much as 100% greater than those in the area corresponding to the northeastern area during 1973–76 and 1977–78; significant areal differences were found in 1977–78 (Wahlen, 1986). If similar differences in MPS by area existed during 1959–72, my estimates of mortality for western/southern spotted dolphins are negatively biased.

For the same reason, my mortality estimates for whitebelly spinner dolphins may also have a negative bias. Observations of MPS of whitebelly spinner dolphins came only from the region of overlap with eastern spinner dolphins; no observations of MPS were from the outside region west of 120°W where whitebelly spinner dolphins are known to occur and where significant fishing effort occurred in 1970, 1971, and 1972 (Punsley, 1983).

The three trips observed prior to 1971 were not part of an established data collection program and, therefore, may have been biased observations. In 1965 and 1968, two trips with tuna boats were observed by scientists, who collected dolphin specimens and also recorded MPS data (Smith and Lo, 1983). These data were not based on random samples, but there is no obvious reason why the data from tuna vessels on which scientists were allowed to collect specimens would tend to have different mortality rates. However, it is not certain a priori in which direction bias would have occurred. Data from the third

Table 3

Average numbers of dolphins killed (M) in purse seine sets in the eastern tropical Pacific by year for the 20 observed trips between 1964 and 1972, for small (≤600 tons carrying capacity) and large (>600 tons carrying capacity) vessels making successful (>1/4 ton yellowfin tuna) and unsuccessful (≤1/4 ton yellowfin tuna) sets on dolphin, pooled over whether the backdown dolphin release procedure was used or not. The number of observed sets (n) and the number of trips (n_{tr}) are given. Numbers of successful sets here are greater than yearly totals calculated from Table 2 because that table excludes sets for which the use or not of backdown was not recorded.

		Successful sets		Unsuccessful sets	
Vessels and year	n_{tr}	M	n	M	n
Small vessels					
1964	1	60.9	20	60.0	1
1965	1	25.9	35	2.6	11
1968	1	130.2	13	4.0	2
1971	3	116.6	19	12.7	3
1972	6	56.5	103	3.7	16
Total	12	62.4	190	5.9	33
Large vessels					
1971	2	41.1	16	0.0	0
1972	6	36.9	117	0.4	12
Total	8	37.4	133	0.4	12

Table 4

Annual estimates of dolphins killed in the eastern tropical Pacific tuna purse-seine fishery, for each year between 1959 and 1972. Coefficients of variation are given in parentheses. The category of all dolphins is the sum of the four stock and other dolphins categories. Estimates were made using mortality-per-set data from 1964 to 1972 (20 trips). See text for scientific names.

Year	All dolphins	Northeastern offshore spotted	Western/southern offshore spotted	Eastern spinner	Whitebelly spinner	All other dolphins
1959	23485 (0.476)	15928 (0.534)	377 (0.540)	6452 (0.472)	0 (0.000)	728 (0.853)
1960	503879 (0.464)	343955 (0.522)	5880 (0.519)	138426 (0.465)	0 (0.000)	15619 (0.842)
1961	558572 (0.421)	365988 (0.476)	21819 (0.478)	153451 (0.433)	0 (0.000)	17314 (0.839)
1962	226396 (0.371)	140952 (0.423)	16231 (0.431)	62196 (0.401)	0 (0.000)	7018 (0.841)
1963	252607 (0.313)	158178 (0.362)	17202 (0.362)	69396 (0.369)	0 (0.000)	7830 (0.847)
1964	410195 (0.240)	272289 (0.282)	12502 (0.282)	112689 (0.338)	0 (0.000)	12715 (0.867)
1965	482331 (0.244)	318528 (0.286)	16346 (0.281)	132506 (0.341)	0 (0.000)	14951 (0.863)
1966	392441 (0.192)	244123 (0.224)	28342 (0.224)	107812 (0.331)	0 (0.000)	12165 (0.893)
1967	262947 (0.195)	171765 (0.227)	10794 (0.221)	72237 (0.333)	0 (0.000)	8151 (0.892)
1968	239051 (0.191)	161234 (0.224)	4735 (0.219)	65672 (0.328)	0 (0.000)	7410 (0.889)
1969	457903 (0.181)	271533 (0.221)	46381 (0.220)	110432 (0.348)	15363 (0.497)	14194 (0.875)
1970	433201 (0.172)	218702 (0.219)	82062 (0.220)	104475 (0.332)	14534 (0.487)	13428 (0.859)
1971	249373 (0.166)	111253 (0.216)	61882 (0.223)	60141 (0.321)	8367 (0.480)	7730 (0.851)
1972	366771 (0.129)	168136 (0.172)	86506 (0.189)	88454 (0.324)	12306 (0.450)	11369 (0.877)

fishing trip in 1964 were recorded and reported by a fisherman who may have reported his observation because of the magnitude of the kill, biasing those data (Smith and Lo, 1983). However, mean MPS's from these three trips were mostly within the range of values from the other observed trips in 1971–72 and therefore do not appear biased (Table 2).

Removing the data from the three trips observed prior to 1971 resulted in minimal changes to the mortality estimates. Annual mortality was higher in each year except 1972. This resulted in an estimate of total dolphin kill for 1959–72 of 5.1 million versus an estimate of 4.9 million when those trips were included. This confirms that my kill estimates were not significantly biased by the three pre-1971 observed trips.

Accepting the assumption of constant MPS rates during 1959–72 is crucial to the accuracy of these kill estimates. Available evidence is consistent with this assumption. For example, the three observed trips from 1964, 1965, and 1968 had MPS rates in the same range as the data collected in 1971–72. There are additional observations prior to 1971 that are also consistent with this assumption. For example, dolphins were noted as being killed in all 28 sets observed on a trip in 1966, but precise counts were made for only the five sets on which the greatest number of dolphins were killed (Smith and Lo, 1983). The average MPS for those five sets was 250.0; thus a minimum estimate of the average MPS for that trip is 45.5, if one assumes that only one dolphin was killed during each of the other 23 sets. Perrin (1969) reported a "rough count" of the total number killed on the trip as 2,000, resulting in an average MPS of 71.4. Most of those sets were known to be successful sets using backdown procedure, and values of 45.5 or 71.4 are within the range (44.2 to 142.5) reported for the small vessel stratum on the 1964–68 trips (Table 2). During the same period of 1964–68, another scientist reported observing two trips with similar MPS rates (Allen[9]). Therefore, there are apparently at least four other observed fishing trips from the 1960's with kill rates similar to those reported here. Finally, fishermen on the 1965 trip and the 1966 and 1968 trips reported to observing scientists that the MPS rates on those trips were the usual rates experienced by the crew of those vessels and others in the fleet at that time[10,11].

Perhaps the greatest uncertainty is due to the lack of MPS data prior to 1964. Historically, MPS rates have decreased in the U.S. fleet because of improvements in the equipment and in the skill and motivation of the fishermen. Use of the backdown procedure was developed on one boat in 1959–60, and its use spread quickly through the majority of the fleet only after 1961 (Barham et al., 1977). Because the procedure saved them time in retrieving the net (Barham et al., 1977), the fishermen likely improved their backdown performance during these first few years. Therefore, the average MPS during backdown sets prior to 1964 may have been higher than in later years. This is consistent with the observation that the proportion of dolphins killed in the net was high during these early years relative to later years (Joseph and Greenough, 1979). For this reason, any substantial bias in these kill estimates is likely a negative bias; the actual kill of dolphins may have been higher, particularly prior to 1964.

Passage of the Marine Mammal Protection Act in 1972 motivated fishermen to kill fewer dolphins, and I expected MPS to decline in 1973, which it did. My calculations of MPS in 1973 for $R_{\bullet 211}$, $R_{\bullet 22\bullet}$, $R_{\bullet 111}$, and $R_{\bullet 12\bullet}$ were 13.1, 7.9, 22.0, and 1.3, respectively, compared with analogous values of 65.8, 5.9, 29.9, and 0.4 in 1959–72 (Table 2). The only dramatically different value was that of the MPS for small vessels with successful set and with backdown procedure, which declined from a value of 65.8 to 13.1. The other values are fairly similar. Kill rates on small vessels prior to 1973 were apparently more than twice as high as those on large vessels. Therefore, it seems reasonable that the most dramatic improvement in MPS rates would have occurred in this category. One technological reason for a decline in kill rates at that time was the increasing use of the Medina panel, an area of finer mesh net in the backdown channel that helped prevent entanglement of dolphins. It was first used experimentally in 1971; by the end of 1972, 40–50% of the U.S. fleet were using it, and 60–70% were using it by the end of 1973 (Barham et al., 1977). In summary, although data available from 1959–72 are sparse, they are consistent with other information available from that period and 1973, which provides support for accepting the assumptions of this analysis and, therefore, accepting these estimates as being reasonably accurate.

Except for the years 1971 and 1972, the coefficients of variation (CV) for the total number of dolphins killed in each year were considerably higher than those reported by Lo and Smith (1986). Since the data in each case are the same, the differences must be due to the use of the bootstrap method versus the analytical equations used in Lo and Smith (1986). The differences in CV's were largest for years 1959–65. For example, they report a CV of 0.31 for 1960

[9] Allen, R., pers. commun., cited in Smith and Lo, 1983.

[10] 1965 trip, David W. Waller, Dept. of Biol. Sci., Kent State Univ., Kent, Ohio. Pers. commun., 1994.

[11] 1966 and 1968 trips, William F. Perrin, Southwest Fish. Sci. Cent., La Jolla, CA. Pers. commun., 1994.

versus my estimate of 0.46. My CV's from 1966 to 1972 (from 0.13 to 0.20) are in the same range as bootstrap CV's reported for 1979–87 (IATTC, 1989) for which there were larger sample sizes of observed sets. These data indicate that there was less variation in MPS between trips in the data set used here than was usual in succeeding years. This may have been an artifact of a relatively small sample size. Alternatively, as MPS declined after 1972, the variance in MPS may have actually increased. One possible explanation for increased variance may be that MPS declined for sets that went as planned but did not decline for high-mortality sets. This could lead to a decrease in average MPS and an increase in the variance.

As expected, CV's of the kill for each stock were higher than those for the total kill because they included additional uncertainty in species proportions. CV's for northeastern spotted dolphins were on average 0.05 more than CV's for total dolphin mortality. CV's were even greater for eastern spinner dolphins, averaging 0.10 more than for total dolphin mortality.

Variance estimates presented here are estimates of the precision given the assumptions of the analysis, such as constant MPS rates in 1959–72. They cannot provide a complete measure of uncertainty of how many dolphins were killed during this period, because some untestable assumptions were made which could lead to bias. However, this is always the case for statistical variance estimates, unless one can be assured that all assumptions have been met or unless one accepts subjective beliefs and incorporates them into a Bayesian statistical analysis (Press, 1989). For example, the assumed linear increase in the use of the backdown procedure between 1959 and 1964 (Lo and Smith, 1986) is probably open to question, but it is unlikely that there are data available to test these kinds of assumptions.

Although my estimates of the numbers of dolphins killed in the early years of the fishery come from a limited set of data on MPS and seem quite large, these estimates are consistent with statements from scientists involved in the fishery then (e.g. "in the early years of the fishery these incidental mortalities were very high," Joseph, 1994). Additionally, my estimates are reasonable when compared with estimates from later years that had substantially more data on MPS. Even after expected declines in MPS due to the passage of the MMPA in 1972 and the increased use of the Medina panel, Wahlen (1986) estimated a kill of 197,000 in 1973, a reduction of about one-third from the average kill of 308,072 per year in the two previous years (Table 4). As recently as 1986, the mortality of dolphin was estimated to be 133,174 (IATTC, 1989). Of those, 52,000 were estimated to be northeastern spotted dolphins, representing 7.1% of the population's estimated abundance in 1986–90 (Wade and Gerrodette, 1993), a level of mortality that is probably not sustainable.

Events in recent years have shown how quickly MPS can change. A variety of efforts to decrease MPS in the fishery (Joseph, 1994) have caused the total kill to decline dramatically to levels of 27,292 in 1991 (Hall and Lennert, 1993), 15,539 in 1992 (Hall and Lennert, 1994), and 3,601 in 1993 (Hall and Lennert, in press). The 1993 mortality of northeastern spotted dolphins was 1,139 or 0.16% of the 1986–90 abundance estimate, and all other stocks had even lower percent mortality levels. The low 1993 levels of mortality (if continued) should allow future growth and recovery of these populations, even if they are currently depleted.

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Abstract.—Depredation of bottomfish on longline catches by killer whales, *Orcinus orca*, has been documented throughout the Bering Sea. Stations where repeated interactions with killer whales had been noted were examined during Japan-U.S. cooperative longline research surveys conducted from 1980 to 1989. During vessel surveys in 1988, killer whales were shown to depredate Greenland turbot, *Reinhardtius hippoglossoides*, sablefish, *Anoplopoma fimbria*, arrowtooth flounder, *Atheresthes stomias*, Pacific halibut, *Hippoglossus stenolepis*, and searcher, *Bathymaster signatus*, selecting the largest fish available for each species. Depredation rate, based on averages of total catch, was higher than calculated from direct counts of damaged fish. The average annual monetary loss to the survey calculated over a 4-month research season as a result of killer whale predation for the years 1982 through 1988 was estimated to range from $2,982 to $34,571 (from ¥402,500 to ¥4,667,110).

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Killer whale, *Orcinus orca*, depredation on longline catches of bottomfish in the southeastern Bering Sea and adjacent waters

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Killer whales, *Orcinus orca*, are cosmopolitan in distribution (Leatherwood and Dahlheim, 1978), and reports of their interference in fishery operations occur worldwide (Sivasubramanium, 1965; Leatherwood et al., 1990; Tasmanian Fisheries Development Authority[1]). In Alaska, killer whales depredate longline catches of bottomfish, such as sablefish (also known as blackcod), *Anoplopoma fimbria*, and Greenland turbot, *Reinhardtius hippoglossoides*, in the southeastern Bering Sea and Prince William Sound, Alaska (Dahlheim[2]). Information from sources in the U.S. domestic longline fishery in the Bering Sea suggests that killer whale depredation occurs on at least 20% of the bottom longline sets (Dahlheim[2]). In Prince William Sound, an estimated 25% of the total catch is lost to killer whales (Matkin[3]).

Annual Japan-U.S. cooperative longline research surveys for sablefish and Pacific cod, *Gadus macrocephalus*, resources have occurred in Alaskan waters since 1979. Research vessels use similar fishing gear to that used during Japanese commercial bottom longline operations. This study reports on the nature and extent of fishery interactions with killer whales on Japan-U.S. research longline operations in Alaskan waters from 1980 to 1989. The survey area included the eastern Aleutian Islands, north into the Bering Sea along the continental slope, eastward following the Alaska Peninsula to the Gulf of Alaska, and then south into Southeast Alaska (Fig. 1). Objectives of the study include 1) definition of the areas where fishery interactions occur; 2) estimation of killer whale depredation on longline-caught fish; 3) iden-

[1] Tasmanian Fisheries Development Authority. 1981. Assessment of impact of interference from *Orcinus orca* (killer whale) on Tasmanian dropline fishery. Australian National Parks and Wildlife Service, Tasmanian Fisheries Development Authority, 23 Old Wharf, Hobart, Tasmania 7000, Australia. Unpubl. manuscr., 35 p.

[2] Dahlheim, M. E. 1988. Killer whale (*Orcinus orca*) depredation on longline catches of sablefish (*Anoplopoma fimbria*) in Alaskan waters. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northwest Alaska Fish. Cent., 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115. Proc. Rep. 88-4, 31 p.

[3] Matkin, C. O. 1986. Killer whale interactions with the sablefish longline fishery in Prince William Sound, Alaska, 1985, with comments on the Bering Sea. Rep. to the National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Unpubl. manuscr. contract 40-HANF-6-0068, 10 p.

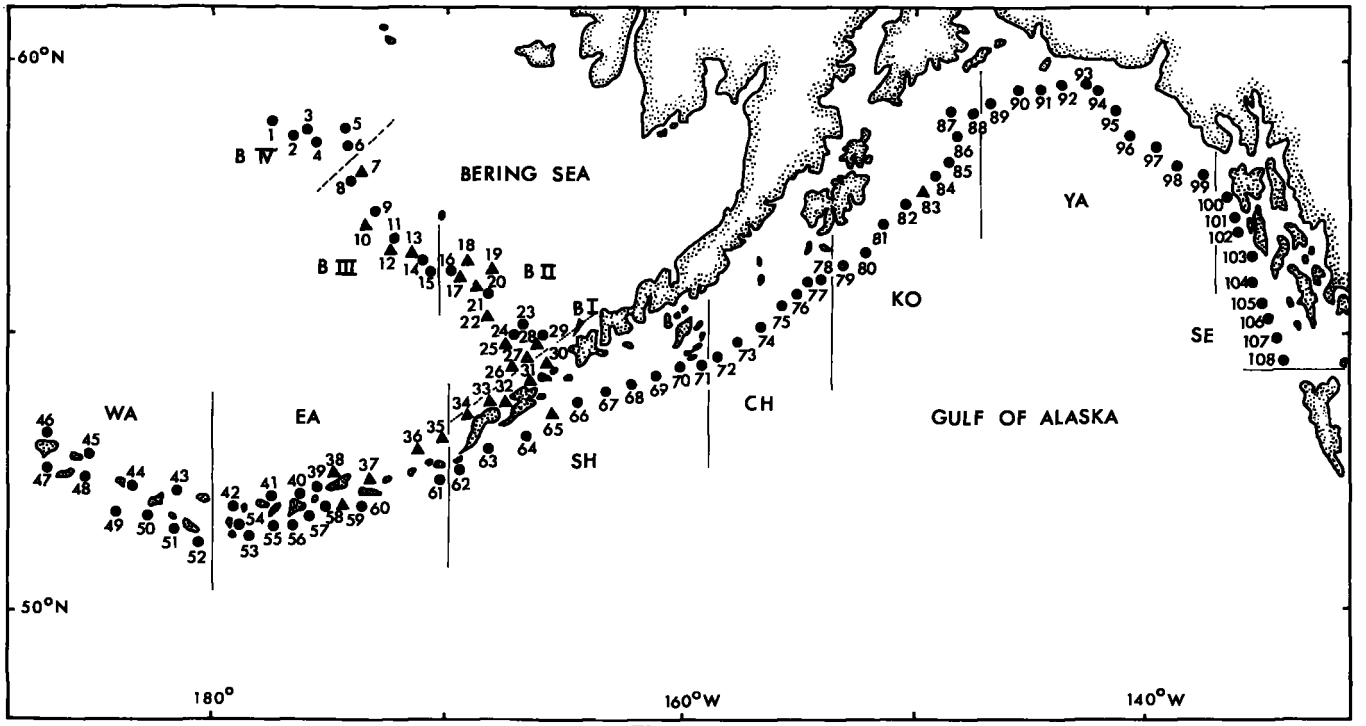

Figure 1

Survey stations of Japan-U.S. cooperative longline surveys in Alaskan waters (1980-89). Surveys were not conducted in the Bering Sea (B-II, B-III, and B-IV) during 1980 and 1981 seasons. (•) = stations where killer whales, *Orcinus orca*, were not encountered; (▲) = stations where whales were encountered (stations 10, 19, and 83 killer whales were observed but no depredation occurred). B = Bering Sea, WA = Western Aleutian Islands, EA = Eastern Aleutian Islands, SH = Shumagin Islands, CH = Chirikof Island, KO = Kodiak Island, YA = Yakutat, SE = Southeast Alaska.

tification of species and size of fish consumed by killer whales; and 4) quantification of the amounts of longline catch lost to killer whales.

Materials and methods

Stations for the Japan-U.S. longline research survey in Alaskan waters were established by the National Research Institute of Far Seas Fisheries, Fisheries Agency of Japan, and the National Marine Fisheries Service (NMFS), Alaska Fisheries Science Center. In 1980 and 1981, 76 stations were fished, excluding areas B-II, B-III, and B-IV (29 stations) in the Bering Sea (Fig. 1). Beginning in 1982, the number of stations (which represent 11 major fishing areas) increased to 108 to include the additional Bering Sea stations (Sasaki, 1985; Fig. 1). Surveys were conducted between May and September each year (1980–89). Weather permitting, one station was fished per day.

The research vessels selected for the surveys were chartered Japanese commercial longline vessels that had been used for previous sablefish and Pacific cod fishing operations in the North Pacific Ocean. The bottom longline was 16 km long and consisted of 160 "hachis" (skates). Each hachi was 100 m long and contained 45 hooks which were spaced 2 m apart. Gangion lengths were 1.2 m. Each hook was baited with squid (total number of hooks=7,200). The hook (standard type: Tara [=cod] no. 18) was 74 mm in length and 21 mm in width. The depth at which fish were caught was estimated by measuring the depth of water under the vessel with an echo sounder at every fifth hachi. The catch was recorded by estimating the numbers of species or species groups for each hachi. The total catch of the major species was weighed to the nearest gram. Total length (TL) or fork length (FL) was measured for each species to the nearest millimeter. Details of the survey methods and longline gear are described in Yano[4,5].

[4] Yano, K. 1989. Japan-U.S. joint survey for stock assessment of sablefish and Pacific cod resources in 1988. Report of the Northern Groundfish Section, Japan Scientific Council on the

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Between 1980 and 1989, stations where killer whales were present were recorded. During vessel surveys in 1988, depredation rates by killer whales were quantified. During the 1988 surveys, as the groundline was retrieved, fish that had been damaged or partially consumed by killer whales were identified by remains left on the hook (e.g. heads, lips, or gills). In addition, head length (HL) or maxillary length (ML) measurements were collected for each damaged fish. Head length (mm) was measured from the most anterior point of the snout of the upper jaw to the most distant point of the posterior margin of the operculum. Maxillary length (mm) was measured along the longest margin on the premaxillary side. Fork length (FL) for sablefish and arrowtooth flounder, *Atheresthes stomias*, and total length (TL) for Greenland turbot were also measured. Fork length and TL were measured from the tip of the snout to the central point of the caudal fin. The relationships between HL and FL or TL and between ML and FL or TL were calculated by the least-square method following the equation:

$$Y = a + bX,$$

where Y is FL or TL (mm), X is HL or ML (mm), and a and b are constants. Average lengths of damaged and undamaged fish were compared by using t-tests with a significance level of 0.05.

To obtain killer whale depredation rates for each station, direct counts were made of the remaining heads, lips, or gills that were brought aboard the research vessel. Empty hooks did not provide evidence of killer whale depredation and were not included in the analysis.

Killer whale depredation rates were calculated by two methods. RNT is the depredation rate calculated from the number of fish preyed upon as a percentage of the total number of fish landed per fishing trip. RNS is the depredation rate calculated from the number of fish preyed upon as a percentage of the number of fish landed from the time the whales were first observed to depredate them.

The two depredation rates were calculated for each station as

$$RNT\ (\%) = NP/(NT+NP) \times 100$$

and

$$RNS\ (\%) = NP/(NS+NP) \times 100,$$

where NP is the number of depredated fish, counted by the remaining heads, lips, or gills; NT is the total number of fish landed with no evidence of killer whale depredation; and NS is the number of fish landed without any physical evidence of depredation counted from the time the whales were first observed to depredate fish (determined by observing heads, lips, or gills on the groundline).

Other depredation rates (REA and REY) were obtained by averaging the catch rates (number of fish per hachi) obtained during the 1980 and 1988 surveys. REA is the depredation rate calculated from the average catch rates for all years at each station. REY is the depredation rate calculated from the average catch rates for all stations for each year. The average catch rates (REA and REY) were obtained through the following formula:

$$REA \text{ or } REY\ (\%) = 100 - (A/B \times 100),$$

where A is the average catch rate during whale depredation for all years at each station (for *REA*) or all stations for each year (for *REY*), and B is the average catch rate with no killer whale depredation for all years at each station (for *REA*) or all stations for each year (for *REY*). We tested for differences in the average catch rates for *REA* and *REY* by using the one-way analysis of variance (ANOVA). The annual survey reports of the Japan Marine Fishery Resources Research Center (JAMARC) by Inada and Sasaki,[6] Onoda and Sasaki,[7] Mizogoshi and Sasaki,[8] Funato and Sasaki,[9] Iwami and Sasaki,[10] Fukui and Sasaki,[11] Takeda and Sasaki,[12] Takeda,[13] and Yano[5] provided fish catch data for the study.

[4] *(continued)* Fisheries Resources (GSK), Tohoku National Fisheries Research Institute, Hachinohe Branch, 25-259 Shimomekurakubo, Samemachi, Hchinohe, Aomori 031, Japan, No. 22, p. 145-173. [In Japanese.]

[5] Yano, K. 1990. Report on sablefish and Pacific cod resource developmental survey, 1988. Japan Marine Fishery Resources Research Center, 3-27 Kioi-cho, Chiyoda-ku, Tokyo 102 Japan, JAMARC Rep. S63/No.11, 195 p. [In Japanese.]

[6] Inada, T., and T. Sasaki. 1981. Report on sablefish and Pacific cod resource developmental survey, 1980. Japan Marine Fishery Resources Research Center, 3-27 Kioi-cho, Chiyoda-ku, Tokyo 102 Japan, JAMARC Rep. S55/No.18, 156 p. [In Japanese.]

[7] Onoda, M., and T. Sasaki. 1982. Report on sablefish and Pacific cod resource developmental survey, 1981. Japan Marine Fishery Resources Research Center, 3-27 Kioi-cho, Chiyoda-ku, Tokyo 102 Japan, JAMARC Rep. S56/No.15, 140 p. [In Japanese.]

[8] Mizogoshi, H., and T. Sasaki. 1984. Report on sablefish and Pacific cod resource developmental survey, 1983. Japan Marine Fishery Resources Research Center, 3-27 Kioi-cho, Chiyoda-ku, Tokyo 102 Japan, JAMARC Rep. S58/No.13, 219 p. [In Japanese.]

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[10] Iwami, T., and T. Sasaki. 1985. Report on sablefish and Pacific cod resource developmental survey, 1984. Japan Marine Fishery Resources Research Center, 3-27 Kioi-cho, Chiyoda-ku, Tokyo 102 Japan, JAMARC Rep. S59/No.12, 223 p. [In Japanese.]

[11] Fukui, J., and T. Sasaki. 1988. Report on sablefish and Pacific cod resource developmental survey, 1985. Japan Marine

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Monetary losses incurred during fishing operations were calculated from data for product (kg) and from price per kilogram (yen) of sablefish, Greenland turbot, and arrowtooth flounder, contained in the annual survey reports of JAMARC by the following formula:

Monetary loss (yen and US dollar) =
(Average product value) × (depredation rate [RNT, RNS, REY or REA])/100,

where average product value is the average of product values calculated by product per operation and by price per kilogram in each area and each year.

Results

Stations with killer whales

Between 1980 and 1989, killer whales were reported at 25 stations (Fig. 1). Eighteen of these stations were in the eastern Bering Sea (B), five stations were near the eastern Aleutian Islands (EA), and one station each was near the Shumagin Islands (SH) and off Kodiak Island (KO). Fishery interactions consistently occurred at several of the sampling locations (Table 1). The highest frequency of killer whale interactions was reported for two areas in the Bering Sea: B-I (stations 31, 32, and 33) and B-II (stations 22, 25, 26, and 27) (Table 1, Fig. 1). Killer whale group size ranged between 4 and 50 animals during the 1988 survey (Table 2). From the 1988 field observations and photographs of killer whales, there appears to be three killer whale groups involved in the Bering Sea fishery interactions (BS1, BS2, and BS3 in Table 2; Yano and Dahlheim[14]).

Depredation by killer whales

During the 1988 survey, when killer whales were observed around the vessel, the hooks on the retrieved groundline frequently contained only fish heads, lips, or gills (Fig. 2), providing evidence that killer whales were responsible for depredation of longline-caught fish. Occasionally, whole fish showed extensive rake marks made by killer whale teeth (Figs. 3 and 4). Whales consumed longline catches of sablefish, Greenland turbot, arrowtooth flounder, and Pacific halibut, the latter remaining whole but showing extensive rake marks. Two heads of searcher were also noted. Other species of fish caught on longlines but not eaten by killer whales included Pacific cod, grenadier, *Coryphaenoides acrolepis*, rockfish, *Sebastes* spp., walleye pollock, *Theragra chalcogramma*, and shortspine thornyhead, *Sebastolobus alascanus*.

Depredation rates

Killer whale depredation rates calculated by four different methods showed that the rates based on averages of total catch (REA and REY) were higher than the rates calculated directly from damaged fish (RNT and RNS). Based on our sampling, depredation rates for Greenland turbot were highest, followed by depredation rates for sablefish, arrowtooth flounder, and Pacific halibut (Table 3). Depredation rates of about 10% or more (based on both RNT and RNS values) were noted for stations 30, 33, 25, 22, and 20. The highest RNT and RNS values were found at station 25 for Greenland turbot and sablefish and at station 22 for arrowtooth flounder. Arrowtooth flounder typically had lower depredation rates than those calculated for Greenland turbot or sablefish. However, a large number of damaged arrowtooth flounder (15-72 specimens) were present in the catch at stations 30, 17, 20, 22, and 25.

Annual catch rates (total number of fish caught per hachi) of sablefish, Greenland turbot, and arrowtooth flounder for each station in the EA, B-I, B-II, B-III, and SH areas (Fig. 1) were used to calculate depredation rates for all years at each station (REA) and for all stations for each year (REY). Twenty-one stations had fishery interactions involving killer whales during the period 1980-88 (Table 4). Depredation rates (REA) calculated from the average fishery catch rates for years with and without killer whale predation showed that the average catch rates of sablefish and Greenland turbot were significantly lower when killer whales were present than when killer whales were absent (ANOVA, $P<0.01$). However, for arrowtooth flounder average catch rates were independent of killer whale depredation (ANOVA, $P>0.05$). In addition average catch of arrowtooth flounder was similar among years regardless of the presence or absence of whales (Table 4). Depredation rates (REA) calculated from the average

[11] *(continued)* Fishery Resources Research Center, 3-27 Kioi-cho, Chiyoda-ku, Tokyo 102 Japan, JAMARC Rep. S60/No.12, 197 p. [In Japanese.]

[12] Takeda, Y., and T. Sasaki. 1988. Report on sablefish and Pacific cod resource developmental survey, 1986. Japan Marine Fishery Resources Research Center, 3-27 Kioi-cho, Chiyoda-ku, Tokyo 102 Japan, JAMARC Rep. S61/No.12, 179 p. [In Japanese.]

[13] Takeda, Y. 1988. Report on sablefish and Pacific cod resource developmental survey, 1987. Japan Marine Fishery Resources Research Center, 3-27 Kioi-cho, Chiyoda-ku, Tokyo 102 Japan, JAMARC Rep. S62/No.11, 191 p. [In Japanese.]

[14] Yano, K., and M. E. Dahlheim. Behavior of killer whales, *Orcinus orca*, during longline fishery interactions in the southeastern Bering Sea and adjacent waters. Fisheries Science (unpubl. manuscript).

Table 1

Areas and stations where killer whales, *Orcinus orca*, were encountered (X) during Japan-U.S. cooperative longline surveys (1980 to 1989). B-II and B-III areas were not surveyed (—) in 1980 and 1981. Asterisks (*) indicate the stations where killer whales were encountered but no depredation occurred.

		Year										Total per station
Area[1]	St. no.	1980	1981	1982	1983	1984	1985	1986	1987	1988[2]	1989	
EA	35				X							1
EA	36					X						1
EA	37							X		X	X	3
EA	38										X	1
EA	59							X				1
B-1	30						X			X		2
B-1	31	X			X	X		X		X	X	6
B-1	32	X	X		X				X			4
B-1	33	X		X	X		X	X	X	X		7
B-1	34			X					X			2
B-II	17	—	—							X	X	2
B-II	18	—	—							X		1
B-II	19	—	—							X*		1
B-II	20	—	—			X		X		X		3
B-II	22	—	—		X				X	X		3
B-II	25	—	—	X			X	X	X	X	X	6
B-II	26	—	—	X				X	X	X	X	5
B-II	27	—	—		X			X	X			3
B-II	28	—	—		X							1
B-III	7	—	—							X		1
B-III	10	—	—							X*		1
B-III	12	—	—		X						X	2
B-III	13	—	—		X							1
SH	65									X		1
KO	83									X*		1
Total per year		3	1	4	9	3	3	8	7	15	7	60

[1] EA = Eastern Aleutian Islands; B = Bering Sea; SH = Shumagin Islands; KO = Kodiak Island, see Figure 1 for areas.
[2] Detailed observations of killer whale predation were documented.

catch rates for years with and without killer whale predation ranged from 9.2 to 92.4% for sablefish, from 2.2 to 90.4% for Greenland turbot, and from 1.4 to 80.3% for arrowtooth flounder (Table 4).

Between-year comparisons (REY) for catches of all species at the same station (except for 1982 of sablefish) indicate catches were lower in years with killer whale depredation (Table 5). The average catch rates of sablefish and Greenland turbot for stations with killer whale depredation were significantly lower than in stations without depredation (ANOVA, $P<0.05$). However, the average catch rate of arrowtooth flounder (for stations with killer whale depredation) was not significantly lower than that for stations without killer whale depredation (ANOVA, $P>0.05$). Depredation rates (REY) calculated from the average catch rates for stations with and without killer whale predation ranged from 33.4 to 84.1% for sablefish, from 53.3 to 82.6% for Greenland turbot, and from 17.0 to 70.8% for arrowtooth flounder (Table 5). REY values calculated from average catch rates for years with and without killer whale depredation were slightly lower than REA values (Table 6).

Predation rates based on the average catch landed (REA and REY values) were higher than those rates (RNT and RNS values) calculated directly from counting heads, lips, and gills of fish remains on the deck during the 1988 survey (Table 6). Depredation rate, based on the four different methods of calculations (i.e. RNT, RNS, REY, and REA), suggested that whales took 14-60% of the sablefish, 39-69% of the Greenland turbot, and 6-42% of the arrowtooth flounder.

Size of fish consumed by killer whales

The size of the fish taken by whales was determined by measurements of HL or ML. The relationships

Table 2

Stations where killer whales, *Orcinus orca*, were encountered during the 1988 Japan-U.S. longline research survey.

Area[1]	St. no.	Date	Operating depth (m)	Estimated number of whales	Arrival time of killer whales	Hachi[2] number when killer whales arrived	Fishing depth of retrieved hachi (m)	First hachi number with evidence of killer whale depredation	Fishing depth of first hachi number that received killer whale depredation (m)	Group[3] identified
EA	37	17 June	160–744	40–50	13:30	50	380	54	440	?
B-I	30	23 June	144–480	20–30	10:25	68	380	76	390	1,3
B-I	31	27 July	110–820	5–6	12:15	120	550	123	600	2
B-I	33	22 June	122–812	20–30	8:40	1	800	7	780	1,3
B-II	17	14 July	174–980	8–10	11:05	86	210	95	300	1
B-II	18	15 July	133–215	8–10	8:30	8	136	24	137	1
B-II[4]	19	17 July	150–245	4	13:16	156	238	—	—	2
B-II	20	18 July	160–820	8–10	9:30	42	160	117	440	2
B-II	22	28 June	197–680	15–30	8:45	1	680	6	670	1
B-II	25	24 June	430–613	10–20	8:30	1	610	6	610	2
B-II	26	21 July	485–720	15–20	8:10	1	485	31	509	?
B-III	7	08 July	130–155	10–15	10:50	46	145	110	150	2
B-III[4]	10	10 July	167–562	—	8:20	1	167	—	—	?
SH	65	30 July	135–765	6–8	13:08	127	455	133	660	1
KO[4]	83	18 August	360–750	7–8	11:00	65	520	—	—	?

[1] EA = Eastern Aleutian Islands; B = Bering Sea; SH = Shumagin Islands; KO = Kodiak Island, see Figure 1 for areas.
[2] A length of groundline equal to 100 m.
[3] See Yano and Dahlheim (See Footnote 14 in text).
[4] No predation observed at station.

Figure 2

Heads, lips, and gills of partially consumed sablefish, *Anoplopoma fimbria*, Greenland turbot, *Reinhardtius hippoglossoides*, and arrowtooth flounder, *Atheresthes stomias*, at station 22. Scale represents 300 mm.

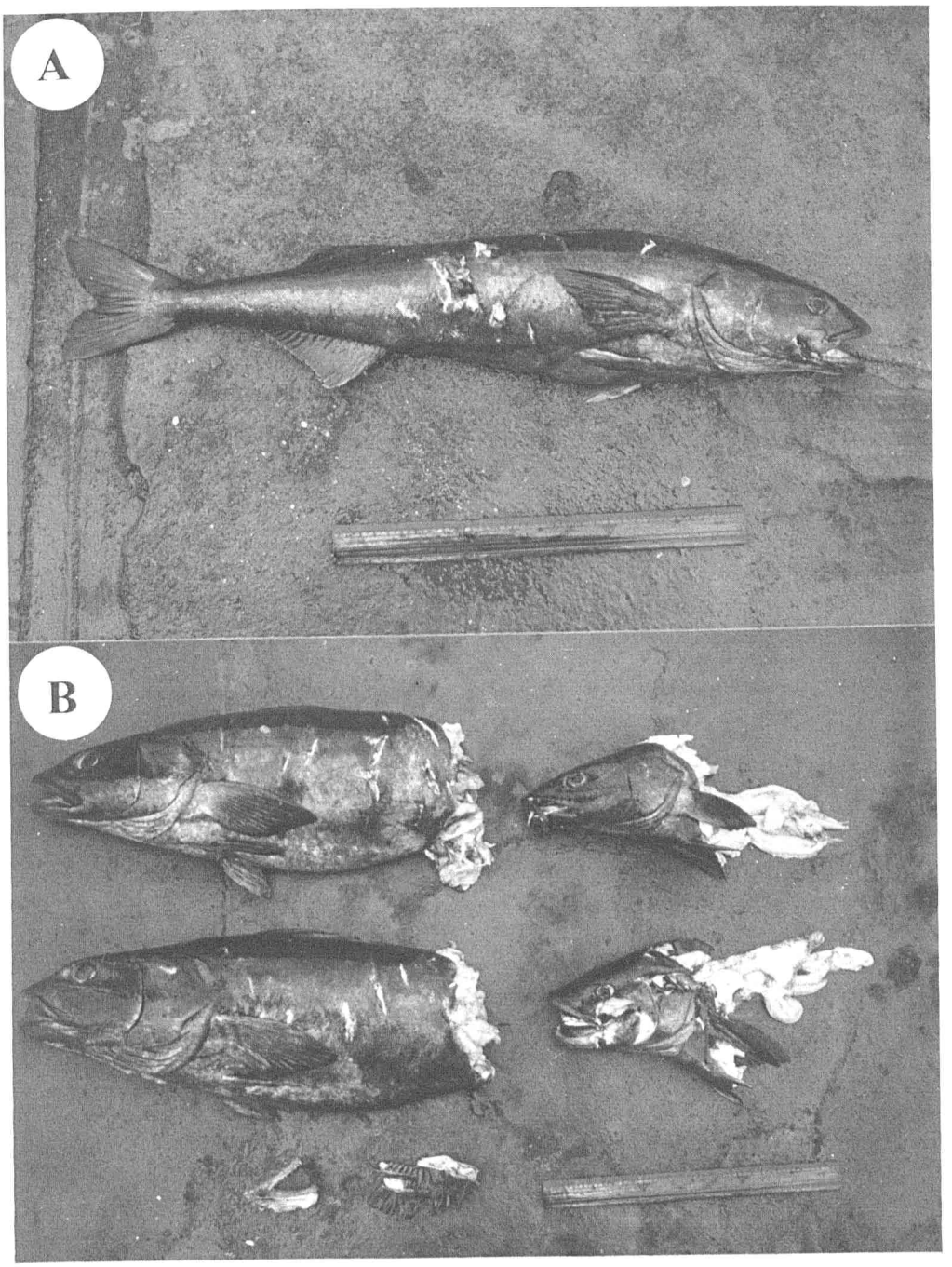

Figure 3

Depredated sablefish, *Anoplopoma fimbria*, at station 33. (**A**) Whole fish with rake marks made by killer whale teeth; (**B**) partially consumed fish showing head, lips, and gills. Scale represents 300 mm.

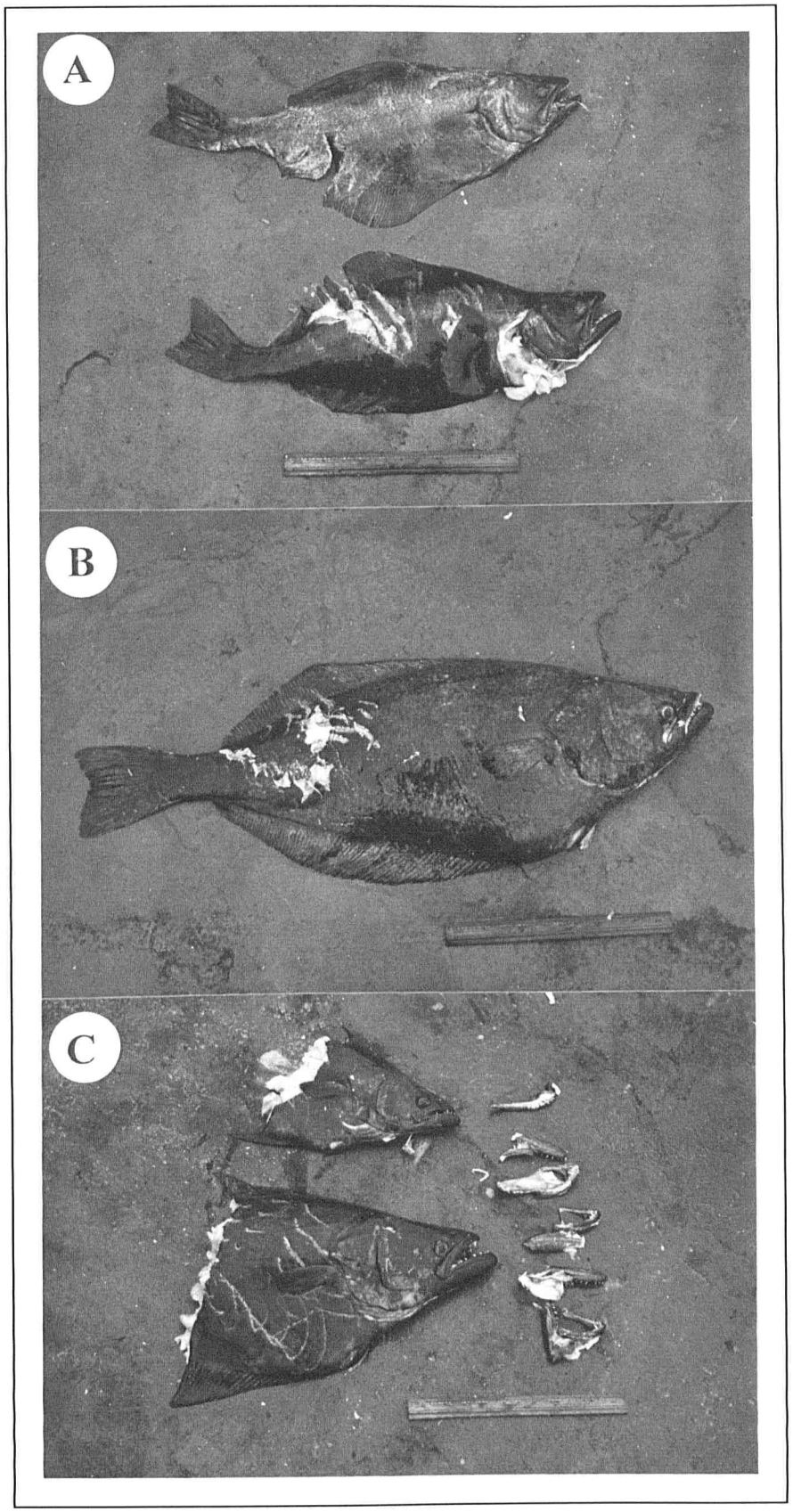

Figure 4

Partially consumed Greenland turbot, *Reinhardtius hippoglossoides*, and arrowtooth flounder, *Atheresthes stomias*. Scales represent 300 mm. (**A**) Arrowtooth flounder with rake marks made by killer whale teeth at station 22; (**B**) damaged Greenland turbot at station 17; (**C**) head and lips of partially consumed Greenland turbot at station 22.

Table 3

Killer whale, *Orcinus orca*, predation rates for 1988 on sablefish, *Anoplopoma fimbria*, Greenland turbot, *Reinhardtius hippoglossoides*, arrowtooth flounder, *Atheresthes stomias*, and Pacific halibut, *Hippoglossus stenolepis*. NPF: number of damaged fish; RNT (%) = (number of partially consumed fish, *NP*)/(number of total catch fish) × 100; RNS (%) = (NP)/(number of fish (remaining heads, lips, or gills seen) counted from the start of depredation by killer whales) × 100.

		Sablefish			Greenland turbot			Arrowtooth flounder			Pacific halibut		
Area[1]	St. no.	NPF	RNT	RNS	NPF	RNT	RNS	NPF	RNT	RNS	NPF	RNT	RNS
EA	37	69	14.11	14.53	33	30.00	30.00	1	2.04	5.88	0	0.00	0.00
B-I	30	13	38.24	43.33	3	60.00	60.00	19	14.29	61.29	0	0.00	0.00
B-I	31	7	2.57	17.07	6	14.63	54.55	0	0.00	0.00	0	0.00	—
B-I	33	27	9.68	9.93	3	9.09	10.34	0	0.00	0.00	0	0.00	0.00
B-II	17	9	7.38	9.47	7	16.28	17.07	15	3.50	17.65	0	0.00	0.00
B-II	18	1	0.26	0.26	0	—	—	3	0.59	0.59	1	0.72	0.72
B-II	20	25	26.04	71.43	27	71.05	77.14	27	7.42	26.21	0	0.00	0.00
B-II	22	8	5.76	6.20	9	37.50	37.50	72	19.46	19.62	0	0.00	0.00
B-II	25	32	62.75	62.75	21	95.45	95.45	15	12.20	12.20	1	8.33	8.33
B-II	26	3	0.64	0.89	11	20.75	23.91	1	8.33	8.33	0	—	—
B-III	7	0	0.00	—	0	—	—	1	0.77	1.64	4	0.57	4.04
SH	65	5	0.28	2.69	0	—	—	0	0.00	0.00	0	0.00	—
Average			13.98	21.69		39.42	45.11		5.72	12.78		0.87	1.46

[1] EA = Eastern Aleutian Islands; B = Bering Sea; SH = Shumagin Islands, see Figure 1 for areas.

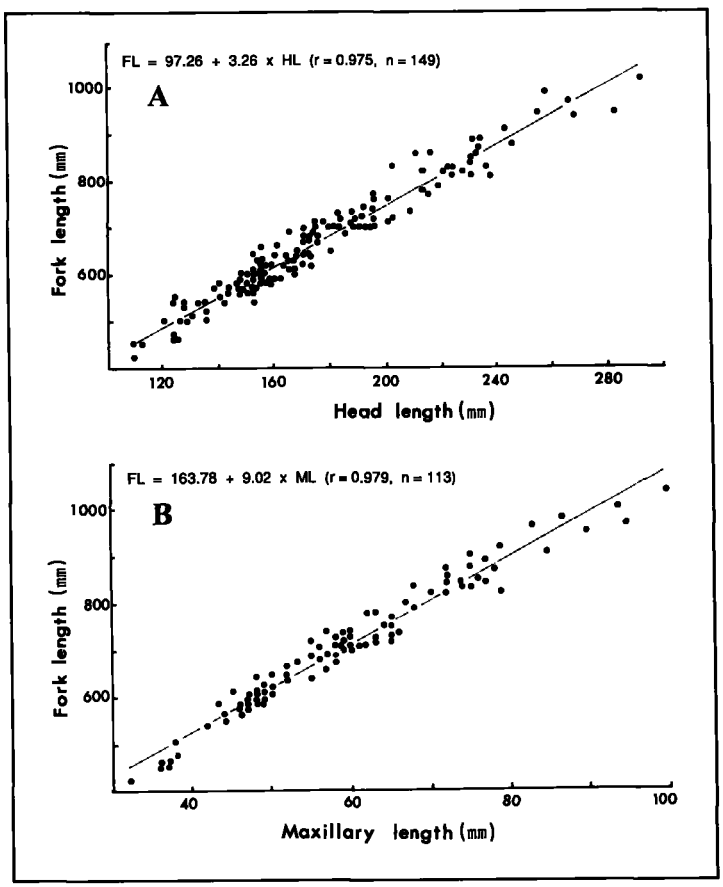

Figure 5

Size of partially consumed sablefish, *Anoplopoma fimbria*. (**A**) The relationship between head length (HL) and fork length (FL); (**B**) the relationship between maxillary length (ML) and fork length (FL).

Table 4

Average catch rates (number of fish per hachi) for years with and without killer whale, *Orcinus orca*, predation (1980–88), and calculated REA [REA = 100 – C (%)]. A = predation occurred; B = no predation occurred; C = A/B × 100 (%); AO = average when C>100% are omitted, and when REA≤0 are omitted.

		Sablefish				Greenland turbot				Arrowtooth flounder				Frequency[2]	
Area[1]	St. no.	A	B	C	REA	A	B	C	REA	A	B	C	REA	D	ND
EA	35	0.20	2.02	9.90	90.10	0.02	0.15	13.33	86.67	0.37	0.24	154.17	-54.17	1	8
EA	36	0.17	0.35	48.57	51.43	0.01	0.04	25.00	75.00	0.31	0.14	221.43	-121.43	1	8
EA	37	5.41	7.65	70.72	29.28	0.72	1.92	37.35	62.65	0.30	0.36	83.33	16.67	2	7
EA	59	1.90	3.66	51.91	48.09	0.01	0.01	100.00	0.00	0.06	0.20	30.00	70.00	1	8
B–I	30	4.22	6.18	68.28	31.72	0.25	1.32	18.94	81.06	0.73	0.74	98.65	1.35	2	7
B–I	31	3.02	6.63	45.55	54.45	0.46	3.26	14.11	85.89	0.37	0.32	115.63	-15.63	5	4
B–I	32	1.34	6.35	21.10	78.90	0.23	0.37	62.16	37.84	0.20	0.49	40.82	59.18	4	5
B–I	33	2.50	5.45	45.87	54.13	0.19	1.88	10.11	89.89	0.20	0.17	117.65	-17.65	7	2
B–I	34	2.89	8.81	32.80	67.20	0.37	2.09	17.70	82.30	0.81	0.40	202.50	-102.50	2	7
B–II	17	0.76	5.66	13.43	86.57	0.28	0.86	32.56	67.44	2.68	0.75	357.33	-257.37	6	1
B–II	18	2.54	2.80	90.71	9.21	—	—	—	—	3.18	0.64	496.88	-396.88	1	5
B–II	20	2.94	3.58	82.12	17.88	0.32	1.79	17.88	82.12	1.06	1.26	84.13	15.87	3	4
B–II	22	0.53	6.94	7.64	92.36	0.13	1.05	12.38	87.62	1.69	1.09	155.05	-55.05	3	4
B–II	25	1.38	6.34	21.77	78.23	0.08	0.83	9.64	90.36	0.34	0.95	35.79	64.21	4	3
B–II	26	2.25	6.87	32.75	67.25	0.45	0.46	97.83	2.17	0.09	0.06	150.00	-50.00	4	3
B–II	27	4.80	11.09	43.28	56.72	0.68	0.78	87.18	12.82	0.75	0.07	70.09	29.91	4	3
B–II	28	1.91	6.73	28.38	71.62	0.39	0.12	325.00	-225.00	0.39	1.98	19.70	80.30	1	6
B–III	7	—	0.02	—	—	—	—	—	—	0.81	0.14	578.57	-478.57	1	6
B–III	12	1.03	4.21	24.47	75.53	0.34	2.33	14.59	85.41	0.75	1.42	52.82	47.18	1	6
B–III	13	1.65	6.06	27.23	72.77	0.23	0.86	26.74	73.26	0.58	0.93	62.37	37.63	1	6
SH	65	11.36	10.86	104.60	-4.60	—	—	—	—	1.23	0.15	820.00	-720.00	1	8
Average		2.64	5.63	43.55	56.45	0.29	1.12	51.25	48.75	0.80	0.64	187.95	-87.95	2.6	5.3
(AO)				(40.34)	(59.66)			(31.09)	(68.91)			(57.77)	(42.23)		

[1] EA = Eastern Aleutian Islands; B = Bering Sea; SH = Shumagin Islands, see Figure 1 for areas.
[2] Frequency of sampling. D = depredation; ND = no depredation.

between HL and FL and between ML and FL for sablefish, Greenland turbot, and arrowtooth flounder are shown in Figures 5–7.

Length-frequency distributions from the 1988 survey data for sablefish, arrowtooth flounder, and Greenland turbot are shown in Figures 8-10. Each figure depicts three different length-frequency distributions for each species: 1) those for all areas fished (EA, B-I, B-II, B-III, and SH) including stations that had reports of killer whale interference with longline operations without estimated length specimens (all areas; Figs. 8A, 9A, and 10A); 2) size distributions of undamaged fish for all stations (station numbers are presented in Table 3) that reported killer whale depredation (all stations; 8B, 9B, and 10B); and 3) size distribution of partially consumed fish and whose estimated length was based on the calculations made through the above formula of HL and ML (partially consumed fish; Figs. 8C, 9C, and 10C).

Average length of sablefish was 635.7 mm FL for all areas fished, 607.5 mm FL for undamaged fish at stations where killer whale depredation was evident, and 633.1 mm FL for the partially consumed fish (Fig. 8, A, B, and C). Significant differences were found between average lengths of damaged fish and undamaged fish for all stations where killer whale predation was evident (t=19.65, P<0.05). However, no significant differences were found between average lengths of damaged fish and undamaged fish for all areas fished (t=0.43, P>0.05). The average length of damaged fish was significantly larger than that of undamaged fish at stations where killer whale depredation was evident (t=19.65, P<0.05), but the total average length was about equal to that for all areas fished.

Average length of arrowtooth flounder was 528.3 mm FL for all areas fished, 506.5 mm FL for stations fished where killer whale depredation was evident, and 575.2 mm FL for fish that were preyed upon. Significant differences were found between average lengths of damaged fish and undamaged fish (t=7.71 and t=10.99, P<0.05). The average size of

Table 5

Average catch rates (number of fish per hachi) for stations with and without killer whale, *Orcinus orca*, depredation (stations indicated in Table 4), and calculated REY [REY=100–C(%)]. A = depredation occurred; B = no depredation occurred; C = A/B × 100(%); AO = average when C≥100% are omitted, and when REY<0 are omitted.

	Sablefish				Greenland turbot				Arrowtooth flounder				Frequency	
Year	A	B	C	REY	A	B	C	REY	A	B	C	REY	D	ND
1980	1.11	2.53	43.87	56.13	0.13	0.60	21.67	78.33	0.19	0.25	76.00	24.00	3	7
1981	0.51	3.20	15.94	84.06	0.48	1.24	38.71	61.29	0.19	0.26	73.08	26.92	1	9
1982	5.03	4.50	11.78	−11.78	0.30	1.18	25.42	74.58	0.14	0.48	29.17	70.83	4	17
1983	2.09	4.56	45.83	54.17	0.38	0.92	41.30	58.70	0.39	0.47	82.98	17.02	9	12
1984	2.04	9.49	21.50	78.50	0.12	0.69	17.39	82.61	0.23	0.31	74.19	25.81	3	18
1985	5.16	7.75	66.58	33.42	0.27	0.72	37.50	62.50	0.33	0.60	55.00	45.00	3	18
1986	3.52	6.69	52.62	47.38	0.36	0.77	46.75	53.25	0.47	0.67	70.15	29.85	8	13
1987	1.42	3.75	37.87	62.13	0.40	1.12	35.71	64.29	0.70	1.31	53.44	46.56	7	14
1988	2.18	4.55	47.91	52.09	0.19	0.48	39.58	60.42	1.33	1.18	112.71	−12.71	12	9
Average	2.56	5.22	49.32	50.68	0.29	0.86	33.78	66.22	0.44	0.61	69.63	30.37	5.56	13.00
AO			41.51	58.49			33.78	66.22			64.25	35.75		

[1] Frequency of sampling. D = depredation; ND = no depredation.

partially consumed fish (Fig. 9C) was significantly larger than that reported from all areas fished (Fig. 9A; t=7.71, P<0.05) and for the stations fished where killer whales were present (Fig. 9B; t=10.99, P<0.05).

There was a bimodal length-frequency distribution for Greenland turbot (Fig. 10, A–C). Average length of Greenland turbot was 744.3 mm TL for all areas fished, 730.8 mm TL for the stations fished where depredation occurred, and 756.1 mm TL for the partially consumed fish. Significant differences were found between average lengths of damaged fish and undamaged fish for all stations with killer whale depredation (t=2.03, P<0.05). However, no significant differences were found between average lengths of damaged fish and undamaged fish for all areas fished (t=1.08, P>0.05). The average length of damaged fish was significantly larger than that of undamaged fish at stations with killer whale depredation (t=2.03, P<0.05) but the total average length was about equal to that for all areas fished.

Monetary loss

For the years 1982–88, data were collected on the product yield of each area and operation, unit price per kilogram (commercial price when landed), and product price per operation for sablefish, Greenland turbot, and arrowtooth flounder (Table 7). The average monetary loss in the total catch per operation (using 160 hachi per operation) was estimated to range from ¥96,853.7 ($717.40 [U.S. dollars] @¥135 calculated from RNT) to ¥790,934.2 ($5,858.80 calculated from REA)(Table 8). The average overall loss incurred for all years at all stations (Table 9) as a result of killer whale depredation ranged from ¥402,499.6 to ¥4,667,109.6 (from $29,181.50 to $34,571.20). The total product value of the 4-month survey for each year (D in Table 9) ranged from ¥98,812,086.0 to ¥283,932,240.0 (from $731,941.40 to $2,103,201.80) and the product values per operation (yearly total product value/number of stations per each survey, F in Table 9) ranged from ¥950,116.2 to ¥2,629.002.2 (from $7,037.90 to $19,474.10; Table 9). The yearly loss was 0.21 to 2.96% (G in Table 9) of the total product value in survey and 3.80 to 34.22% (H in Table 9) of the product value per station (per operation). These values suggest that the rate of yearly overall loss is not large (less than 3%) in total product (survey area is extensive, ranging from the Aleutian Islands to Southeast Alaska in Figure 1),

Table 6

Estimated depredation rate (%) calculated by remaining heads, lips, or gills (RNT and RNS) and by averaging the catch rates (REY and REA).

Depredation rate	Sablefish	Greenland turbot	Arrowtooth flounder	$\bar{x}$
RNT	13.98	39.42	5.72	19.71
RNS	21.69	45.11	12.78	26.53
REY	58.49	66.22	35.75	53.49
REA	59.66	68.91	42.23	56.93

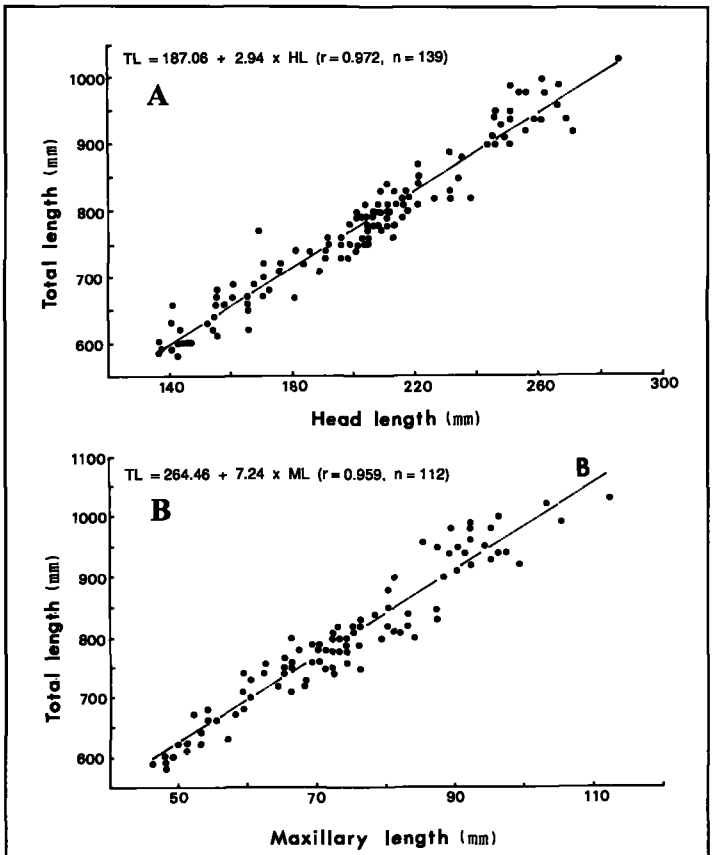

Figure 6

Size of partially consumed Greenland turbot, *Reinhardtius hippoglossoides*. (**A**) The relationship between head length (HL) and total length (TL); (**B**) the relationship between maxillary length (ML) and total length (TL).

but the rate of yearly loss per station (per operation) is relatively large in product per station.

Discussion

Although killer whales range throughout Alaskan waters (Braham and Dahlheim, 1982), fishery interactions are restricted to the Bering Sea and Prince William Sound (Dahlheim[2]). In the Bering Sea, two areas, B-I and B-II, were repeatedly noted for predation by killer whales on longline-caught fish. Despite considerable fishing effort in areas outside the Bering Sea, killer-whale-longline interactions have not been reported for most of the western Aleutian Island chain, Alaska Peninsula, Gulf of Alaska, or Southeast Alaska. However, in September 1991 in Glacier Bay National Park, fishermen reported that a small number of halibut showed evidence of tooth rake marks made by killer whales and consequently were unmarketable fish (Matkin[15]). In Canadian waters, 85% of the commercial harvest of sablefish is taken by pot gear. There have been no reports of killer whales interfering with this pot fishery. There are, however, two isolated accounts of killer whales raiding Pacific halibut longline operations in Hecate Strait, British Columbia (Ellis[16]). Sablefish longlining operations also range from Washington State to central California. Records of killer whale interference with this fishery have not been found (Parks[17]).

The only other area within Alaska where killer whales have been reported raiding longline gear is Prince William Sound. Interactions in this area are well documented (Dahlheim[2]; Matkin[3]). At least 19

[15] Matkin, D. R. Box Gustavus, AK. Pers. commun., October 1991.

[16] Ellis, G. Box 215, Station A, Nanaimo, B.C., Canada V9R 5K9. Pers. commun., March 1990.

[17] Parks, N. Alaska Fisheries Science Center, 7600 Sand Point Way N.E., Seattle, WA 98115. Pers. commun., May 1990.

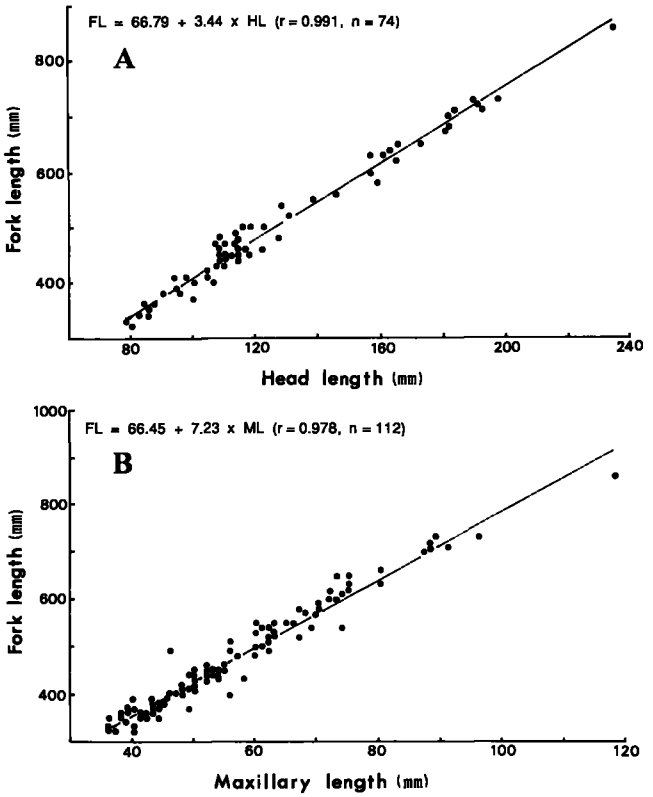

Figure 7

Size of partially consumed arrowtooth flounder, *Atheresthes stomias*. (**A**) The relationship between head length (HL) and fork length (FL); (**B**) the relationship between maxillary length (ML) and fork length (FL).

killer whale pods are known to exist within the area but only two pods have been involved in fishery interactions. Although killer whales may frequently travel between Prince William Sound and offshore waters of the Gulf of Alaska, fishery interactions have not been reported in the waters adjacent to Prince William Sound. One encounter with killer whales was reported off Kodiak Island during this study but no depredation occurred. Whales probably learned to depredate longline-caught fish by long-term exposure to fishing activities. Accounts of killer whales feeding off the discard of fish-processing vessels for a period of over 30 days has been noted in the Bering Sea (Dahlheim, unpubl. data). Active depredation may begin once the whales learn to associate fishing operations with a feeding opportunity.

An examination of the yearly catch data suggested that killer whales depredate 39–69% of the Greenland turbot, 14–60% of the sablefish, and 6–42% of the arrowtooth flounder. Whales took the largest fish for each species consumed. Although available, fish species not eaten by killer whales included Pacific cod, grenadier, rockfish, walleye pollock, and shortspine thornyhead. Little is known of the food habits of Bering Sea killer whales. The fish species consumed by the whales during this study have not been previously reported in the diet of North Pacific killer whales (Rice, 1968), perhaps because few stomachs were examined.

Within- and between-year comparisons of catch rates of sablefish, Greenland turbot, and arrowtooth flounder showed that fewer fish were landed when killer whales were present. Although annual changes in fish biomass and composition by region have been reported (Yano[4,5]; Sasaki and Yano[18]), catch rates (for

[18] Sasaki, T., and K. Yano. 1990. Report on Japan-U.S. joint longline survey by *Tomi Maru No. 88* in the eastern Bering Sea, Aleutian Region, and Gulf of Alaska, 1988. National Research Institute of Far Seas Fisheries, 5-7-1 Orido, Shimizu, Shizuoka 424 Japan, 163 p.

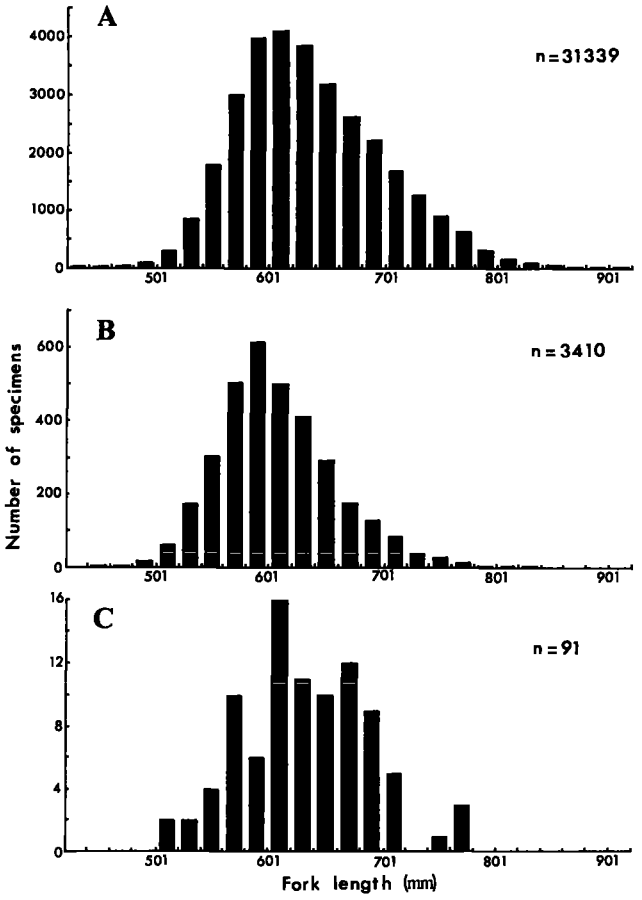

Figure 8

Length-frequency distribution of sablefish, *Anoplopoma fimbria*. (**A**) All areas (see Fig. 1); (**B**) all stations fished where depredation occurred; (**C**) calculated length (head length and maxillary length) of partially consumed fish.

the 10-year period) were typically lower when killer whales were reported as present.

Depredation rates based on average catch rates (REY and REA values) were higher than those calculated from direct counts of damaged fish (RNT and RNS values). Calculated values of RNT and RNS did not consider empty hooks. It is possible that parts of the fish that were preyed upon were pulled off or dropped off the line as it was being retrieved. Thus the rate of predation based on a direct-count method may underestimate the overall rate of depredation. However, RNT and RNS values were used as direct evidence of depredation by killer whales. RNS values indicated that killer whales actively depredate at least 22% of the sablefish, 45% of Greenland turbot, and 13% of the arrowtooth flounder. Large numbers of arrowtooth flounder are found in shallower depths where killer whales do not actively prey on fish, but sablefish and Greenland turbot are found in deeper depths where active depredation has been observed (Yano[4]). However, a greater number of damaged arrowtooth flounder prevailed in the catch (higher RNS values). Depredation rates by killer whales on the U.S. domestic Bering Sea fishery could easily be higher because some vessels (due to overall size and limited range) are forced to fish repeatedly in the same area. If a particular area is in a region of high killer whale density, the vessel may experience continual problems. Reports of killer whales following vessels over short distances from one fishing area to another have been documented (Onodera[19]).

[19] Onodera, S. Fishing master of *Tomi Maru No. 88*, 6-3-25 Irifune, Kushiro, Hokkaido 085 Japan. Personal commun., October 1988.

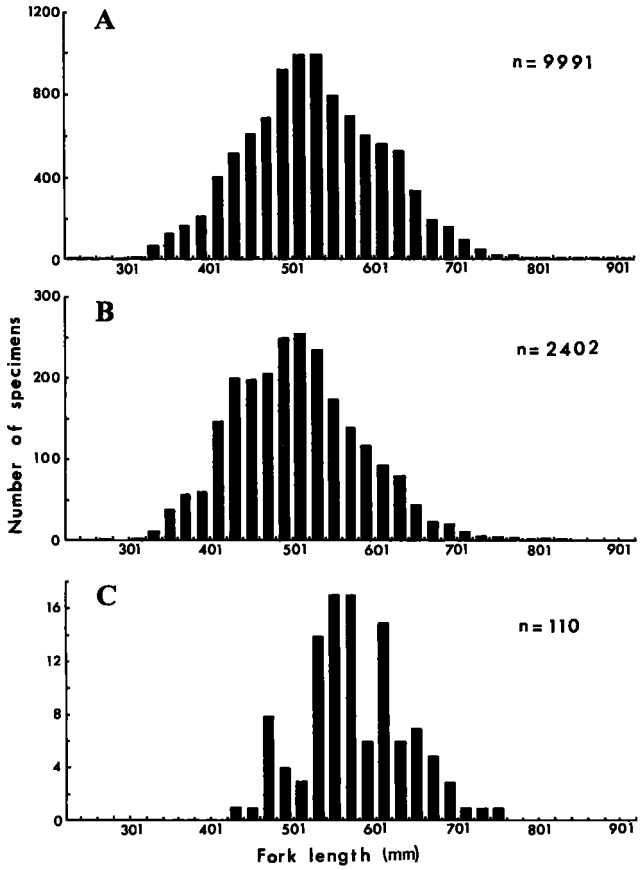

Figure 9

Length-frequency distribution of arrowtooth flounder, *Atheresthes stomias*. (**A**) All areas (see Fig. 1); (**B**) all stations fished where depredation occurred; (**C**) calculated length (head length and maxillary length) of partially consumed fish.

Dahlheim[2] estimated that the U.S. domestic longline fishery in the Bering Sea incurred an average loss of $2,300 per day during the winter of 1988, similar to the values ($928.90 in RNT and $3,373.50 in REA per operation [per day]) reported for this study. However, losses reported for this study may be underestimated. For example, monetary losses would be greater if the time spent by fishermen traveling from one area to another to escape whales was considered. Also the price per kilogram of sablefish is greater than that for larger fish. Since whales were shown to prefer larger fish, the actual monetary losses per operation may be greater than those reported (values based on an average cost/kg). Matkin et al.[20] estimated sablefish losses of $34,300 to $55,500 over the entire season for the 1986 Prince William Sound sablefish longline industry. During the 4-month research survey, a minimum value (calculated from RNT) of $2,982.00 and a maximum value (calculated from REA) of $34,571.00 was estimated.

Acknowledgments

We express our sincere appreciation to T. Sasaki (National Research Institute of Far Seas Fisheries) and M. Kuroiwa (Japan Marine Fishery Resources Re-

[20] Matkin, C. O., G. Ellis, O. von Ziegesar, and R. Steiner. 1987. Killer whales and longline fisheries in Prince William Sound, Alaska 1986. Alaska Fisheries Science Center, National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Unpubl. manuscr., contract 40ABNF6 2262, 18 p.

Table 7

Product of each area, product per operation, price per kilogram, and product price per operation for sablefish, *Anoplopoma fimbria*, Greenland turbot, *Reinhardtius hippoglossoides*, and arrowtooth flounder, *Atheresthes stomias*. B = product, C = product per operation (C = B/A), D = price per kilogram, and E = product value per operation (E=C × D)

			Sablefish				Greenland turbot				Arrowtooth flounder			
Year	Area[1]	No. of operation (A)	B (kg)	C (kg)	D (yen)	E (yen)	B (kg)	C (kg)	D (yen)	E (yen)	B (kg)	C (kg)	D (yen)	E (yen)
1982	EA	17	5,300.0	311.8	722	225,094.1	1,306.4	76.8	383	29,432.4	652.3	38.4	158	6,062.6
	B-I	5	5,100.0	1,020.0	722	736,440.0	2,101.6	420.3	383	160,982.6	296.5	59.3	158	9,369.4
	B-II	14	5,700.0	407.1	722	293,957.1	4,203.2	300.2	383	114,987.5	1,008.1	72.0	158	11,377.1
	B-III	9	2,700.0	300.0	722	216,600.0	4,430.4	492.3	383	188,538.1	474.4	52.7	158	8,328.4
	$\bar{x}$			509.7	722	368,003.4		322.4	383	123,479.2		55.6	158	8,784.8
1983	EA	15	10,172.2	678.1	506	343,142.2	2,369.3	158.0	277	43,753.1	483.9	32.3	155	5,000.6
	B-I	5	6,883.0	1,376.6	506	696,559.6	3,145.9	629.2	277	174,281.8	234.4	46.9	155	7,267.3
	B-II	14	13,388.5	956.3	506	483,898.6	2,418.4	172.7	277	47,849.4	957.5	68.4	155	10,600.6
	B-III	8	3,356.8	419.6	506	212,317.6	2,829.5	353.7	277	97,972.5	564.8	70.6	155	10,943.4
	$\bar{x}$			857.7	506	433,996.2		328.4	277	90,966.8		54.5	155	8,447.5
1984	EA	17	11,303.0	664.9	865	575,123.2	1,665.8	98.0	417	40,860.4	323.9	19.1	154	2,933.9
	B-I	5	7,378.3	1,475.7	865	1,276,445.9	2,068.1	413.6	417	172,482.9	253.0	50.6	154	7,793.0
	B-II	14	11,813.2	843.8	865	729,887.0	1,038.5	74.2	417	30,933.7	693.0	49.5	154	7,622.6
	B-III	9	5,526.4	614.0	865	531,148.4	2,673.8	297.1	417	123,887.0	541.9	60.2	154	9,271.8
	$\bar{x}$			899.6	865	778,154.0		220.7	417	92,031.9		44.8	154	6,899.2
1985	EA	17	18,592.8	1,093.7	978	1,069,632.8	1,399.2	82.3	305	25,103.3	405.6	23.9	170	4,063.0
	B-I	5	10,614.0	2,122.8	978	2,076,098.4	2,130.6	426.1	305	129,966.6	338.0	67.6	170	11,492.0
	B-II	14	13,249.2	946.4	978	925,551.3	1,478.7	105.6	305	32,214.5	1233.7	88.1	170	14,980.6
	B-III	9	7,960.5	884.5	978	865,041.0	3,021.0	335.7	305	102,378.3	794.3	88.3	170	15,003.4
	$\bar{x}$			1,261.8	978	1,234,040.4		237.4	305	72,407.0		67.0	170	11,390.0
1986	EA	16	14,219.0	888.7	737	654,962.7	874.0	54.6	436	23,816.5	266.0	16.6	152	2,527.0
	B-I	5	7,759.0	1,551.8	737	1,143,676.6	1,646.0	329.2	436	143,531.2	407.0	81.4	152	12,372.8
	B-II	14	9,864.0	704.6	737	519,269.1	1,361.0	97.2	436	42,385.4	1,239.0	88.5	152	13,452.0
	B-III	9	10,486.0	1,165.1	737	858,686.9	2,201.0	244.6	436	106,626.2	531.0	59.0	152	8,968.0
	$\bar{x}$			1,077.5	737	794,117.5		181.4	436	79,090.4		61.4	152	9,332.8
1987	EA	16	13,832.0	864.5	894	772,863.0	1,767.0	110.4	347	38,321.8	990.5	61.9	105	6,500.2
	B-I	5	2,223.0	444.6	894	397,472.4	3,021.0	604.2	347	209,657.4	990.5	198.1	105	20,800.5
	B-II	14	3,629.0	259.2	894	231,737.6	2,394.0	171.0	347	59,337.0	3,366.0	240.4	105	25,245.0
	B-III	9	3,534.0	392.7	894	351,044.0	2,394.0	266.0	347	92,302.0	1,603.8	178.2	105	18,711.0
	$\bar{x}$			490.2	894	438,238.8		287.9	347	99,901.3		169.7	105	17,818.5
1988	EA	17	13,851.0	814.8	831	677,069.5	2,008.8	118.2	193	22,805.8	1,107.8	65.2	50	3,258.2
	B-I	5	4,807.0	961.4	831	798,923.4	744.0	148.8	193	28,718.4	592.1	118.4	50	5,921.0
	B-II	14	6,004.0	428.9	831	356,380.3	558.0	39.9	193	7,692.4	6,242.9	445.9	50	22,296.1
	B-III	9	6,745.0	749.4	831	622,788.3	2,176.2	241.8	193	46,667.4	2,005.5	222.8	50	11,141.7
	$\bar{x}$			738.6	831	613,776.6		137.2	193	26,479.6		213.1	50	10,655.0
Minimum			2,223.0	259.2	506	212,317.6	558.0	39.9	193	7,692.4	234.4	16.6	50	2,527.0
Maximum			18,592.8	2,122.8	978	2,076,098.4	4,430.4	629.2	436	209,657.4	6,242.9	445.9	170	25,245.0
Average			8,428.2	833.6	790.4	658,877.4	2,122.3	245.1	336.9	82,574.2	1,021.3	95.3	134.9	12,856.0

[1] EA = Eastern Aleutian Islands; B = Bering Sea, see Figure 1 for areas.

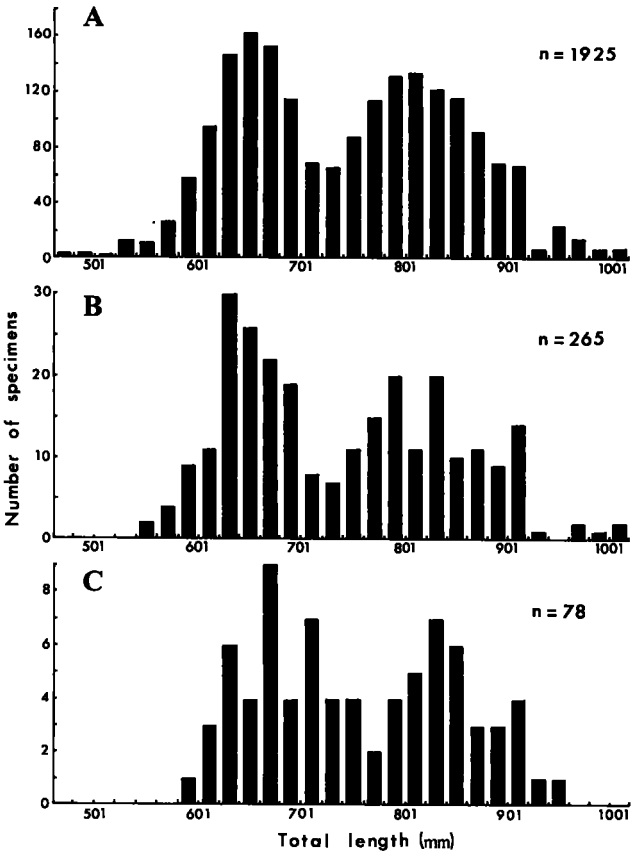

Figure 10

Length-frequency distribution of Greenland turbot, *Reinhardtius hippoglossoides*. (**A**) All areas (see Fig. 1); (**B**) all stations fished where depredation occurred; (**C**) calculated length (head length and maxillary length) of partially consumed fish.

Table 8

Average monetary loss per station (1982–88) estimated by depredation rates (RNT, RNS, REY, and REA) for sablefish, *Anoplopoma fimbria*, Greenland turbot, *Reinhardtius hippoglossoides*, and arrowtooth flounder, *Atheresthes stomias*. Total given for all three species.

	Sablefish		Greenland turbot		Arrowtooth flounder		Total	
Depredation rate	Yen	U.S. $	Yen	U.S. $	Yen	U.S. $	Yen	U.S. $
RNT	92,111.1	682.30	32,550.7	241.10	735.4	5.40	125,397.2	928.90
RNS	142,910.5	1,058.60	37,249.2	275.90	1,643.0	12.20	181,802.7	1,346.70
REY	385,377.4	2,854.60	54,680.6	405.00	4,596.0	34.00	444,654.0	3,293.60
REA	393,086.3	2,911.80	56,901.9	421.50	5,429.1	40.20	455,417.3	3,373.50

Table 9

Yearly monetary loss per station and overall loss estimated by depredation rate of RNT (minimum value) and RNA (maximum value), and yearly total product value per survey and product values per station calculated from total product value.

Year		Yearly monetary loss per station (A) Yen	U.S. $	No. of depredated stations (B)	Overall monetary loss (C=AxB) Yen	U.S. $	Yearly total product value in Yen (U.S. $)	No. of stations per survey (E)	Product value/station (F=D/E) in Yen (U.S. $)	Rate of loss per yearly product (G=C/Dx100) (%)	Rate of loss per station product (H=A/Fx100) (%)
1982	max.	100,624.9	745.40	4	402,499.6	2,981.50	121,346,699	108	1,123,580.5	0.33	8.96
	min.	308,350.2	2,284.10		1,233,400.8	9,136.30	(898,864.40)		(8,322.80)	1.02	27.44
1983	max.	97,015.0	718.60	9	873,135.0	6,467.70	98,812,086	104	950,116.2	0.88	10.21
	min.	325,174.7	2,408.70		2,926,572.3	21,678.30	(731,941.40)		(7,037.90)	2.96	34.22
1984	max.	145,459.5	1,077.50	3	436,378.5	3,232.40	176,102,713	108	1,630,580.7	0.25	8.29
	min.	530,579.4	3,930.20		1,591,738.2	11,790.70	(1,304,464.50)		(12,078.40)	0.90	32.54
1985	max.	201,713.2	1,494.20	3	605,139.6	4,482.50	283,932,240	108	2,629,002.2	0.21	7.67
	min.	790,934.2	5,858.80		2,372,802.6	17,576.30	(2,103,201.80)		(19,474.10)	0.84	30.08
1986	max.	142,728.9	1,057.30	8	1,141,831.2	8,458.00	238,057,678	107	2,224,838.1	0.48	6.42
	min.	532,212.9	3,942.30		4,257,703.2	31,538.50	(1,763,390.20)		(16,480.30)	1.79	23.92
1987	max.	101,666.1	753.10	7	711,662.7	5,271.60	271,467,224	107	2,537,076.9	0.26	4.01
	min.	337,820.0	2,502.40		2,364,740.0	17,516.60	(2,010,868.30)		(18,793.20)	0.87	13.32
1988	max.	96,853.7	717.40	12[1]	1,162,244.4	8,609.20	275,277,684	108	2,548,867.4	0.42	3.80
	min.	388,925.8	2,880.90		4,667,109.6	34,571.20	(2,039,094.00)		(18,880.50)	1.70	15.26
Overall	max.	96,853.7	717.40		402,499.6	2,981.50				0.21	3.80
		790,934.2	5,858.80		4,667,109.6	34,571.20				2.96	34.22

[1] Three stations where no depredation was evident.

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Abstract.—To enable accurate ageing of orange roughy, *Hoplostethus atlanticus*, eggs caught in egg production surveys for biomass estimation, eggs were cultured at four experimental temperatures, and the results were fitted to a regression model of age-at-stage for the culture temperatures used. Water column ascent and descent rates of early stage eggs were estimated by using a combination of experimental observation and theory. Young eggs ascended rapidly (>300 m·day^{-1}), middle-aged eggs approached neutral buoyancy, and the oldest eggs sank rapidly. The ascent and development rate results were combined with data on water column thermal structure to produce a "thermal history model" of orange roughy egg development, enabling the thermal history of eggs to be considered in ageing them as they rise through the stratified layers into the mixed layer. The ascent and descent rates and modelled depth-at-stage were compared with field data on depth distributions of stages from MOCNESS tows over the North Chatham Rise, New Zealand. For the dominant and subdominant egg stages, predictions closely matched the field results. The model therefore provided a robust method for ageing eggs caught in an egg production survey for orange roughy. The ontogenetic pattern of buoyancy in the eggs may partially explain the distributions of early juvenile orange roughy on the North Chatham Rise. The bias in predicted egg ages, caused by the assumption that temperature of development was constant for eggs below the mixed layer, was shown to be important in egg production estimation.

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Fishery Bulletin 93:373–385 (1995).

Ascent rates, vertical distribution, and a thermal history model of development of orange roughy, *Hoplostethus atlanticus*, eggs in the water column

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Orange roughy, *Hoplostethus atlanticus* (family: Trachichthyidae), are slow-growing, deep water (700–1,500 m) fish that have been found in large quantities mainly in New Zealand[1] and Australia (Kailola et al., 1993). In winter, orange roughy aggregate to spawn near banks, pinnacles, and canyons, and these aggregations attract large amounts of fishing effort. Fisheries for orange roughy began in 1978–79 in New Zealand. The largest fishery is on the Chatham Rise (Fig. 1) where reported catches reached 13,800 metric tons (t) in 1992–93.[1] The stock assessment for the Chatham Rise fishery is based on stock reduction modelling of biomass in which commercial catches, biological parameters, and time series of relative biomass estimates from research trawl surveys are used. The next largest fishery (with reported catches of 9,128 t in 1992–93 [Field et al., 1994]) is off the east coast of New Zealand, and a large proportion of the catch is taken from the winter spawning aggregations on the Ritchie Bank (Fig. 1). The stock reduction analysis for this fishery prior to 1993–94 was based primarily on catch-per-unit-of-effort data which were highly uncertain and made the biomass estimate very uncertain (Field et al., 1994). Consequently, there was a need for a reliable, absolute biomass estimate.

After reviewing aspects of the biology of orange roughy planktonic eggs and adult fecundity, Zeldis (1993) concluded that both the annual egg production method (AEPM; Saville, 1964) and the daily fecundity reduction method (DFRM; Lo et al., 1992) would be feasible for the estimation of absolute spawning biomass of orange roughy on the Ritchie Bank. Both the AEPM and the DFRM were applied during an egg production survey of Ritchie Bank orange roughy biomass in June–July 1993.[2]

Because egg production methods rely on calculating egg production rates from estimates of abundance-at-age of planktonic eggs, a means of ageing the eggs is required. This is done by determining ages of identifiable morphological stages of egg

[1] Annala, J. (Compiler) 1994. Report from the Special Fishery Assessment Plenary, 17 August 1994: stock assessments and yield estimates for ORH 3B, 24 p. Unpubl. rept. held in MAF Fisheries, Greta Point library, Wellington, N.Z.

[2] Zeldis, J., R. I. C. C. Francis, J. K. V. Ingerson, M. Clark, and P. J. Grimes. 1994. A daily fecundity reduction method estimate of Ritchie Bank and east coast North Island orange roughy biomass. Draft New Zealand Fisheries Assessment Research Document. MAF Fisheries, Greta Point, Wellington, N.Z.

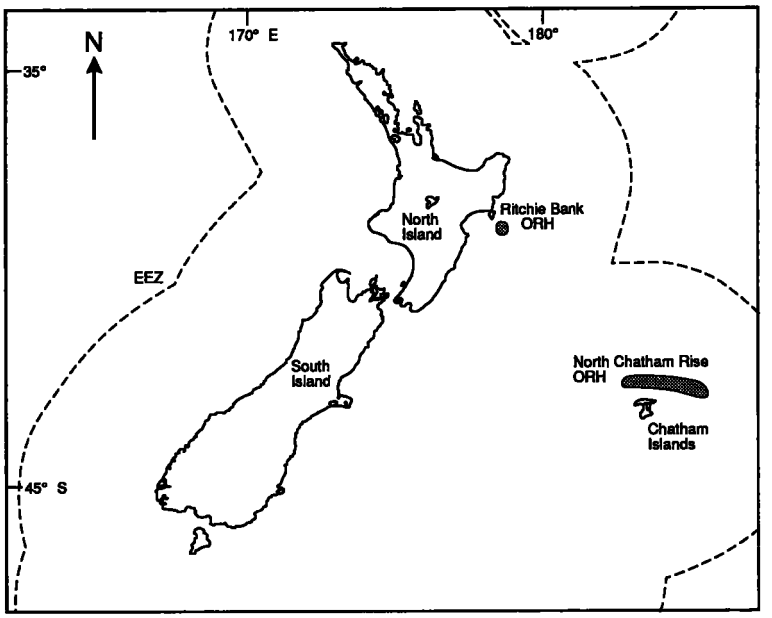

Figure 1

Map of New Zealand and Exclusive Economic Zone and location of Chatham Rise and Ritchie Bank orange roughy, *Hoplostethus atlanticus*, fisheries.

development. Embryogenesis and larval development of orange roughy are undescribed, as are the vertical distributions of the eggs and larvae (Zeldis, 1993). Orange roughy produce large eggs (2.32-mm mean diameter) with a large oil droplet (0.60-mm mean diameter), suggesting that their eggs would be strongly positively buoyant (Robertson, 1981). Since egg development rate in teleosts is strongly temperature dependent (Pauly and Pullin, 1988; Pepin, 1991), changes in the vertical distribution of orange roughy eggs during embryogenesis will have a strong effect on their development rate, because they are spawned in thermally stratified waters below the mixed layer (Zeldis, 1993). Therefore, in order to estimate egg production for orange roughy accurately, a model was needed which considers the thermal history of an egg when the observed stage of development is used to estimate age.

To create and test this model, this study had the following objectives: 1) to describe the temperature dependence of egg development rate; 2) to estimate ascent rates of egg stages with experimentation and theory; 3) to combine results on development rate and ascent rate to develop a 'thermal history model' of orange roughy development in the water column; and 4) to test predictions of this model against observed vertical distributions of egg stages in the water column.

In this study a generalized description of embryology is used to address these objectives. Photographs of some of the egg and larval stages have been published (Grimes and Zeldis, 1993), and detailed descriptions of orange roughy embryological and larval stages will be published separately.

Methods

Embryological, ascent rate and vertical distribution studies were conducted on the North Chatham Rise (Fig. 1) from 7 to 28 July 1992 with the MAF Fisheries RV *Tangaroa*, a 70-m research stern trawler (voyage TAN9206). Additional embryological and ascent rate studies were conducted on the Ritchie Bank from 6 June to 8 July 1993 during an egg production survey (*Tangaroa* voyage TAN9306).

Embryology and development rates

To study embryology and development rates, orange roughy eggs were cultured under controlled-temperature conditions in a shipboard laboratory. The culturing facility had four insulated, plastic 20-L bins, in which plastic jars with mesh tops were submerged to hold the eggs. Each bin had flow-through supplies

of seawater (500 mL·min^{-1}) filtered to 5 microns. Water was cooled to 6°C by a refrigeration system, then heated to desired culture temperatures by aquarium heaters controlled with digital thermistors. The 6°C inlet and heater for each bin were within a central PVC "upwelling stem" driven by an airstone and provided stable culture temperatures during the study (±0.2°C). The jars and bins were disinfected with weak ammonia about every three days.

Culture temperatures used were 6, 8, 10, and 12°C, which spanned the temperature range from the depth of spawning to the sea surface in orange roughy spawning areas. The eggs used for the 6°C culture were fertilized from stripped fish (on voyage TAN9306), and the eggs used for the 8, 10, and 12°C cultures were captured from the plankton (on voyage TAN9206). Growing captured planktonic eggs was generally more successful than starting with stripped eggs and sperm. Only a few hundred strip-fertilized eggs were successfully grown, as opposed to thousands of captured eggs. Strip-fertilizing was most successful when free-flowing, ovulating females and freely expressible males were taken from the wings of the trawl and when cooled seawater and dilute sperm infusions were used with the eggs. The eggs that were selected from the plankton samples for culturing were those that floated in the plankton catches.

Eggs were staged by using the criteria and figures for killifish *Fundulus heteroclitus* from New (1966), in which most relevant features of orange roughy development were identifiable, up to and including New's stage 25. Subsequent stages were defined by the degree the tail was free of the yolk (as a proportion of total tail length), and stage 30 was defined as the hatching stage. Stage numbers used in this paper are assumed to represent the midpoints of the time periods of the stages. Eggs were sampled from the jars and examined under a binocular microscope every 3 or 4 hours at 6°C, and less frequently (see Fig. 2) at 8, 10, and 12°C, until stage 9 (morula formation). The 6°C eggs were sampled more frequently because they were the only culture temperature used on voyage TAN9306 and more time was available to sample and observe eggs. After morula formation, eggs from all temperatures were sampled once or twice a day until stage 19 (blastopore closure) and then once every 1 or 2 days until hatching was imminent. After examination, the sampled eggs were either replaced in the culture vessels (if they were rare) or more commonly preserved in 4% buffered formaldehyde in seawater.

Since the eggs used in the 8°C, 10°C, and 12°C series were caught from the plankton, their absolute ages at the start of their series (at stage 5) were not known. To estimate the absolute ages of the observed stages, the cumulative time up to each stage since stage 5 was regressed against the observed stage for each series for each temperature. This meant all regression lines effectively had a common x-axis intercept at stage 5, with age = 0. The absolute age at stage 5 for each temperature was estimated by continuing the lines to 0 on the x-axis and taking the absolute values of the resulting negative y-axis in-

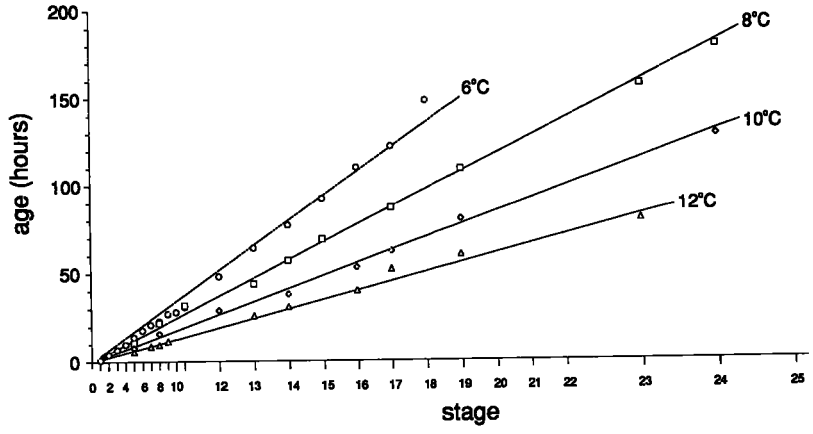

Figure 2

Orange roughy, *Hoplostethus atlanticus*, egg development stages at four temperatures from culturing experiment with curves fitted from Equation 1. The stage numbers should be interpreted as indicating the midpoint of the period of each stage.

tercepts. These predicted y-axis intercepts had small standard deviations (SD) ranging from 1.3 h to 1.5 h, so this source of error in age estimation was considered negligible. The absolute values of the intercepts were then added to the cumulative times of all the observations to estimate the absolute ages for each observed stage for each temperature (Fig. 2). The model was then reestimated by using these absolute ages (the fitted lines in Fig. 2). The regression model predicted egg age as an exponential function of temperature and a linear function of stage:

$$age = 8.803\ e^{-0.158temp} \times stage \qquad (1)$$

The fit had r^2 of 0.96.

The justification for assuming that egg age was a linear function of stage was as follows. The mean duration of the stages given by New (1966) at 20°C for killifish were 1.0 ±0.35 (1 SD) h for stages ≤10, 4.1 ±1.14 h for stages 11 and 21, and 9.0 ±1.15 h for stages 22 and 25. Thus, stage durations were similar within each of these stage groups and differed between the groups by the ratios 1.0: 4.1: 9.0. Evidently, these ratios also applied to orange roughy development, judging by the linear appearance of the orange roughy age-at-stage data for each temperature (Fig. 2) when the x-axis (stage) was scaled by these ratios for stages 1 to 10, 11 to 21, and 22 to 25, respectively. Thus, to use Equation 1 to estimate age from stage, the input value for stage had to be scaled by these ratios (e.g., the appropriate input value for stage 13 would be (11)(1) + (2)(4.1) = 19.2). Orange roughy egg stages from 26 to 30 deviated from that of New (1966) and were not of a consistent length. Therefore, scaling of these stages was not done and ages for stages ≥26 were not modeled.

The justification for assuming that egg age was an exponential function of temperature was that the egg development period for 140 species of pelagic, spherical marine fish eggs was well predicted as an exponential function of temperature and egg size by Pauly and Pullin (1988).

Egg ascent and descent rates

To estimate egg ascent and descent rates, a graduated, perspex cylinder (7×100 cm) was suspended from the ceiling of a shipboard laboratory; its bottom was open in a bucket of seawater and the cylinder was filled with surface seawater (35.00 ppt salinity; see below for the temperatures used). Orange roughy eggs of various stages were introduced at the bottom of the cylinder and, following an initial ascent of 10 cm (to allow the eggs to reach terminal velocity), subsequent ascent was timed over four to seven 10-cm intervals. Older eggs sank; therefore these were introduced to the top of the cylinder and descent rates were measured by following an initial descent of 10 cm. Means and standard deviations of these rates were estimated from estimators for a two-stage sampling design, weighted for unequal subsample sizes (Eq. 5 in Picquelle and Stauffer [1985]).

The water temperature within the cylinder for the experiments on younger eggs (unfertilized, newly fertilized, cell division, and morula-early blastula eggs: stages 0–11 in Fig. 3) was between 6 and 7 degrees and characteristic of the water column at the depth of the spawners. Since these eggs were very positively buoyant, it was clear (see Results section) that the older of these stages occurred shallower in the water column, so it was necessary to predict how fast they would ascend under the temperature-salinity conditions at shallower depths. This was done by using a combination of experimental observation and theory in the following way.

First, it was observed that unfertilized and stage-1 eggs ascended the experimental cylinder at a mean rate of 275 m·day^{-1} at 6°C and 35.00 ppt (Fig. 3). This ascent rate was used to predict the density of these eggs by using the theoretical relationships in Robertson (1981), the seawater density, and seawater viscosity (Sverdrup et al., 1964) in the cylinder. The predicted density was 1.02488 g·cm^{-3}. To test this theoretical density against experimental determinations, the density of unfertilized and stage-1 eggs was measured by diluting the seawater medium (35.00 ppt, 10°C) of the eggs with distilled water until the eggs became neutrally buoyant and by calculating the density of the seawater (1.02425 g·cm^{-3}). The theoretical and experimental densities can be compared if the former value (determined at 6°C) is adjusted to 10°C by using the coefficient of thermal expansion of seawater to account for the decrease in density of the eggs with increase in temperature (taken to be equal in seawater and fish eggs: Coombs et al., 1985). The coefficient of thermal expansion was interpolated from Table 3.1 in Neumann and Pierson (1966) at 35.00 ppt and 8.0°C and atmospheric pressure and was 151·10^{-6} per 1°C change in temperature. The resulting theoretical density was 1.02428, virtually the same density as determined experimentally. This strongly suggests that the theoretically determined density was realistic and that the theory could be used to adapt experimental ascent rates determined at particular temperatures and salinity to various conditions in the oceanic water column.

Accordingly, Robertson's (1981) theoretical relationships were used to calculate the density of stage 1–11 eggs from their experimentally determined

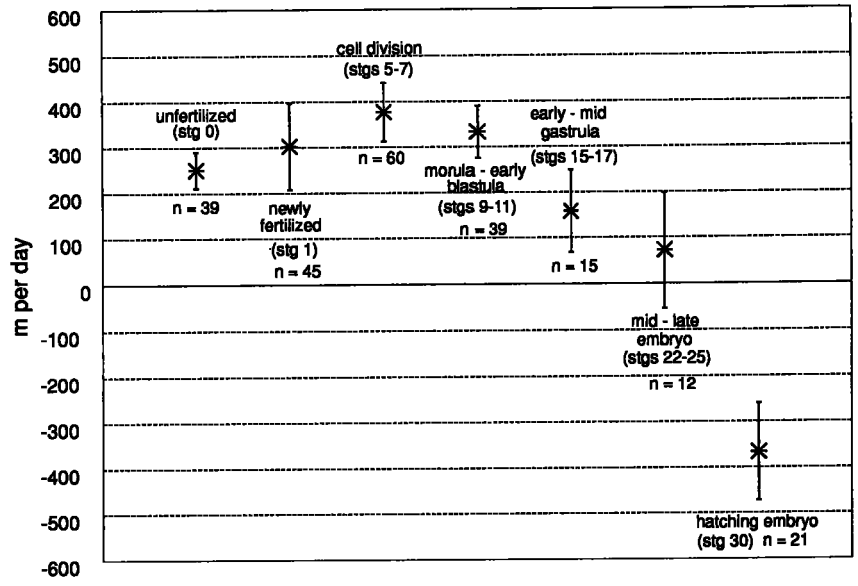

Figure 3

Orange roughy, *Hoplostethus atlanticus*, egg ascent and descent rates in the experimental cylinder for groups of egg stages. Points are means ±95% confidence limits, n = total number of determinations in each group.

ascent rate (mean of 350 m·day^{-1}; Fig. 3) at 6.0°C and 35.00 ppt in the experimental cylinder. This density (1.02406 g·cm^{-3}) and the coefficient of thermal expansion were then used to estimate the ascent rates (Table 1) for stage 1–11 eggs through the water column. This was done for depth strata corresponding to 1°C increases, from 6.0 (the bottom at 870 m) to 11.25°C (the bottom of the mixed layer at 250 m). The analysis accounted for the change in density of the eggs (via the coefficient of thermal expansion), change in density of the surrounding water (from MOCNESS-CTD data), and change in seawater viscosity, as the eggs ascended the water column. Neither the viscosity or coefficient of thermal expansion were corrected to account for changes in salinity and pressure during the ascent (p. 69 in Sverdrup et al., 1964; Table 3.2 in Neumann and Pierson, 1966) because they both changed less than 5% over the salinity and pressure gradients considered here.

Ascent rates of early to mid gastrula and mid to late embryo stages (stages 15–25) were estimated in the cylinder at surface temperature (11–12°C) and

Table 1

Predicted ascent rates of stage 1–11 eggs of orange roughy, *Hoplostethus atlanticus*, at various depths and temperatures in the water column based on relationships between egg density, water column sigma-t and viscosity given by Robertson (1981).

Temp. (°C)	Depth (m)	Salinity (ppt)	Sigma-t (g·cm^{-3})	Viscosity (g sec^{-1}·cm^{-1})	egg density (g·cm^{-3})	Ascent rate (m·day^{-1})
6.0	870	34.40	1.02710	0.0159	1.02406	305.7
7.0	700	34.48	1.02703	0.0156	1.02391	316.9
8.0	550	34.55	1.02694	0.0152	1.02376	330.8
9.0	400	34.65	1.02686	0.0149	1.02361	335.4
10.0	315	34.75	1.02677	0.0146	1.02346	350.8
11.0	265	34.89	1.02671	0.0142	1.02331	360.6
11.25	250	35.00	1.02675	0.0141	1.02327	368.4

salinity (35.0 ppt). These conditions emulated seawater densities that are experienced by eggs at these stages in nature, because the embryos are approaching neutral bouyancy and reside primarily within the mixed layer (see Results section).

The descent rate of hatching-stage eggs (stage 30) was measured at 9.0°C. These eggs were very negatively buoyant and were probably sinking rapidly through the water column. Because surface salinity water was used in the experimental cylinder, the measured descent rate (366 m·day^{-1}) is probably an underestimate for waters below the mixed layer because of decreasing salinity. The measured descent rate of these eggs at 9.0°C and surface salinity were used to predict their density: 1.02707 g·cm^{-3}. This was then used to predict their descent rates at 9.0°C and 34.65 ppt (the salinity at 9°C in the water column) which was 381 m·day^{-1}.

A thermal history model

As orange roughy eggs ascend the oceanic water column, it can be assumed that they will develop at the rate governed by their immediate environmental temperature (Pauly and Pullin, 1988). However, their actual stage at any age is determined by an accumulating average of their previous and present temperatures. A model which enables this "thermal history" of an orange roughy egg to be considered, when the egg's observed stage is used to estimate its age, was created in the following way.

First, it was observed that the temperature-at-depth data for the five MOCNESS profiles (Fig. 4) below the mixed layer had three segments for which the depth change per 1°C change was nearly constant. These were 870 m to 450 m, 450 to 315 m, and 315 to 250 m (the bottom of the mixed layer). These depth changes were divided by the predicted egg ascent rates at each of these 1°C depth intervals (Table 1) to determine the amount of time eggs would spend in each of the 1°C temperature strata. Next, a family of age-at-stage curves was graphed by using Equation 1 from 6.0°C (the near-bottom temperature) to 11.0°C, each curve representing development over an interval of ±0.5°C. Eggs were then "developed" graphically, by moving along the 6.0°C curve until the change in age equalled the amount of time eggs spent in that stratum (in this case 9.4 h, since this stratum was truncated by the bottom at 5.75°C). The point reached was age = 9.4 h, stage = 2.8 (Fig. 5). Then, these stage 2.8 eggs were developed further by "dropping down" to the 7°C curve and moving along it until the change in age was 11.4 h (the length of time required to ascend through the 6.5–7.5°C stratum). The point reached was cumulative age = 20.8 h, stage = 6.7, which was the stage the eggs had reached after accounting for development at 7°C and the previous development at 6°C. This procedure was repeated until eggs were aged through to 11.25°C (at 250 m; the bottom of the mixed layer) at cumulative age = 46.0 h. The eggs at this age were in stage 13. Subsequent egg development to stage 26 occurred in

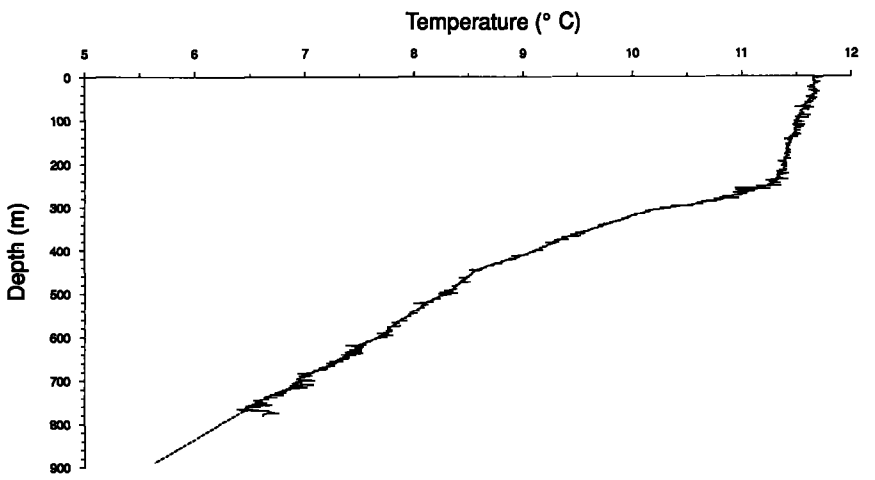

Figure 4

Temperature profile in MOCNESS survey area on the north Chatham Rise during TAN9206. Data are mean temperatures in each 1-m depth stratum across the 5 MOCNESS tows. Temperatures from 780 m to 870 m are extrapolated from temperatures below 450 m for use in modelling.

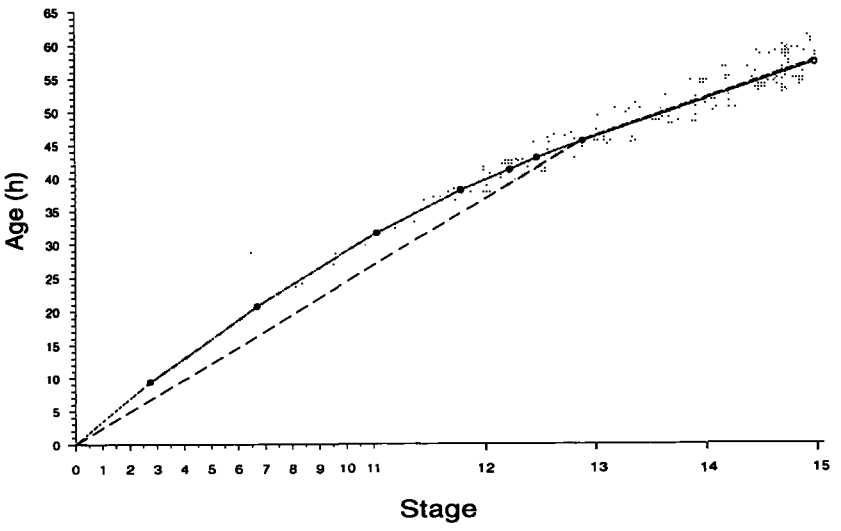

Figure 5

Orange roughy, *Hoplostethus atlanticus*, egg age-at-stage (h) determined from the thermal history model. Dots indicate age-at-stage for each 1°C temperature stratum in the water column. Shaded area shows 95% confidence limits for age-at-stage estimated from 95% confidence limits for ascent rates (Fig. 3). Dashed line shows age-at-stage when temperature of development is assumed to be mean temperature of the stratified layer. Stage numbers represent midpoints of time periods of stages.

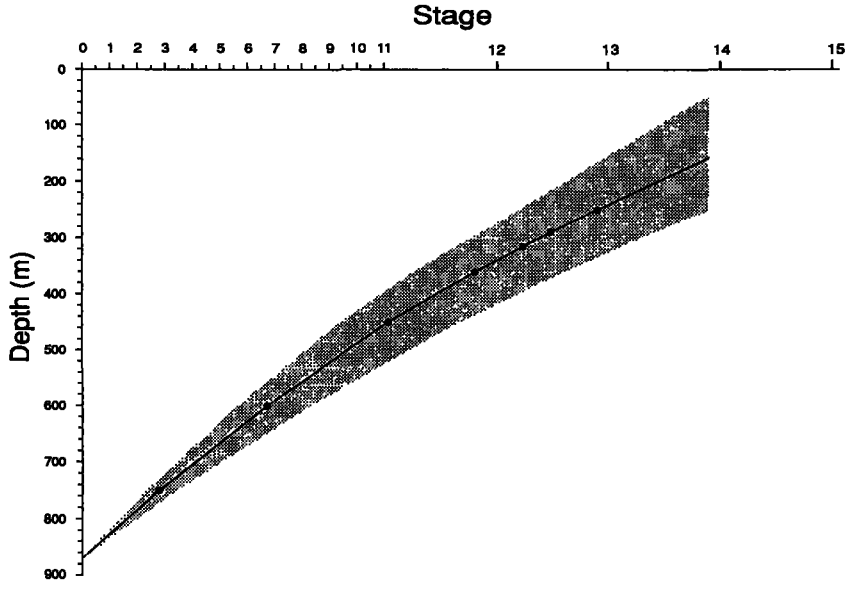

Figure 6

Orange roughy, *Hoplostethus atlanticus*, egg depth-at-stage (m) from surface determined from thermal history model. Dots indicate depth-at-stage for each 1°C temperature stratum in the water column. Shaded area shows 95% confidence limits for depth-at-stage estimated from 95% confidence limits for ascent rates (Fig. 3). Stage numbers represent midpoints of time periods of stages.

the mixed layer, at a constant, mean temperature of 11.25°C, until about cumulative age 150 h was reached (shown only to stage 15 or cumulative age 57.4 h in Fig. 5).

To examine the effect of variability of the laboratory-determined ascent rates on the predictions of age-at-stage, the model was rerun by using the ascent rates in Table 1 ±their 95% confidence intervals (taken to be 60 m·day^{-1} from Fig. 3), to give 95% confidence intervals about the mean age-at-stage. Depth reached at each stage was also determined (Fig. 6) from the ascent rates and time intervals used to run the model, along with the depths reached when the ascent rates ± their 95% confidence intervals were used.

Modeling of age- and depth-at-stage from stage 26 onward was not attempted because of uncertainty in modeling age-at-stage at temperature for these older eggs (see embryology and development rates above). Also, the descent rate data (Fig. 3) were insufficient to describe the rate at which eggs in these stages increase in sinking rate and the position of the eggs in the mixed layer when sinking starts was not known. It is likely that mixing would redistribute neutrally buoyant eggs in the mixed layer before the eggs begin to sink.

Field vertical distribution

To study vertical distribution of eggs in the field, a multiple opening-closing net and environmental sensing system (MOCNESS) was used on the North Chatham Rise to take plankton, temperature, and salinity samples from known depth strata. The MOCNESS tows were made at various times of day in areas where catch rates of adults had been relatively high or where exploratory plankton tows conducted in previous days had produced relatively high catch rates of orange roughy eggs. On three of the MOCNESS tows, the first of the nine nets was used for an integrated haul from the surface to within about 90 m of the bottom at 870 m; then the ascent was stratified into approximately 100-m intervals by the remaining nets (see Fig. 7 for exact stratum intervals). On two of the tows, both descent and ascent were stratified into approximately 200 m intervals. Eggs caught in the tows were either staged on board and then grown in the culture facility or were preserved in 4% buffered formaldehyde in seawater and staged in the land-based laboratory. Preservation had little effect on staging accuracy, because stage frequencies of eggs staged in the laboratory were very similar to those staged in the fresh state on board. However, in three of the nets some of the young eggs had embryos which were damaged and could not be staged with certainty. The damaged eggs were all ≤stage 7 (32 cell); all other samples with eggs older than this had no damaged eggs. The damage was observed prior to preservation and evidently occurred during the hauling of the plankton net. These eggs were staged by proration, from the frequencies of undamaged eggs ≤stage 7 in these nets. In tow 546 (Fig. 7), the nets fishing to 783 and 672 m contained 34% and 32% of eggs damaged, respectively, and the bottom net in tow 545 contained 61% damaged, as percentages of total eggs ≤stage 7.

Field vertical distributions of egg stages (Fig. 7) were compared with their predicted depths from the thermal history model (Fig. 6). To facilitate this comparison, the depth intervals of stages 1 to 14 were determined (Table 2) by using the 95% confidence intervals around the depths reached at the beginning and end of each stage (Fig. 6). These depth intervals were compared with the egg densities-at-stage summed over all MOCNESS tows within 200-m strata (summary column in Fig. 7; Table 3) and with catches from individual nets within these 200-m strata.

Results

Two features were evident in the egg catches from the MOCNESS series. First, the abundance of dif-

Table 2

Predicted mean depth (m) and depth range of egg stages of orange roughy, *Hoplostethus atlanticus*, from the thermal history model. Maximum and minimum depths were predicted from the lower and upper 95% confidence limits in Fig. 6 for the beginning and end of each stage, respectively. The stage numbers represent the midpoint of the period of each stage.

	Depth (m)		
Stage	mean	max	min
1	840	870	800
2	785	840	740
3	740	795	695
4	700	745	645
5	660	710	605
6	625	685	565
7	585	655	530
8	555	625	485
9	520	590	430
10	480	565	415
11	450	535	320
12	335	470	220
13	240	370	100
14	155	285	45

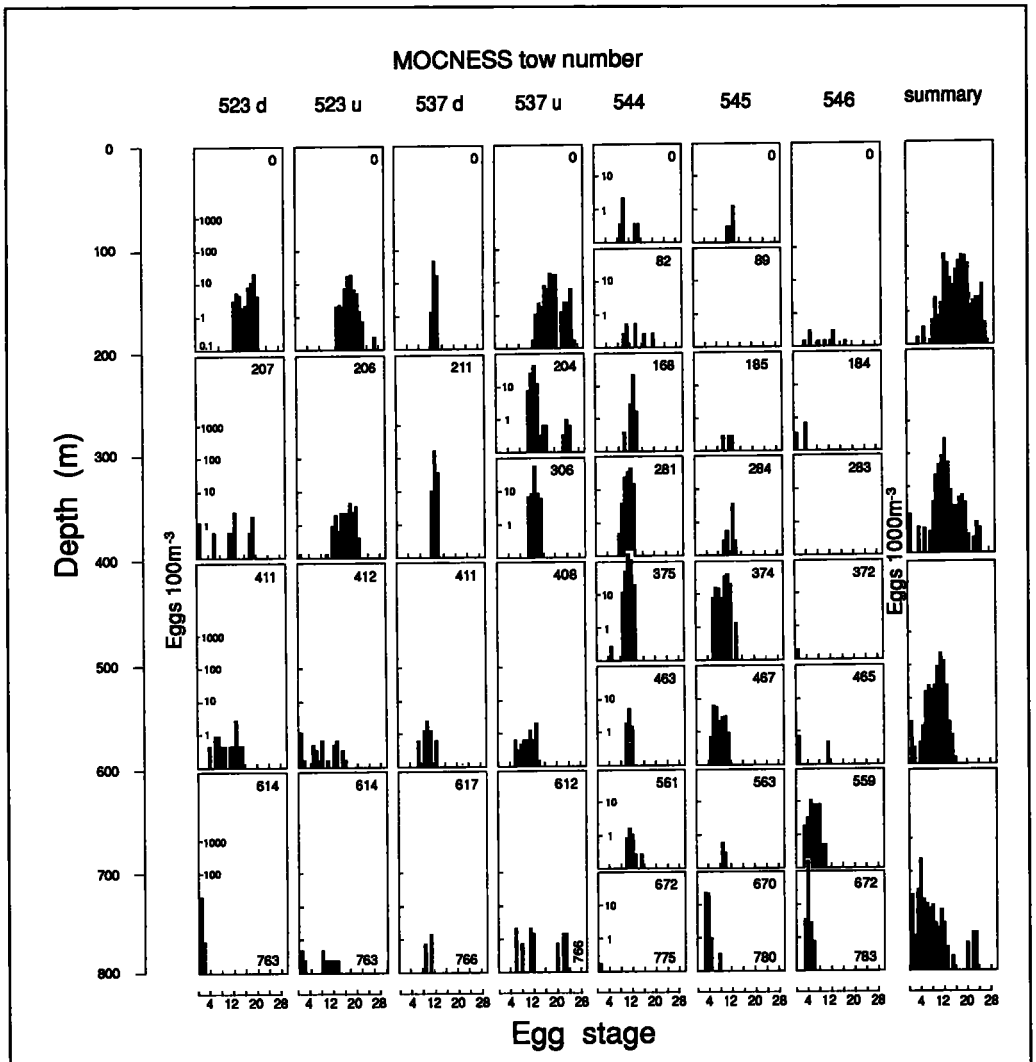

Figure 7

Orange roughy, *Hoplostethus atlanticus*, egg densities-at-stage (standardized to eggs·100 m^{-3}) from the MOCNESS tows conducted over the North Chatham Rise during TAN9206. Tows labelled with 'd' ('u') indicate the descent (ascent) phase of that tow. Box size around each histogram is an approximation of the depth range sampled by that net; the actual minimum depths of each net are annotated (also maximum depths for bottom nets). The "summary" column shows the egg densities-at-stage (standardized to eggs·1,000 m^{-3}) summed over all the tows within each 200-m stratum.

ferent egg stages at the various depths of the MOCNESS nets (Fig. 7) depended on the distance of the tows from concentrations of spawning adults. Two tows were conducted near an aggregation of spawning adults at 177°W (tows 545 and 546; Fig. 8A) in which most eggs were in young and middle ages (up to stage 13) and were caught from the bottom to middle depths (Fig. 7). In three tows conducted to the west of the aggregation (tows 544, 523, and 537; Fig. 8A), most eggs were middle-aged and older and were caught from middle depths to the upper water column. This distribution suggested that the eggs were advecting horizontally away from the spawners as they aged and ascended the water column.

Second, as the eggs developed, their depth changed in a manner consistent with predictions of the ascent and descent rate experiments and the thermal history model (Figs. 3 and 6; summary column in Fig. 7). The young eggs ascended from the spawners toward the surface, middle-aged eggs approached neutral buoyancy in the mixed layer, and oldest eggs sank. In the 0 to 200 m MOCNESS stratum, stage-13

eggs were the youngest to appear in significant quantities (17.9% of total eggs in the stratum; Table 3). The thermal history model (Table 2) predicted that stage-13 eggs should have occurred between 370 and 100 m depth, which is within the sampling ranges of the nets (tow 537, descent) which caught the great majority of them (Fig. 7). Stage-14 eggs were predicted to be from 285 to 45 m (Table 2), and these eggs were found evenly distributed between the 1–200 and 200–400 m strata (Table 3). Stage-15 to stage-26 eggs approached neutral buoyancy (Fig. 3) and accumulated in the mixed layer on the basis of their high proportional occurrence (Table 3; summary column in Fig. 7).

Table 3

Percentages of orange roughy, *Hoplostethus atlanticus*, eggs occurring in each stage for each 200-m stratum sampled by the MOCNESS (derived from the summary column in Fig. 7). Given stratum depth ranges are only approximate: see Fig. 7 for actual sampling depth ranges of the nets.

	MOCNESS stratum			
Stage	0–200 m	200–400 m	400–600 m	600–800 m
1	0.0	0.2	0.3	5.6
2	0.0	0.0	0.0	0.3
3	0.0	0.0	0.0	8.0
4	0.0	0.1	0.0	68.4
5	0.0	0.0	0.2	4.1
6	0.1	0.1	2.7	3.0
7	0.0	0.0	4.0	2.1
8	0.0	0.0	3.1	2.7
9	0.1	0.6	4.1	0.7
10	0.8	4.2	16.0	0.5
11	0.2	8.7	40.3	1.9
12	0.5	16.1	23.8	0.7
13	17.9	53.6	4.3	0.1
14	9.8	10.3	0.3	0.0
15	3.3	1.5	0.1	0.0
16	2.0	0.5	0.0	0.0
17	6.1	0.5	0.0	0.0
18	11.2	0.8	0.0	0.0
19	16.9	1.0	0.0	0.0
20	15.8	0.6	0.0	0.2
21	9.2	0.0	0.0	0.0
22	0.5	0.0	0.0	0.4
23	0.6	0.0	0.0	0.4
24	0.8	0.1	0.0	0.0
25	0.8	0.1	0.0	0.0
26	2.1	0.0	0.0	0.0
27	0.1	0.0	0.0	0.0

In the 200 to 400 m MOCNESS stratum, stages 12 and 13 were most common (Table 3), and the model (Table 2) predicted that these stages would be centered in this stratum. Stages 11 and 14 were also common (Table 3). Their expected mean depths were 50 m deeper and shallower than this stratum, respectively (Table 2), and most of the stage-11 and stage-14 eggs in this stratum were caught in the deeper and shallower parts of it (tows 544 and 537, ascent, respectively; Fig. 7). Eggs approaching neutral buoyancy were caught in the upper part of this stratum (tow 537, ascent), which could be expected since this net sampled the lower mixed layer.

In the 400 to 600 m MOCNESS stratum, the dominant stages were 10, 11, and 12 (Table 3). The model (Table 2) predicted that all these stages would be most common in the upper half of this stratum, and the nets that caught the great majority of them were in tows 544 and 545, fishing between 467 and 374 m; Fig. 7). Of the total eggs in this stratum, 4.3% were in stage 13, which was unexpected from the model, even taking into account the modelled ranges of occurrence (Table 2). It is likely that a low rate of misidentification of stages (between stages 12 and 13) caused these unexpected results. This would be expected of any staging system that attempts to place eggs into discrete categories when they are actually undergoing a continuous growth process.

In the 600 to 800 m MOCNESS stratum, the dominant stage was 4 (Table 3). This stage was predicted to occur between 745 and 645 m (Table 2) which was within the sampling range of the nets that caught the great majority of them (tows 545 and 546, fishing between 783 and 670 m; Fig. 7). The next most abundant stage was 3 and was predicted to occur between 795 and 695 m. The deep net on tow 545 caught most of these eggs and fished between 780 and 670 m. Tow 537 (ascent) caught some older eggs (stages 20–24) that evidently were sinking. These eggs were somewhat younger than were predicted to sink (Fig. 3), suggesting that there is some variability in the stage when sinking begins.

In summary, over all depth strata the predictions of modelled depth-at-stage were consistent with depth distributions of the dominant and subdominant stages caught in the MOCNESS tows. This consistency suggests that the basic parameters of the model are sound and are reasonably well estimated. One factor that might have caused the expected vertical distributions of eggs to deviate from the observed distributions may have been significant amounts of spawning far off the bottom. However, there was no evidence of this, in that significant numbers of very young eggs were seen only in the deepest stratum (Fig. 7, Table 3), and no "spawning plumes" of fish

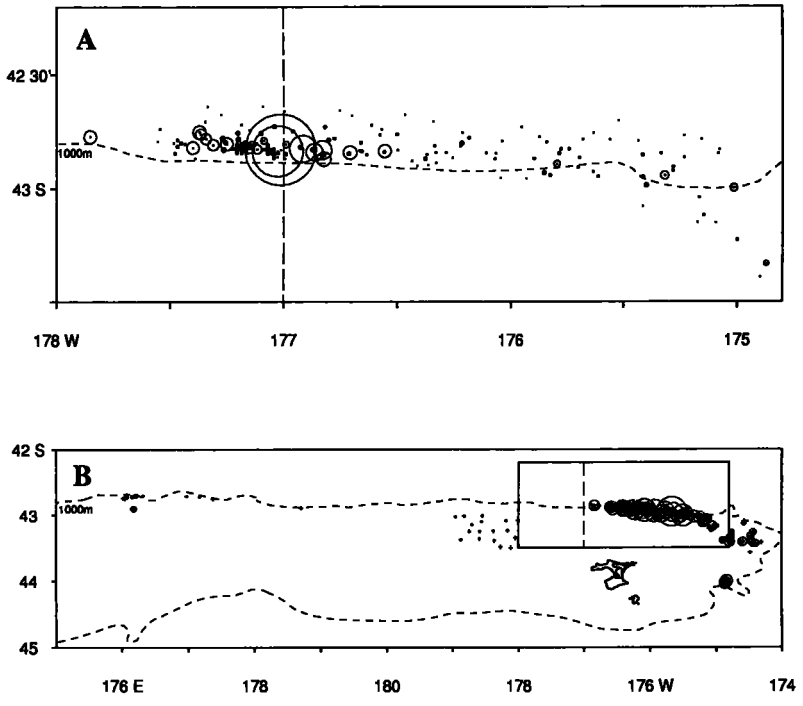

Figure 8

(**A**) Start positions (crosses) of MOCNESS tows on North Chatham Rise for orange roughy, *Hoplostethus atlanticus*, eggs, and start positions and relative adult catch rates (circle areas) from trawls conducted coincidentally with this study on TAN9206. MOCNESS tow numbers from west to east are 544, 523, 537, 546, and 545. (**B**) Relative catch rates (circle areas) of 0+ and 1+ (≤6 cm tail length) juvenile orange roughy during juvenile surveys done in 1988 and 1989 (Mace et al., 1990). Crosses show that tow positions and crosses with no circle had zero catch rate. The inset is the area of the survey shown in (A) and the dashed vertical line indicates the longitude of the spawning aggregation in (A).

(Pankhurst, 1988) were seen on echo sounders during these surveys.

Discussion

In culturing experiments, orange roughy eggs hatched after 235 h of development at 10°C. This was close to the prediction of Pauly and Pullin (1988) that the development period for orange roughy eggs at egg diameter 2.32 mm and 10°C would be 217 h. This result is in the upper part of the scatter in Pauly and Pullin's plot of development period vs. temperature (their Fig. 1), which would be expected, because orange roughy eggs are relatively large and will take longer to develop than will smaller eggs when both are measured at the same temperature (Pepin, 1991).

The eggs changed from positive to neutral to negative buoyancy as they aged (Fig. 3). This was unlikely to have been caused by poor condition of the cultured eggs, because many eggs were neutrally buoyant when captured and were later grown to hatching. Also, older eggs, all of which had been sitting on the bottom of the culture vessels for some days during late development, had virtually 100% hatching success. Finally, late-stage eggs were caught in MOCNESS samples deep in the water column (Fig. 7), albeit in low numbers. This ontogenetic pattern of change in bouyancy is a common one in marine fish eggs (reviewed by Page et al., 1989) and could be the consequence of density changes in the egg as high initial concentrations of yolk are converted to embryonic tissue during ontogeny (Mangor-Jensen and Huse, 1991).

Thus, it is likely that orange roughy eggs undergo extensive movement (both in ascent and descent) through the water column as they develop. Young eggs ascend rapidly to the mixed layer, reaching it

by about age 50 h (stage 13), where they reside until about age 150 h (stage 26); then they sink rapidly for about 50 more h before hatching. Since the hatching eggs sink at about 381 m·day^{-1} and their density is greater than seawater near the bottom in the spawning area on the North Chatham Rise (870 m), they may hatch near the bottom. This vertical distribution pattern of the eggs may partially explain the distributions of early juvenile orange roughy on the North Chatham Rise. The spawning aggregation at 177°W (Fig. 8A) forms each year and has supported the highest measured orange roughy biomasses on the North Chatham Rise since the inception of the trawl surveys on the stock (Zeldis, 1993). There are high concentrations of 0+ to 1+ annual cohort orange roughy about 50 to 175 km east of this aggregation (Fig. 8B; Mace et al., 1990) and this is the only area on the rise where early juveniles have been found in large quantities. Mean, residual currents are directed eastwards along the North Chatham Rise (Heath, 1983; Chiswell, 1994). These currents are generally weak (about 6 cm·sec^{-1} in the mixed layer), and the current velocity decreases with depth (Heath, 1983; Chiswell, 1994). During their 10-day development period, orange roughy eggs spend about 6 days in the mixed layer and a total of about 4 days ascending to and sinking out of the mixed layer. Therefore, on average, eggs spawned in the aggregation at 177°W would be expected to drift somewhat less than 50 km east before hatching near the bottom. The subsequent distribution of the newly hatched larvae is unknown, but since the larvae are more dense than bottom waters of the North Chatham Rise (Grimes and Zeldis, unpubl. data) they may remain near the bottom and drift into the area of high 0+ and 1+ juvenile density just downstream.

In this study, middle-age and older eggs were displaced in near-surface waters some 18 km to the west of the concentration of spawning adults (Figs. 7 and 8A), contrary to the expected eastward drift. This unexpected location may have resulted from smaller-scale eddy and tidal flow embedded in the large-scale mean eastward flow on the North Chatham Rise (Chiswell, 1994).

This study has determined the age-at-stage of orange roughy egg development as vertical distribution changes during ontogeny. These results were formerly unknown for this species. They are, however, essential for egg production estimation of orange roughy biomass where they are used for estimating egg mortality rates and rates of egg production at spawning. A further step is to ask how sensitive egg production estimation is to inaccuracies in egg age determination. This is significant in regard to other studies which may have less information than this one on vertical distributions of eggs during ontogeny. An example is the egg production study by Lo et al. (1992) for Dover sole, *Microstomus pacificus*, biomass, in which eggs were aged on the assumption that the temperature of development was the mean temperature of the stratified layer for the eggs they found in that layer. This assumption does not use depth-specific development rates to age eggs in the stratified layer and if it were applied to orange roughy, would cause egg age to be underestimated (dashed line in Fig. 5). To examine this effect on orange roughy egg production estimates, these underestimated egg ages were used to estimate the production rate of orange roughy eggs from the Ritchie Bank egg production survey and were compared with the result when the thermal history model (solid line in Fig. 5) was used to age eggs. Maximum likelihood fits of both sets of egg abundance-at-age data were done by using only stages ≤10, because older eggs were advected out of the survey area.[2] Egg production rate was biased upward by 31% for the fit with underestimated ages relative to the fit in which ages from the thermal history model were used. This happened because the same numbers of eggs-at-age were assumed to have occurred but over a shorter time for the fit with underestimated ages.

Dover sole eggs have a similar diameter and spawning depth range to that of orange roughy eggs (Lo et al., 1993). Therefore, they should ascend the water column at a similar rate, excluding large differences in water column density and egg density. Therefore, the ages of young Dover sole eggs may be underestimated by a similar extent as shown above for orange roughy, and their production rate may be similarly overestimated when they are aged without using depth-specific development rates. Thus, it seems prudent to reduce ageing bias by using a method that accounts accurately for thermal history of eggs. This is especially important if eggs found below the mixed layer contribute exclusively or substantially to the data set used for estimating egg production. This was the case for the Ritchie Bank egg production survey and has been suggested by Lo et al. (1993) for future Dover sole egg production surveys.

The consistency between the thermal history model results and field results on orange roughy egg vertical distributions suggests that age-at-stage should be predictable in other orange roughy spawning areas (e.g. the Ritchie Bank) where egg production surveys are conducted, provided data are available on water column density and temperature structure. It should also be possible to age other pelagic fish eggs by using depth-specific development rates, as long as ascent rates are not affected by chorionic sculpturing (Robertson, 1981). This would require data

on egg size, egg density, temperature dependent development rates, and water column density and temperature structure.

This study appears to be the first to model the depth-specific development rate of teleost eggs. Orange roughy eggs also appear to have the deepest distribution of any eggs for which a development rate has been studied in detail (see literature summary in Page et al., 1989); most studies have concerned continental shelf dwelling stocks. These two points are probably related, in that it is probably not important to model depth-specific development rate for eggs that are spawned in shallow water where the water column is either completely mixed or has a relatively small vertical thermal gradient (e.g. Coombs et al., 1985; Page et al., 1989). However, if a shelf-dwelling stock spawns near the bottom in stratified waters (e.g. in summer) and if the eggs are small and rise slowly, the development rate of the younger stages of these eggs might be variable with depth to an extent sufficient to significantly affect egg production estimates.

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Consistent yearly appearance of age-0 walleye pollock, *Theragra chalcogramma*, at a coastal site in southeastern Alaska, 1973–1994

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Walleye pollock, *Theragra chalcogramma*, are found throughout the North Pacific Ocean; their abundance is centered in the Bering Sea and Gulf of Alaska, where they are of great economic importance and a key species in the ecosystem. Pollock presently support the world's largest single-species fishery, averaging over 5 million metric tons (t) annual catch since the early 1980's (Lloyd and Davis, 1989). They made up 5% (4.9 million t) of the total world catch of all species in 1991 (FAO, 1993).

Adult pollock are found over the continental shelf, mainly in the mid-range of the water column; the greatest biomass has been found between 100 and 300 m deep (Smith, 1981). Most spawning takes place in spring (Kendall and Picquelle, 1990), during late March and April in the Gulf of Alaska (Kim, 1989). Spawning pollock broadcast pelagic, nonadhesive eggs in mid-water (Serobaba, 1974).

Larval pollock are found near the surface and in mid-water, above 100-m depths and they make diel vertical migrations (Serobaba, 1974; Kamba, 1977; Pritchett and Haldorson, 1989). In Southeast Alaska, abundant larvae (5–7 mm standard length [SL]) were found during mid-May in Auke Bay; peak hatching occurred about 28 April (Haldorson et al., 1990). Later-stage larvae (4–17 mm SL) were found throughout the water column from near surface to 55 m depths during June and July in Auke Bay; they became demersal (absent from the plankton, found only near the bottom during day) after reaching 20–30 mm SL (Salveson, 1984).

The presence of young pollock has been documented from mid-water and near bottom depths during summer (Smith, 1981; Krieger and Wing, 1986; Hinckley et al., 1991) and fall (Carlson et al.[1]). Available information on their distribution generally covers only a few years or wide geographic areas. During August–December trawl surveys from 1969 through 1981, age-0 pollock were taken near the bottom at 30–60 m depths at various bays and inlets in southeastern Alaska (Carlson et al.[1]).

Although general distribution of some young pollock is documented, patterns of long-term use of specific sites by successive generations of young-of-the-year (age-0) pollock are little known. Because pollock year-class strength can be established after the larval stage (Bailey and Spring, 1992), sampling these sites may provide useful information for establishing an index of population characteristics.

This paper documents the yearly first appearance, from 1973 through 1994, of newly metamorphosed juvenile walleye pollock at a specific site in Auke Bay, Southeast Alaska, and describes the young fish living near bottom during their initial growing season.

Methods

The 1,344 diving observations reported in this study took place in or near northeastern Auke Bay (Fig. 1), 20 km west of Juneau, Alaska, and focused on two adjacent, submerged (20–25 m depths) rocky ledges at a site within 200 m of the Auke Bay Laboratory. The diving effort included sites within a 15-km radius of Auke Bay that were surveyed periodically to explore possible presence of age-0 pollock elsewhere in the area.

Conventional scuba gear was used and no decompression procedures were followed. I averaged 8.8 (range 0–17) diving days per month from June through December and covered intertidal to 20–30 m depths for 22 consecutive years (Table 1). Nearly all dives took place during daylight until November and December, when night dives became equally routine. Most diving days involved a single dive; an average dive was made to a depth of 23 m and lasted 25 minutes. On each dive, I routinely swam the equivalent of transects over a set of underwater landmarks (e.g. rock ledges, cobble slope), noted and later recorded all identi-

[1] Carlson, H. R., R. E. Haight, and K. J. Krieger. 1982. Species composition and relative abundance of demersal marine life in waters of southeastern Alaska, 1969–81. U.S. Dep. Commerce, NMFS, NWAFC Processed Rep. 82-16, 106 p.

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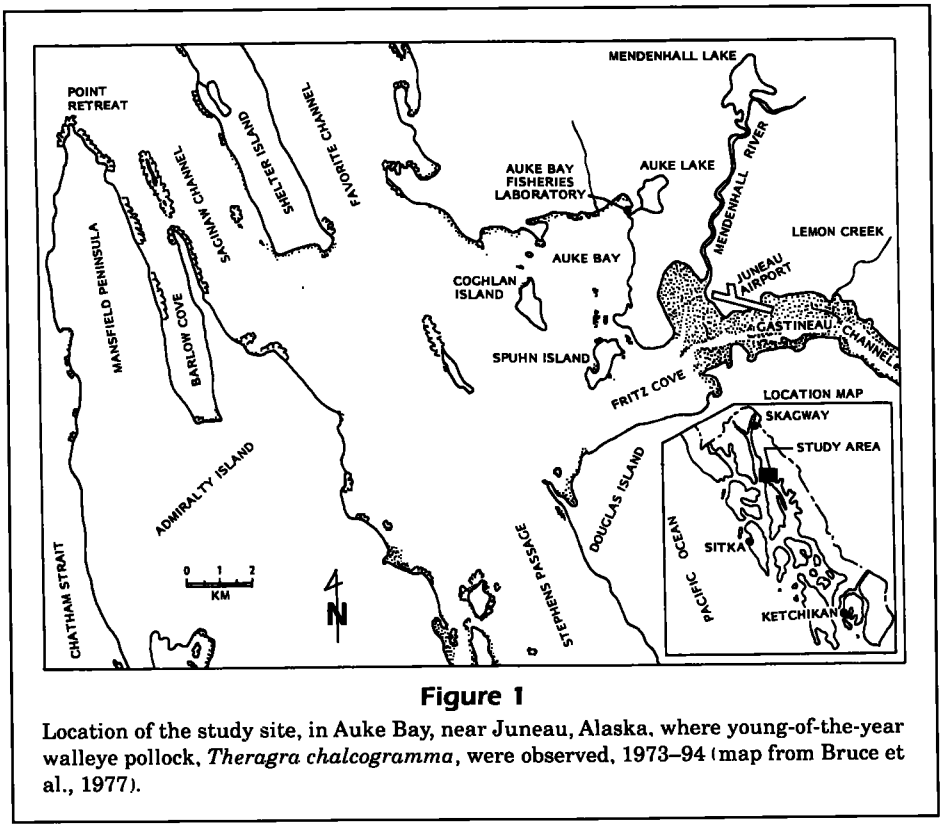

Figure 1

Location of the study site, in Auke Bay, near Juneau, Alaska, where young-of-the-year walleye pollock, *Theragra chalcogramma*, were observed, 1973–94 (map from Bruce et al., 1977).

fiable fish and invertebrate species, and documented life stage and relative abundance of commercially valuable species. For age-0 walleye pollock, I visually estimated total length (TL) of individuals to the nearest cm. These size-composition estimates were corroborated by Salveson (1984), who collected and measured hundreds of young pollock concurrently with my diving observations in 1978 and 1979, during growth and distribution studies in northern Stephens Passage, including my site in Auke Bay. These samples included 511 age-0 pollock collected (by using explosives) during August and September 1979 from the same shoals that I observed.

Results

The first sightings of demersal age-0 walleye pollock (Table 2) occurred most often in July (14 years) and sometimes in August (5 years); the first sighting was later than August in only 3 of 22 years.

General appearance and behavior of the young pollock at the Auke Bay study site was similar throughout summer and fall and from year to year. Over the course of the study, size estimates of individual fish were consistently 3–6 cm TL in July and 8–10 cm TL by October (Table 2). No size differences or environmental anomalies (sea temperature, salinity profiles) were apparent in the three years of later first sightings. The young fish formed shoals composed of hundreds to a few thousand loosely aggregated individuals within 1 m above the bottom or off rocky ledges at 20–30 m. Currents were normally slight, and these shoals moved and milled slowly, apparently feeding on zooplankton.

Each year, just before the shoals of demersal young pollock appeared, I observed great sculpins, *Myoxocephalus polyacanthocephalus*, distributed over the slope and rocky ledges where the young pollock later appeared. These large (many >60 cm) predators were unusually abundant, often numbering as many as 20–30 sculpins along a 15–20 m length of rocky ledge. They lay in wait on the bottom and after the young pollock appeared, were often seen pursuing and capturing them. Some sculpins appeared so gorged with young pollock that their gut was greatly distended.

As the juvenile pollock grew, they moved down the slope into deeper waters. After reaching approximately 10 cm TL by October or November, they were seen less frequently. By then the pollock were inhabiting waters 30 m or deeper, approaching the limits of normal scuba operations. By December and into winter, the juvenile pollock were seen infrequently

Table 1

Survey effort (number of diving days) in Auke Bay and vicinity, Southeast Alaska, to observe juvenile walleye pollock, *Theragra chalcogramma*, June–December 1973–94.

	Month							
Year	June	July	August	Sept	Oct	Nov	Dec	Total
1973	0	1	1	3	6	6	5	22
1974	3	4	3	2	5	10	6	33
1975	7	9	8	0	0	0	0	24
1976	4	5	13	7	7	7	15	58
1977	10	5	9	9	4	7	5	49
1978	6	7	10	11	8	11	13	66
1979	17	14	14	13	17	14	17	106
1980	16	4	9	15	9	6	10	69
1981	9	4	11	17	17	14	16	88
1982	3	6	14	9	7	4	11	54
1983	16	7	8	9	12	10	8	70
1984	7	2	7	8	6	6	6	42
1985	8	1	4	6	6	7	12	44
1986	5	3	4	5	9	13	15	54
1987	16	17	8	9	15	13	16	94
1988	6	16	10	13	16	11	17	89
1989	9	5	9	10	15	12	15	75
1990	14	14	8	15	5	11	16	83
1991	4	12	8	11	8	15	17	75
1992	6	10	12	6	8	9	13	64
1993	3	3	5	6	8	9	7	41
1994	6	9	3	8	14	4		44
Total	175	158	178	192	202	199	240	1,344

during daylight. During darkness in November and December, they moved into shallows of 9 m or less and became more loosely aggregated; some individuals remained on the bottom and motionless under a light beam. At dawn the loose aggregations became shoals and moved downslope again to depths >30 m.

Discussion

The consistent appearance of the age-0 pollock that I observed each year for 22 years at the Auke Bay site agrees during 1986–89 with the earlier appearance for those years of pollock larvae observed in Auke Bay by Haldorson et al. (1990). They found that little hatching occurred after the major larval cohort appeared and concluded that pollock spawn during the relatively short period when larval feeding conditions are optimal.

By July, I observed that the larvae had usually settled out from a planktonic existence and had become demersal juveniles. Typically at this time, sea surface temperatures in Auke Bay are near a yearly peak (Bruce et al., 1977), a thermocline has formed around 12 m depth, zooplankton abundance in the upper water column approaches its yearly maximum (Carlson, 1980), and 3–4 cm juvenile pollock feed mostly on the copepod *Acartia clausi* (Krieger, 1985). Similar to my findings, the sculpin *Myoxocephalus* sp. is a major predator of age-0 juvenile pollock in the Bering Sea (Smith, 1981).

By October, when the young pollock were 8–10 cm TL, they appeared sufficiently motile to evade most bottom-dwelling predators. They moved to deeper water in the fall around the time that, typically, storms mix the surface and mid-water strata, the thermocline breaks down, and sea temperatures decrease sharply and become nearly uniform through-

Table 2

Dates of first sightings and estimated size range of young-of-the-year walleye pollock, *Theragra chalcogramma*, in Auke Bay, Southeast Alaska, 1973–1994. No est. = no estimate; TL = total length.

Year	Date	Size range (TL, cm)
1973	2 August	7
1974	11 October	5–6
1975	17 July	3
1976	15 July	3–5
1977	2 August	5–6
1978	19 July	3–4
1979	14 July	3–4
1980	12 August	4–8
1981	27 July	4–5
1982	27 July	no est.
1983	10 July	4–6
1984	12 September	no est.
1985	28 August	no est.
1986	4 November	no est.
1987	18 July	3
1988	23 July	4–5
1989	2 July	4–5
1990	14 July	5
1991	17 August	5
1992	7 July	4–6
1993	24 July	3–6
1994	16 July	3–5

Summary
Month of first sightings

July	14 years
August	5 years
September	1 year
October	1 year
November	1 year
Total	22 years

out the water column (Bruce et al., 1977). Generally, by this time zooplankton abundance had declined, daylight was greatly reduced (Carlson, 1980), and juvenile pollock feeding had shifted from copepods to larger prey—mainly mysids and euphausiids (Krieger, 1985). The young pollock appeared to move deeper in response to these changing oceanographic and trophic conditions.

Each year, this pattern of appearance of juvenile pollock repeated itself with few exceptions and with remarkable predictability; it was generally consistent in timing, location, depth, and size of fish. The consistent residency at the same site, around the same time, by young-of-the-year walleye pollock for 22 consecutive years, demonstrates the long-term significance and potential importance of locales such as Auke Bay as nursery grounds for this species.

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Radiometric analysis of blue grenadier, *Macruronus novaezelandiae*, otolith cores

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Blue grenadier, *Macruronus novaezelandiae*, is a major commercial fish species in the upper continental slope waters of southeastern Australia and New Zealand. An accurate knowledge of age and growth rate of this species is required for management of the fishery. Several ageing studies have provided estimates of age for blue grenadier (hoki) from New Zealand waters (reviewed by Paul, 1992), with the maximum age ranging from 12 to 15 years. Kenchington and Augustine (1987) examined whole otoliths and thin transverse sections from blue grenadier caught in southeastern Australian waters and reported a maximum age of 25 years. However, Kenchington and Augustine (1987) were unable to validate their ages for fish >3 years of age. They found that conventional techniques of validating age estimates, such as tagging, modal analysis, marginal increment or edge-type analysis, and back calculation of lengths at age, could not be applied to blue grenadier.

The possibility that radiometric analysis of fish otoliths, a technique pioneered by Bennett et al. (1982) for ageing fish, might validate the ages of blue grenadier led to a study by Fenton et al. (1990). Unfortunately radiometric analysis of ^{210}Pb and ^{226}Ra in whole blue grenadier otoliths was unsuccessful for estimating fish ages (Fenton et al., 1990). This was due to an exponential reduction in ^{226}Ra incorporation into the otoliths of blue grenadier during their life, a reduction that was believed to result from an ontogenetic change in habitat from juvenile to adult fish.

Recent advances with radiometric ageing of fish indicate that ages can be determined radiometrically from otolith cores (Campana et al., 1990, 1993; Smith et al., 1991). The coring method removes all the layers of otolith growth beyond the earliest year(s) and thus avoids problems of changes in ^{226}Ra or ^{210}Pb uptake patterns in later life. Furthermore, an analysis of otolith cores circumvents the need to model the mass growth rate of otoliths, which is necessary in determining age from whole otoliths (Smith et al., 1991).

Radiometric analysis of otolith cores has been successfully used to age redfish, *Sebastes mentella* (Campana et al., 1990), and splitnose rockfish, *Sebastes diploproa* (Smith et al., 1991), with $^{210}Pb/^{226}Ra$. In addition, otolith cores have been analyzed with $^{228}Th/^{228}Ra$ to age flying fish, *Hirundichthys affinis* (Smith et al., 1991; Campana et al., 1993), and silver hake, *Merluccis bilinearis* (Smith et al., 1991). While the isotope pair $^{228}Th/^{228}Ra$ is useful for short-lived fish up to about 5 years (Campana et al., 1993), analysis of $^{210}Pb/^{226}Ra$ is appropriate for medium-aged to long-lived fish up to about 120 years.

In the present study measurements of $^{210}Pb/^{226}Ra$ disequilibria have been conducted on cores of adult female blue grenadier otoliths in an attempt to provide independent age data for this species.

Materials and methods

Field collection

Blue grenadier, *Macruronus novaezelandiae*, were collected by bottom trawling (500–850 m depth) during cruises conducted northwest of Sandy Cape off the west Coast of Tasmania by the Tasmanian Department Primary Industry, Division of Sea Fisheries, and the CSIRO Division of Fisheries between 1985 and 1986. Sagittal otoliths were removed and stored dry. This collection of otoliths was used by Kenchington and Augustine to estimate age by annulus counts (1987) and was subsequently made available for the present study.

Otolith morphometrics

The linear dimensions of blue grenadier otoliths (maximum length, width, and thickness with respect to the primordia) were measured to the nearest 0.1 mm with calipers. Otolith weight was also determined for n=172 blue grenadier otoliths

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from fish previously aged by Kenchington and Augustine (1987). The dimensions of otoliths from 1+ fish (ages assigned by Kenchington and Augustine, 1987) were examined and the average linear dimensions and weight for a 1+ fish determined. The average otolith dimensions of 1+ fish were selected as the shape of the core to be removed. This core size was chosen 1) because it ensured minimal influence of changing ^{226}Ra (as reported in Fenton et al., 1990); 2) because it represented the minimum core size that could be repeatably isolated (attempts to remove smaller cores, e.g. 0+ dimensions, resulted in the otolith shattering or splitting, and being unusable; and 3) because it fitted the age estimate of 1+ otoliths by Kenchington and Augustine (1987) who were able with confidence to validate fish age for individuals under 3 years old.

Removal of otolith core

Blue grenadier otoliths chosen for coring were selected from females collected from the same site, on the same date, and of similar fish length and otolith weight. Cores were removed from the otoliths by sanding the outer layers away by hand (with respect to the primordia) with wet and dry sand-paper (silicon carbide paper) in progressively finer grades until the desired core dimensions were achieved. The mean core dimensions were compared with the mean whole otolith dimensions for 1+, 2+, and 3+ fish. New, wet and dry sand paper was used for each otolith to eliminate the risk of ^{210}Po cross contamination between otoliths. The cores of 2 or 3 fish were pooled to produce the 1-g sample necessary for radiometric analysis.

Radiometric analysis

Cores were cleaned of adventitious ^{210}Po by exposure to an alkaline H_2O_2 solution for 1/2 hour. The analysis of ^{210}Pb via its alpha-emitting, short-lived daughter proxy ^{210}Po followed the method we have previously described (Fenton et al., 1991), employing high resolution alpha-spectrometry. Polonium-210 was assumed to be in equilibrium with ^{210}Pb in all samples, and ^{210}Pb concentrations were corrected back to the date of fish collection. Mean ^{210}Po reagent blank was 0.0071 ±0.0012 disintergrations per minute (dpm·g^{-1}). Recovery of ^{210}Po was invariably >90%. Instrumental background counts (for ^{208}Po and ^{210}Po) were less than 1 count per day. Analysis of ^{226}Ra was by a direct alpha spectrometry technique (Fenton et al., 1991). The mean activity of the ^{226}Ra blanks was 0.0174 ±0.002 dpm·g^{-1}. Both ^{210}Po and ^{226}Ra blank values were reduced to lower values than those from previous studies because of tighter quality control of reagents and minor improvements in technique.

Stable element analysis

The levels of lead (Pb) and barium (Ba) are presumed to act as stable equivalents of ^{210}Pb and ^{226}Ra (Fenton and Short, 1992) and, as such, can potentially be used to assess the uptake of the radioactive isotopes and for normalizing the radiometric data. Therefore the concentrations of stable lead, barium, calcium (Ca), and strontium (Sr) in each otolith core sample were measured. An aliquot of the same dissolved otolith core solution used for ^{210}Pb and ^{226}Ra analysis was analyzed. Lead and barium were analyzed by inductively coupled plasma mass spectrometry (ICP-MS) and strontium and calcium by inductively coupled plasma atomic emission spectrometry (ICP-AES).

Calculation of fish age

Fish age was calculated by using the model proposed by Campana et al. (1990) and described in Smith et al. (1991). The ^{210}Pb/^{226}Ra activity ratio of the otolith core during growth, assuming a constant mass growth model for the period of core formation only, is given by the equation:

$$\frac{A_{Pb^{210}}}{A_{Ra^{226}}} = 1-(1-R)\left(\frac{1-e^{-\lambda T}}{\lambda T}\right),$$

where A = specific activity (i.e. activity concentration);
R = initial activity ratio (i.e. uptake activity ratio);
λ = decay constant of ^{210}Pb (year^{-1});
T = period of core formation (years).

The activity ratio of the core at any subsequent time in the life of the fish is unaffected by mass growth of the otolith and is therefore given by the equation:

$$\frac{A_{Pb^{210}}}{A_{Ra^{226}}} = \left(1-e^{-\lambda(t-T)}\right)+\left[1-(1-R)\left(\frac{1-e^{-\lambda T}}{\lambda T}\right)\right]e^{-\lambda(t-T)},$$

where t= age of the fish (years).

The fish age is found by solving for t by the Newton-Raphson iterative method. All radiometric age values are given with an error value of ±1 standard deviation.

Table 1

Comparison of core dimensions and the otolith dimensions of 0+, 1+, 2+, and 3+ blue grenadier, *Macruronus novaezelandiae*. Probability (*P*) values are given for *t*-test comparison of the mean core dimensions and mean whole otolith dimensions SD= standard deviation and *n* is the number of otoliths measured.

	Core dimension	0+ otolith	1+otolith	2+ otolith	3+ otolith
Otolith length (mm)					
Mean	12.50	7.20	12.26	15.94	18.66
SD	0.20	0.29	0.68	1.37	1.09
n	24	48	38	12	14
P		< 0.001	>0.02	<0.001	<0.001
Otolith width (mm)					
Mean	5.44	3.27	5.40	6.73	7.64
SD	0.14	0.15	0.30	0.69	0.33
n	24	47	38	12	14
P		<0.001	> 0.50	<0.001	<0.001
Otolith Thickness (mm)					
Mean	1.28	0.74	1.25	1.69	1.79
SD	0.05	0.07	0.10	0.04	0.14
n	24	46	38	12	14
P		<0.001	> 0.10	<0.001	<0.001
Otolith Weight (g)					
Mean	0.2008	0.0197	0.0961	0.1870	0.2750
SD	0.007	0.020	0.013	0.043	0.030
n	24	57	38	13	14
P		<<0.001	<<0.001	0.50-0.20	<<0.001

Results

Otolith core dimensions

Otolith growth in linear dimensions and weight for juvenile blue grenadier (0+, 1+, 2+, and 3+) was rapid (Table 1). The cores that were removed approximated the linear dimensions of 1+ fish, but they were heavier than the average 1+ fish with a weight that was not significantly different from that of 2+ fish (t=1.15;P>0.20). The dimensions and weight of 3+ fish otoliths were significantly greater than the isolated core dimensions. Therefore, in view of the core weight our calculation of age assumed that the cores analyzed represented 2 years of growth.

Stable element analysis

Low levels of both stable lead and barium were found in all the samples (Table 2). Stable lead ranged from 0.269 to 1.78 ppm. Barium levels were low, ranging from 1.50 to 2.28 ppm, consistent with the relatively low ^{226}Ra levels in these blue grenadier otolith cores. The ratio of Pb/Ba was relatively high, ranging from 0.17 to 0.78. From this Pb/Ba data we concluded that there is some allogenic uptake of ^{210}Pb from the environment. However the extent of uptake was difficult to assess given the low levels of Pb and Ba measured. The Sr/Ca ratio ranged between 0.0034 and 0.0042.

Radiometric results

^{210}Pb ranged from 0.0040 ±0.0045 to 0.0078 ±0.0025 dpm·g^{-1} (Table 3). The ^{226}Ra content of the otolith

Table 2

Blue grenadier, *Macruronus novaezelandiae*, stable element data from inductively coupled plasma mass spectrometry (ICP-MS) and inductively coupled plasma atomic emission spectrometry (ICP-AES) analysis of otolith core solutions.

Sample number	Pb ppm	Ba ppm	Pb/Ba ppm/ppm	Sr ppm	Ca ppm	Sr/Ca ppm/ppm
LH 2269	0.749	1.50	0.50	1590	400300	0.0040
LH 2270	1.78	2.28	0.78	1620	387800	0.0042
LH 2271	0.389	1.57	0.22	1810	448380	0.0040
LH 2272	0.269	1.55	0.17	1920	483570	0.0040

Table 3

Blue Grenadier, *Macruronus novaezelandiae*, otolith core radiometric results and ages calculated by using individual ^{226}Ra and mean ^{226}Ra activity ratios.

Sample number	Mean fish length (cm)	Mean otolith mass (g)	No. of otoliths	^{210}Pb (dpm·g^{-1})	^{226}Ra (dpm·g^{-1})	$^{210}Pb/^{226}Ra$ activity ratio from individual ^{226}Ra activity ratio	$^{210}Pb/^{226}Ra$ activity ratio from mean ^{226}Ra activity ratio	Otolith core age (years) from individual ^{226}Ra activity ratio	Otolith core age (years) from mean ^{226}Ra activity ratio
LH 2269	95.63 ±0.44	0.5395 ±0.009	6	0.0051 ±0.0023	0.0290 ±0.0036	0.174 ±0.082	0.227 ±0.111	5.5 (+3.4, –3.0)	7.6 (+5.0, –4.3)
LH 1817	99.3 ±0.52	0.7116 ±0.078	6	0.0040 ±0.0045	0.0203 ±0.0042	0.197 ±0.225	0.179 ±0.205	6.4 (+10.6, –7.9)	5.7 (+9.2, –7.2)
LH 2270	104.0 ±1.79	0.7136 ±0.053	6	0.0078 ±0.0025	0.0179 ±0.0026	0.438 ±0.153	0.351 ±0.129	17.9 (+10.2, –7.7)	13.3 (+7.1, –5.8)
LH 2271	107.2 ±3.06	0.8896 ±0.073	6	0.0074 ±0.0031	0.0222 ±0.0039	0.332 ±0.151	0.331 ±0.151	12.3 (+8.2, –6.5)	12.2 (+8.2, –6.5)
LH 2272	110.3 ±1.37	0.9531 ±0.076	6	0.0058 ±0.0030	0.0223 ±0.0039	0.259 ±0.142	0.259 ±0.143	9.0 (+6.8, –5.6)	9.0 (+6.9, –5.7)

cores ranged from 0.0179 to 0.0290 dpm·g^{-1} and showed a mean value of 0.0223 ±0.0036 dpm·g^{-1}. The ^{226}Ra values found for the cores were consistent with our earlier analysis (Fenton et al., 1990) of whole otoliths (see Discussion section) and further confirmed that the core represents approximately a 2+ fish.

In order to select the value of R, the initial activity ratio used in the calculation of age, we examined our previous data for whole otoliths (Fenton et al., 1990) and the stable element analysis of Pb and Ba (discussed above). From the data for a 1+ fish a value of $R<0.06$ is indicated; however, data for 0+ fish indicate R could be as high as 0.1. A value of $R=0.05$ appears to be the best estimate for the initial activity. If R were as high as 0.1, it would lower the age estimate by approximately 9 months. Conversely, if $R=0$, ages would be higher by 2.6 years. The difference that a lower or higher value makes to the age estimates is well within the error associated with each radiometric age calculated by using $R=0.05$.

Otolith core ages were calculated by using both the individual sample ^{226}Ra value and the mean ^{226}Ra value. This has little effect on the average age of all the cores analyzed (e.g. 10.2 ±5.0 years [with individual ^{226}Ra] and 9.6 ±3.2 years [with mean ^{226}Ra]), but the maximum age recorded changes from 17.9 (+10.2, –7.7) years (with individual ^{226}Ra) to 13.3 (+7.1, –5.8) years (with mean ^{226}Ra) depending on which radium value is used. Since all individual ^{226}Ra activity ratios are similar within experimental error, it follows that the best age estimates are calculated by using the mean ^{226}Ra activity.

Age estimates from annulus counts conducted by Kenchington and Augustine (1987) relative to fish length and otolith weight are plotted together with the radiometric core age estimates in Figure 1. The radiometric analysis of otolith cores are similar to those assigned by Kenchington and Augustine (1987), although there is some indication that the radiometric ages may be slightly lower. However, the core samples represent the average age of only three fish, the errors associated with the radiometric analyses are large, and limited sample sizes preclude any meaningful statistical analysis.

Discussion

Radiometric analysis of otolith cores has successfully provided age estimates for blue grenadier, in contrast to the unsuccessful analysis of whole otoliths by Fenton et al. (1990). The average age of the otolith core samples was approximately 10 years for fish 95–110 cm in length.

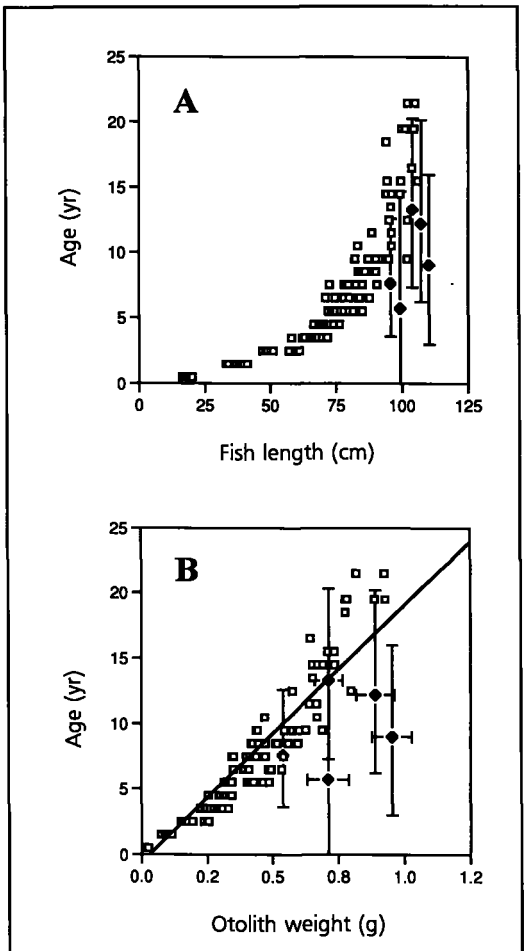

Figure 1

Blue grenadier, *Macruronus novaezelandiae*, core ages (□) calculated by using mean ^{226}Ra values together with ages (◆) determined by the study of Kenchington and Augustine (1987). (**A**) Age versus fish length; (**B**) age versus otolith weight (where $y = 19.633x - 0.603$, $r^2 = 0.910$ for the Kenchington and Augustine [1987]data set).

The ^{226}Ra concentrations in the blue grenadier otolith (0.022 ±0.004 dpm·g^{-1}) cores are low compared with other fish species. For example, orange roughy, *Hoplostethus atlanticus*, whole otoliths had a mean ^{226}Ra concentration 2–3 times higher (Fenton et al., 1991), and the otolith cores of three species of tropical snapper had ^{226}Ra values 6–10 times higher (Milton et al., 1995). The main consequence of the relatively low radium in blue grenadier cores is that the error associated with their age estimates are higher ±4–8 years than those for tropical snapper otolith cores ±1–2 years (Milton et al., 1995).

Furthermore, the ^{226}Ra concentrations in the blue grenadier otolith cores were lower than the concentrations we reported earlier in whole otoliths from east coast 1+ fish (0.050 ±0.005 to 0.075 ±0.008 dpm·g^{-1}) but higher than the values for 4+ fish (0.016±0.010 to 0.018±0.009 dpm.g^{-1}) (Fenton et al., 1990). The ^{226}Ra concentrations found in Fenton et al. (1990) for whole blue grenadier otoliths ranged from 0.084 ±0.009 dpm·g^{-1} for 0+ fish caught in the Derwent estuary to 0.005 ±0.005 dpm·g^{-1} for 21+ fish caught off the west coast of Tasmania and exhibited a clear exponential reduction in ^{226}Ra with fish length/age. The ^{226}Ra found in cores in the present study are consistent with our earlier data for whole otoliths and also confirm that the core represents approximately a 2+ fish.

Reexamination of the radiometric data in our earlier study shows that data for a 1+ fish sampled from the east coast of Maria Island can also be used to estimate age. The sample had a ^{226}Ra value of 0.050 ±0.005 dpm·g^{-1} and ^{210}Pb of 0.003 ±0.003 dpm·g^{-1} which corresponds to a linear otolith mass growth radiometric age (see Fenton and Short, 1992, for the linear mass growth radiometric equation) of 0.68 ±0.68 years. This is consistent with the age of 1+ determined by Kenchington and Augustine (1987). The remaining data in our earlier study cannot be used to determine age because of the exponential reduction in ^{226}Ra through life and the lack of a priori knowledge of the relationship between R and increasing otolith mass.

The age of Australian blue grenadier derived by radiometric age of otolith cores gives age estimates in approximate agreement with those derived by Kenchington and Augustine (1987) and New Zealand studies (reviewed Paul, 1992). Further radiometric ageing of otolith cores may be useful in examining apparent differences in the growth curves for New Zealand and Australian blue grenadier fisheries. For such a comparison, it would be worthwhile to include analysis with the radioisotope pair $^{228}Th/^{228}Ra$ because this should increase the precision of the age estimates particularly for fish under 5 years (Smith et al., 1991; Campana et al., 1993). In conclusion, the results of this study offer an independent assessment of age in blue grenadier and in doing so demonstrate the applicability of radiometric ageing of otolith cores for medium-aged temperate fish.

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Seasonal depth distribution of the crystal shrimp, *Penaeus brevirostris* (Crustacea: Decapoda, Penaeidae), and its possible relation to temperature and oxygen concentration off southern Sinaloa, Mexico

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With an estimated value of 30 million U.S. dollars, red or crystal shrimp, *Penaeus brevirostris*, is the sixth most important fishery resource in Mexico (Edwards, 1978; Rodriguez de la Cruz, 1981; Hernandez-Carballo, 1988). However, until recently very little was known about its general biology, ecology, and seasonal variation in relative abundance.

Penaeus brevirostris is a species limited to the eastern tropical Pacific off northern Sinaloa, Mexico, to southwest of Cabo Blanco, Peru, and Islas Galapagos (Perez-Farfante, 1988). In Mexico, it is normally fished in two areas: from southern Sinaloa to northern Nayarit and in the Gulf of Tehuantepec (Edwards, 1978; Hernandez-Carballo, 1988). *Penaeus brevirostris* occupies a wide range of depths. Postlarvae are found near the shore and in coastal lagoons (Calderon-Perez and Poli, 1987). Preadults and adults have been found at depths of 45–90 m off Mexico (Rodriguez de la Cruz, 1981; Hendrickx et al., 1984; Chapa-Saldaña[1]) and Peru (Cobo and Loesch, 1966) and at 3 m in estuarine channels (esteros) in Ecuador (Loesch and Avila[2]). The deepest record of crystal shrimp is 183 m (Perez-Farfante, 1988). In spite of its rather wide depth distribution, *P. brevirostris* is usually found deeper than *P. stylirostris* (estuarine and marine to 27 m, rarely to 45 m; Rodriguez de la cruz, 1981; Hendrickx, 1986; Perez-Farfante, 1988), *P. vannamei* (estuarine and marine to 36 m) (Rodriguez de la Cruz, 1981; Hendrickx, 1986) and *P. californiensis* (estuarine and marine to 50 m, rarely to 180 m) (Perez-Farfante, 1988). Occasionally, it is found co-existing with the latter (Chapa-Saldaña[1]). In two separate fishing surveys during the closed (nonfishing) season, the species was not found on traditional trawling grounds off Sinaloa and Nayarit (Barreiro and Lopez-Guerrero, 1972; Magallon-Barajas and Jacquemin-Poulet, 1976).

The purpose of this study is to determine whether the distribution of *P. brevirostris* varies seasonally with respect to depth (presumably, because of the bathymetric movements of the species) and to relate its distribution to temperature and oxygen variation near the bottom.

Material and methods

The study area (Fig. 1) lies at the entrance of the Gulf of California (Alvarez-Borrego, 1983) off the mouths of the Piaxtla River to the north (23°42'N, 106°49'W) and the Teacapan-Agua Brava Lagoon complex to the south (22°32'N, 105°45'W). It has been described as a transitional zone that has a complex and dynamic structure (Alvarez-Borrego, 1983). At the surface, there are three different types of water: 1) cold California Current water of low salinity (S ≤34.6 ppt) which flows southward along the west coast of Baja California; 2) warm eastern tropical Pacific water of intermediate salinity (34.65 ppt ≤ S ≥34.85 ppt) which flows into the area from the southeast; and 3) warm, highly saline (S ≥34.9 ppt) Gulf of California water (Roden and Groves, 1959; Stevenson 1970; Alvarez-Borrego, 1983). This region experiences upwelling events during the spring (Roden, 1964; Roden and Groves, 1959; Alvarez-Borrego and Schwartzlose, 1979). The oxygen content in the upper 100 m layer is greater than 1 mL/L; below 150 m the oxygen concentration falls to less than 0.5 mL/L and at intermediate depths (500–1,100 m) oxygen may be undetectable by the Winkler method (Alvarez-Borrego et al., 1978).

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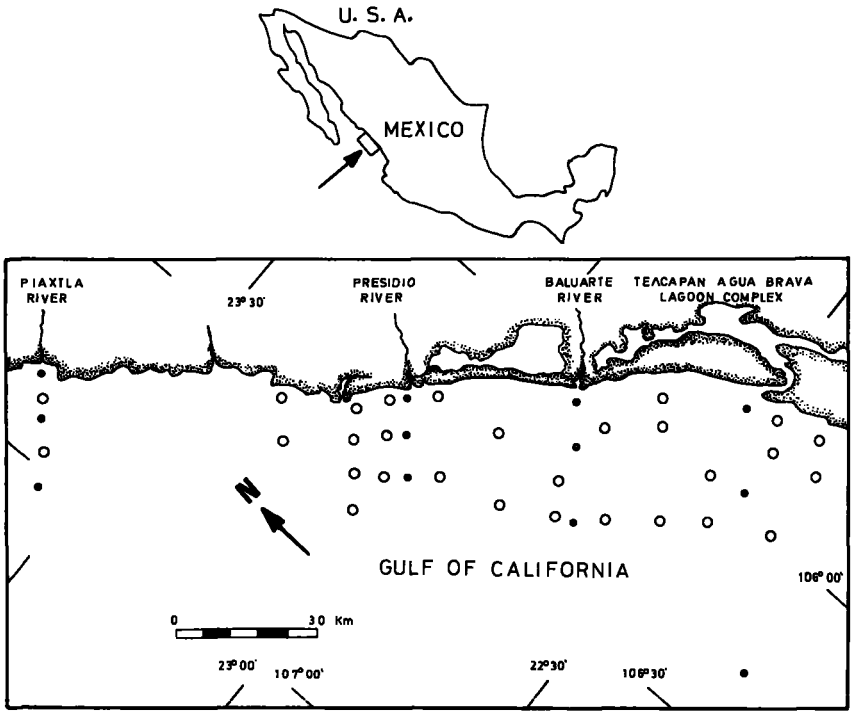

Figure 1

Study area (1981–86) located off the mouths of the Piaxtla River and the Teacapan-Agua Brava lagoon complex, Mexico. Twenty-nine stations from the CRIP-INP cruise series are denoted by empty circles. Stations from the BIOCAICT series are indicated with solid circles.

Seventeen survey cruises were made by the Centro Regional de Investigaciones Pesqueras of the Instituto Nacional de la Pesca (CRIP) on board commercial shrimp trawlers during the years 1981, 1982, 1984, 1985, and 1986, and four cruises were made by the Universidad Nacional Autonoma de Mexico between November 1985 and August 1986 on board the vessel *MARSEP XI* (BIOCAICT cruises). On all cruises, a pair of 22.9-m otter trawl nets was used. The nets have a progressively reducing mesh size from 6.4 cm on the body of the net to 3.8 cm at the cod end. Eleven sampling stations of the BIOCAICT series were located on four transects perpendicular to the coast line off the mouths of Piaxtla, Presidio, and Baluarte rivers and off the Teacapan-Agua Brava lagoon complex. Sampling depth varied from 9 to 90 m. Data from the more extensive CRIP cruises were selected to match the location of the BIOCAICT series (Fig. 1).

In all BIOCAICT cruises, surface, mid-water, and bottom water samples were taken with 8-L niskin bottles. Temperature was measured in situ with reversing thermometers to the nearest 0.1°C. Dissolved oxygen (DO) was determined by using a modification of the Winkler method (Strickland and Parson, 1972). At each sampling station, shrimps were sorted, identified, and counted for each catch. Color in fresh animals (Chapa-Saldaña[1]) proved to be a very reliable character for species identification.

CRIP monthly samples from 29 stations within a depth span of 9–80 m were averaged at intervals of 18 m (10 fathoms), except for the initial interval of 9 m (9–18 m), and pooled across years into four bimonthly periods. The term sample refers to the number of shrimp per twin net haul divided by the number of hours (ind./h) at each station. The first period (April–May) had a total of 87 samples (April 1985, May 1981, 1982 at 29 stations [Fig. 1], distributed in five depth intervals [9–18 m, 19–36 m, 37–54 m, 55–72 m, and 73–80 m]). June–July had 203 samples (June 1981, 1982; July 1981, 1982, 1984, 1985, and 1986) while August–September had 145 samples (August 1981, 1985, 1986; September 1982, 1985), and there were 87 samples for October–December (October 1981; December 1985, 1986). The sampling periods between June and September had higher

numbers of samples because the CRIP cruises were primarily intended to sample the closed season that, in those years, was imposed for that period. Catch data were averaged by period and depth interval and are reported as mean number of individuals per hour (ind./h ±SE) of trawling. Seasonal abundance data from BIOCAICT cruises, on the other hand, are reported for only three depth intervals: 9–15 m, 40–45 m, and 70–90 m. Catch figures were averaged for every 2.0°C interval of temperature and 0.5 mL/L interval of dissolved oxygen within the observed ranges and are presented as the average number of individuals per hectare (ind./ha ±SE).

Nonparametric single factor analysis of variance by ranks (Kruskal-Wallis test for tied ranks) was used to test for differences in shrimp abundance between the five depth intervals in each of the four bimonthly periods and between four dissolved oxygen levels. A nonparametric multiple range test (NMRT) was used in cases where Kruskal-Wallis test were significant (α=0.05, Zar, 1974).

Results and discussion

Penaeus brevirostris specimens were collected over a wide depth range, although generally higher catches were taken between 50 and 80 m. The depth distribution varied throughout the sampling period (Fig. 2). Most catches were monospecific, except in August 1986, when both *P. brevirostris* and *P. californiensis* were sampled at 80 m on the Piaxtla transect. During the period April–May, shrimp were more abundant between 9 and 18 m (5.8 ±3.6 ind./h) but specimens were also caught at most depth intervals except at 73–80 m (Fig. 2A). Differences in mean abundance between the five depth intervals were not significant (Kruskal-Wallis, P>0.05). During June-

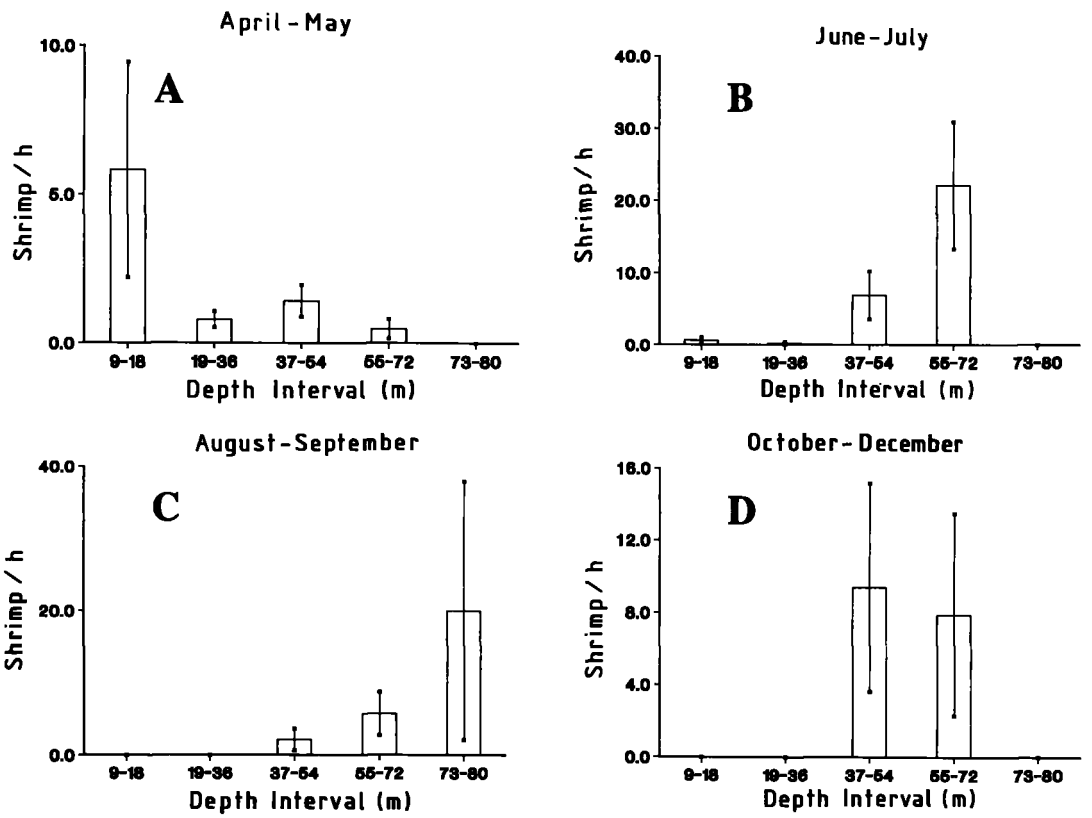

Figure 2

Mean abundance (shrimp/h ±SE) of crystal shrimp, *P. brevirostris*, at five depth intervals. Data combined from CRIP cruises in 1981, 1982, 1985, and 1986. (**A**) April–May 1981, 1982, and 1985; (**B**) June–July 1981, 1982, 1984, 1985, and 1986; (**C**) August–September 1981, 1982, 1985, and 1986; and (**D**) October–December 1981, 1985, and 1986. Abundance refers to mean number of shrimp caught at stations located within each depth interval in one hour trawling (paired 22.86-m otter trawl).

July, higher catches were obtained between 55 and 72 m (22.1 ±8.855), but abundance was also considerable at 37–54 m (6.9 ±3.3) (Fig. 2B, Kruskal-Wallis test, $P<0.001$). Mean abundance was significantly different between depth interval 55–72 m and all other intervals (NMRT, $P<0.01$), between depth interval 37–54 m and the remaining three intervals (NMRT, $P<0.01$), and was not significantly different between depth intervals 9–18, 19–36, and 73–80. In August–September, red shrimp was found only at depths beyond 55 m (Fig. 2C, Kruskal-Wallis, $P<0.025$). Mean abundance was significantly different between depth interval 55–72 m and all other depth intervals (only three categories were considered, as three intervals with zero abundance were regarded as one; NMRT, $P<0.005$). Abundance between depth intervals 9–18 m, 19–36 m, 37–54 m, and 73–80 m was not significantly different. During the October–December period, *P. brevirostris* catches were taken mainly at depth intervals 31–40 and 41–50 m (Fig 2D, Kruskal-Wallis, $P>0.05$). Although there appears to be a distinct difference in abundance between depth intervals, the test was not significant because the number of zero catches was high (79 cases out of 84), making the sum of ranks very similar in all intervals. The high standard error indicates the extent of data dispersion.

These results suggest that although *P. brevirostris* is generally found at greater depth intervals in the summer and autumn, its presence at mid-depths and shallower waters in spring may be an indication of seasonal changes in bathymetric distribution, i.e. onshore in spring and offshore in summer and autumn.

The distribution and abundance of *P. brevirostris* observed during the BIOCAICT cruises (Fig. 3) were very similar to those described earlier, i.e. the shrimp were mostly distributed in deeper waters except for the capture of some individuals at a depth of 10 m in June 1986 (Presidio and Baluarte transects). In November 1985 (Fig. 3A) and January 1986 (Fig. 3B), most individuals were caught at the deepest stations (70–90 m; 11.47 ±3.99 and 53.07 ±18.01 ind./ha,

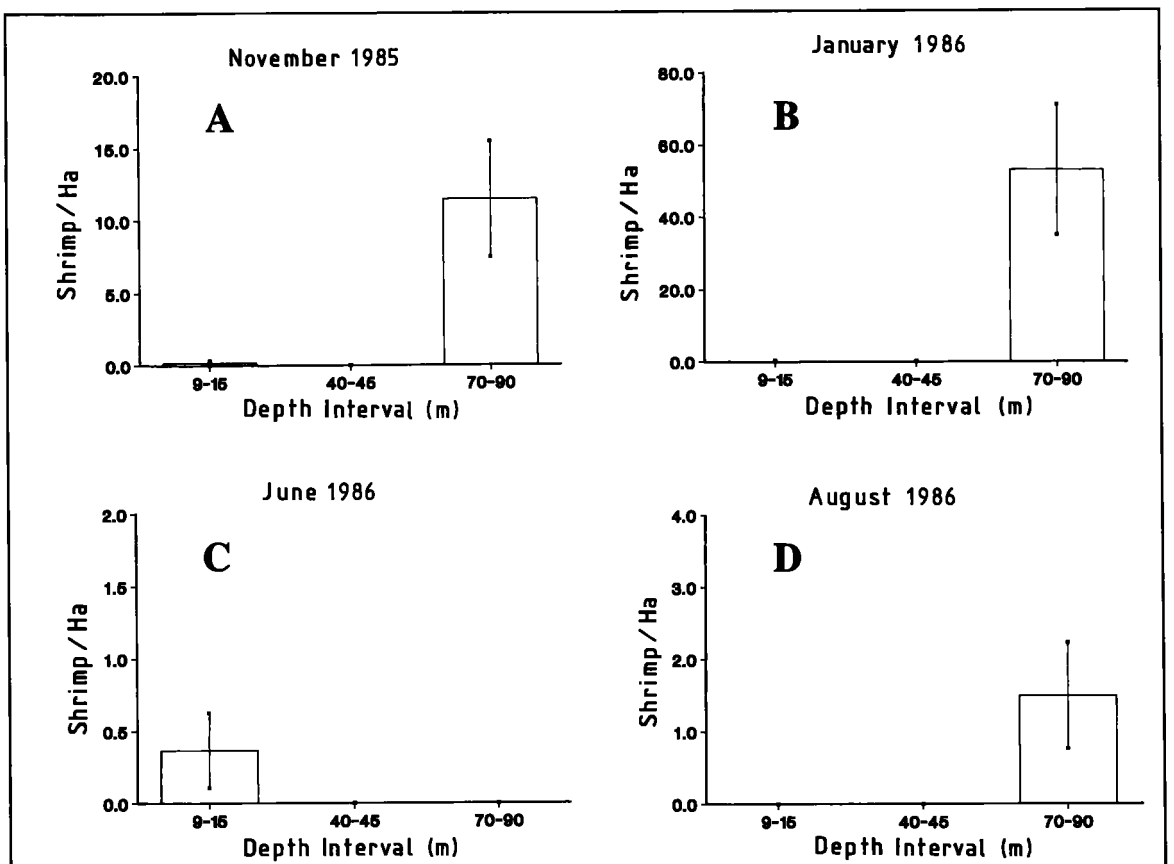

Figure 3

Mean abundance (shrimp/ha ±SE) of crystal shrimp, *Penaeus brevirostris*, at depth intervals observed during the BIOCAICT cruises in (**A**) November 1985, and (**B**) January, (**C**) June, and (**D**) August 1986.

respectively), except for a small catch in the former at the 9–15 m depth interval (0.13 ±0.19 ind./ha). In mid-June, very few specimens were collected (0.37 ±0.26 ind./ha), all in the Presidio and Baluarte transects at depths of about 10 m (Fig. 3C). During the summer cruise (August 1986) all individuals were caught at the deeper stations, (>70 m, 1.50 ±0.73 ind./ha; Fig. 3D).

The distribution of *P. brevirostris* observed during the BIOCAICT cruises, at all the stations, appeared to be limited to a narrow temperature range. The majority of individuals were caught at temperatures between 14.1 and 18.0°C and, although some individuals were also found at about 24.0°C, the average mean abundance at this temperature was rather low (0.1 ind./ha; Fig. 4).

Similarly, the main distribution of *P. brevirostris* appears to be limited to a narrow bottom dissolved oxygen range (Fig. 5). Mean shrimp densities were highest at the DO levels of 0.9–1.5 mL O_2/L while at higher (2.9–4.1 and 4.2–6.0 mL O_2/L) and lower levels (0.1–0.8 mL O_2/L), mean shrimp abundance was lower (Kruskal-Wallis test, $P<0.005$). Crystal shrimp abundance was significantly higher at the DO interval 0.9–1.5 mL/O_2 than at the other DO intervals (NMRT, $P<0.005$. Abundance differences among other DO intervals were not significant.

The former suggests that *P. brevirostris* occupies waters with lower oxygen content than do the other members of the genus. Most studies emphasize their distinct avoidance of hypoxic water and the negative consequences of exposure to it. Renaud (1986) found that *P. aztecus* and *P. setiferus* were able to detect and avoid hypoxic water below 2 ppm (1.4 mL O_2/L) and 1.5 ppm (1.05 mL O_2/L), respectively. Broom (1971) found a slightly higher threshold for the latter species (2 ppm, 1.4 mL O_2/L). Rubright et al. (1981) and Bassanesi-Poli (1987) reported surface oriented movements of *P. vannamei* when dissolved oxygen in culture ponds dropped below 2 mL/L. Egusa and Yamamoto (1961) observed stress in *P. japonicus* for oxygen concentrations below 2 mL/L and evacuation of their burrow at a DO level of 0.7 ppm (0.5 mL O_2/L). Regarding prolonged effects of hypoxia, Clark (1986) reported that *P. latisulcatus* showed molt inhibition and increased mortality under the hypoxic conditions of 2 ppm (1.4 mL O_2/L).

The disappearance of *P. brevirostris* from traditional fishing grounds in the summer may be due to the occurrence of temperature and dissolved oxygen levels outside its tolerable range. The population may move to deeper regions where low temperature and DO conditions, to which they are better adapted, prevail. Calderon-Perez[3] found a substantial number of shrimps of this species 120 m deep in June 1992 but none in shallower areas where temperature and DO were higher.

Thus, the seasonal variation in depth distribution of *P. brevirostris* in the eastern Pacific ocean may be due to bathymetric movements which, for most animals (Figs. 4 and 5), seem to be determined by seasonal changes in environmental parameters.

[3] Calderon-Perez, J. A. 1992. Data from the *BIOCAPESS VI* cruise on board the B/O (R/O) *El Puma*, carried out between 24–30 June 1992. Estación Mazatlán, Instituto de Ciencias del Mar y Limnología, U.N.A.M., apdo. Postal 811, Mazatlán, Sinaloa, México, CP 82000.

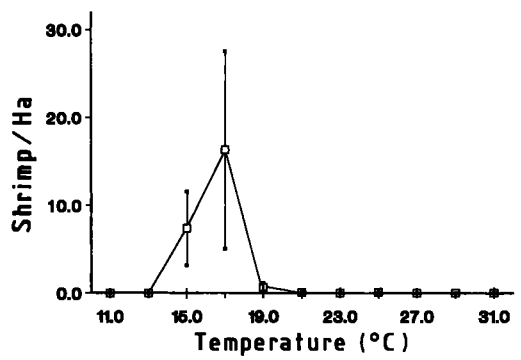

Figure 4

Mean abundance (shrimp/ha ±SE) of crystal shrimp, *Penaeus brevirostris*, in relation to bottom temperature (°C). Vertical lines represent standard error of the mean for each 2°C interval.

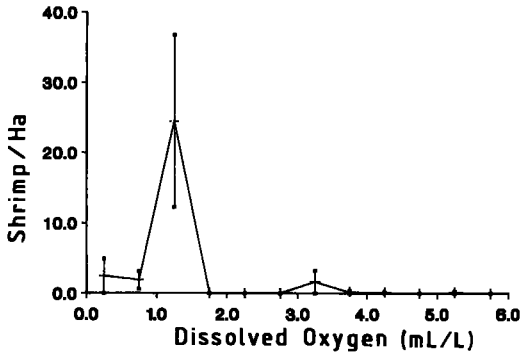

Figure 5

Mean abudance (shrimp/ha ±SE) of crystal shrimp, *Penaeus brevirostris*, in relation to dissolved oxygen (DO) concentration. Vertical lines represent standard error of the mean calculated for each DO interval of 0.5 mL/L.

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The diet of the swordfish *Xiphias gladius* Linnaeus, 1758, in the central east Atlantic, with emphasis on the role of cephalopods

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The swordfish *Xiphias gladius* Linnaeus, 1758, is a mesopelagic teleost with a cosmopolitan distribution between 45°N and 45°S latitude. It is an opportunistic predator feeding mainly on pelagic vertebrates and invertebrates (Palko et al., 1981). The diet of the swordfish has been studied mainly in the western Atlantic Ocean (Tibbo et al., 1961; Scott and Tibbo, 1968, 1974; Toll and Hess, 1981; Stillwell and Kohler, 1985). Earlier reports reflected the importance of fish in the swordfish diet, but recently Stillwell and Kohler (1985) cited squid as the predominant component in the diet of swordfish. Azevedo (1989) and Moreira (1990), reporting from off the Portuguese coast, mentioned fish (principally *Micromesistius poutssou*) and cephalopods as the main prey groups of swordfish. This finding was corroborated by Guerra et al. (1993) from the Northeastern Atlantic where cephalopods were found to be the most important component of the diet. Maksimov (1969) studied the diet of swordfish in the eastern tropical Atlantic Ocean. Cephalopods were a major component of the diet in all areas sampled and although no cephalopod species were identified, the genus *Ommastrephes* was present among the five genera found in stomach contents.

Stomach content analysis is an important tool in ecological and fisheries biology studies. Oceanic vertebrates are often more efficient collectors of cephalopods than any available sampling gear (Bouxin and Legendre, 1936; Clarke, 1966). The purpose of this study was to expand knowledge of the diet of the swordfish from the central east Atlantic Ocean, with special emphasis on the role of cephalopod species.

Material and methods

Sampling areas and capture methods

The stomach contents of 75 swordfish, *Xiphias gladius*, were analyzed. Specimens were caught at night in three different areas of the central east Atlantic Ocean (Fig. 1) from the commercial landings of the Spanish fleet:

Zone A Strait of Gibraltar (35°53'–35°42'N and 6°35'–6°30'W). Thirty five swordfish were caught with drift nets (2.5 miles long × 20 m deep) between 10 and 22 September 1990.

Zone B South of the Canary Islands (23°–26°N and 17°–22°W). Twenty-five swordfish were obtained from a longline vessel between 1 and 15th March 1991 by using mackerel, *Scomber* spp., as bait.

Zone C Gulf of Guinea (3°09'–0°36'N and 26°27'–4°17'W). Fifteen swordfish (standard length [SL] between 140–209 cm) were selected on the basis of the presence of cephalopods in their stomachs. These were taken from catches made by a longliner between May and July of 1991 by using mackerel and squid, *Illex* sp., as bait.

Stomach preservation and analysis

In zones A and B, fish were stored in ice. After landing, fish were measured from the tip of the lower jaw to the fork of the tail (SL). During commercial operations the internal organs were removed before the fish were weighed. The stomach contents of each fish, including all hard parts found in the stomach wall folds (otoliths, very small beaks, and lenses), were weighed (in grams) and preserved in 70% ethyl alcohol. Otoliths were also removed from the fish prey. Nematodes were found in some stomachs in small quantities, but these were assumed to be parasites and were not considered prey. In general, stomach contents showed an advanced level of digestion. A stomach fullness index (*SF*) was calculated as *SF* = (wet weight of the stomach content / wet weight of the swordfish without internal organs) × 100.

In zone C only cephalopods were preserved frozen. Fish were frozen immediately after capture without internal organs. This material was not included in comparative analyses because the main objective was to record the relative proportions of cephalopod species that were preyed upon in this zone.

Scomber spp. and *Illex* sp. were not considered prey from zones B

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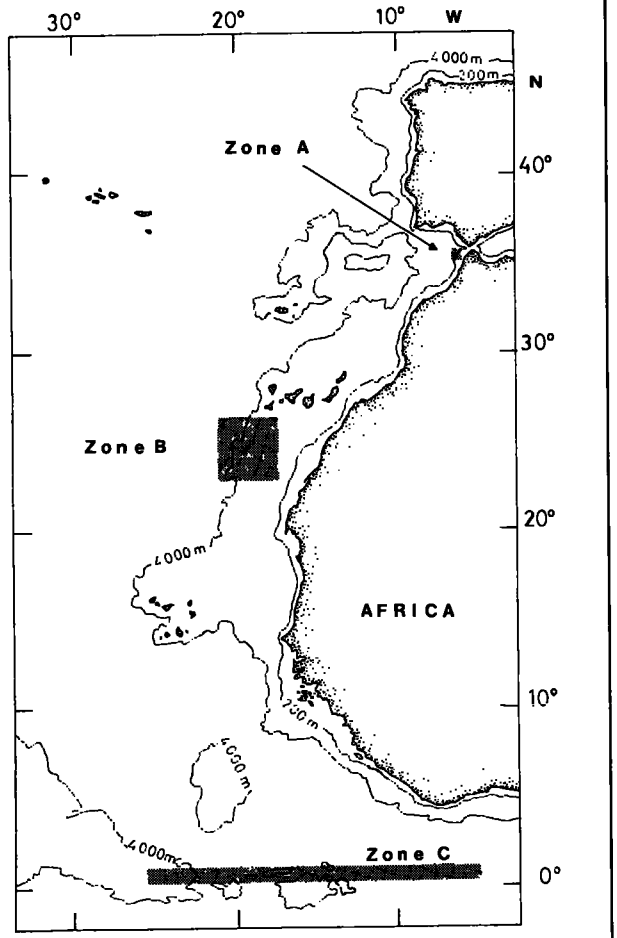

Figure 1

Locations of the swordfish *Xiphias gladius* fishing grounds in the central east Atlantic Ocean where samples were obtained in 1990–91.

and C respectively because they were used as bait. Prey items were identified to the lowest taxonomic category possible. Fish were identified from otoliths and bones (otolith guides of Härkönen (1986), Hecht and Hecht (1979), and author's collection). Crustaceans were classified from external parts of the skeleton (Zariquiey-Alvarez, 1968). Lower beaks (LB) were used as the primary means for classification of cephalopods, and beak identity was established by methods described by Clarke (1962, 1980, 1986a) and supplemented by a collection of cephalopod beaks (including beaks removed from locally caught cephalopods); upper beaks, other morphological characters (Hess and Toll, 1981), and distributional knowledge (Nesis, 1987) were used in some cases as well. Nearly all the beaks collected were fresh. All lower beaks were identified to the lowest taxon possible and the lower rostral length (LRL) or, in the order Sepiida, the hood length (LHL) (defined in Clarke, 1962, 1980) were measured by digital caliper or steroscopic microscope and eyepiece micrometer. Mantle lengths (ML in mm) and weights (W in g) of the cephalopods from which lower beaks came were then estimated from LRL's or LHL's by using relationships published elsewere (Clarke 1962, 1980, 1986a; Pérez-Gándaras, 1983; Wolff, 1982 (cited by Clarke, 1986a), Wolff and Wormuth, 1979).

Despite the advanced state of digestion of stomach contents, an attempt was made to examine the importance of each prey item. Two methods of stomach content analysis were used: percent numerical abundance and percent occurrence (Hyslop, 1980). A coefficient of prey numerical frequency, % No. = $(Ni/Nt) \times 100$, and a coefficient of prey frequency, % occurrence = $(Nsi/Nsf) \times 100$ were calculated; where Ni is the number of prey of each group i, Nt is the total number of prey, Nsi is the number of stomachs containing each group i, and Nsf is the total number of stomachs with food. An index of prey numerical importance (Castro, 1993) was also obtained as % importance = $(\%\ \text{No.} \times \%\ \text{occurrence})^{1/2} \times 100$.

Comparative analysis of degradation of hard structures

Free hard structures (otoliths, beaks, and eye lenses) were often found in the stomach contents. To estimate the importance of each prey item from the refractory or hard structures, it is important to know the rate of degradation by stomach acids.

Otoliths (sagittae) from four chub mackerel, *Scomber japonicus* (18 to 20 cm SL), similar in size to those found in the swordfish stomachs, and five otoliths of blue whiting, *Micromesistius poutassou*, from head-specimens found in swordfish stomachs were used to determine the rate of otolith degradation. Otolith lengths, taken on the longest axis, were between 3.70 and 4.10 mm for *Scomber* and between 10.81 and 13.53 mm for *Micromesistius*. Beaks from eleven *Illex coindetii* and two *Todarodes sagittatus* were used, with LRL's between 3.90 and 6.19 mm and 7.53 and 8.41 mm, respectively. Degradation of six eye lenses, three belonging to *T. sagittatus* and three belonging to fish species, were also analyzed.

Hard structures were placed in a hydrochloric acid (HCl) solution (pH=1.1; value lower than the range reported by Jobling and Breiby [1986] for fish in which the digestive process had begun), and the temperature was maintained between 18 and 20°C. The experiment was carried out for 48 hours. Old acid solutions were replaced with fresh solutions after 24 hours.

Cephalopod beak digestion (measured as decreasing upper rostral length, lower rostral length, and

lower wing length) and eye lens digestion (measured as decreasing lens diameter) were measured every 12 hours. Otolith digestion (measured as decrease of the longest axis length) was measured at intervals of 12 hours for blue whiting, although the third interval was divided into two intervals (measuring each 6 hours). Otolith digestion was measured at intervals of 2.5 or 1 hour for the chub mackerel.

Results

Stomach fullness analysis

Data on fish length (SL), weight (W), and stomach fullness (SF) from zones A and B are given in Table 1. Values of SF in zone A were higher than those in zone B. In the latter area four stomachs were empty whereas in zone A all stomachs had contents.

Stomach contents analysis

Zone A The swordfish diet consisted of fish, cephalopods, and decapods (Table 2). Fish were the most important item by number (93.33%, Table 2), although in 20% of the stomachs analyzed fish were represented by only otoliths and bones. A total of 832 otoliths were collected. Most bone remains could not be identified. Many of them consisted of a large spinal column (as long as 78.5 cm). It was estimated that otoliths and spines belonged to a total of 476 fish. Blue whiting, *Micromesistius poutassou*, was the most important prey species by number (37.81%, Table 3).

Cephalopods were detected in 17.14% of the stomachs sampled, and the number of specimens was estimated as 26 (Table 2). They were always present in those fish with the highest SF. The Ommastrephidae was the most important family by number (35.6%) and *Todarodes sagittatus* was the predominant species (23.4%). The Histioteuthidae ranked second in importance (21.4%) and *Histioteuthis bonnellii* was the dominant species (11.4%, Table 4).

Decapods of the order Natantia were found in the stomach contents of two individuals (Table 2), and a large specimen was identified as *Acanthephyra purpurea*.

Zone B In zone B the swordfish diet consisted of cephalopods and fish. Cephalopods represented the most common food item in this area, revealing the highest index of numerical importance (67.89%, Table 2). A group of six pairs of beaks and one free upper beak with the same shape could not be assigned to any family. These were called "Unknown A." A description and sketches of this beak type (Fig. 2) are given in the Appendix. Ommastrephidae was the

Table 1

Swordfish *Xiphias gladius* data from zones A and B: length (SL) in cm, weight (W) in Kg, and stomach fullness (SF). *n* is the number of fish collected in each zone.

		SL			W			SF		
	n	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Zone A	35	103–193	142.4	17.72	20–132	56.95	29.71	0.1–9.0	2.46	2.29
Zone B	25	112–201	153.3	24.54	13–102	40.40	24.36	0–5.3	0.75	1.37

Table 2

Comparison of the dietary importance of the three major forage categories observed in swordfish stomachs from zones A (35 fish) and B (21 fish). Data are given in terms of numerical frequency, frequency of occurrence, and index of numerical importance.

	Zone A				Zone B		
Forage category	% number	% occurrence	% importance	Forage category	% number	% occurrence	% importance
Fish	93.33	100.0	88.78	Fish	28.57	42.85	32.10
Cephalopods	5.09	17.14	8.54	Cephalopods	71.42	76.19	67.89
Decapod crustacea	1.56	5.71	2.66	Decapod crustacea	0.0	0.0	0.0

Table 3

Fish species occurring in the diet of the swordfish *Xiphias gladius* in zones A and B (35 and 9 swordfish stomachs containing fish, respectively) expressed in terms of numerical frequency, frequency of occurrence, and index of numerical importance.

	Zone A				Zone B		
Species	% number	% occurrence	% importance	Species	% number	% occurrence	% importance
Micromesistius poutassou	37.81	80.00	38.61	*Diaphus* sp.	16.66	22.22	18.35
Scomber japonicus	3.78	22.85	6.53	*Thunnus* sp.	5.55	11.11	7.49
Capros aper	2.10	8.57	2.97	Not identified	77.77	77.77	74.16
Lepidopus caudatus	1.47	20.00	3.80				
Trachurus sp.	1.26	14.28	2.97				
Merluccius merluccius	0.84	5.71	1.53				
Thunnus sp.	0.21	2.85	0.54				
Not identified	52.52	71.42	43.00				

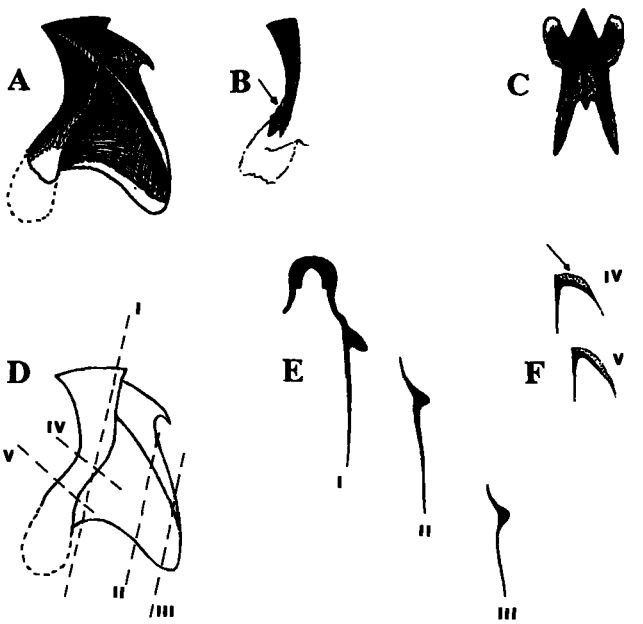

Figure 2

Illustration of the characteristic, unidentified, lower beak (called "Unknown A"). Lower rostral length = 3.4 mm. (**A**) profile of the beak; (**B**) profile of the anterior part with one side removed to show the shoulder and the anglepoint; (**C**) top view; (**D**) outline of the beak showing the positions of sections shown in E and F; (**E**) three sections of the crest and one lateral wall taken at positions indicated in D to show thickening; and (**F**) two sections of the wing and shoulder region at positions shown in D. Cartilage is indicated by arrows and dotted area.

Table 4

Cephalopods in the diet of the swordfish *Xiphias gladius* from zones A, B, and C (6, 16, and 15 swordfish with cephalopod remains, respectively). Number of cephalopods (*n*), index of numerical importance (IN), range of lower rostral length (LRL), range of estimated mantle length (ML), and range of estimated body weight (W) in each zone. The percentage by number of each species in all areas together is also given. The equation used is given under the symbol (A) (a = Clarke, 1962; b = Clarke, 1980; c = Clarke, 1986; d = Pérez-Gándaras, 1983; e = Wolff and Wormuth, 1979; f = Wolff, 1982). A specimen identified and counted from upper beaks is indicated by an asterisk (*). Broken beaks are indicated by (R).

	Zone A					Zone B					Zone C					All zones
Group or Species	*n*	% IN	LRL (mm)	ML (mm)	W (g)	*n*	% IN	LRL (mm)	ML (mm)	W (g)	*n*	% IN	LRL (mm)	ML (mm)	W (g)	% A
Family Spirulidae																
Spirula spirula						1	2.6	0.7	20.4	1.0						0.9 c
Family Sepiidae																
Sepia officinalis	1	5.0	4.0	97	34											0.9 d
Family Loliginidae																
Loligo vulgaris						2	3.7	3.9–4.2	286–311	437–542						1.7 c
Family Ancistrocheiridae																
Ancistrocheirus lesueuri	1	5.0	5.6	186	379						1	3.0	—	170	—	1.7 b
Family Octopoteuthidae																
Octopoteuthis rugosa	1	5.0	12.4	215	401											0.9 b
Family Onychoteuthidae																
Onychoteuthis A						3	6.5	3.2–4.5	166–245	132–466	1	3.0	6.6	373	1,923	3.5 f
Onychoteuthis B											1	3.0	3.0	154	105	0.9 f
Onychoteuthis C											6	17.2	3.0–4.4	154–243	109–451	5.3 f
Family Gonatidae																
Gonatus sp. ?	1*	5.0	—	—	—											0.9 —
Family Histioteuthidae																
Histioteuthis bonnellii	5*	11.4	6.4–7.9	74–88	247–377											4.4 b
Histioteuthis dofleini	1	5.0	7.0	128	435						3	8.3	5.4–6.9	95–121	235–435	3.5 bf
Histioteuthis A	1	5.0	2.8	48	53											0.9 b
Family Brachioteuthidae																
Brachioteuthis sp.						1	2.6	1.6	48	3						0.9 c
Family Ommastrephidae																
Todaropsis eblanae	2	7.2	R–4.3	R–141	R–189											1.7 d
Todarodes sagittatus	7*	23.4	4.4–6.9	172–274	149–517	2*	5.6	6.5	260	448						8.0 ba
Ommastrephes bartrami	1	5.0	8.5	303	1,383	3	8.0	4.5–8.1	180–289	185–1,170						3.5 a
Sthenoteuthis pteropus						10*	20.6	8.1–12.9	336–531	787–7,508	22*	41.6	5.3–10.8	218–442	375–4,052	28.3 e
Ommastrephid species						1	2.6	1.6	—	—						0.9 —
Family Thysanoteuthidae																
Thysanoteuthis rhombus						4	7.5	3.3–7.6	252–727	670–8,613	4*	11.8	4.2–5.9	351–543	1,402–4,052	7.0 c
Family Mastigoteuthidae																
Mastigoteuthis sp.	1	5.0	5.6	—	—											0.9 —
Family Grimalditeuthidae																
Grimalditeuthis bomplandi											1	3.0	3.9	—	—	0.9 —
Family Cranchiidae																
Teuthowenia megalops	1	5.0	4.1	179	56											0.9 c
Teuthowenia sp.											1	3.0	2.8	—	—	0.9 —
Megalocranchia sp.						2	5.3	5.1–5.4	276–297	—						1.7 b
Family Argonautidae																
Argonauta sp.	1*	5.0	—	—	—	6	13.0	3.8–7.2	—	—						6.2 —
Unknown A						7*	14.0	3.0–4.4	—	—						6.2 —
Not identified	2	7.2	—	—	—	3	8.0	—	—	—	2	5.9	—	—	—	6.2 —

most important family by number (36.8%), and the orangeback squid, *Sthenoteuthis pteropus*, was the most important species (20.6%, Table 4).

Eighteen fish were counted from spinal columns and otoliths with an index of numerical importance of 32.10% (Table 2). Fish were found together with cephalopods in 19.0% of the stomachs containing food. In zone A the numbers of free lenses of fish and cephalopods were similar. However, only 32 cephalopod lenses were found in zone B; fish lenses were not found.

Zone C A total of 46 cephalopods were found in stomachs from zone C. The family Ommastrephidae, represented solely by *Sthenoteuthis pteropus*, was the most important species by number (41.6%) and estimated weight (Table 4). The Onychoteuthidae ranked second in importance by number but not by weight.

In the combination of all three zones, the Ommastrephidae, Onychoteuthidae, Histioteuthidae, and Thysanoteuthidae were the most important cephalopod families by number in swordfish diet (67.9%); other families are probably occasional prey. The most important species was *Sthenoteuthis pteropus* (28.3%, Table 4). The *S. pteropus* collected were mostly females, as evidenced by their large ML's (females can reach 650 mm ML and males 280 mm ML, Zuev et al., 1985) and by the presence of large oviducts. Moreover of the "Unknown A" species, five cephalopod species (*Brachioteuthis* sp., *Grimalditeuthis bomplandi*, *Megalocranchia* sp., *Octopoteuthis rugosa*, and *Spirula spirula*) were identified for the first time in swordfish stomach contents.

Comparative analysis of hard structure degradation

Otoliths (sagittae) of *Scomber japonicus* were dissolved after an average time of 6 hours and 47 minutes (% decrease of otolith length=2.121 + 14.424T, SD=5 min; Fig. 3). Otolith length decreased significantly over a period of one hour (ANOVA, df=14, P=5.0425 × 10^{-5}).

Otoliths of *Micromesistius poutassou* showed a significant decrease in length after an interval of 12 hours (ANOVA, df=8, P=1.7605 × 10^{-2}). After 48 hours, they had lost 40% of their length (% decrease of otolith length=1.932 + 0.843T, Fig. 3) but still maintained their original shape.

Lower rostral length and upper rostral length did not differ significantly after 48 hours in acid (ANOVA, df=24, P=0.95588 and df=24, P=0.93221, respectively). In addition, wing length of the lower beak did not differ significantly after 48 hours (ANOVA, df=24, P=0.97319). No significant differences were found for fish and cephalopod eye lense diameter after 48 hours (ANOVA, df=4, P=0.50454 and df=4, P=0.89424, respectively).

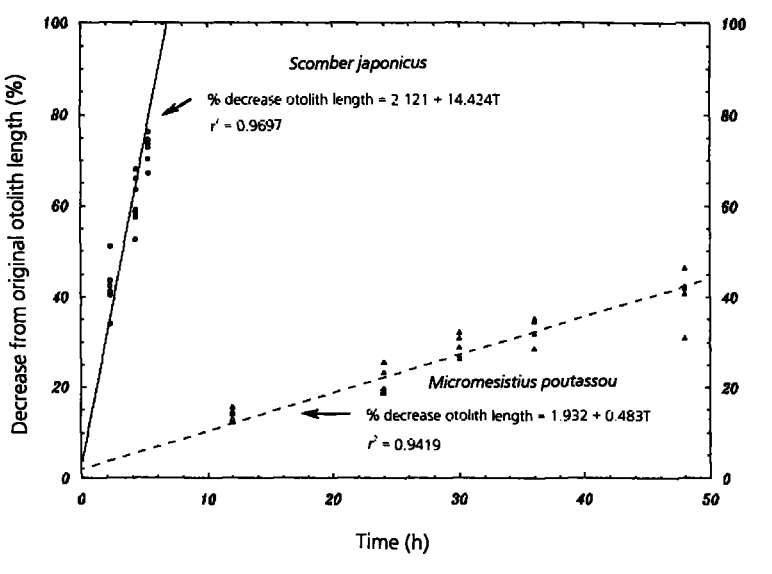

Figure 3

Decrease in otolith length of chub mackerel, *Scomber japonicus*, and blue whiting, *Micromesistius poutassou* (measured on the longest axis) after immersion in hydrochloric acid (pH=1.1) for 48 hours.

Discussion

Commercial longline fishing generally lasts for 12–14 hours and the fish caught can remain alive for many hours (Boggs, 1992); thus digestion of stomach contents is continuous. Moreover, regurgitation regularly occurs (Tibbo et al., 1961). This may bias values of stomach fullness. The period of study was limited in each area and sample sizes were not large, precluding statistical analysis. However, the diet of swordfish appeared to show substantial variation between areas. In neritic areas (zone A) swordfish preyed upon pelagic and benthic species of fish and squids, whereas in oceanic areas (zone B) they preyed mainly on squids (Table 2). This pattern was also observed by Maksimov (1969). In addition, Carey and Robison (1981) showed that in neritic areas swordfish have a different ecology and migration pattern from that found in oceanic waters. In neritic areas, swordfish are found near the bottom during the daylight, feeding mainly on benthic species (i.e. *Capros aper* and *Merluccius merluccius* in this study, Table 3); at night, they move offshore to feed actively on squid and other migrating fauna concentrated near the surface (i.e. *Todarodes sagittatus* in this study, Table 4). In oceanic waters, swordfish undergo a diel vertical migration reaching about 600 m at noon and ascending to shallow waters at night; they can prey actively on oegopsid squids at both ends of the migration (Carey and Robison, 1981). The mean number of cephalopods per stomach was 0.7 in zone A, similar to data reported by Moreira (1990). In zone B (oceanic waters) the mean was 1.8, similar to the value of 2.1 calculated from data obtained by Guerra et al. (1993). In zone C, the mean number of cephalopds per stomach was 3. Bane (in Fonteneau and Marcille, 1991) also showed that cephalopod-prey are more important in oceanic waters than inshore for yellowfin tuna, *Thunnus albacares*.

From analysis of degradation, otoliths were strongly eroded by acid; large, thick otoliths dissolved more slowly than small, thin ones. Cephalopod beaks and eye lenses and fish eye lenses were not affected by acid. Fish were the item with the highest index of numerical importance (Table 2) in zone A. However, the value obtained must be treated with caution because the otoliths of *Micromesistius poutassou* may accumulate owing to the structure of the stomach wall and the time necessary to dissolve them (Fig. 3). The otoliths of *Scomber japonicus* were not found free, a feature that accords with the results of the analysis of degradation. Therefore, if evaluation of fish biomass is based on the presence of otoliths, biomass may be overestimated for fish with large and dense otoliths (i.e. *M. poutassou*). Fish with smaller and weak otoliths may be underestimated as was observed by both da Silva and Neilson (1985) and Jobling and Breiby (1986). However, the rate of degradation of otoliths in this study may be overestimated because the acidity was greater than the value reported in general for fish stomach acids (pH=2.0–3.0) after the digestive process has begun. Because cephalopod eye lenses and fish eye lenses are not affected by acid, as noted by Clarke (1986b), the number of lenses found in a stomach may be a means of estimating the relative importance of cephalopods and fish in the diet. However, the percentage of occurrence of fish (counted from whole fish and free otoliths) was similar to that obtained by Azevedo (1989) and Moreira (1990) in areas nearest to zone A. In zone B, if eye lenses of fish and cephalopods are considered, both of which experience a similar rate of digestion, the relative importance of fish in the diet is less than what was indicated by data from the otoliths.

The importance (based on % number) of *Sthenoteuthis pteropus* in zone C is not surprising given the large abundance of this species at these latitudes (Voss, 1966; Zuev et al., 1985). The preferred temperature range for swordfish is from 25° to 29°C (Ovchinnikov, 1970) which is nearly the same as that for adult squid females (24°–30°C, Zuev et al., 1985). These temperatures are almost constant at these latitudes throughout the year. Around zone C, there is a complex system of currents and frontal zones where there is a high biomass (Blackburn, 1965; Ovchinnikov, 1970): in addition, high swordfish CPUE values have been obtained in these areas by the Spanish fishing fleet (Mejuto et al., 1991) and the Japanese longline fishery (Palko et al., 1981). Therefore, the availability of prey may be partially responsible for the distribution of swordfish in these waters.

Guerra et al. (1993) found that *Sthenoteuthis pteropus* was the most common species in the swordfish diet in the Northeastern Atlantic; this species is possibly one of the unidentified ommastrephid species found by Maksimov (1969). *Todarodes sagittatus* and *Ommastrephes bartrami* were also found. These three species ascend to the upper epipelagic layer and feed actively on myctophids and small squid at night (Nigmatullin et al., 1977; author, unpubl. data). During the day, *S. pteropus* descend to 350 or 400 m (Moiseyev, 1988). These ommastrephids have a high growth rate and their life span is no longer than 1.5 years (Arkhipkin and Mikheev, 1992; Rosenberg et al., 1980; Ishii, 1977). Therefore, squid may be an efficient means of energy transfer in oceanic food webs.

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Appendix

Description of the "unknown A" lower beak

Terms and measurement used to describe the characteristic beak (the "Unknown A") are the same as those used by Clarke (1980, 1986a). The beak (Fig. 2) belongs to an unidentified species of oegopsid, and its general shape is similar to the beak of *Discoteuthis*. It is taller than it is long (Fig. 2A) and although five of them had digested wings, the largest beak (lower rostral length=4.4 mm) had a full wing with an isolated spot.

The rostrum is distinctly shorter than deep (g/a=0.67, where g is the hood length in the midline and a is the length of the rostral edge visible in profile) and narrow (i/j=2.8, where i is the LRL and j is the distance between the jaw angles). There is no hook in the rostral edge, but rather this is sharp-edged and thickened. The crest is short and has a notch in the lateral wall to the side of the crest (Fig. 2, A and C). The hood does not lie close to the crest. The surface of the hood has a very soft fold. The jaw angle is obtuse and a sharp anglepoint is present (Fig. 2B). Jaw angle is obscured from the side by a very low wing fold (Fig. 2, A, B, and F) which is covered by cartilage (dotted area). A distinct lateral wall ridge forms a fin (Fig. 2, E, I), similar to *Histioteuthis* beaks (type A) described by Clarke (1980). This runs toward the midpoint of the posterior edge of the lateral wall (Fig. 2, E, III). The beaks of *Discoteuthis* lack this ridge.

Length-weight relationships for 13 species of sharks from the western North Atlantic

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The rapid expansion of sport and commercial fisheries for sharks in the western North Atlantic has created the need to manage the stocks of several species of large sharks. A fishery management plan for sharks within the U.S. exclusive economic zone (EEZ) of the Atlantic Ocean (USDOC, 1992) was implemented in 1993. The 39 species of sharks included in the fishery management plan are not managed on an individual species basis, but are grouped into three species groups—large coastal, small coastal, and pelagic. Basic biological information needed for stock assessment is lacking for many of these Atlantic sharks, including minimum, maximum, and average sizes, as well as length-to-weight and length-to-length relationships. These data are essential for understanding the growth rate, age structure, and other aspects of shark population dynamics.

Size conversions also have a practical value in fisheries. One measure currently in practice at nearly all shark tournaments on the Atlantic coast is the establishment of minimum size limits and usually a minimum weight. Since sizes must be estimated at sea, means for converting lengths to weights are essential to anglers. Moreover, the National Marine Fisheries Service (NMFS) conducts an extensive Atlantic Shark Tagging Program using volunteer assistance of recreational and commercial fishermen. Commercial fishermen generally are more confident in estimating the weight of sharks being released, and recreational fishermen in estimating lengths. Conversions are needed to change these estimates into common size units for analysis.

Length data on sharks worldwide have been reported as total length (Strasburg, 1958; Stevens, 1975, 1983; Stevens and Wiley, 1986; Stevens and Lyle, 1989), alternate length (Cailliet and Bedford, 1983; Stick and Hreha, 1989), dorsal length (Aasen, 1963, 1966), precaudal length (Nakano et al., 1985; Cliff et al., 1989), standard length (Guitart Manday, 1975) and fork length (Mejuto and Garces, 1984; Casey and Pratt, 1985; Berkeley and Campos, 1988). Most studies include formulas to convert their measurements to total length. Total length measurements, however, can vary considerably depending on the placement of the caudal fin (Branstetter et al., 1987).

Published size relationships for sharks from various regions of the Atlantic Ocean and Gulf of Mexico include studies on the blue shark, *Prionace glauca* (Aasen, 1966; Stevens, 1975); tiger shark, *Galeocerdo cuvier* (Branstetter, 1981; Branstetter et al., 1987); silky shark, *Carcharhinus falciformis* (Guitart Manday, 1975; Branstetter, 1987; Berkeley and Campos, 1988); bull shark, *C. leucas* (Branstetter, 1981); spinner shark, *C. brevipinna* (Branstetter, 1981); night shark, *C. signatus* (Guitart Manday, 1975; Berkeley and Campos, 1988); oceanic whitetip shark, *C. longimanus* (Guitart Manday, 1975); finetooth shark, *C. isodon* (Castro 1993); shortfin mako, *Isurus oxyrinchus* (Guitart Manday, 1975; Mejuto and Garcés, 1984); white shark, *Carcharodon carcharias* (Casey and Pratt, 1985); porbeagle shark, *Lamna nasus* (Aasen, 1963; Mejuto and Garcés, 1984); bignose shark, *C. altimus* (Berkeley and Campos, 1988); bigeye thresher shark, *Alopias superciliosus* (Guitart Manday, 1975); and scalloped hammerhead, *Sphyrna lewini* (Branstetter, 1987). In response to the immediate needs of tournament officials and fishermen, and for management initiatives, we present length and weight data for thirteen species of large Atlantic sharks collected by the Apex Predator Investigation (API) of NMFS over a 29-year period.

Materials and methods

Length and weight data were collected from sharks caught by recreational and commercial fishermen and biologists along the U.S. Atlantic coast from the Gulf of Maine to the Florida keys during 1961 through 1989. Sharks were caught primarily on rod and reel at sport fishing tournaments and on longline gear aboard research vessels and commercial fishing boats. Some data were obtained from sharks that were harpooned or taken in gill nets. Measurements from a large white shark captured off Rhode Island in 1991 were also

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included in the analysis because of the shark's unusual size. Data were obtained opportunistically throughout each year but most (88%) were collected in the months of June, July, and August off the northeast United States between North Carolina and Massachusetts. Only lengths and weights measured by the authors and other members of the API or by cooperating biologists are included in this report. Measurements of embryos and fish known to be pregnant were excluded from the data set.

All lengths were measured with a metal measuring tape to the nearest centimeter in a straight line along the body axis; the caudal fin was placed in a natural position. Fork length (FL) was measured from the tip of the snout to the fork of the tail. Total length (TL) is defined as the distance from the snout to a point on the horizontal axis intersecting a perpendicular line extending downward from the tip of the upper caudal lobe to form a right angle.

Total weight (WT) of each shark was measured to the nearest pound and converted to kilograms. The majority of the fish were weighed hanging from the caudal peduncle which allowed any water in the stomach, and in some cases stomach contents, to drop out prior to weighing. Many fish were examined internally and, if unusually large amounts of water or contents were found in the stomach or abdominal cavity, the weights were subtracted to obtain a more accurate weight.

Fork-total length relationships for 13 species of shark (n=5,065) were determined by the method of least squares to fit a simple linear regression model. Linear regressions of fork-to-total length were calculated with their corresponding regression coefficients, sample sizes, and mean lengths. These data were then combined into four family groups: Alopiidae (thresher sharks), Lamnidae (mackerel sharks), Carcharhinidae (requiem sharks), and Sphyrnidae (hammerhead sharks), and linear regressions and TL/FL percentages were calculated for each group.

An allometric length-weight equation was calculated by using the method of Pienaar and Thomson (1969) for fitting a nonlinear regression model by least squares. The form of the equation is $WT=(a)FL^b$, where WT=total weight (kg), FL=fork length (cm), and a and b are constants. Length-weight relationships, mean lengths and weights, and size ranges were determined for 13 species of sharks (n=9,512). Literature values for maximum fork length and fork length at maturity were also included. The regressions of the length-weight equations expressed logarithmically were tested for possible significant differences ($P<0.05$) between males and females by using an analysis of covariance test for homogeneity of slopes.

Fork length is used throughout this report as the basis for all conversions and comparisons. We have found fork length to be a more precise measurement. For comparative purposes, all values published elsewhere as total lengths were converted to fork lengths by using the species' equations presented in this paper.

Minimum sizes at maturity reported here are from published accounts with their original sources referenced, with the exception of *Alopias vulpinus* and *Carcharodon carcharias*. Minimum size at maturity for the thresher shark and the male white shark were determined by Pratt[1] who used the following criteria: smallest male with calcified claspers that rotate at the base and smallest gravid female. When considerable variation occurred among published accounts, traditional sizes at maturity were chosen primarily from Atlantic populations. The maximum sizes and maximum sizes at birth used here are summarized in Pratt and Casey (1990).

Results and discussion

Linear regressions of fork-to-total length were calculated for 13 species of shark and four family groups (Table 1). The slopes of the regression lines of the four families decrease with the increasing length of the upper caudal lobe. The mackerel sharks have lunate tails with the upper and lower caudal lobes almost equal in size. The requiem sharks, hammerhead, and thresher sharks have heterocercal tails with the upper lobe longer than the lower. The latter group have very long upper caudal lobes with the fork length approximately 60% of the total length. The fork length represents 92%, 84%, and 77% of the total length for the mackerel, requiem, and hammerhead sharks, respectively.

A total of 9,512 sharks representing 13 species were measured, sexed, and weighed. There were no significant differences in slope or intercept of the length-weight relationships between males and females for any of the species and therefore one equation, calculated with the sexes combined, was used to represent the data for each species (Table 2).

Size at maturity for males and females is difficult to determine for pelagic sharks and can vary in different parts of the world (Pratt and Casey, 1990). The discrepancy is due, in part, to the use of variable criteria in determining a precise length at sexual maturity (Springer, 1960; Clark and von Schmidt, 1965; Pratt, 1979) and thus maturity is often reported

[1] H. L. Pratt, National Marine Fisheries Service, Narragansett, RI 02882. Pers. commun., May 1993.

Table 1

Fork length (FL)-total length (TL) relationships for 13 species of sharks and four family groups from the western North Atlantic: $FL = (a)TL+b$. Fork length and total length means and ranges were taken from data presented in this study.

Species	n	Mean total length (cm)	Total length range (cm)	Mean fork length (cm)	Fork length range (cm)	$FL = (a)TL+b$ a	b	r^2
Alopiidae	69					0.4882	37.9566	0.8577
Alopias superciliosus (bigeye thresher)	56	312	155–371	192	100–228	0.5598	17.6660	0.8944
A. vulpinus (thresher shark)	13	373	291–450	211	168–262	0.5474	7.0262	0.8865
Lamnidae	324					0.9352	−3.3292	0.9972
Carcharodon carcharias (white shark)	112	204	122–517	187	112–493	0.9442	−5.7441	0.9975
Isurus oxyrinchus (shortfin mako)	199	171	70–368	157	65–338	0.9286	−1.7101	0.9972
Lamna nasus (porbeagle)	13	201	119–247	182	106–227	0.8971	1.7939	0.9877
Carcharhinidae	4561					0.8290	1.1309	0.9963
Carcharhinus altimus (bignose shark)	10	174	132–228	148	112–192	0.8074	7.7694	0.9872
C. falciformis (silky shark)	15	173	90–258	142	73–212	0.8388	−2.6510	0.9972
C. obscurus (dusky shark)	148	153	92–330	125	74–277	0.8396	−3.1902	0.9947
C. plumbeus (sandbar shark)	3734	123	51–249	103	42–211	0.8175	2.5675	0.9933
C. signatus (night shark)	38	154	72–235	130	60–195	0.8390	0.5026	0.9883
Galeocerdo cuvier (tiger shark)	44	247	145–375	203	116–318	0.8761	−13.3535	0.9887
Prionace glauca (blue shark)	572	214	64–337	179	52–282	0.8313	1.3908	0.9932
Sphyrnidae	111					0.7756	−0.3132	0.9868
Sphyrna lewini (scalloped hammerhead)	111	206	82–278	160	64–216	0.7756	−0.3132	0.9868

as a size range rather than as a specific length. An individual author's definition of maturity is sometimes ambiguous or obscure. The sizes at maturity (Table 2) are from multiple reference sources and therefore may be mixed in definition and criteria. The original published sources should be consulted as the basis for defining sexual maturity among different authors.

An attempt was made to obtain samples representative of the full size range of each species. The minimum, maximum, and mean lengths and weights by species of sharks examined in this study are reported (Tables 1 and 2). A reliable maximum size is difficult to verify. Lengths or weights, or both, for large fish are often reported inaccurately and published accounts usually qualify maximum lengths with such words as "probably reach," "possibly to," or "may grow up to." Maximum lengths (FL) reported in Pratt and Casey (1990) are included for comparison with the sizes measured in this study (Table 2). With the exception of the porbeagle and the tiger shark, our data are within 62 cm (2 ft) of published maximum sizes. The porbeagle shark is less common in our study area; fewer specimens were examined (<30), and therefore the full size range of this species is not represented. Although the tiger shark is purported worldwide to grow to 469 cm FL (15.4 ft) (Castro, 1983; Compagno, 1984; Pratt and Casey, 1990),

Table 2

Fork length (FL)-total weight (WT) relationships for the 13 species of sharks from the western North Atlantic: $WT = (a)FL^b$. Fork length and weight means and ranges were taken from data presented in this study. The maximum fork length and sizes at maturity for each species were obtained from the literature.

Species	Sex	*n*	Mean fork length (cm)	Fork length range (cm)	Max fork length (cm)	Fork length at maturity (cm)	Mean weight (kg)	Weight range (kg)	$WT = (a)FL^b$ a	b	r^2
Alopias superciliosus (bigeye thresher)	Combined	55	190	100–228	270[1]		99	11–170	9.1069×10^{-6}	3.0802	0.9059
	Male	34	188	100–221		180[1]	92	11–150			
	Female	21	194	123–228		214[1]	110	23–170			
A. vulpinus (thresher shark)	Combined	88	201	154–262	276[4]		122	54–211	1.8821×10^{-4}	2.5188	0.8795
	Male	46	197	154–228		184[2]	116	54–181			
	Female	41	207	155–262		226[2]	129	59–211			
Carcharodon carcharias (white shark)	Combined	125	186	112–493	555[3]		141	12–1554	7.5763×10^{-6}	3.0848	0.9802
	Male	65	203	117–493		332[3]	208	16–1554			
	Female	59	168	112–310		454[12]	69	12–297			
Isurus oxyrinchus (shortfin mako)	Combined	2081	172	65–338	336[4]		63	2–531	5.2432×10^{-6}	3.1407	0.9587
	Male	1007	169	70–260		179[5]	59	2–210			
	Female	1054	174	65–338		258[5]	68	3–531			
Lamna nasus (porbeagle)	Combined	15	185	106–227	329[1]		83	19–143	1.4823×10^{-5}	2.9641	0.9437
	Male	13	180	106–216		159[6]	77	19–113			
	Female	2	214	201–227		204[6]	117	91–143			
Carcharhinus altimus (bignose shark)	Combined	38	151	97–210	235[1]		42	6–143	1.0160×10^{-6}	3.4613	0.8958
	Male	12	158	115–205		182[7]	45	14–99			
	Female	26	148	97–210		190[7]	41	6–143			
C. falciformis (silky shark)	Combined	85	118	73–212	253[8]		22	4–88	1.5406×10^{-5}	2.9221	0.9720
	Male	39	117	73–196		178[11]	22	4–88			
	Female	46	119	78–212		186[11]	22	4–88			
C. obscurus (dusky shark)	Combined	247	162	79–287	303[7]		69	5–270	3.2415×10^{-5}	2.7862	0.9649
	Male	103	136	79–276		231[8]	39	5–216			
	Female	144	181	83–287		235[8]	90	6–270			
C. plumbeus (sandbar shark)	Combined	1548	129	44–201	198[7]		30	1–104	1.0885×10^{-5}	3.0124	0.9385
	Male	577	115	45–183		150[8]	20	1–68			
	Female	961	138	44–201		152[8]	36	1–104			
C. signatus (night shark)	Combined	124	111	60–203	235[1]		15	3–102	2.9206×10^{-6}	3.2473	0.9502
	Male	69	112	93–195		—	14	8–64			
	Female	55	111	60–203		150[7]	16	3–102			
Galeocerdo cuvier (tiger shark)	Combined	187	203	92–339	469[1]		110	5–499	2.5281×10^{-6}	3.2603	0.9550
	Male	92	209	95–318		258[9]	113	7–348			
	Female	92	197	92–339		265[9]	107	5–499			
Prionace glauca (blue shark)	Combined	4529	195	52–288	320[1]		52	1–174	3.1841×10^{-6}	3.1313	0.9521
	Male	3095	205	54–288		183[10]	59	1–174			
	Female	1398	172	52–273		185[10]	34	1–140			
Sphyrna lewini (scalloped hammerhead)	Combined	390	158	79–243	239[11]		47	5–166	7.7745×10^{-6}	3.0669	0.9255
	Male	189	166	107–224		139[11]	53	11–126			
	Female	199	151	79–243		194[11]	41	5–166			

[1] Castro (1983).
[2] Pratt (personal commun.).
[3] Randall (1987).
[4] Pratt and Casey (1990).
[5] Stevens (1983).
[6] Aasen (1961).
[7] Compagno (1984).
[8] Springer (1960).
[9] Branstetter et al. (1987).
[10] Pratt (1979).
[11] Branstetter (1987).
[12] Casey and Pratt (1985).

Atlantic specimens may not attain that size. Our longest tiger shark was 339 cm FL (11.1 ft) (Table 2). The maximum reported length examined by Branstetter (1981) in a study of tiger sharks in the north central Gulf of Mexico was 346 cm FL (11.4 ft). The maximum reported length for the U.S. Atlantic coast is 391 cm FL (12.8 ft) (Bigelow and Schroeder, 1948). These lengths are more in agreement with individuals sampled in this study.

Specimens from three species of sharks exceeded the maximum reported lengths (Table 2): sandbar shark, shortfin mako shark, and scalloped hammerhead shark. The 211 cm FL (6.9 ft) female sandbar shark in this study (Table 1) was measured by one of the authors (J. Casey) and is the largest measured sandbar reported to date. This fish was caught in September of 1964 by a sport fisherman approximately 10 miles east of Asbury Park, New Jersey. Unfortunately, the fish was not weighed. Two mako sharks measured in this study were longer than the 336 cm FL (11.0 ft) maximum size fish published in the literature. Both of these fish were 338 cm FL (11.1 ft) females caught by sport fishermen south of Montauk Point, New York. One was landed in July of 1977 and weighed 471 kg (1,039 lbs). The other was caught in August of 1979 and weighed 382 kg (841 lbs). The largest scalloped hammerhead (243 cm FL, 8.0 ft; 166 kg, 365 lbs) was measured at a sportfishing tournament in July of 1985 and was caught 36 miles southeast of Highlands, New Jersey.

The lower ends of the length-weight curves also compare well with published estimates of size at birth for each species of shark. Pratt and Casey (1990) give maximum size at birth in TL for 11 of the 13 species of sharks sampled here and all except the thresher shark are within 40 cm (16 in) of those sizes. Our smallest thresher shark is 64 cm (25 in) larger than the reported birth size.

All of the larger fish were female with the exception of the white and the blue shark (Tables 1 and 2). The larger size attained by females is typical of sharks in general (Pratt and Casey, 1983; Hoenig and Gruber, 1990), and thus larger female blue and white sharks very likely occur outside of our western North Atlantic sampling area which only covers a small portion of their extensive oceanic range.

Blue sharks have a complex life history cycle and large females are infrequent visitors to the continental shelf and slope waters off North America. The shelf area serves as a mating ground where the catch consists primarily of juvenile males and females, subadult females, and adult males (Casey, 1985). The occurrence of considerable numbers of the larger females (>240 cm, 7.9 ft) is rare in the western North Atlantic, but numerous large gravid females have been reported in the eastern Atlantic from the Mediterranean Sea and around the Madeira and Canary Islands (Aasen, 1966; Pratt, 1979).

The white shark distribution pattern may be as complex as that of the blue shark but is more obscure. Although no mature female white sharks were examined, adult females have been reported from the western North Atlantic. Casey and Pratt (1985) describe a 483 cm FL (15.8 ft) fish harpooned off Montauk, New York, in 1964 and a 526 cm FL (17.3 ft) female which became entangled in a gill net near Prince Edward Island, Canada, in July, 1983. Elsewhere, large female white sharks have been reported in the Gulf of Maine (Bigelow and Schroeder, 1948; Skud, 1962), in the Mediterranean Sea (Ellis and McCosker, 1991) and off the west coast of Florida (Springer, 1939). Catching a large white shark of either sex, however, is an uncommon event. White sharks are likely to occur singly or as scattered, unassociated individuals over vast geographical areas (Casey and Pratt, 1985). Owing to their immense size, they are difficult to catch and are capable of breaking free of most conventional fishing gear.

Factors affecting weight

Weights of individual sharks of the same length may differ depending on several factors, including the amount of stomach contents, the stage of maturity, the liver weight, and the condition of the shark. The effects of stomach contents on the weight of the fish were minimal in this study. In many instances, the sharks everted their stomachs prior to being weighed. For the bigger fish, when large amounts of food were present, the weight of the stomach contents was subtracted to obtain the total body weight. Since not every shark was examined internally, some pregnant fish may have been inadvertently included in the database.

Differences in body weight also reflect differences in the condition of an individual. Sharks have large livers which store high energy, fatty acids for buoyancy and for use as a food reserve (Bone and Roberts, 1969; Oguri, 1990). The weight of this organ is thus a good indicator of the health or condition of a shark (Springer, 1960; Cliff et al., 1989). The liver is the largest organ by weight in the shark and can vary from 2–24% of the body weight depending on the species (Cliff et al., 1989; Winner, 1990). Variation in the liver size accounted for the majority of the weight difference in individuals of the same species with corresponding lengths. In six of the eight largest white sharks, the liver weights ranged from 14.6–22.7% of the body weight (hepatosomatic index, HSI) (Table 3). The 458 cm (15.0 ft) FL white shark

in this group had the lowest HSI value (14.6%) although it was longer than four heavier fish. The difference in body weight between the 458 cm (15.0 ft) FL and the 463 cm (15.2 ft) FL fish is 360 kg (793 lbs). When the weights of sharks without livers are compared, the difference between these two fish is reduced to 239 kg (526 lbs). Thus, eliminating the liver accounted for 34% of the weight difference between these two sharks of similar length. The same is true for large mako sharks. The HSI for one of the longest mako sharks (338 cm, 11.1 ft FL; 382 kg, 841 lbs) was 5.4% as contrasted with 17.9% for the 323 cm (10.6 ft) FL fish weighing 490 kg (1,080 lbs). When the two makos are compared without livers, the difference in body weights is reduced from 108 kg (239 lbs) to 41 kg (91 lbs).

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Table 3

Fork length, body and liver weight, and hepatosomatic index (HSI) for large white sharks, *Carcharodon carcharias*, from the western North Atlantic.

Fork length (cm)	Whole body weight (kg)	Liver weight (kg)	HSI (%)
463	1,245	250	20.1
458	885	129	14.6
446	1,261	206	16.3
444	1,320	232	17.6
437	1,084	246	22.7
425	941	179	19.0

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An analysis of the length-weight relationship of larval fish: limitations of the general allometric model

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Substantial morphological and physiological changes occur during the early ontogeny of fish. After hatching, both shape and size undergo significant alterations in association with yolk absorption and a subsequent increase in musculature. In fish, the larval stage generally consists of a period of rapid growth, which can vary substantially in duration within and among species (Sinclair and Tremblay, 1985, Ware and Lambert, 1985; Houde, 1989; Pepin, 1991). Length and weight may increase by factors of approximately 10 and 1,000, respectively, over a time interval that often spans less than 10% of a species' life time. Such high development rates are associated with high metabolic rates (Giguère et al., 1989) which can lead to substantial variation in condition as a result of fluctuations in food availability (Houde and Schekter, 1980; Werner and Blaxter, 1980). Studies of variations in growth characteristics and condition have been an important keystone in understanding early life history survival (Houde, 1987).

Changes in length or weight through time have been used to assess the general growth rates of populations. Most often, the model used to describe length-weight relationships of fish larvae is a general allometric function

$$W = aL^b, \qquad (1a)$$

where W is weight, L is length, and a and b are constants. A logarithmic transformation of Equation 1 leads to a linear relationship

$$\log W = \log a + b \log L \qquad (1b)$$

that can be estimated with minimal computing power, by using least squares, and for which the fit is generally strong (e.g. Laurence, 1978). The latter point may seem reason enough to assume that a general allometric model is an adequate description of the data. However, some inferences derived from this type of information concern variation in condition. For example, deviations from a general length-weight relationship (e.g. Fulton's (1911) index of condition [$K=W/L^3$, where W and L are the weight and length of individuals]) have been used to describe the relative state of health of individuals (e.g. Westernhagen and Rosenthal, 1981; Checkley, 1984; Ciechomski et al., 1986; Harris et al., 1986; Frank and McRuer, 1989; Drolet et al., 1991). It is therefore necessary to ensure that the model used to describe the length-weight relationship not only provides a strong fit to the data but also that it accurately describes the functional form of that relationship.

Zweifel and Lasker (1976) suggest that changes in length or weight of fish larvae through time can be described by a Gompertz model

$$L = L_0 e^{K(1-e^{-\alpha t})} \qquad (2a)$$

$$W = W_0 e^{K'(1-e^{-\alpha' t})}, \qquad (2b)$$

where L_0 and W_0 are the length and weight at time t=0, K and K' are the specific growth rates at time t=0, and α and α' are the rates of decay in growth rates. Only when $\alpha=\alpha'$ does the length-weight relationship reduce to the form shown in Equation 1b. Otherwise, the logarithmic length-weight relationship will exhibit a degree of nonlinearity (Laird et al., 1968; Zweifel and Lasker, 1976). Barton and Laird (1969) noted that fitting the general allometric model is relatively insensitive to slight departures from the true time relations for growth in length and weight (i.e. $\alpha\neq\alpha'$). Consequently, a general allometric relationship (Eq. 1b), with only two parameters, may be considered to provide an adequate description to the data, despite the fact that a more complex model (e.g. a Gompertz length-weight relationship) better describes the patterns of growth in length and weight. Although the importance of such subtle differences may appear to be minor, consistent departures from a general allometric model can lead to significant bias in predicting or interpreting weight at length. This can be particularly important when trying to model growth during the early life history (e.g. Rose and Cowan, 1993) or in estimating size-dependent metabolic processes (e.g. Checkley, 1984; Kiørboe, 1989; Giguère et al., 1989). Furthermore, there is potential for inaccurate inferences in instances where condition is being studied (e.g. W/L^3). Westernhagen and Rosenthal (1981) and Ciechomski et al. (1986) noted a decrease in Fulton's condition index after hatch, followed by an increase some time after first feeding. Although this pattern may be due to food deprivation, it can also arise because of a developmentally determined nonlinear allometric length-weight relationship (i.e $\alpha\neq\alpha'$).

In this study, I present evidence that, despite a strong fit to a general allometric length-weight rela-

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tionship (Eq. 1b), the use of such a model may be inappropriate for the study of fish larvae.

Materials and methods

Ichthyoplankton samples were obtained during two surveys of Conception Bay (47°45'N, 53°00'W), Newfoundland, Canada. Cruises were held during the periods from 27 June 1990 to 15 July 1990 and from 25 September 1990 to 30 September 1990. Sampling was conducted during daylight hours (0700–1900) with a 4-m^2 Tucker trawl equipped with panels of 1,000-, 570-, and 333-μm mesh nitex. At each station, a single oblique tow of approximately 15 minutes was made at 2 knots (1 $m \cdot s^{-1}$). The net was lowered to 40 m at a rate of approximately 0.25 $m \cdot s^{-1}$ and retrieved at 0.064 $m \cdot s^{-1}$. After the net was washed, samples were preserved in 2% buffered formaldehyde. Within three to six months after collection, ichthyoplankton were sorted and identified to species or to the lowest taxonomic level possible (Atlantic Reference Centre, Huntsman Marine Science Centre, St. Andrews, New Brunswick, Canada). Sorted specimens were stored in 95% ethanol for approximately three years. Sixteen species were used in this analysis. For each species, 20 to 80 larvae were measured and weighted, depending on abundance, general condition, and the range of sizes available.

Larvae were measured to the nearest 0.1 mm by using an image analysis system mounted on a Wild M3C dissecting microscope that was equipped with an S-type mount fitted with a 0.5× objective. Each larva was placed on a preweighted aluminium sheet and dried in an oven at 65°Celsius. After 24 hours, larvae were transferred to a desiccator for no less than 1 hour and no more than 3 hours. Each larva was weighted to the nearest 0.1 μg by using a Cahn–31 microbalance.

Length-weight relationships of $\log_{10}$-transformed data were evaluated by using two models. In the first instance, a general allometric model of the form

$$\log W = a' + b \log L + \varepsilon, \quad (3)$$

where W and L are weight and length, a' is equal to log(a) from Equation 1b, b is the exponent in Equation 1, and ε is error, was fit by using a general linear algorithm (procedure GLM, SAS, 1988). In the second case, a model of the form

$$\log W = a'' + b''(\log L)^{c''} + \varepsilon, \quad (4)$$

where W and L are weight and length, respectively, and a", b", and c" are constants, and ε is error, was fit by using a nonlinear iterative least squares algorithm (procedure NLIN, SAS, 1988). When the value of c" is not significantly different from 1, Equation 4 reduces to the general allometric model (Eq. 3). Equation 3 is a well-recognized and general functional form used in the estimation of length-weight relationships (Ricker, 1975; Zweifel and Lasker, 1976; Cone, 1989). Equation 4 is not a common form (e.g. a Gompertz model; Laird et al., 1968; Zweifel and Lasker, 1976) but represents a first-order increase in complexity over the general allometric model (Eq. 3). I chose not to use the more complex Gompertz length-weight model, which has been used in other studies (e.g. McGurk, 1987) for two reasons. First, a Gompertz model is best suited for data that cover the entire range of sizes for a developmental stage. Such data were not available from the surveys conducted as part of this study. Second, preliminary analysis revealed that Equation 4 is numerically more stable than the Gompertz model for the data used in this study.

To establish whether there was a significant departure from loglinearity (Eq. 3), a second order polynomial was fit to the residuals ($Y = a + bX + cX^2$, where Y are the residuals and X is the log-transformed length). If the second order coefficient (c) is not significantly different from 0, then there is no departure from loglinearity and all other terms will also not differ from 0.

Results

Despite the wide variation in the range of information available for each species considered in this analysis (Table 1), the relationship between length and weight appears to be strong in all instances (Fig. 1). Analysis with the general linear allometric model (Eq. 3) shows a very highly significant fit for all species (Table 1). Evidence of a nonlinearity in the allometric relationship between length and weight is apparent in an analysis of the residuals from the general allometric model (Eq. 3). In 10 of 16 species, the second-order polynomial fit to the residuals in relation to log-transformed length was significant (Table 2).

The value of c" (Eq. 4) was significantly different from 1 for 11 of the 16 species used in this study (Table 3). In the case of *Ammodytes* sp., the value of c" indicates an asymptotic relationship. An exponential length-weight relationship of the log-transformed data is indicated in the 10 other species with values of c" significantly different from 1. Fitting Equation 4 to the data resulted in a decrease in residual sum of squares in 14 of the 16 species which averaged

Table 1

General characteristics of the length data for the 16 species used in this study. Three groups could only be identified to genus. Parameters of the general allometric model (Eq. 3) were estimated for the 16 species used in this analysis. The r^2, and the number of observations (n) are also provided. All relationships are significant at $P<0.001$. Values in brackets represent the standard error of the estimated parameters.

Species	Range in length (mm)	Median length (mm)	Intercept (a')	Slope (b)	r^2	n
Ammodytes sp.	7.3–28.6	18.0	–3.41	2.97 (0.14)	0.93	37
Aspidophoroides monopterygius	6.4–24.9	13.1	–2.83	2.49 (0.20)	0.89	20
Clupea harengus	6.8–28.9	9.7	–4.19	3.45 (0.11)	0.97	34
Gadus morhua	2.2–12.2	4.8	–2.68	2.65 (0.12)	0.92	40
Glyptocephalus cynoglossus	5.6–37.6	10.6	–3.12	2.63 (0.18)	0.85	40
Hippoglossoides platessoides	2.7–24.5	7.7	–3.53	3.42 (0.10)	0.94	80
Liparis atlanticus	2.8–7.5	4.0	–2.85	3.15 (0.10)	0.98	20
Liparis gibbus	5.3–12.5	7.5	–3.01	3.13 (0.20)	0.93	20
Lumpenus sp.	9.9–28.8	16.2	–3.11	2.70 (0.10)	0.95	36
Mallotus villosus	4.2–24.0	8.5	–3.55	2.79 (0.06)	0.98	40
Pleuronectes americanus	2.1–6.2	3.8	–3.08	3.11 (0.16)	0.91	40
Pleuronectes ferrugineus	1.9–14.4	3.6	–3.35	3.54 (0.09)	0.97	40
Sebastes sp.	4.4–9.5	7.5	–2.39	2.27 (0.19)	0.76	46
Stichaeus punctatus	8.8–22.0	13.5	–3.96	3.71 (0.13)	0.95	40
Tautogolabrus adspersus	3.3–9.3	5.3	–3.73	4.22 (0.25)	0.90	59
Ulvaria subbifurcata	4.5–13.3	6.4	–3.23	3.13 (0.13)	0.92	50

19% (range: 2–47%). In the cases of *Lumpenus* sp. and *Sebastes* sp., the use of Equation 4 resulted in an increase in the residual sum of squares of 15% and 8%, respectively.

Although lengths and weights were not corrected for shrinkage, Hay's (1984) and Johnston and Mathias' (1993) studies show that proportional weight loss due to preservation is greater than shrinkage in length and is proportionally greater as size of larvae decreases. If correction factors had been available, the net result would have been to increase the departure from log-linearity.

Discussion

Despite the apparently strong fit to the general allometric relationship between length and weight of larval fish, this analysis clearly shows a consistent nonlinear pattern in the log-transformed data. Although the curvature appears subtle, incorrect assumptions about model form may cause bias in the prediction of weights from lengths as well as in the interpretation of size-related variations in the physical condition of fish larvae. The significance of such inaccuracies may be minor for some aspects of the early life history (e.g. range of weights based on a mean functional relationship [Houde, 1989]) but may become more important in the calculation of metabolic processes (e.g. Checkley, 1984; Kiørboe, 1989; Giguère et al., 1989). Furthermore, the interpretation of gross measures of condition could also be influenced by the nonlinear nature of the length-weight relationship of larval fish. For example, calculation of Fulton's K, an index of condition, relies on the assumption that the general length-weight relationship of organisms follows a linear logarithmic function, specifically an isometric one (i.e. b=3). Increases or decreases in this coefficient are believed to be related to variations in condition. Not only is the general isometric assumption violated in 11 of 16 species (Table 1), but also that of linearity (Table 3). The significance of a departure from an isometric relationship in the interpretation of measures of condition relative to changes in body shape has been discussed in general terms by Cone (1989) and in relation to larval fish by Laurence (1978). As Ricker (1975) points out, Fulton's K can be used only to contrast individuals of approximately the same length. However, this is only true if the logarithmic length-weight relationship is linear and may not be appropriate when there is a significant departure from linearity, as shown in this study.

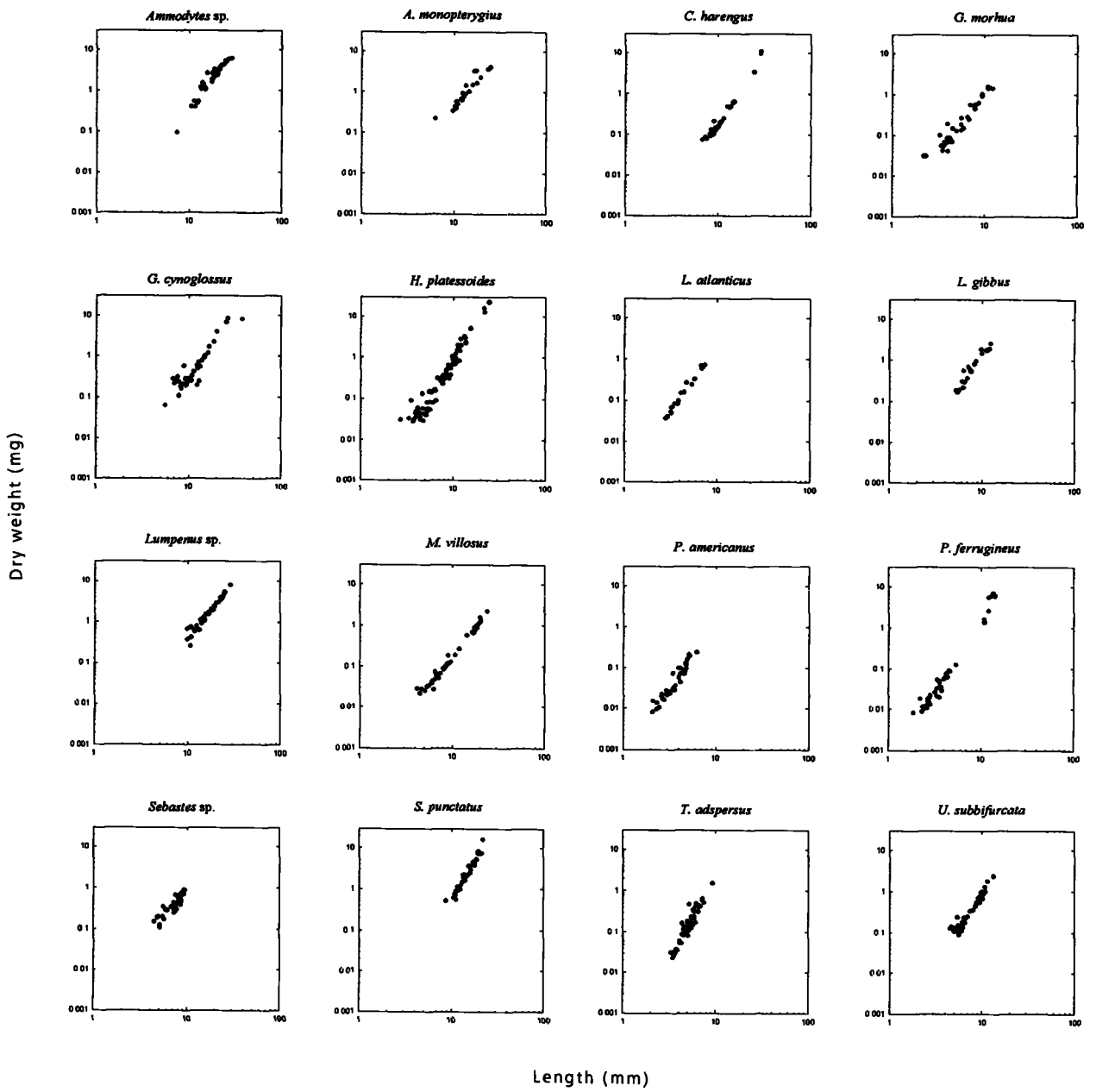

Figure 1

Logarithmic plot of the length-weight data for the 16 species considered in this analysis. Each point represents an individual larva.

Ontogenic development is characterized by notable changes in functional morphology that impact motility, foraging ability, and predator avoidance (Blaxter, 1986; Neilson et al., 1986; Olla and Davis, 1992). Developmental changes in body form or composition can result in differences in proportional growth in terms of length and weight and thus lead to a nonlinear allometric length-weight relationship. Alternatively, nonlinear variation in the length-weight relationship could be considered as evidence of changes in condition induced by some degree of food deprivation within a population of larval fish (e.g. Grover and Olla, 1986; Frank and McRuer, 1989; Drolet et al., 1991). Under such circumstances, varia-

Table 2

Estimated parameters of a second-order polynomial ($Y = a + bX + cX^2$) fit to the residuals (Y) from the general allometric model, estimated for the entire data set, in relation to log-transformed length (X). The right-most column provides the significance level of a two-tailed t-test evaluating the hypothesis that c=0.

Species	a	b	c	P
Ammodytes sp.	–3.21	5.45	–2.28	0.003
Aspidophoroides monopterygius	0.79	–1.43	0.63	0.54
Clupea harengus	2.79	–4.99	2.17	0.001
Gadus morhua	0.92	–22.62	1.74	0.003
Glyptocephalus cynoglossus	1.96	–3.56	1.57	0.03
Hippoglossoides platessoides	1.19	–2.83	1.59	0.001
Liparis atlanticus	–0.48	1.50	–1.13	0.23
Liparis gibbus	–2.30	5.11	–2.80	0.15
Lumpenus sp.	1.48	–2.47	1.02	0.26
Mallotus villosus	1.06	–2.19	1.08	0.001
Pleuronectes americanus	0.66	–2.56	2.37	0.05
Pleuronectes ferrugineus	0.80	–2.47	1.67	0.001
Sebastes sp.	3.70	–9.07	5.49	0.01
Stichaeus punctatus	2.57	–4.47	1.92	0.14
Tautogolabrus adspersus	–0.79	2.26	–1.58	0.26
Ulvaria subbifurcata	3.93	–9.16	5.23	0.001

Table 3

Parameter estimates for the nonlinear logarithmic length-weight relationship (Eq. 4). Values in brackets represent the asymptotic standard error of the estimated parameters. An asterisk next to the parameter in column c" denotes that the exponent is significantly different from 1 (two-tailed t-test). The right-most column provides the percent change in residual sum of squares relative to the fit provided by Equation 3. A positive value indicates an increase in the residual sum of squares whereas a negative value represents a decrease in the residual sum of squares.

Species	a"	b"	c"	Percent
Ammodytes sp.	–18.4	18.0	0.19 (0.05) *	–22
Aspidophoroides monopterygius	–1.84	1.52	1.55 (0.92)	–3
Clupea harengus	–1.92	1.15	2.44 (0.29) *	–47
Gadus morhua	–1.78	1.80	1.94 (0.33) *	–23
Glyptocephalus cynoglossus	–1.53	1.02	2.22 (0.59) *	–11
Hippoglossoides platessoides	–2.27	2.11	1.78 (0.19) *	–21
Liparis atlanticus	–4.66	4.87	0.53 (0.37)	–9
Liparis gibbus	–30.6	30.7	0.09 (0.51)	–9
Lumpenus sp.	–1.56	1.18	1.91 (0.81)	15
Mallotus villosus	–2.39	1.58	1.76 (0.23) *	–25
Pleuronectes americanus	–2.37	2.83	1.80 (0.39) *	–9
Pleuronectes ferrugineus	–2.42	2.58	1.66 (0.16) *	–47
Sebastes sp.	–0.99	0.93	3.80 (1.28) *	8
Stichaeus punctatus	–1.65	1.42	2.18 (0.59) *	–6
Tautogolabrus adspersus	–8.02	8.24	0.40 (0.51)	–2
Ulvaria subbifurcata	–1.35	1.26	3.41 (0.60) *	–29

tion in condition, or the scatter about the length-weight relationship, should be greatest at the developmental stage most vulnerable to food deprivation (i.e. yolk absorption). However, the pattern of scatter about the length-weight relationship shows little evidence of a consistent pattern associated with that stage of the early life history (Fig. 1). It is possible that the majority of larvae undergo a degree of starvation associated with the period of yolk absorption (e.g. Theilacker, 1986; Drolet et al., 1991; Marguiles, 1993), which would result in a uniform pattern in the deviation from a general allometric length-weight relationship. However, there is also evidence that suggests that only a limited fraction of a larval fish population suffers from substantial food deprivation (O'Connell, 1981; Canino et al., 1991; McGurk et al., 1992). The consistent nonlinear pattern in the length-weight relationship among a suite of species with different life histories, which could result in substantial differences in vulnerability to environmental factors (Miller et al., 1988; Pepin, 1991), suggests that developmental processes in the early ontogeny of fishes are important factors governing the form of this relationship. The degree of curvature in the logarithmic relationship (c": Eq. 4) is not significantly correlated with size at hatch (r=0.45, P>0.05, n=14; Fig. 2), which may be a measure of vulnerability to starvation (Miller et al., 1988; but see Pepin, 1991). In fact, the positive trend is opposite that expected on the premise that species that produce small larvae should be more vulnerable to starvation.

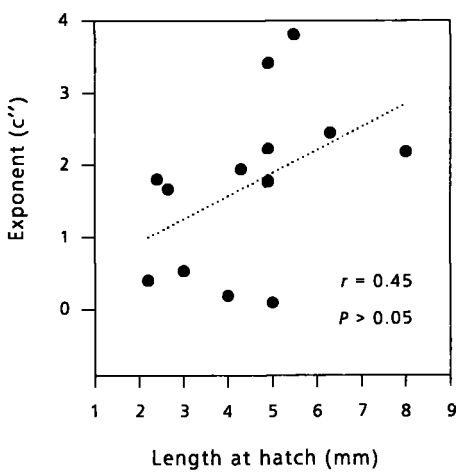

Figure 2

The value of c" in relation to the size at hatch for 14 of the 16 species used in this study. The value of c" provides a measure of the curvature in the logarithmic length-weight relationship. Data on size at hatch were obtained from general reference sources detailing fish life history characteristics (Fahay, 1983; Scott and Scott, 1988). Data were unavailable for *Aspidophoroides monopterygius* and *Lumpenus* sp.

Whether physiological processes rather than developmental constraints result in the nonlinear logarithmic length-weight relationship described in this study is uncertain. There are a number of approaches that may be indicative of the physiological condition of larval fish (e.g. Theilacker, 1986; Clemmensen, 1988; Fraser, 1989), but they may never the less be highly correlated with morphometric indices of condition (e.g. Theilacker, 1978; Harris et al., 1986; Setzler-Hamilton et al., 1987). Furthermore, there may remain considerable uncertainty about the interpretation of variation in such condition indices of larval fish (e.g. Bergeron and Boulhic, 1994). To interpret variation in length-weight relationships correctly, it is essential that thorough studies be conducted to establish the proper functional form and how this may vary under different feeding conditions.

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Early life history of black sea bass, *Centropristis striata*, in the mid-Atlantic Bight and a New Jersey estuary*

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Abstract.—This study focuses on composite field collections and in situ observations from the mid-Atlantic Bight continental shelf and a New Jersey estuary in order to elucidate aspects of the early life history of age 0+ black sea bass, *Centropristis striata*. Spawning in the mid-Atlantic Bight is prolonged (April through November, with a peak between June and September) and is most intense in the southern portion of this range. Between 1977 and 1987, larvae were collected between Cape Hatteras, North Carolina, and Long Island, New York. In New Jersey coastal waters larvae first appear in July but can occur into November. Recently settled individuals (15–24 mm total length [TL]) were collected at an inner continental shelf site and an adjacent estuary from July through October. By fall, fishes from these areas were 18–91 mm TL, and many had moved offshore from New Jersey estuarine waters and other estuaries to inner continental shelf waters between southern Massachusetts and Cape Hatteras. Subsequently, they continued to move offshore and during their first winter, they were concentrated near the shelf or slope break in the southern portion of the mid-Atlantic Bight. Some age 0+ individuals moved back into New Jersey estuaries in early spring, at sizes approximating those of the previous fall (50–96 mm TL). Thus, black sea bass reach relatively small sizes after 12 months of growth partly because little or no growth occurs during their first winter. This year class reached sizes of 78–175 mm TL by midsummer and 134–225 mm TL by the following fall.

During summer, benthic juveniles were collected or observed primarily in a variety of structured habitats. On the inner continental shelf they were found among accumulations of surfclam *Spisula solidissima* valves or among smaller pieces of shell, and occasionally in burrows in exposed clay. While in the estuary, they were collected from areas with a variety of structured habitats, such as shell accumulations in marsh creeks and peat banks. The data suggest that during their first summer, black sea bass have similar densities and growth rates in estuarine and inner continental shelf habitats, and thus both areas serve as nurseries.

Manuscript accepted 5 January 1995.
Fishery Bulletin 93:429–445 (1995).

The black sea bass, *Centropristis striata*, is an important component of recreational and commercial fisheries along much of the east coast of the United States (U.S. Dep. Commerce, 1993). Despite its importance we know relatively little of the early life history of this species (Kendall, 1972). The best efforts to date are studies on larval distribution (Cowen et al., 1993), with comments on presumed estuarine nursery areas (Kendall, 1972), and studies on seasonal distribution and size attained at different seasons (Musick and Mercer, 1977) as well as at the end of the first year (Briggs, 1978). Faunal surveys in the mid-Atlantic Bight from Massachusetts (Lux and Nichy, 1971), New York (Perlmutter, 1939), New Jersey (Bean, 1888; Nichols and Breder, 1927), Maryland (Schwartz, 1961, 1964a), and Virginia (Hildebrand and Schroeder, 1928) have also contributed to our understanding of the seasonal distribution of juveniles. A general summary of the biology, population size, and fisheries is provided by Kendall and Mercer (1982).

In this study we limit our observations to black sea bass in the mid-Atlantic Bight, the area between Cape Cod and Cape Hatteras, because this population is considered a separate stock from those south of Cape Hatteras, North Carolina (Mercer, 1978; but see Bowen and Avise, 1990). This interpretation appears to be supported by studies that show movements inshore and north in spring and offshore and south in the fall within the mid-Atlantic Bight (Pearson, 1932; Nesbitt and Neville, 1935; Lavenda, 1949; June and Reintjes, 1957; Frame and Pearce, 1973) but only localized movements in the South Atlantic Bight (Parker, 1990; Low and Waltz, 1991). Recently, variations in meristic and morphometric characteristics have led to the suggestion that stock structure may not be homogenous within the mid-Atlantic Bight (Shepherd, 1991).

The objectives of this study are to elucidate aspects of the reproduc-

* Contribution 94-30 of the Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ.

tive periodicity, seasonal distribution, growth, and nursery habitats during the first year (age 0+) of black sea bass. We used composite data from a variety of field collections for larvae and juveniles, in situ observations on the mid-Atlantic Bight continental shelf, and intensive collections from a New Jersey estuary.

Materials and methods

Data sources for planktonic larvae and benthic juveniles (age 0+) from the mid-Atlantic Bight (Fig. 1) and southern New Jersey (Fig. 2) are summarized in Table 1. Larval sampling was conducted as part of the National Marine Fisheries Service (NMFS) Marine Resources Monitoring, Assessment, and Prediction (MARMAP) surveys (Sherman, 1980, 1986). Further details of the sampling methodology are provided by Sibunka and Silverman (1984, 1989) and Morse et al. (1987). Larval distribution and abundance are displayed as average number of larvae per 10 m^2 of sea surface calculated by month for the mid-Atlantic Bight study area for 1977–87. Larvae were also collected as part of a characterization of the Long-term Ecosystem Observatory (LEO-15) around Beach Haven Ridge off southern New Jersey (von Alt and Grassle, 1992) (Fig. 2). Samples were collected with an opening and closing Tucker trawl (1-m^2, 505-μ mesh) with multiple codends that were fished in a step-oblique manner from the surface to near bottom for 7.5–15 minutes. The mouth of the net was equipped with a flowmeter to determine the volume of water sampled.

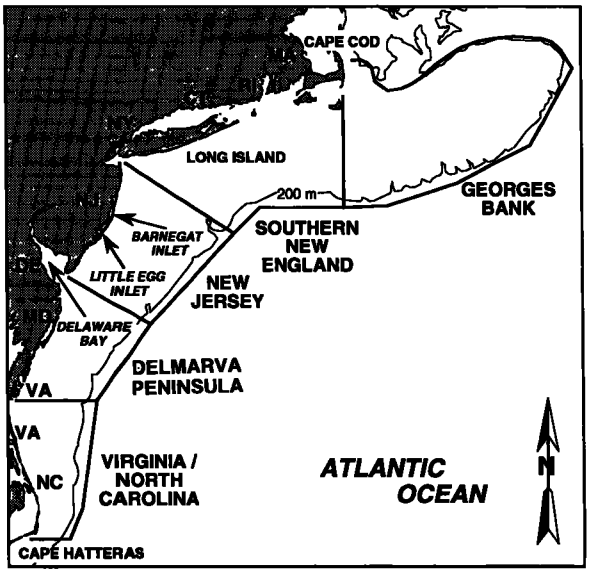

Figure 1

Collection sites for larval and juvenile black sea bass, *Centropristis striata*, in the mid-Atlantic Bight.

Age 0+ juveniles, as determined from length frequencies, were collected from the mid-Atlantic Bight continental shelf during the NMFS-Northeast Fisheries Science Center (NEFSC) bottom trawl surveys. Samples were collected at stratified random stations between Cape Hatteras, North Carolina, and Nova Scotia on the continental shelf. Details of the sample distribution and technique are provided by Azarovitz (1981). Seasonal sampling occurred during fall (September–October), winter (January–February) and spring (March–April). After additional depths were stratified, random sampling occurred seasonally with otter trawls in inshore continental shelf waters off Massachusetts by the Massachusetts Division of Marine Fisheries (MADMF) (Howe, 1989) and off New Jersey by the New Jersey Department of Environmental Protection (NJDEP) (Byrne[1]; Byrne et

[1] Byrne, D. M. 1988. Inventory of New Jersey's coastal waters. New Jersey Division of Fish, Game, and Wildl., Trenton, NJ, 3 p.

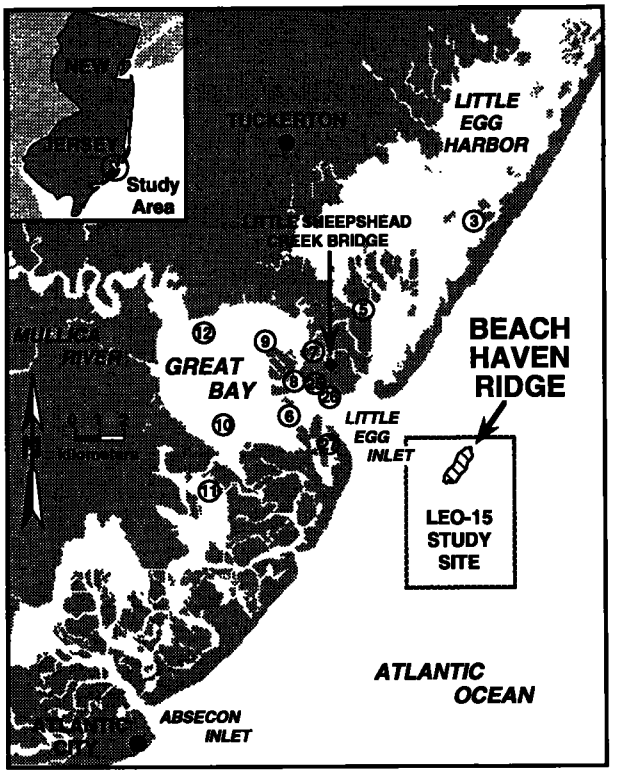

Figure 2

Collection sites for larval and juvenile black sea bass, *Centropristis striata*, from inner continental shelf and estuarine study areas off southern New Jersey. Circled numbers indicate otter trawl sampling sites; number 25, however, is the location of trapping sites at Rutgers University Marine Field Station. Little Sheepshead Creek is the location of the plankton sampling site. LEO-15 = Long-term Ecosystem Observatory.

Table 1

Summary of data sources for larval and juvenile (age 0+) black sea bass, *Centropristis striata,* examined during this study. See Figures 1 and 2 for study areas.

Study area	Sampling method	Sampling period	Sampling depths	Frequency of sampling	Sources
Great Bay–Little Egg Harbor, New Jersey	Plankton net (1 m, 3-mm mesh)	1989–91	0–4 m,	Weekly	Witting, Able, and Fahay, unpubl. data
	Otter trawl (4.9 m, 6-mm mesh codend)	1989–91	1–8 m	Monthly	Szedlmayer and Able[1]
	Traps (6-mm mesh)	1991–92	1-3 m	Daily-weekly	This study
Vicinity of Beach Haven Ridge, off southern New Jersey	Tucker trawl (1 m, 1-mm mesh)	1991–92	0–15.5 m	Bimonthly-monthly	This study
	Beam trawl (2 m, 6-mm mesh)	1991–92	6–23.5 m	Bimonthly-monthly	This study
	Otter trawls (7.6 m, 13-mm mesh codend)	1974	2–19 m	Monthly	Milstein and Thomas, 1977
	In situ observations with SCUBA	1992	10–20 m	Variable during summer	This study
Mid-Atlantic Bight	Otter trawl (10.4 m, 12.5-mm mesh)	1982–90	9–365 m	Seasonal	Azarovitz, 1981
	Bongo plankton nets (61 cm, 505-μ mesh)	1977–87	8–1,500 m	Monthly-bimonthly	Sibunka and Silverman, 1984
Nearshore off Massachusetts	Otter trawl (15 m, 12-mm mesh codend)	1982–90	7–147 m	Seasonal	Howe, 1989
Nearshore off New Jersey	Otter trawl (30 m, 6-mm mesh codend)	1988–91	5–27 m	Seasonal	Byrne (Footnotes 1 and 2 in the text)

[1] Szedlmayer, S. T., and K. W. Able. Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey estuary. In review.

al.[2]). More temporally intensive sampling with beam trawls (2-m, 6-mm mesh) was conducted outside Little Egg Inlet in southern New Jersey in the vicinity of Beach Haven Ridge at the LEO-15 site (Fig. 2). Additional length-frequency information was adapted from an environmental impact study in 1974 at this site (Table 1). In the Great Bay-Little Egg Harbor estuarine system (Fig. 2), juveniles were collected with otter and beam trawls and traps over several years in a variety of habitats and depths (Table 1). For all samples, larval size was recorded as notochord length (NL) or standard length (SL), and juveniles as total length (TL).

Visual observations and video records of juveniles and available habitat at several locations in the study area in inner continental shelf waters were made during 1991 and 1992 (Table 1). Near Beach Haven Ridge, 30-m transects were made across a variety of habitat types during 1992.

[2] Byrne, D. M., A. W. Burnett, and D. J. Vareha. 1990. Inventory of New Jersey coastal waters. New Jersey Div. Fish, Game, and Wildl., Trenton, NJ, 39 p.

Results

Temporal and spatial distribution of larvae

Black sea bass reproduction throughout the mid-Atlantic Bight occurs over a fairly prolonged period on the basis of occurrence of larvae from April through November (Fig. 3; Table 2). It appears that reproduction progresses seasonally from south to north on the basis of collections off Virginia and North Carolina as early as April, and off New Jersey and Long Island beginning in July (Fig. 3). The smallest larvae (2–3 mm NL) occurred off New Jersey from July through October (Table 3). At Beach Haven Ridge off southern New Jersey, larvae (4–12 mm TL) were collected in late July and early August.

Larvae occurred in samples from April through November and into January in the mid-Atlantic Bight, although their occurrence varied with geographic location (Table 2; Fig. 3). For all regions, the peak in abundance was from July through September or October (Table 2). The largest larvae collected

Table 2

Abundance of black sea bass, *Centropristis striata*, larvae in the mid-Atlantic Bight expressed as no./10 m^2 of sea surface by month and area during 1977–87. Areas are indicated in Figure 1.

Area	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan
Georges Bank									6		
Southern New England				4	22	88	42				
New Jersey			7		110	370	150	216	5		
Delmarva				79	376	1672	670	15	8		
Virginia/North Carolina		126	76	100	534	1561	502	53	16		20

Table 3

Monthly totals of black sea bass, *Centropristis striata*, larvae by length collected over the continental shelf off New Jersey during 1977–87. Total number of stations refers to collections containing black sea bass larvae.

		Length (mm NL)									
Month	Total number of stations	2	3	4	5	6	7	8	9	10	Total number of larvae
April	—										
May	1								1		1
June	—										
July	12		3	5	7	3		1			19
August	31	15	66	36	18	13	3	1			152
September	18	2	22	13	6	5	3			1	52
October	13	3	23	12	11	10	2				61
November	2						1	1			2
Totals	77	20	114	66	42	31	9	3	1	1	287

were 8–10 mm NL but most were <8 mm NL. The larvae were distributed across much of the mid-Atlantic Bight continental shelf; the greatest abundance occurred between Cape Hatteras and Delaware Bay (Fig. 3). At the northern limit of occurrence, off New Jersey and Long Island, larvae were most abundant on the inner half of the continental shelf. Only a few larvae were found north and east of the eastern end of Long Island (July, Fig. 3). A single 6.4-mm larva was collected on Georges Bank in November 1982. During weekly night-time sampling in the Great Bay estuary at a site just inside Little Egg Inlet, New Jersey (Table 1; Fig. 2), larvae were never collected during the period from 1989 to 1991 (Witting et al.[3]).

[3] Witting, D. A., K. W. Able, and M. P. Fahay. Marine Field Station, Institute of Marine and Coastal Science, Rutgers Univ., Tuckerton, NJ 08087. Unpubl. data.

Temporal and spatial distribution of benthic juveniles

Benthic age 0+ individuals smaller than 25 mm TL were collected from both inner continental shelf (Beach Haven Ridge) and estuarine (Great Bay) habitats from July through October (Figs. 4–6). Collections from these areas indicate that two length modes occurred during the summer and fall of 1992. The first mode appeared in late July and could be followed through the fall when the fish have reached lengths >50 mm TL. The second mode appeared at the inner shelf site in late September at sizes >10 mm TL. This group reached an apparent minimum size of 30 mm TL by the fall (Fig. 4).

Movement out of the estuary in the fall is indicated by the reduction in the number of age 0+ individuals by November-December (Figs. 4–6). This same pattern of movement out of the estuary also was reflected in the catch per unit of effort (CPUE)

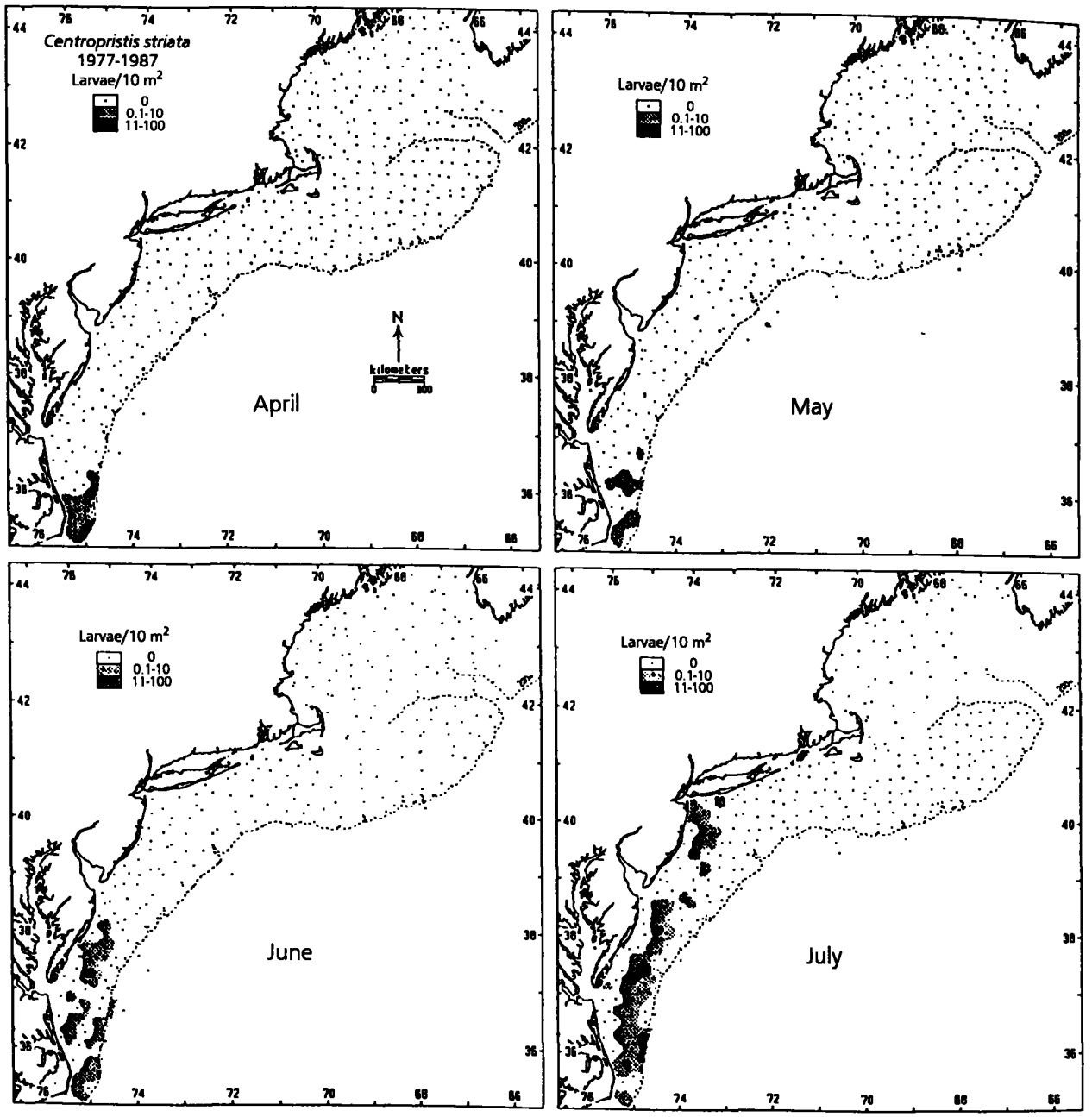

Figure 3

Monthly distribution and abundance of black sea bass, *Centropristis striata*, larvae in the mid-Atlantic Bight based on NMFS-MARMAP surveys during 1977–87.

from trap collections in the Rutgers University Marine Field Station (RUMFS) boat basin in 1992 (Fig. 7). At the same time, catch rates increased dramatically, compared with those for summer, on the inner continental shelf off New Jersey (Fig. 8), owing, presumably, to the addition of individuals moving from the estuary as well as to recently settled fishes. Age 0+ individuals were absent in the winter. Catches at Beach Haven Ridge were zero from December through February and few individuals were caught in March (Fig. 7) in 1991 and 1992. Catches increased in April or May, or during both months, depending on the year, and then decreased through the spring and early summer. This same general seasonal pat-

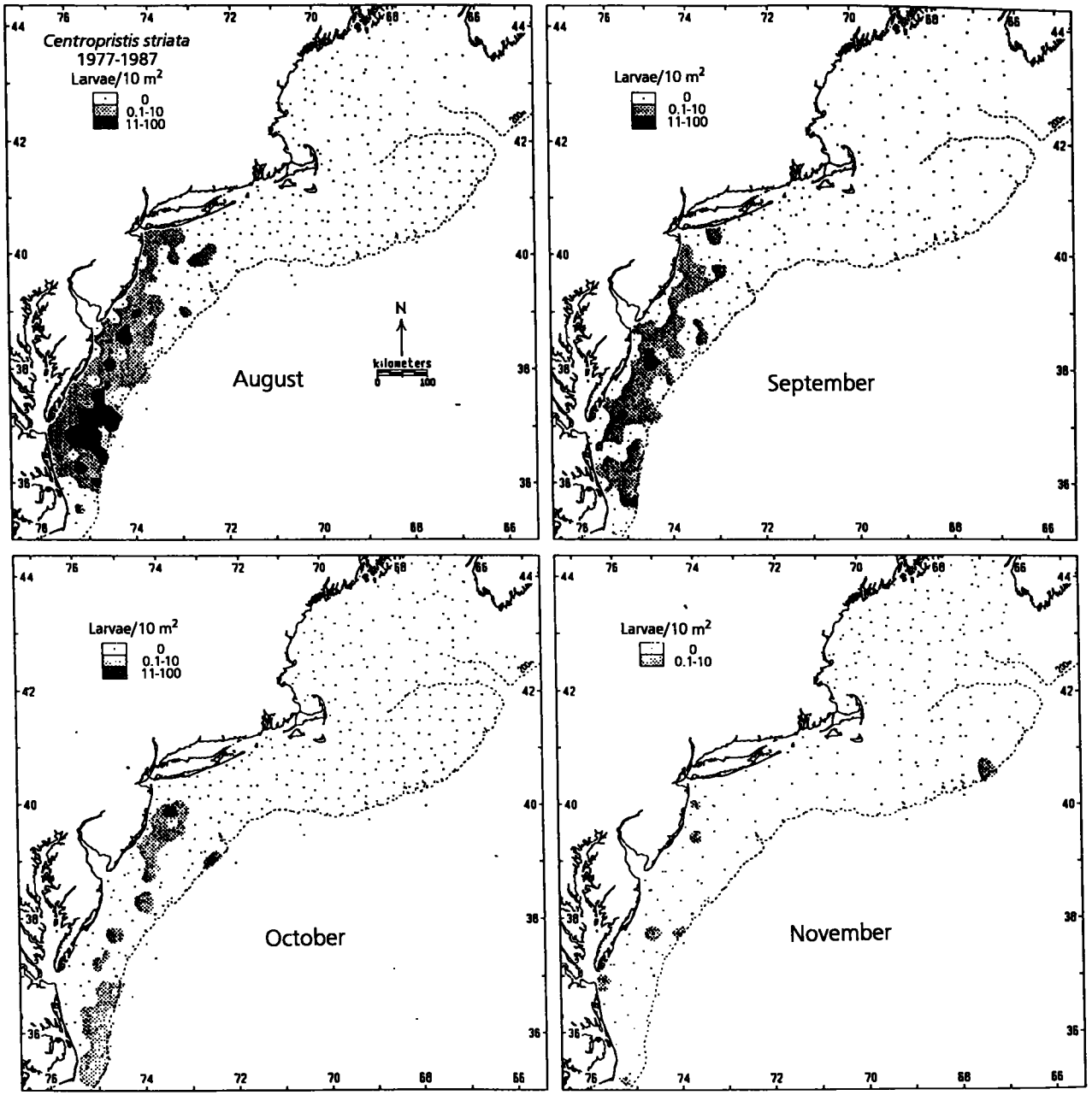

Figure 3 (continued)

tern occurred in the Great Bay estuary between 1988 and 1992 (Fig. 5) and during 1974 (Fig. 6) when most individuals were present from March through May and from August through November and were absent during the winter.

Fall otter trawl sampling from the continental shelf off New Jersey (Fig. 8) and from elsewhere in the mid-Atlantic Bight (Fig. 9) collected age 0+ individuals of the same lengths (3–9 cm TL) as those in the fall estuarine sampling (September and October, Figs. 4–6). These individuals were distributed throughout the inshore portions of the mid-Atlantic Bight (Figs. 8 and 10). Interestingly, the largest collections of age 0+ individuals were taken off eastern Long Island, Rhode Island, and off Massachusetts, both north and south of Cape Cod (Fig. 10). These are areas where larvae were virtually absent in extensive collections between 1977 and 1987 (Fig. 3).

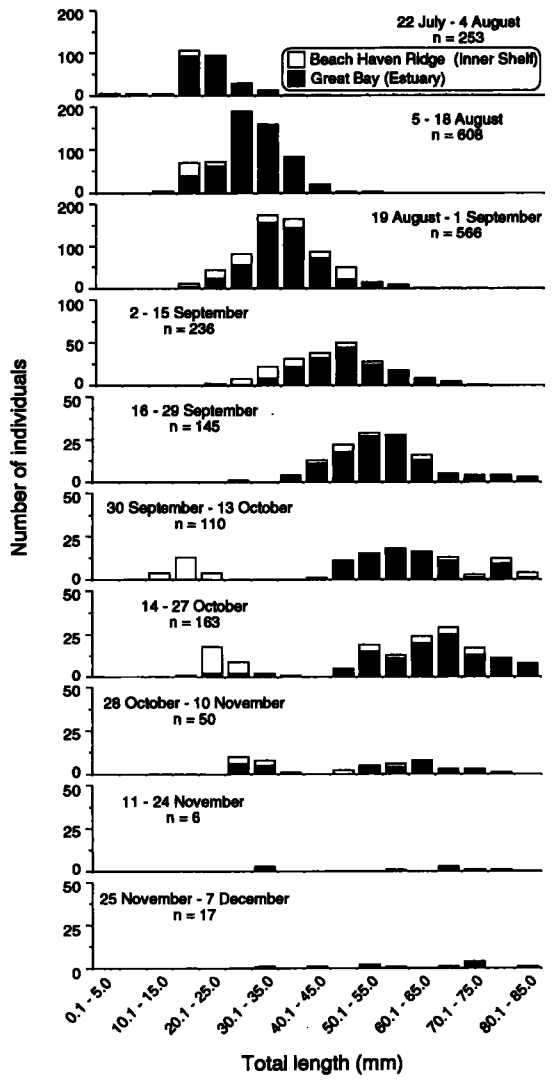

Figure 4

Occurrence and length of black sea bass, *Centropristis striata*, larvae and juveniles collected near Beach Haven Ridge (in plankton, beam trawl, and trap samples) on the inner continental shelf and in the Great Bay estuary (in trap samples) during 1992. See Figure 2 for localities.

Large numbers of 0+ individuals were found in intensive fall surveys in shallower inner continental shelf waters off Massachusetts (Figs. 9 and 10). In the winter, no age 0+ individuals were collected in inner continental shelf waters off New Jersey (Figs. 8 and 10). Most individuals in the winter (January–February) offshore surveys were collected near the edge of the continental shelf. In spring (March–April) surveys over the continental shelf, age 0+ individuals were evident over most depths. Most of these fish were found south of Delaware Bay (Fig. 10), some at a variety of depths off New Jersey. No individuals were collected in inshore spring (April–May) surveys of Massachusetts coastal waters.

Growth

The 1992 year class attained sizes of 18–101 mm TL by October after spawning, which occurred primarily in August (Figs. 4 and 5; Tables 2 and 3). Our estimates of growth rate are confounded somewhat by the occurrence of two length modes of 0+ benthic juveniles (Fig. 4), but calculations, based on the progression of these modes through October, yielded growth rate estimates of 0.45 mm/day for the first and 0.42 mm/day for the second length mode. The 1974 year class appeared to have reached similar lengths by the fall (Fig. 6). In both 1974 and in more recent year classes, sizes of fall fish and those reappearing the following spring were similar (Figs. 5 and 6), indicating very little growth over the intervening winter.

Growth resumed at a relatively fast rate in the spring and continued through the summer. Based on monthly increases (April–September, Fig. 5) in mean size, growth rate was 0.77 mm/day during the period. By July, approximately one year after spawning, these fish were 70–180 mm TL (Fig. 5). By September, when these fish were approximately 14–17 months old, they were 134–251 mm TL. A similar pattern was evident for 1974 (Fig. 6).

Habitat

Juveniles (age 0+) were collected and observed in a variety of habitat types both on the continental shelf and in the estuary. Densities of age 0+ individuals were similar between the inner continental shelf (Beach Haven Ridge) and estuarine study sites in the fall (August and September). When all the values for all habitats were combined, they were virtually identical with 0.33 (±0.007) ind·m^{-2} in the estuary (1-m beam trawl, n=144) and 0.32 ind·m^{-2} (±0.006) on the inner continental shelf (2-m beam trawl, n=57) (Table 1). Age 0+ individuals, both on the inner shelf and in the estuary, were found in habitats with some structure. Visual observations and video records provided evidence that individuals occurred in large linear accumulations or "windrows" of the Atlantic surfclam valves, *Spisula solidissima*, during the day in depths of 14–20 m on the inner continental shelf near Beach Haven Ridge in 1991 and 1992 (Petrecca[4]). Estimates made from video-

[4] Petrecca, R. Institute of Marine and Coastal Sciences, Rutgers Ur.iv., New Brunswick, NJ 08903. Personal commun., 1992.

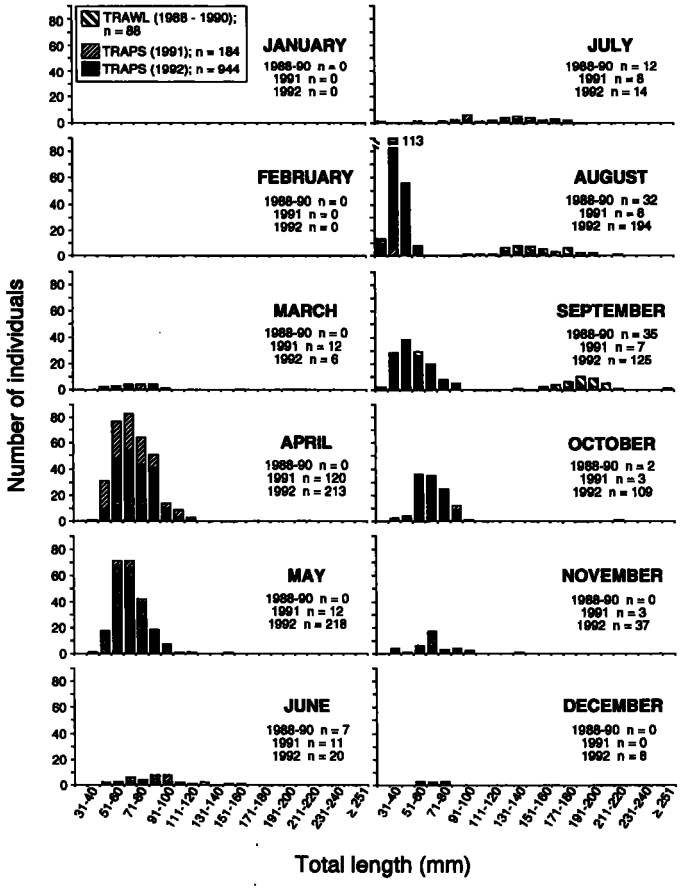

Figure 5

Monthly length frequencies of black sea bass, *Centropristis striata*, from the Great Bay-Little Egg Harbor estuarine system during 1988–92.

tapes taken during 1991 indicated that there were as many as five individuals/m^2 in the surfclam shell habitat. During the same periods they were not observed in adjacent open sand bottom, sand with pronounced megaripples, nor in exposed clay substrate habitats. In situ observations at other locations found age 0+ individuals at a number of continental shelf sites off Barnegat Inlet, New Jersey, in 19–26 m depths. In many of these instances the juveniles were associated with broken mollusk shells on the bottom and were seldom seen over sand substrate without shells (Witting[5]).

In the Great Bay-Little Egg Harbor estuary system (Fig. 2), patterns of habitat use for age 0+ black sea bass were derived primarily from beam trawl catches in 1992 (Fig. 11). They were most abundant in habitats (Fig. 2) with sand and shell (Stn. 5) and in habitats with sand with seasonally varying amounts of amphipod (*Ampellisca*) tubes (Stn. 9). They also occurred frequently in channels with silt substrate (Stn. 10), over silt and shell (Stn. 12), over bare sand (Stn. 8), over sand with seasonally occurring macroalgae (*Ulva lactuca*) (Stn. 11), in marsh creeks (Stns. 25–27), and were less abundant in an area with extensive hydroids (Stn. 6). They were absent in eelgrass (*Zostera marina*, Stn. 3) and in a habitat mixture of sand, shell, sponge, and peat (Stn. 7). All of these habitats were located at depths of 1–8 m in the polyhaline portion of the lower estuary. Separate trap sampling in marsh creeks directed at deep holes (2–3 m) confirmed the presence of age 0+ individuals in these holes but not in uniform, shallow areas (approx. 1 m).

Temperatures of areas where juvenile black sea bass occurred varied seasonally. In the estuary at

[5] Witting, D. A. Marine Field Station, Institute of Marine and Coastal Sciences, Rutgers Univ., Tuckerton, NJ 08087. Personal commun., 1994.

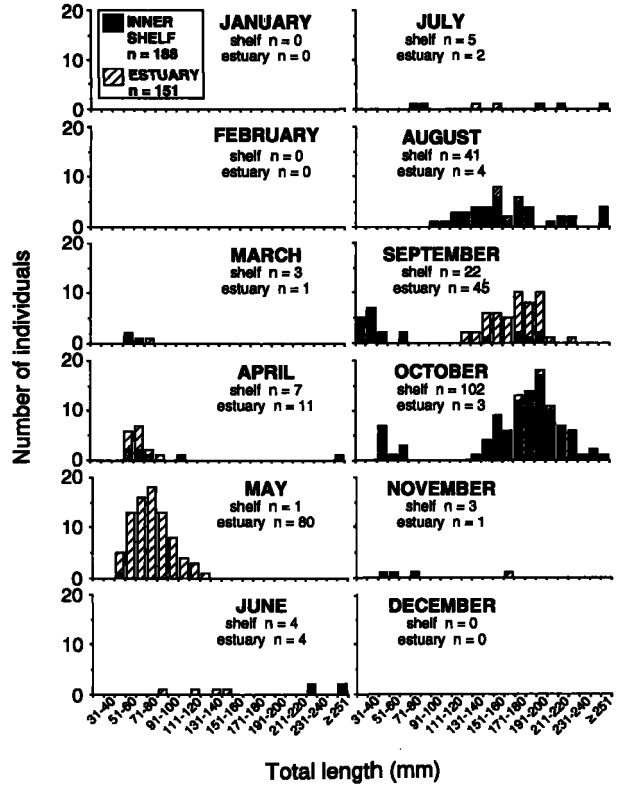

Figure 6

Monthly length frequencies, based on otter trawl collections, of black sea bass, *Centropristis striata*, from the inner continental shelf in the vicinity of Beach Haven Ridge and Great Bay-Little Egg Harbor estuary during 1974.

the time of first spring collections, temperature was approximately 10°C for individuals age 1+ (approximately 9 months old), whereas in the summer temperature was approximately 23°C for age 0+ individuals (Fig. 7). In the vicinity of Beach Haven Ridge, the age 0+ individuals first occurred at approximately 15°C and were most abundant when bottom temperatures reached 20°C (Fig. 7). Over the continental shelf in the fall, the age 0+ cohort was collected primarily at bottom temperatures of 14–17°C (Fig. 12) and at higher average temperatures of 16–21°C in Massachusetts inshore waters (Fig. 12). During winter, most individuals were collected at 6–9°C (Fig. 12), a temperature that probably reflects their greater abundance in deeper waters at that time (Fig. 10). In the spring, this same cohort was abundant at 6–11°C and 15–17°C. In every instance on the continental shelf, with the possible exception of inshore Massachusetts, the fish were found at higher average temperatures than those represented by most of the stations sampled (Fig. 12).

Discussion

Annual cycle in the early life history

Spawning of black sea bass in the mid-Atlantic Bight proceeds from south to north, presumably with warming temperatures. Our interpretation of this geographical pattern is based on extensive collections during 1977–87 and is consistent with that reported for 1966–67 (Kendall, 1972; Kendall and Mercer, 1982). The occurrence of larvae of all sizes in all areas suggests that spawning and development occurs throughout most of the mid-Atlantic Bight. In addition, most larvae were <8 mm TL in our continental shelf collections and were similar to those

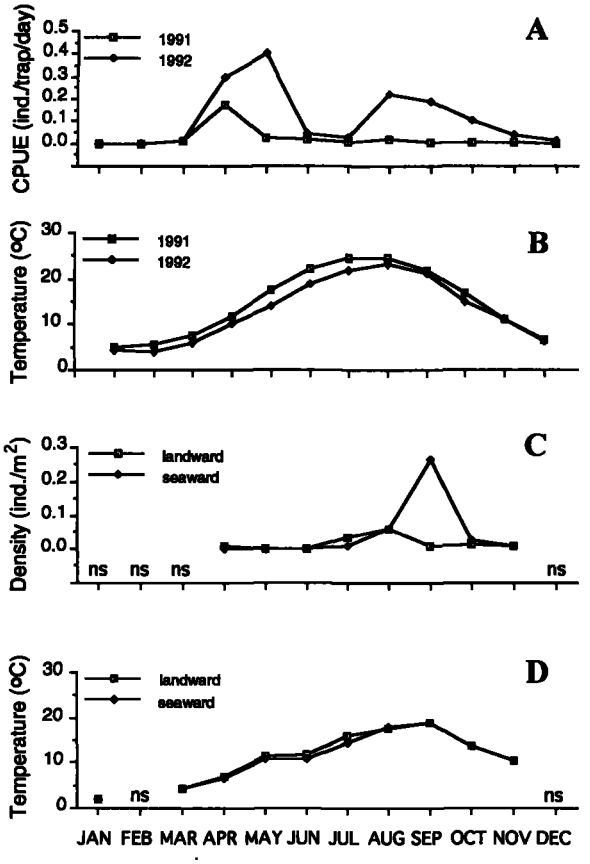

Figure 7

Monthly averages of abundance of age 0+ black sea bass, *Centropristis striata*, and temperature in the estuary (**A** and **B**) and on the inner continental shelf in the vicinity of Beach Haven Ridge (**C** and **D**). Abundance was based on trap collections in the estuary and on beam trawl sampling landward and seaward of the ridge.

reported by Kendall (1972). Thus, black sea bass may settle to the bottom at sizes between 10 and 16 mm TL. This size range also corresponds to the size at which ossification of fin rays and vertebrae is completed (Kendall, 1972). The smallest individual previously reported from the continental shelf was one of 43 mm (Massman et al., 1962). Settlement on the inner continental shelf and in the estuary occurred from July through October according to our estimations based on collections of small individuals (<20 mm TL) throughout that period (Fig. 4). The identification of two length modes during 1992 in both the estuary and on the inner continental shelf (Fig. 4) was not as obvious at the same continental shelf location in 1991 when small juveniles (10–20 mm TL, n=35) occurred from August through October. On the basis of consistent occurrence of age 0+ individuals, it is evident that both the inner continental shelf and estuaries function as nurseries (see below) during the first summer and fall.

Black sea bass (age 0+) appear to leave the estuary and the inner continental shelf off New Jersey during the fall and to move to deeper waters as indicated by the decline in CPUE in the estuary, by the simultaneous increase in numbers on the inner shelf, and by the subsequent complete disappearance of fish from both of these areas by winter. This pattern is evident on the continental shelf throughout the mid-Atlantic Bight from fall collections of the same year class, especially south of Delaware Bay (Fig. 10) as previously observed (Musick and Mercer, 1977). These movements are likely initiated in the fall by decreasing temperatures as suggested by the decrease in fish abundance with declining estuarine

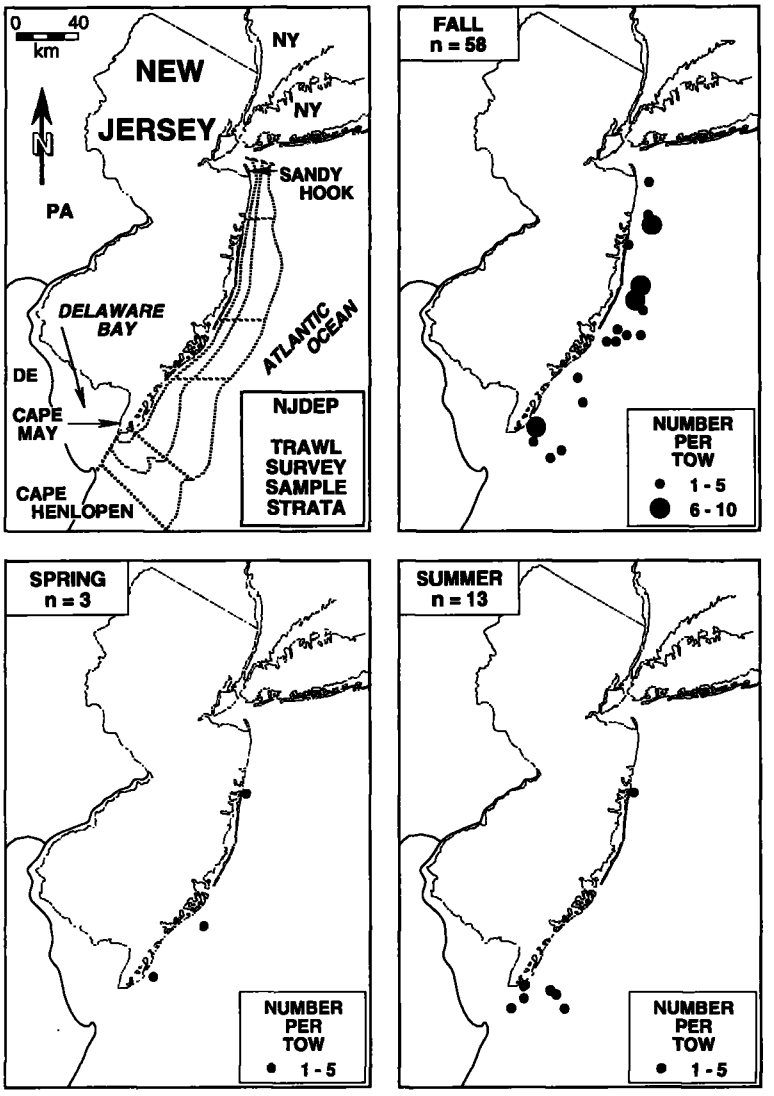

Figure 8

Distribution of age 0+ black sea bass, *Centropristis striata*, during the fall, spring, and summer in inner continental shelf sampling areas off New Jersey during 1988–91. No fish were collected during winter.

temperatures (Fig. 7). This same trend was also noted in Chesapeake Bay estuaries (Musick and Mercer, 1977) and off the coast of Massachusetts (Lux and Nichy, 1971). This response is not surprising given the inability of young (Schwartz, 1964b) and age 0+ (Hales and Able, in press b) black sea bass to tolerate temperatures below 2–3°C, which can occur in the Great Bay estuary during the winter (Able et al., 1992; Szedlmayer et al., 1992). Age 0+ individuals apparently spend the winter on the outer continental shelf, but by early spring they can be found over most of the shelf (Fig. 10). Musick and Mercer (1977) have suggested that they overwinter on the continental shelf in somewhat shallower depths (56–110 m). This year class reenters New Jersey estuaries in the spring, where it spends the summer, then migrates offshore again in the fall. A similar seasonal pattern occurs in Chesapeake Bay estuaries (Musick and Mercer, 1977, and references cited therein).

The 70–180 mm TL size range attained during the first year (ending July) is similar to that reported from back-calculated lengths from scales (approximately 40–159 mm TL; Briggs, 1978) and otoliths (75–107 mm SL; Alexander, 1981). The 1+ age class

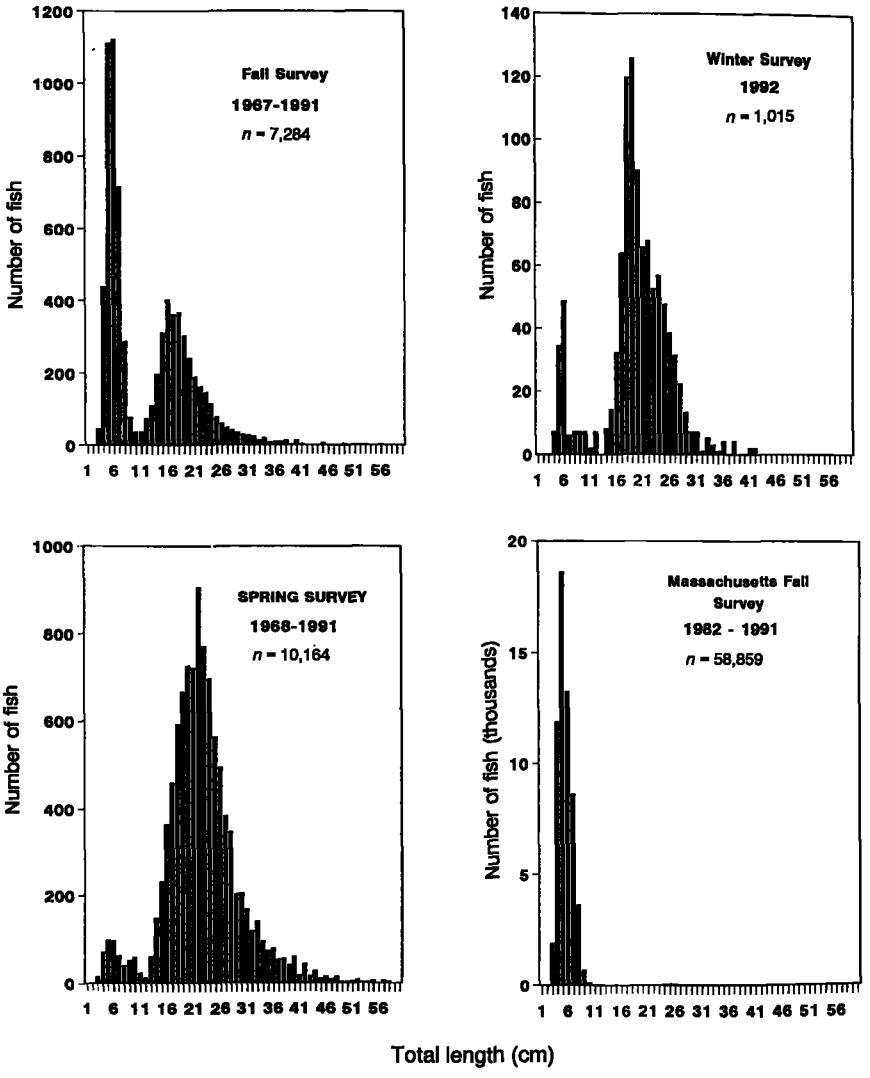

Figure 9

Composite lengths of black sea bass, *Centropristis striata*, from bottom trawl surveys in the mid-Atlantic Bight in (**A**) fall, (**B**) winter, and (**C**) spring, and in Massachusetts waters during the fall (**D**).

appears to follow a similar pattern of inshore-offshore movements as indicated by catches in the estuary over a number of years (Figs. 5 and 6). Thus this annual pattern may be characteristic for age 0+ and 1+ black sea bass for the entire mid-Atlantic Bight.

Nursery habitats

There are inconsistencies between the available data on larval distribution and presumed nursery areas in southern New England. The northern limit of larvae from MARMAP samples for the period 1977–87 was off Long Island (Fig. 3). Earlier studies noted the absence of black sea bass larvae from Block Island Sound (Merriman and Sclar, 1952), Narragansett Bay (Bourne and Govoni, 1988), Long Island Sound (Wheatland, 1956; Richards, 1959), Great South Bay, Long Island (Monteleone, 1992), and offshore of these areas (Kendall, 1972). The only exception was the collection of a few larvae from Georges Bank (Table 2), Cape Cod Bay (Scherer, 1984), and Narragansett Bay (Herman, 1963). However, there was some documentation of spawning aggregations in southern Massachusetts coastal waters (Wilson, 1889).

Despite the scarcity of larvae in southern New England, age 0+ individuals have been very abun-

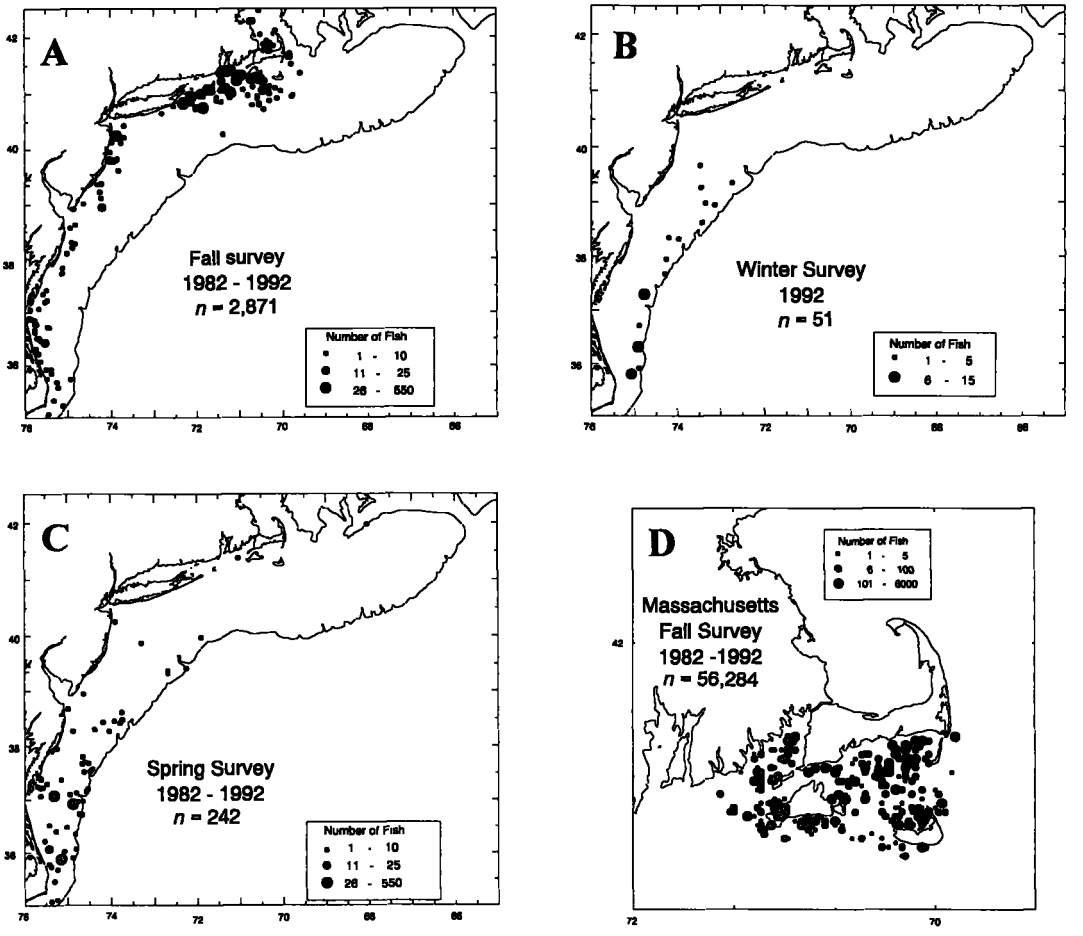

Figure 10

Distribution of age 0+ black sea bass, *Centropristis striata*, in the fall, winter, and spring based on composite collections (1982–92) from the mid-Atlantic Bight and in the fall off the coast of Massachusetts (1982–92).

dant in nearshore waters off Massachusetts (Fig. 10). The age 0+ year class from some estuaries on the south shore of Massachusetts has been described as either rare (Waquoit Bay-Eel Pond estuary [Curley et al., 1967]) or common (Quisset Harbor and Wareham River [Sumner et al., 1913]; Bass River [Curley et al., 1975]; Little Sippewisset Marsh [Werme, 1981]; Great Harbor near Woods Hole [Lux and Nichy, 1971]). In Bass River, where juveniles represented 9.3% (n=69) of the total catch, they were most abundant in deeper (1–3 m) otter trawl catches from August to October (Curley et al., 1975). In Little Sippewisset Marsh they were found in the channels of shallow marsh creeks (Werme, 1981), and juvenile black sea bass were regularly collected in Buzzards Bay and Vineyard Sound during the autumn bottom trawl survey (Fig. 10). The abundance of age 0+ individuals in the region indicates that further

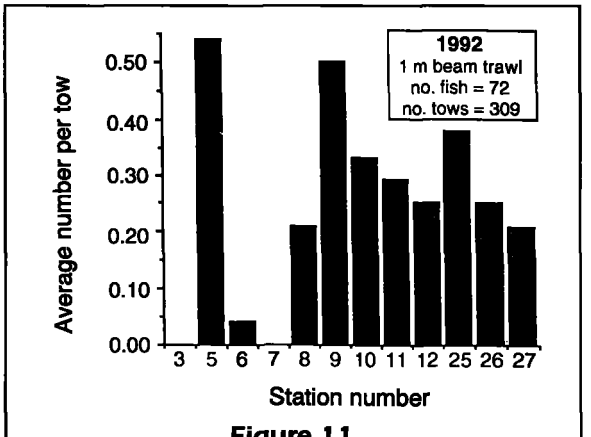

Figure 11

Abundance of age 0+ black sea bass, *Centropristis striata*, in the Great Bay-Little Egg Harbor estuary during 1992. See text for habitat designations and Figure 2 for locations.

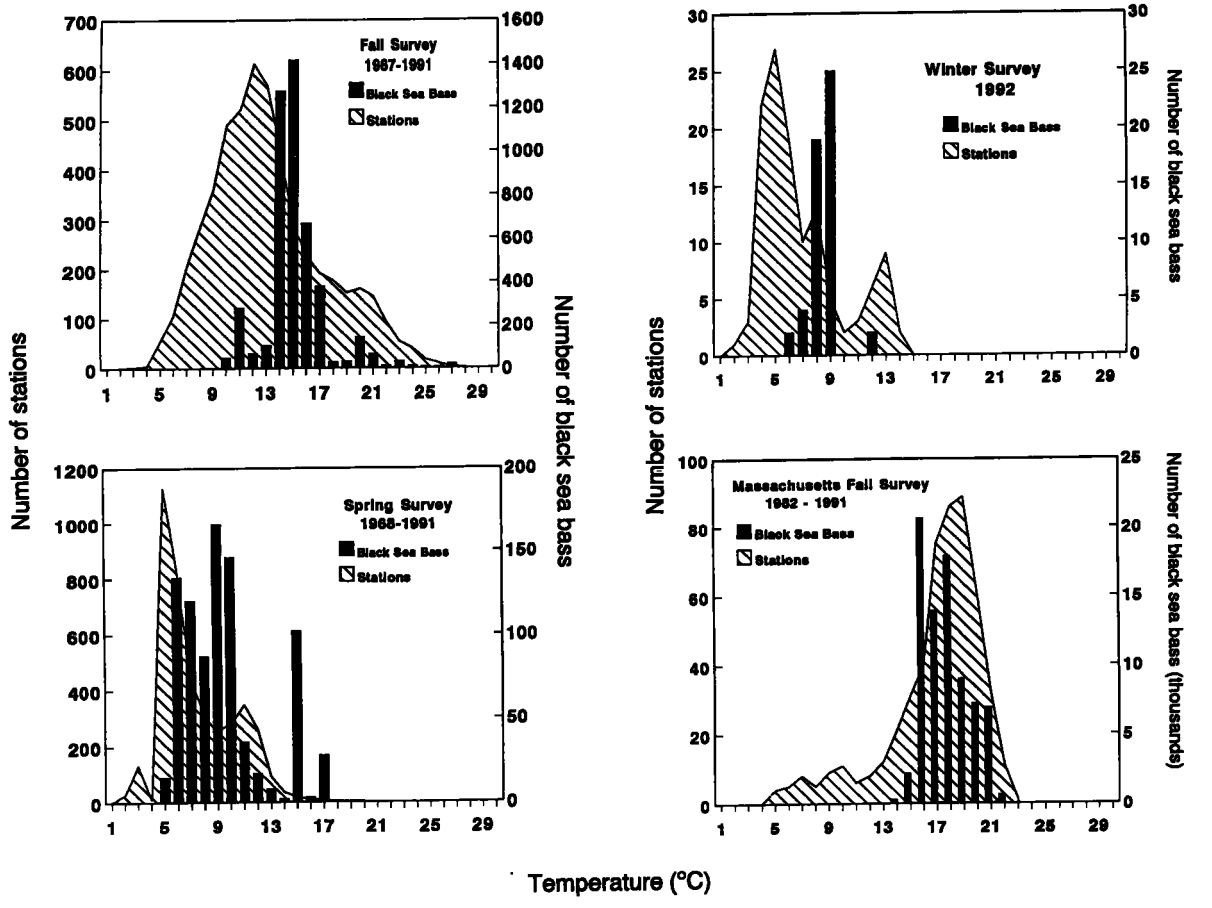

Figure 12

Abundance of age 0+ black sea bass, *Centropristis striata*, relative to bottom temperature in the spring, fall, and winter on the mid-Atlantic Bight continental shelf and off the coast of Massachusetts, based on Northeast Fish. Sci. Cent. and Massachusetts Div. Marine Fisheries bottom trawl surveys (1982–92).

studies are warranted to understand the possible significance of the region as a nursery.

In southern New Jersey, spawning and nursery areas are somewhat better delineated. The larvae clearly occur on the inner continental shelf off New Jersey (Figs. 3 and 4; Kendall, 1972), but there is no evidence of larvae in estuaries and bays in New Jersey (Croker, 1965; Himchak, 1982; Witting[3]) or Delaware (Pacheco and Grant, 1965; Wang and Kernehan, 1979). The apparent absence of larvae in estuaries and the occurrence of larvae and small juveniles (<20 mm TL) at Beach Haven Ridge suggest that settlement may initially occur on the inner continental shelf and that some individuals may remain there while some move into estuaries. Larvae 15–17 mm were reported in late July near Hereford Inlet, New Jersey (Allen et al., 1978), but further details are not available. The only other prior reports of small juveniles in New Jersey estuaries are of 25-mm individuals from Great Egg Harbor (Bean, 1888), 20-mm individuals from Raritan Bay (Nichols and Breder, 1927) and 25–35 mm specimens from lower Delaware Bay (Wang and Kernehan, 1979). The occurrence of juveniles in the York River in Chesapeake Bay (Musick and Mercer, 1977) was based on individuals that may have overwintered on the continental shelf and reentered the estuary as occurs in New Jersey. In other Chesapeake Bay habitats black sea bass (some of them 140–165 mm) were more abundant in eelgrass, *Zostera marina*, both day and night, than in adjacent unvegetated areas (Orth and Heck, 1980).

Our observations suggest that suitable summer nursery habitats, either on the continental shelf or in estuaries, are presumably related to the occurrence of some type of bottom structure, such as peat and shell accumulations. This is further substantiated

by the increase in catch rates of black sea bass juveniles when shell was added to estuarine substrate to improve oyster recruitment (Arve, 1960). Dissolved oxygen also may influence patterns of habitat use because juveniles are intolerant of low levels (Hales and Able, in press a). The similarities in the densities and in sizes attained in the fall by juveniles in the estuary and in the adjacent inner continental shelf suggest that habitat quality is similar for both these areas, if one assumes that size differential predation or movements did not occur at either site during the sampling period. In summary, these data indicate that both estuaries and the inner continental shelf are important as nursery areas and that juvenile black sea bass are not strickly estuarine dependent.

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Population estimates of Pacific coast groundfishes from video transects and swept-area trawls

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Abstract.—Demersal fish surveys are used for two purposes: to detect trends in multispecies communities for environmental assessment and to provide fishery independent stock assessments for management. We compared remotely operated vehicle (ROV) and swept-area trawl surveys to evaluate their strengths and weaknesses for these two purposes. ROV abundance estimates tended to be higher and have lower coefficients of variation than did trawl abundance estimates. This trend is greatest for benthic species and particularly so for small, cylindrically shaped fishes. For patchily distributed, off-bottom fishes such as rockfish, *Sebastes* spp., sablefish, *Anoplopoma fimbria*, and Pacific whiting, *Merluccius productus*, the results vary between ROV and trawl estimates. For environmental assessment, the ROV estimates are superior because, for most species, abundances are higher and smaller changes can be detected. For fisheries management of commercially important species, the results are divided. Dover sole, *Microstomus pacificus*, and thornyheads, *Sebastolobus* spp., have higher ROV abundance estimates and lower coefficients of variation than the trawl. Sablefish, which exhibit more off-bottom behavior, have higher trawl estimates at two of three depths. The ROV and trawl provide different types of information not available from other gear. Much of the difference between the two types of surveys stems from the nature of the sampling gear and from the behavior, body shape, and size of the fishes.

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Estimates of population abundance are essential to research for understanding the impact of human activities on marine demersal fish populations. Traditionally, swept-area trawl surveys have been used to obtain abundance estimates aimed at fisheries management. Recently, environmental surveys, used to monitor the impacts of pollution and coastal development, have become more widespread and important. These two types of surveys have different goals. Data from fisheries surveys are used as input for predictive models to forecast the results of alternative fisheries management strategies and are usually directed toward either a single species or a small species group. Environmental surveys are used to detect trends in populations over time, to distinguish those trends from natural variation, and are usually directed at an entire multispecies fish community.

Both types of survey population estimates are subject to the problems of bias and precision. Bias is a particular problem for fisheries surveys. Fishery stock assessment is based on models that integrate fishery catch-at-age data with fishery-independent survey estimates of abundance (Deriso et al., 1985). The catch-at-age data, sampled from the commercial fishery, document the trend of population change resulting from recruitment of young fish into the population and from removal of individuals out of the population due to fishing and natural mortality. The fishery-independent survey data are used as a measure of either relative or absolute abundance (Doubleday and Rivard, 1981). These survey data are used to calibrate or "tune" the trend ob-

tained from the catch-at-age data to determine how close the population is to a threshold value of overfishing (Kimura, 1989). Survey data also yield valuable information on migration routes, or biological parameters such as age-at-maturity, fecundity, and feeding. Biased survey estimates can result in very precise estimates of population abundance which are either lower or higher than the true population abundance.

For environmental surveys, the problem of precision is the major concern. Here, the goal is to detect a trend in population size, often of all the fish in the habitat, and to distinguish that trend from natural variation in fish populations. Abundance estimates from trawl surveys tend to have very large variances; often means and variances are correlated (see Lenarz and Adams, 1980). Resulting confidence intervals around means range from 50 to 100% for flatfish species and are greater than 100% for rockfish, *Sebastes* spp. (Raymore and Weinberg, 1990). As a result, all but the most extreme changes in population size are masked by these large confidence intervals. Methods commonly used to deal with this variability are transformations using the negative binomial (Lenarz and Adams, 1980) or the Delta distribution (Pennington, 1986). Data transformed by using these distributions often result in the variance being independent of the mean; however, the large confidence intervals and low statistical power remain.

In this study we examined video transects conducted from a remotely operated vehicle (ROV) as an alternative method for making population estimates of demersal fishes and compared these estimates to those from a conventional swept-area trawl survey.

Methods

Study site

The study site off central California lies along a cone-shaped ridge which runs southwest from Santa Cruz, California, and separates Monterey Canyon to the south from Ascension Canyon to the north (Fig. 1). Surface topography of the ridge is smooth and relatively unbroken (Greene[1]). The ridge is composed of sandstone, is covered with mud of pelagic origin, and is characterized by occasional areas of exposed bedrock. The stations where ROV and trawl operations were conducted were located along the ridge at depths of 200, 400, and 600 m (see Fig. 1).

[1] Greene, G. U.S. Geological Service, Pacific Marine Geology, 345 Middlefield Rd., Menlo Park, CA 94025. Personal commun., 1992.

ROV operations

ROV operations were conducted by using the Monterey Bay Aquarium Research Institute's ROV *Ventana* aboard the RV *Point Lobos*. The ROV was equipped with a Sony DXC-3000 video camera with a 5.5–44 mm zoom lens, illuminated by four 400-W sodium scandium lights. The zoom lens was used only for identification off the transect. Fiber-optic cable was used for viewing and recording images. The ROV was also equipped with a combined dual signal, a global positioning system and sonar system, which recorded the ROV position every 10 seconds. Depth, altitude off bottom, and various camera settings were also recorded.

At least three replicate transects were made at each depth. Transects at the 200-m, 400-m, and 600-m depths were sampled (for dates, see Table 1). Because a video transect covering the same total area as a trawl was not practical, a transect length of similar distance covered by a trawl was chosen (approximately 1.8 km or 1 nmi). Strip transects were used rather than line transects because the orientation of the lights produced a very sharp boundary between illuminated width of the transect and the darkness (Burnham et al., 1980; Butler et al., 1991). Transects were made at a speed of approximately 1.8 km/hr (1 knot) parallel to the isobath, interrupted occasionally by stops for fish identification or vehicle maintenance. Transects were made with a camera angle of 30° off the parallel horizon to the bottom and with a camera height averaging 0.7 m off the bottom. Fish were identified from videotapes by two independent viewers, and the response of each fish to the ROV was recorded as follows: 1) strongly attracted (rapidly moving into the frame); 2) weakly attracted

Table 1

Dates of remotely operated vehicle (ROV) and trawl sampling cruises at 200-m, 400-m, and 600-m depth strata off central California. The number in parentheses is the number of transects or trawls occurring during that month.

Depth stratum (m)	ROV	Trawl
200	Oct 1991 (3)	Apr 1991 (2) Sep 1991 (3) Jan 1992 (3)
400	Mar 1991 (1) Oct 1991 (1) Oct 1992 (2)	Apr 1991 (1) Sep 1991 (3) Jan 1992 (4)
600	Jul 1991 (1) Sep 1991 (2)	Apr 1991 (2) Sep 1991 (4) Jan 1992 (3)

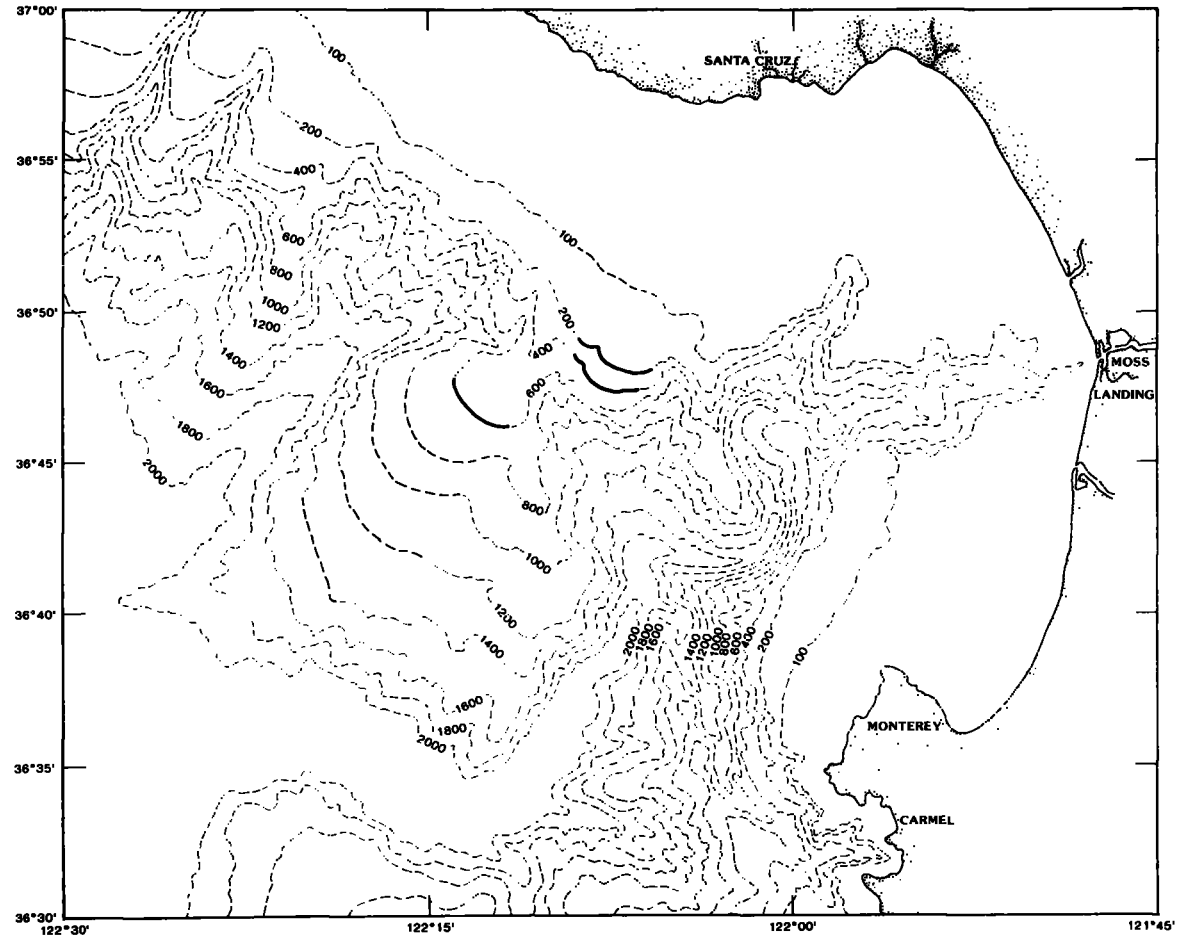

Figure 1

Study site off central California marked for 200-m, 400-m, and 600-m depth comparisons of population estimates from video transects conducted from an ROV survey and from swept-area trawl surveys.

(slowly moving into the frame); 3) no response (no movement); 4) weakly avoided (slowly moving out of the frame); and 5) strongly avoided (rapidly moving out of the frame). A time line, at which the fish were counted, was chosen in the center of the viewing area. To determine transect width at the time line, the ROV was transected over a 5-m square grid, and known lengths from the grid were measured on the monitor. From these lengths and standard photometric equations (Wakefield and Genin, 1987), the transect width was calculated to be 1.8 m (see Fig. 2). The vertical perspective of the video ranged from a height of 0.7 m at the camera to a visual horizon of 2.4 m in front of the ROV. The number of fish per transect was converted to fish per hectare by dividing the number of fish observed by the area covered (transect distance multiplied by transect width).

Trawl operations

Trawling was conducted on separate cruises on the RV *David Starr Jordan*. Three trawl surveys were conducted and a sample size of at least three trawls per station was taken per cruise (for dates, see Table 1). During the April 1991 cruise, all three replicates were not completed owing to inclement weather. Parallel tows were made along the same isobath as the ROV transect at a speed of approximately 3.7 km/hr (2 knots) for 30 minutes, although control of the trawl was not as exact as that of the ROV. The net, an Aberdeen high-rise trawl net with a 29-m (96-ft) headrope, was equipped with 1.5 × 2.1 m steel doors. Trawl openings were not measured; this type of trawl has an average horizontal opening of 13.5 m (see Fig. 2) and an average vertical opening of 5.5 m

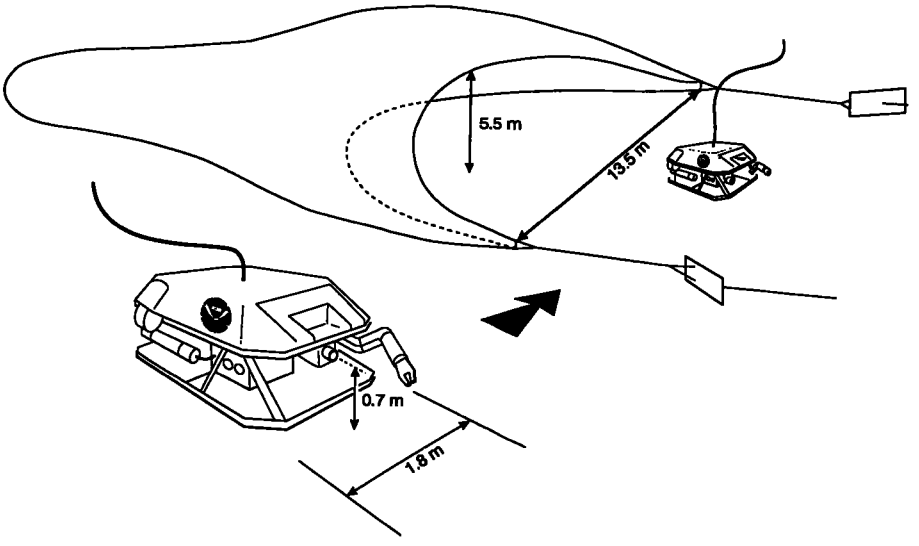

Figure 2

Sampling dimensions of a remotely operated vehicle (ROV) video transect and a trawl. Drawings of gear and sampling volumes are made to scale.

(Rose[2]). On deck, catches were handled with standard protocol (Smith and Bakkala, 1982) and were sorted to species, weighed, and measured. Lengths were measured for either a subsample of 100 fish or the entire catch, if it comprised less than 100 fish. When the catch was greater than 100 fish for a species, total species number was extrapolated from total species weight by using the average weight per fish from the subsample weight and numbers. Numbers of species per hectare were expanded by dividing the total species number by the area covered (distance traveled by a tow multiplied by the average width of the trawl).

Differences in ROV and trawl abundance estimates for individual species at each depth were tested by using t-tests for differences of unpaired log-transformed means. A sign test was used to determine whether the number of times that an ROV abundance estimate (or coefficient of variation) was higher than the trawl was greater than would have been expected randomly (i.e. a 50/50 ratio).

Statistical power is defined as $1-\beta$, where β is the probability of failing to reject a hypothesis when it is false, and therefore power is the probability of correctly rejecting a false hypothesis (Peterman, 1990). The power of the ROV and trawl abundance estimates was evaluated by calculating the required sample size to detect a 50% reduction from the log-transformed mean abundance at a fixed level of α (0.05) and at a high level of power ($1-\beta$, 0.80). Comparisons were made for the commercially important species (Dover sole, *Microstomus pacificus*; thornyheads, *Sebastolobus* spp.; and sablefish, *Anoplopoma fimbria*) and for a group of other abundant taxa (catsharks, Scyliorhinidae; skates, Rajidae; and eelpouts, Zoarcidae) at the 400-m depth (the only depth where all of these taxa occurred in both the ROV and the trawl surveys).

Results

More fish per hectare were observed from the ROV than were captured in the trawl at the 400-m and 600-m depths, whereas more fish were captured in the trawl at the 200-m depth (Fig. 3). However, the differences in the log-transformed total ROV and trawl estimates were only significant at the 400-m and 600-m depths (400 m: t=5.50, P<0.001; 600 m: t=3.28, P=0.011) and not at the 200-m depth (200 m: t=0.32, P=0.713). Numbers captured in the trawl at the 200-m depth were higher owing to a single large catch of two species of rockfish in one trawl. The ROV estimates of fish numbers were higher for most individual species or taxonomic groups that occurred in

[2] Rose, C. National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA, 98115–0700. Personal commun., 1992.

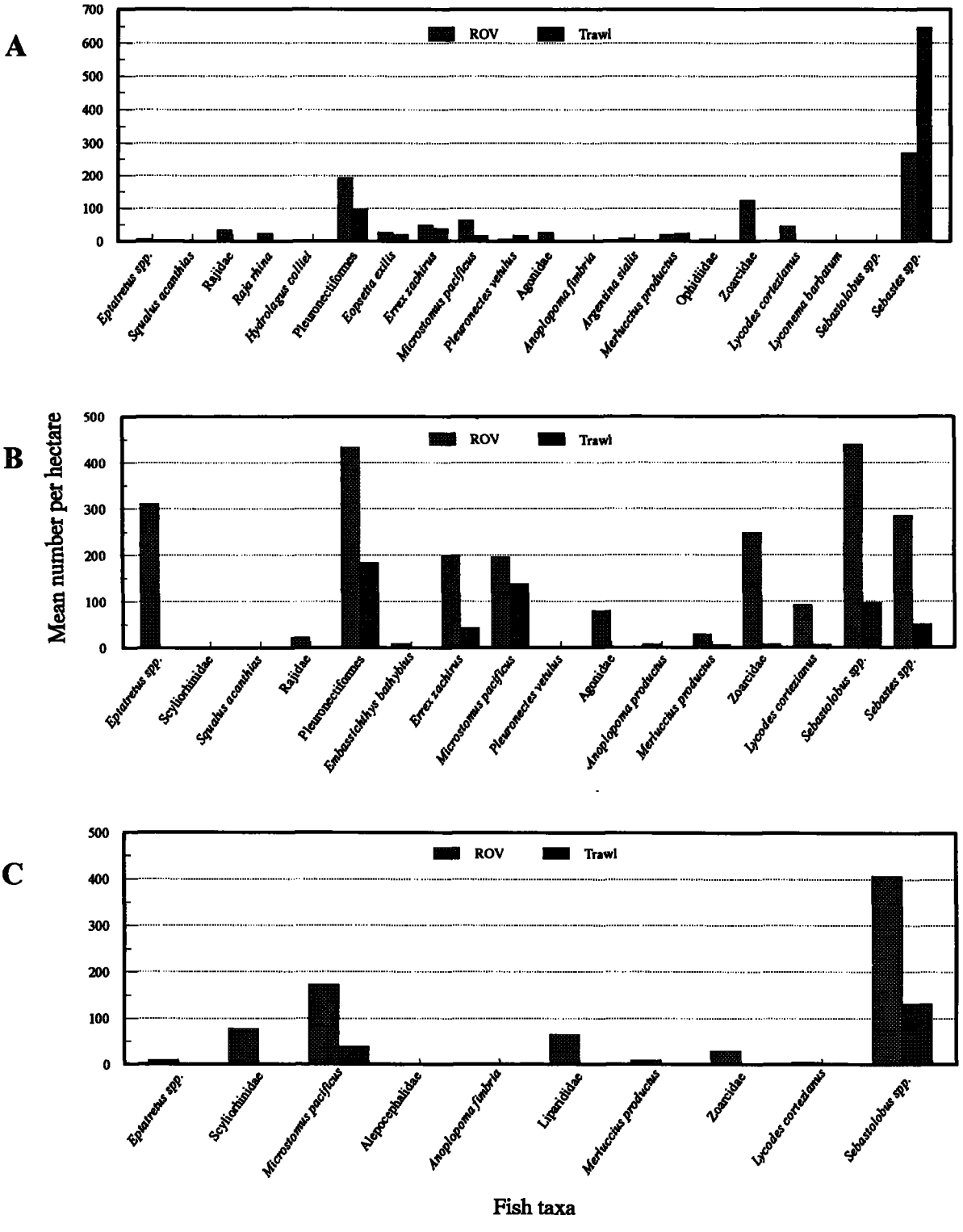

Figure 3

Mean numbers of fish per hectare estimated from an ROV video strip-transect survey and a swept-area trawl survey from (**A**) the 200-m depth station (ROV, n=3 and trawl, n=8); (**B**) the 400-m depth station (ROV, n=4 and trawl, n=8); and (**C**) the 600-m depth station (ROV, n=3 and trawl, n=9).

any abundance (greater than 1 fish/hectare in either estimate). For the 200-m, 400-m, and 600-m depths (Fig. 3), the mean ROV estimates were higher than the trawl estimates for 13 of 20, 15 of 16, and 9 of 10 comparisons, respectively (sign test 200 m: P=0.180; 400 m: P=0.001; and 600 m: P=0.011).

Especially large differences between the ROV and trawl estimates existed for strongly bottom-associated groups: skates, flatfish (Pleuronectiformes), and thornyheads, and particularly for small, cylindrically shaped fish that remained on the bottom: hagfish (*Eptatretus* spp.) poachers (Agonidae), and eelpouts. No significant differences were found between ROV and trawl estimates for fishes with more off-bottom behavior ("roundfish"), such as Pacific whiting, *Merluccius productus*, sablefish, and rockfish. Spiny dogfish, *Squalus acanthias,* were captured at every depth in low numbers in the trawls and were the only species to occur consistently in the trawls that were not seen with the ROV.

Coefficients of variation were generally smaller for the ROV estimates than for the trawl estimates. For species that occurred in both the ROV and the trawls, the coefficients were smaller for the ROV estimate in 10 of 15 comparisons at the 200-m depth, in 10 of 13 comparisons at the 400-m depth, and in 8 of 10 comparisons at the 600-m depth ([Fig. 4] sign test; 200 m: P=0.170; 400 m: P=0.050; and 600 m: P=0.050). ROV coefficients of variation were always larger for catsharks only and were mixed for Pacific whiting and some species of flatfish. At all depths, ROV coefficients of variation were smaller for rockfish and thornyheads, species typically with very large variances. Coefficients of variation for total fish number were much larger for the trawl estimates than for the ROV estimates at all depths (200-m, 2.4 times; 400-m, 4.6 times; and 600-m depths, 3.0 times).

The required sample sizes to detect a 50% reduction in the log-transformed means for a fixed level of power (1–β, 0.80) were smaller for the ROV than for the trawl, except for catsharks (Table 2). When the ROV sample sizes were smaller, the difference in sample sizes ranged from 1.3 to 19 times. For catsharks, a taxon with high variability, the ROV sample size was nearly six times larger than that for the trawls.

Most fishes showed no response to the ROV (Table 3). Considering all fish taxa observed, 80% showed no response to the ROV, 6% were attracted, and 14%

Table 2

The required sample size to detect a 50% reduction from the log-transform mean abundance of commercially important and abundant fish taxa at the 400-m depth from ROV and trawl surveys. The calculations were made at a fixed level of α (0.05) and power (1–β, 0.80).

	ROV	Trawl
Commercially important taxa		
Microstomus pacificus	5	95
Anoplopoma fimbria	25	55
Sebastolobus spp.	29	38
Abundant taxa		
Scyliorhinidae	251	43
Rajidae	9	104
Zoarcidae	14	90

Table 3

Response of commonly occurring fish taxa to the remotely operated vehicle (ROV). Fish from all depths (n=10) were recorded. Unid. = unidentified.

	Strongly attracted	Weakly attracted	No response	Weakly avoided	Strongly avoided
Eptatretus spp.	0	8	182	5	9
Scyliorhinidae	0	2	22	19	0
Rajidae unid.	0	2	42	4	8
Errex zachirus	0	1	89	3	26
Microstomus pacificus	0	3	326	10	21
Anoplopoma fimbria	0	4	5	2	2
Merluccius productus	0	45	28	11	7
Lycodes cortezianus	0	1	69	12	8
Sebastolobus spp.	0	2	173	8	10
Sebastes spp.	0	0	14	2	0
All taxa	0	68	950	76	91

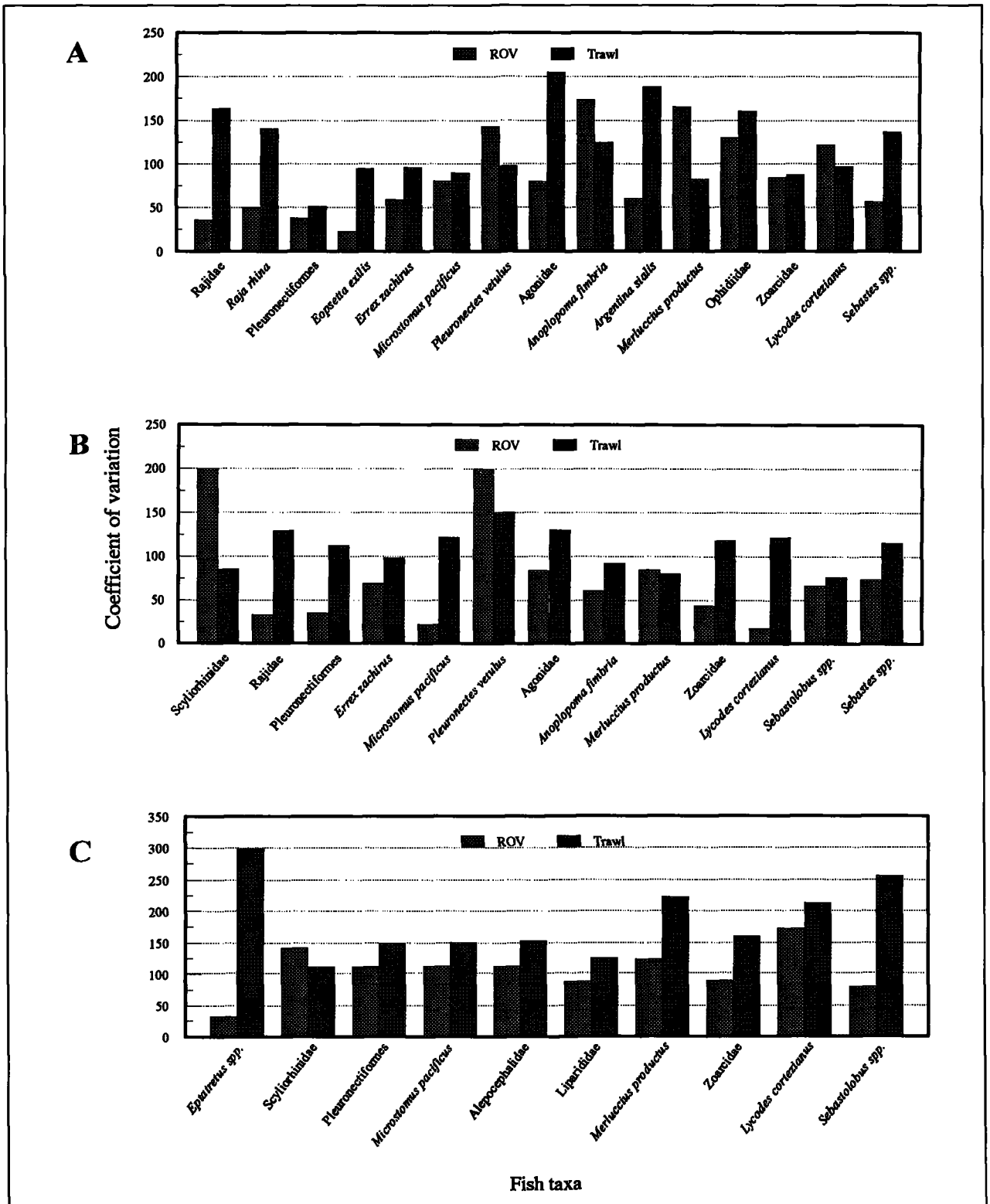

Figure 4

Coefficients of variation of the mean number of fish per hectare estimated from an ROV video strip-transect survey and a swept-area trawl survey from (**A**) the 200-m depth station (ROV, n=3 and trawl, n=8); (**B**) the 400-m depth station (ROV, n=4 and trawl, n=8); and (**C**) the 600-m depth station (ROV, n=3 and trawl, n=9).

avoided it. Pacific whiting had the strongest response (69%), appearing to be attracted to the ROV. Sablefish had the next strongest response (62%), but their numbers were low, averaging 3.75 individuals over all depths. Their behavior was variable: some animals swam away, some swam toward the ROV, and some ignored the ROV. Catsharks showed approximately equal numbers responding and not responding, and those that did respond consistently avoided the ROV.

Finally, the red octopus, *Octopus rubescens*, was the most abundant animal counted from the ROV. It was observed from the ROV only at the 200-m depth at numbers of 1,610 per hectare (SE=516.4) and was not captured in the trawls. The ROV red octopus abundance estimates were higher than any fish estimate from the trawls.

Discussion

Much of the difference between the ROV and trawl estimates was due to the different mechanical nature of the sampling gear and to the body shape and behavior of the fishes. The ROV intensively sampled a narrow area directly in front and extending up a short height off the bottom. The trawl sampled a much wider area, including a larger area off the bottom, but with what must have been a great deal of escapement. The result was that ROV abundance estimates were higher and had lower coefficients of variation for fishes either strongly associated with the bottom or with a body shape and size, or both, that would pass through the mesh (such as the red octopus). Conversely, animals with highly patchy distributions and off-bottom behavior (catsharks, rockfish at the 200-m depth) had higher abundance estimates from the larger volume trawl. Although both the ROV and trawl estimates were adjusted to the same surface area, there was no adjustment made to reflect the 7.7 times greater off-bottom height sampled by the trawl (Fig. 2). Probably neither method does a particularly good job of estimating off-bottom fishes that are patchily distributed. Visual estimates of fish abundance either from submersibles (Uzmann et al., 1977) or from divers (Kulbicki and Wantiez, 1990) are reported to be higher than those from otter trawl estimates for multispecies assessments, but the reverse was true in this study for rockfishes (see also Krieger, 1993).

The smaller sample sizes required to detect a 50% reduction of the ROV abundance estimates would improve the ability to detect trends in abundance such that a smaller increment of change would be detectable. The degree on improvement would vary with species. Reductions of the order of 1.3 to 19 times in required sample size are sufficient to increase the ability to detect true changes in population size. Much of the decrease in required sample size (and increase in statistical power) comes from the much higher ROV abundance estimates. If samples are drawn from two populations with similar levels of variation, a 50% decrease in abundance of the larger estimate is much larger and therefore easier to detect. Unfortunately, a great deal of variation due to patchiness in fish distribution remains.

For an environmental assessment, the ROV estimates provide a better overall picture of the community than do the trawl estimates. While the similarity in the presence and absence of species in the two methods was surprisingly high, the ROV abundance estimates generally tended to be higher and had lower coefficients of variation. Species that were usually in direct contact with the bottom had much higher ROV abundance estimates than did those captured in the trawl. Small, cylindrically shaped fishes (hagfish, poachers, and eelpouts) had particularly large differences between ROV and trawl abundance estimates, probably owing to escapement under the footrope or through the trawl webbing. The most obvious example of escapement or avoidance was that provided by the red octopus, which was more abundant in the ROV sampling than any fish, but which was not captured by the trawl.

For the commercially important species at these depths (Dover sole, thornyheads, and sablefish), the results were mixed. For Dover sole and thornyheads, ROV abundance estimates were higher and coefficients of variation were lower. For sablefish, abudance estimates were higher for the trawl sampling at 200-m and 600-m depths. Although rockfish at the 200-m depth are not commercially important, the trawl estimates for this taxon were higher, and this is likely to be true of commercially important rockfishes.

Stock assessment integrates patterns of removals and information on year-to-year variation in recruitment from catch-at-age data with mean levels of abundance and longer term trends from survey data (Deriso et al., 1985; Methot, 1990). Using simulations, Kimura (1989) showed that, if survey data are biased, the results can be a precise, but biased, inference regarding the population. The higher ROV abundance estimates mean that trawl estimates are biased too low and that there is actually a larger difference between years of low population size and threshold levels of overfishing set by these assessments. The risk of overfishing is actually lower than that which was assumed. A more dangerous situation arises when bottom trawl estimates are larger than the ROV estimates, as with rockfish (also see Krieger, 1993). Here the difference between years of

low population and threshold levels of overfishing is actually less than that which was realized, a difference that increases the risk of overfishing.

ROV's have the ability to identify the degree of species' attraction to or avoidance of the sampling gear. Three species showed a strong response to the ROV: Pacific whiting, sablefish, and catsharks. Pacific whiting was the only species that was attracted to the ROV (Table 3). These three species are usually observed off-bottom and in motion, rather than resting in contact with the bottom. Fishes that are commonly in motion should be in a better position to respond quickly to stimuli (motion, light, etc.) around them. Understanding and accounting for fish behavior could improve the accuracy of an estimate. For trawl gear, the level of attraction or avoidance is unknown. Anecdotal evidence for attraction (crowding of fish between doors suggested by Krieger [1993]) and for avoidance (net sounder readings of rockfish rising up out of the path of the net [Adams[3]]), have been reported, but there is no simple way of evaluating these phenomena for trawl gear.

While the presence of large seasonal or interannual variation in fish numbers could have introduced bias into the estimates, there is no reason to believe this occurred. None of the 20 most common species captured by the three trawl surveys, which covered almost the entire study period, exhibited a consistent seasonal or overall trend in fish abundance. Also, the consistency of trends in abundance derived from ROV's and trawls from all depths, even though they were sampled at different times, suggests that large varations in abundance were not an important source of bias. However, if this bias had occurred, it would have been a larger problem for the ROV estimates than for the trawl estimates. The ROV samples at depth were taken during one time period, with the exception of the 400-m depth, whereas the trawl samples were taken at all depths during three cruises over nearly the entire time period.

Both ROV and trawl surveys contain additional information that may be critical to the goals of an abundance study. ROV surveys provide much biological information, particularly on habitat and species association. In two instances, we observed feeding behavior. Trawl surveys deliver the fish on deck; for common types of biological studies, such as ageing or food habits, these specimens are critical. In addition, these specimens enable accurate species identification. Identifcation, however, is expected to become less of a problem as video technology improves.

[3] Adams, P. National Marine Fisheries Service, Tiburon Laboratory Southwest Fisheries Science Center, 3150 Paradise Dr., Tiburon, CA 94920. Personal commun., 1986.

Finally, there is the chronic problem of the low statistical power of tests of these abundance estimates owing to large, associated variances. Since increasing the sample size is often not practical, the only alternative is to stratify the sampling more effectively rather than simply on the basis of depth. Better stratification can come only from a greater understanding of the biological factors responsible for fish distributions. An adequate understanding would include the association of fish with microhabitat and the biological behavior of fishes that leads to patchiness. Surveys could then be stratified on the basis of areas where fish are occurring at background levels and in large patches. Trawl surveys have been unsuccessful in achieving such separation. Information gained from the ROV could lead to the biological understanding necessary to achieve more efficient stratification designs.

Acknowledgments

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Abstract.—The impact of predation by staghorn sculpin, *Leptocottus armatus*, on newly settled Dungeness crab, *Cancer magister*, in the Washington coastal estuary of Grays Harbor was studied. Staghorn sculpin are known to be generalist, opportunistic feeders, with relatively high food requirements for estuarine growth during warm summer months. During late spring or early summer, vast numbers of crab megalopae reach the estuary and settle on intertidal flats and in subtidal channels. During the next two months the young-of-the-year (0+) crab population is rapidly reduced by predation, including cannibalism. Crab without appropriate refuge habitat are highly vulnerable to predation by fish, and accordingly survival of young crab is highest in intertidal shell and eelgrass beds. Abundance and summer growth of crab and sculpin within the estuary were documented by monthly trawling surveys (April to August) in 1989. Stomach contents of sculpin were analyzed to characterize the overall summer diet, to note monthly shifts in major prey items within two age classes of sculpin (0+ and 1+), and to contrast sculpin prey consumed in eelgrass with that consumed in shell habitats. The predominant prey species varied across the categories above but generally included ghost and blue mud shrimp, *Neotrypaea californiensis* and *Upogebia pugettensis*, a nereid polychaete (*Nereis brandti*), juvenile Dungeness crab, *Cancer magister*, and sand shrimp (*Crangon* spp.). Some combination of these species composed 85% of the total diet (on the basis of percentage of total Index of Relative Importance; %IRI) across time and between habitats. A comparison of diets of sculpin collected at eelgrass and shell habitats was significantly different; a strong preponderence of 0+ crab were consumed at the shell habitat. *Nereis brandti* was the most important prey for 0+ sculpin, whereas *Neotrypaea californiensis* was the most important for 1+ and older sculpin. The importance of shell as refuge habitat for *C. magister* and the apparent contradiction in the observation that a large number of 0+ crab were taken by sculpin at the shell habitat are discussed.

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Food habits of estuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab, *Cancer magister**

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Staghorn sculpin, *Leptocottus armatus*, are common in major estuaries throughout their range from Baja California through the Gulf of Alaska (Hart, 1974). Young sculpin inhabit brackish water streams and channels and move down into the estuary as they grow larger during their first year. Older juvenile and adult sculpin are broadly distributed throughout estuarine nursery areas utilized by juvenile crab and are known predators of Dungeness crab, *Cancer magister*, within estuaries (Reilly, 1983). Staghorn sculpin have wide gapes and relatively large mouth areas in relation to their size compared with other species of fish predators commonly found in estuaries during the summer.[1,2] They are opportunistic, generalist predators (Jones, 1962; Hart, 1974; Birtwell et al., 1984) and feed heavily on decapod crustaceans such as the yellow shore crab, *Hemigrapsus oregonensis*,[5] the ghost shrimp *Neotrypaea californiensis*, and pea crab, *Pinnixa* sp. (Tasto, 1975; Posey, 1986). Staghorn sculpin are described as visual predators that move onto estuarine tideflats with the incoming tide (Tasto, 1975); their foraging behavior may contribute to the high mortality rate of small 0+ crab (Wainwright et al., 1992).

The Grays Harbor estuary, Washington, contains extensive intertidal tracts of eelgrass and shell that serve as critical nursery areas for young-of-the-year (0+) and one-year-old (1+) Dungeness crab[3] (Gutermuth and Armstrong, 1989; Gunderson et al., 1990; Jamieson and Armstrong, 1991). During high tides in May and June, vast numbers of crab megalopae reach estuaries, settle to the benthos, and metamorphose to the first juvenile instar (J1). Crab settle over broad expanses of the intertidal sandflats

* Contribution 903 of the University of Washington, School of Fisheries, Seattle, WA 98195.

[1] Smith, J. L. 1976. Impact of dredging on the fishes in Grays Harbor. Appendix G *in* Maintenance dredging and the environment of Grays Harbor, Washington. Final Rep. by U.S. Army Corps of Engineers, Seattle District, 94 p.

[2] McGraw, K., and D. A. Armstrong. 1990. Fish entrainment by dredges in Grays Harbor, Washington. *In* C. A. Simenstad (ed.), Effects of dredging on anadromous Pacific coast fishes; workshop proceedings, Seattle, WA, 8–9 Sep. 1988. Washington Sea Grant Program, Univ. Washington, Seattle, WA 98195, 160 p.

[3] Armstrong, D. A., T. C. Wainwright, J. M. Orensanz, P. A. Dinnel, and B. R. Dumbauld. 1987. Model of dredging impact on Dungeness crab in Grays Harbor, Washington, Final Rep. FRI-UW-8702 to Battelle Northwest Laboratories and U.S. Army Corps of Engineers, Seattle, District, Seattle, WA,167 p.

and in subtidal channels but within a few weeks can be found only in areas that afford some refuge[4] (Dumbauld et al., 1993; Fernandez et al., 1993a). First year survival, based on five years of trawl survey data in the estuary (Gunderson et al., 1990), has been estimated at approximately 8% (Wainwright et al., 1992). Different assemblages of predators affect survival of Dungeness crab during each phase of their life history (Reilly, 1983; Stevens and Armstrong, 1985; Thomas, 1985). Estuarine and nearshore fishes, wading birds, and older crab are known to prey upon the young crab instars (Stevens et al., 1982; Fernandez et al., 1993b), causing high mortality rates in the summer months (Wainwright et al., 1992).

Predation, including cannibalism, is considered to be the prime cause of the rapid decline in crab abundance through the summer. Stevens et al. (1982) showed that during years of high 1+ crab abundance, cannibalism can account for a significant portion of 0+ crab mortality. Even early settling 0+ crab are capable of cannibalizing later settlers of the same year class (Fernandez et al., 1993b). However, aside from Reilly's study (1983) in California estuaries, predation by estuarine fish and wading birds has received little attention as a source of crab mortality. Although sea birds are known to take a toll on megalopae[5] and on newly settled crab (Mace, 1983), fish and crab predators are more likely to exert the greatest predation pressure on the highly abundant, small instars during settlement and early development.

In this study, we discuss the estuarine summer feeding patterns of staghorn sculpin with respect to a broad spectrum of crustacean prey but focus on their possible significance as predators of 0+ *C. magister* and on the role of refuge habitat on the basis of spatial patterns of predation in the estuary. A temporal shift in consumption of certain prey taxa is also discussed as indicative of opportunistic feeding by staghorn sculpins with seasonal patterns of prey abundance or with life history events which make prey more susceptible to predators.

Materials and methods

Sampling scheme

Grays Harbor (46°55'N, 124°05'W) is a major Washington coastal estuary of about 8,545 hectares (Gunderson et al., 1988) marked by numerous subtidal channels. These channels extend across extensive sandflats that become exposed and represent 67% of surface area during spring low tides. Refuge habitat is provided by epibenthic shell exposed from remnant *Mya arenaria* and *Crassostrea gigas* bivalve populations and by eelgrass. Shell coverage has been calculated to account for 19% of the total intertidal area,[6] whereas eelgrass (*Zostera marina* and *Z. noltii*) was reported to cover 42% of the tidal flat area.[7]

Staghorn sculpin were collected from Grays Harbor during six sampling trips from April through August 1989. Sampling was timed to coincide with the following periods: April–May prior to the main pulse of annual crab settlement, June (two trips) during recruitment of 0+ crab, and July–August during the post-settlement summer growth period. Two intertidal sandflat sites located about 10 km apart were routinely trawled at high tide as a means of contrasting diet in two common epibenthic habitats of the estuary: an eelgrass (*Zostera* spp.) bed in North Bay, and shell piles (*Mya arenaria*) in South Channel (Fig. 1). In order to ensure reasonable sample sizes of fish for each trip and site (target of $n>20$), two trawls each were conducted at both an intertidal station (during slack flood tide) and at an adjacent subtidal station (at low slack) within 6 h on the same day, and fish were pooled for analyses of differences in diet over time. Additional subtidal trawls were made as time permitted for a total of 9–11 trawls per trip.

All trawl samples were collected with a 3-m beam trawl (Gunderson and Ellis, 1986) deployed from a 7-m Boston Whaler. The net had an effective fishing width of 2.3 m and a 4-mm codend liner to retain juvenile crab and fish. Trawls in subtidal channels were run for about four minutes at a speed of 3.7 to 5.6 km/h. Distance fished was determined by optical range finder fixes between buoys deployed at the beginning and end of each tow (see Gunderson et al., 1990, for details of trawl procedure); such distances ranged from 200 to 350 m. Intertidal tows were made between two staked points 160 m apart. Distance fished and fishing width of net were used to estimate area swept for calculation of catch per unit of effort (CPUE; number per hectare). Trawl contents were characterized as to type of vegetation (e.g. algae,

[4] Armstrong, D. A., L. Botsford, and G. S. Jamieson. 1990. Ecology and population dynamics of juvenile Dungeness crab in Grays Harbor estuary and adjacent nearshore waters of the southern Washington coast. Rep. to U.S. Army Corps of Engineers, Seattle District, Seattle, WA, 140 p.

[5] Armstrong, D. Personal observation at Whitcomb Flats sea gull nesting site, Grays Harbor, WA, May 1988.

[6] Dumbauld, B. R., and D. A. Armstrong. 1987. Potential mitigation of juvenile Dungeness crab loss during dredging through enhancement of intertidal shell habitat in Grays Harbor, Washington. Final Rep. FRI-UW-8714 to U.S. Army Corps of Engineers, 64 p.

[7] Smith, J., L. D. R. Mudd, and L. W. Messmer. 1977. Impact of dredging on the vegetation in Grays Harbor. Appendix F *in* Maintenance of dredging and the environment of Grays Harbor, Washington. Final Rep. by U.S. Army Corps of Engineers, Seattle District, 94 p.

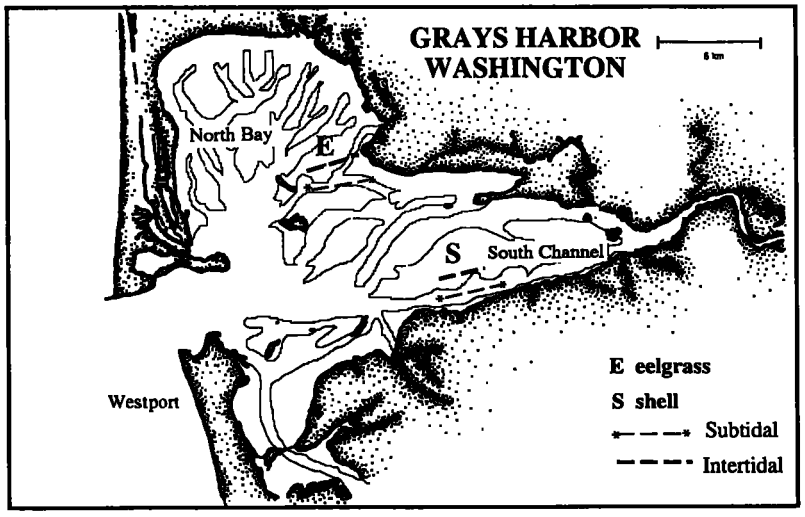

Figure 1

Grays Harbor, Washington, sampling locations for staghorn sculpin, *Leptocottus armatus*, and Dungeness crab, *Cancer magister*, at eelgrass (E) and shell (S) sampling sites. Bold dashed line denotes intertidal trawls and lighter dashed line indicates subtidal channel trawls.

eelgrass, terrestrial leaves), shell, and underlying substrate. All fish and crab were sorted from the catch, identified to species, and counted. Crab were measured (carapace width [CW] inside the 10th lateral spine), sexed, and returned to the water. Staghorn sculpin were picked from the catch and killed. Their body wall was slit, and the fish were preserved in 10% formalin in sea water and later transferred to 70% ethanol in the lab for measurement (total length, TL) and stomach content analyses.

Length-frequency data for sculpin and crab were used to determine instar and year-class composition. Crab length-frequency histograms by trip were used to establish the presence of the 1989 year class of 0+ crab from first tentative appearance in May, at peak settlement in early June, and at the time of summer growth through August. Size modes for crab instars (juvenile crab 6–40 mm CW) were visually determined from length-frequency histograms (hereafter crab instars 1 through 7 will be referred to as J1–J7 and conform to instar sizes specified by Wainwright and Armstrong [1993] and Dinnel et al. [1993]). Evaluation of size ranges and modes as compared with stage (CW for crab; TL for sculpin, Tasto, 1975) were used to set the upper size limits for 0+ and 1+ age classes each month during the summer.

Sculpin gape measurements

Sculpin mouth widths (measured for 466 sculpin) were used as an index of mouth gape size. The mouth of a preserved specimen was gently pried open as far as possible and the internal distance from the intersections of upper and lower jaws was measured. Since fish body lengths are more commonly reported as standard lengths (SL), sculpin total lengths (TL) were converted to standard length for a discussion of mouth gape to body length relationship[8]:

$$SL = 0.87338\ TL - 2.7584$$
$$(r^2 = 0.995,\ n = 53).$$

Stomach content analyses

Stomach contents of all staghorn sculpin from a trawl were examined up to a total of 20 fish. When catches were higher, the fish were separated into 5-mm size intervals, then proportionally subsampled until a total of 20 fish were selected for stomach analyses. Sculpin were measured (TL), blotted on paper towels, and weighed wet to the nearest 0.1 g. Then their stomachs were removed, blotted, and weighed with and without contents to derive stomach content weight. An estimate of relative stomach fullness was derived by using six categories corresponding to empty, 1/4, 1/2, 3/4 full, full, and "distended." In the latter case, quantity of prey within the stomach resulted in pronounced distention of the body wall beyond the normal lines and curvature of the fish. Sculpin stomachs were analyzed to document the frequency of occurrence of Dungeness crab, the overall proportion of the diet attributed to major prey categories, and the relationship between sculpin size and size of juvenile crab prey.

Food items were generally identified to species unless obscured by digestion. Prey species consumed frequently were analyzed as a distinct prey category, but species that were consumed infrequently were combined to form a more general prey taxon that also included prey items obscurred by digestion. As an example, the amphipod *Eogammarus confervicola* was recorded as a separate prey category owing to its high frequency of occurrence, but several species of fishes (*Gasterosteus aculeatus*, *Lumpenus sagitta*, *Cymatogaster aggregata*, *Leptocottus armatus*, *Pleuronectes vetulus*, and *Citharichthys* sp.) were consumed infrequently and were thus grouped as "fish." Analysis of stomach content data was done by

[8] Williams, G. Pacific Estuarine Research Labs., San Diego State Univ., San Diego, CA. Unpubl. data, 1991.

calculation of a modified form (Stevens et al., 1982) of the Index of Relative Importance (IRI) (Pinkas et al., 1971; Hyslop, 1980) based on estimated food weight rather than food volume. For a particular prey category, an IRI value was calculated as

$$IRI = (NC + GC)FO,$$

where *NC* (numerical composition) is the number of a particular prey item divided by the total number of all prey items in that sample multiplied by 100, *GC* (gravimetric composition) is the combined weight of a particular prey item divided by the total weight of all stomach contents in the sample multiplied by 100, and *FO* (frequency of occurrence) is the number of stomachs from a sample containing a given prey item divided by the total number of fish sampled multiplied by 100. IRI values from all prey categories were summed to derive a grand total IRI value. The relative importance of each prey category was then expressed as a percentage of this total IRI (hereafter referred to as %IRI).

Data analysis

Sculpin stomach content data were analyzed from four perspectives. First, an overall summer diet for staghorn sculpin was derived by combining all fish from both sites (E and S), inter- and subtidal, across months to determine dominant prey taxa. Second, a temporal comparison of sculpin diets from late spring through summer was made by examination of sculpin stomachs grouped by sampling trip. Third, the effect of sculpin size (and thus age) on diet was investigated for two size groupings derived from length-frequency histograms of sculpin caught during the six trips. Size ranges and age equivalents were set from the literature (Anaheim Bay, CA, [Tasto, 1975]; Yaquina Bay, OR [Bayer, 1985]) to group fish by age class as either 0+ (n=210) or ≥1+ (n=256). IRI analyses were run separately on 0+ and ≥1+ sculpin to determine whether there were changes in diet composition based on predator size. Fourth, prey composition of sculpins feeding at different epibenthic habitats was compared by examining diets of fish collected from the intertidal eelgrass site (n=55) and diet of sculpin caught at the intertidal shell site (n=44).

To compare dietary overlap of sculpin of the two size/age categories or of sculpin collected at the two different habitats (eelgrass vs. shell), Schoener's (1970) index of overlap (S_{IO}) was calculated as

$$S_{IO} = 1 - 0.5\left(\sum_{j=1}^{n}\left|P_{x_i} - P_{y_i}\right|\right),$$

where P_{xi} = the proportion of prey i (%IRI) in the diet of sculpin of size x (or from habitat x);
P_{yi} = the proportion of prey i (%IRI) in the diet of sculpin of size y (or from habitat y),
and j = the number of prey types. An overlap value of $S_{IO} \geq 0.6$ (Schoener, 1970) was considered significant in this study.

Results

Overall summer diet

A total of 482 staghorn sculpin stomachs were collected from April to August 1989, of which 458 had some stomach contents. Sculpins averaged 118 mm TL (range: 61–215 mm TL) during the five-month sampling period (Table 1). Mouth gape width ranged from 13 to 17% of standard length (gape width = 0.1818 SL–2.6487, r^2=0.909; Fig. 2). Average fish length and weight varied by sampling month and were generally greater in April and May when samples were composed primarily of 1+ fish, decreased in June as 0+ sculpin moved into the sampling sites, and increased in July and August as individuals grew through summer (Fig. 3; Table 1). Size-frequency data indicated the presence of two modes equivalent to 0+ and 1+ age classes. Young of the year ranged from 60 to 94 mm TL in April and had grown to 75–119 mm by August (Fig. 3). For purposes of analyses of diet based on size-age composition of sculpin, 118 mm TL was used as the boundary between 0+ and 1+ groups. These size-age categories were corroborated by otolith annuli determinations of a similar size range of staghorn sculpins from Vancouver Island, British Columbia, estuaries by Mace (1983, p. 369).

The mean number of individual prey items per sculpin was 3.4, and gut fullness was generally high; 75% of all stomachs examined were rated 50% full or greater whereas fewer than 5% were empty (Fig. 4). Sculpin stomach contents included 23 prey taxa (Armstrong, 1991) which were grouped into 14 prey categories for IRI analyses (Table 2). Principal categories of sculpins' overall summer diet (% IRI) were the polychaete *Nereis (Neanthes) brandti* (30% IRI), the ghost shrimp *Neotrypaea californiensis* (27% IRI), sand shrimps *Crangon* spp. (13% IRI, including *C. franciscorum*, *C. nigracauda*, and *C. stylirostris*), juvenile *Cancer magister* (9% IRI), and the mud shrimp *Upogebia pugettensis* (6% IRI).

Temporal changes in diet

Stomach contents were analyzed on a per trip basis to note change in sculpin diet over the course of the

Table 1

Summary data for groups of staghorn sculpin, *Leptocottus armatus*, sampled during monthly trips and for all sculpin combined from April to August 1989 from Grays Harbor, Washington, for stomach content analysis. During each trip all sculpin were caught from both sites, eelgrass and shell habitats, inter- and subtidal trawls combined. SD = 1 standard deviation, TL = total length.

	Fish size (mm TL)			Fish wet wt. (g)			Mean gape			
Dates	Mean	1 SD	Range	Mean	1 SD	Range	(mm)	No. stomachs examined	% empty	Mean no. prey per sculpin
Apr 7–8	113	21	(61–190)	17	11	(2–70)	14.8	111	0	7.1
May 6–7	138	27	(94–215)	36	28	(9–133)	18.9	38	3	2.5
Jun 4–6	108	25	(72–173)	17	14	(3–62)	14.7	62	0	2.7
Jun 18–19	99	19	(70–162)	12	9	(4–55)	12.2	126	4	2.3
Jul 19–20	121	23	(78–169)	21	13	(4–53)	16	61	11	1.4
Aug 15–18	127	28	(84–213)	24	19	(6–102)	16.7	84	8	3.3
Combined grand mean	118	27	(61–215)	20	17	(2–133)	15.6	482	5	3.4

summer. Entry of small sculpin into our sampling areas in June was inferred by the decrease in mean sculpin size and wet weight (Table 1) and supported by examination of length-frequency histograms (Fig. 3).

Diet composition changed appreciably from month to month. During the spring, sculpin primarily consumed the gammarid amphipod *E. confervicola* (46% IRI), *Crangon* spp. shrimp (24% IRI), and fish (13% IRI) in April (Fig. 5), whereas the nereid polychaete *N. brandti* (34% IRI), the thalassinid shrimps *N. californiensis* (45% IRI), and *U. pugettensis* (12% IRI) were the most abundant prey in stomachs in May (Fig. 5). Sculpin consumed few crab, reflecting the relative scarcity of 0+ instars in late spring; J1 instars were found in only 5% of sculpin stomachs in May and represented less than 1% IRI. Minimal settlement of Dungeness crab during May was indicated by low catches of 0+ crabs (Fig. 6; only three J1 were caught in 10 trawls).

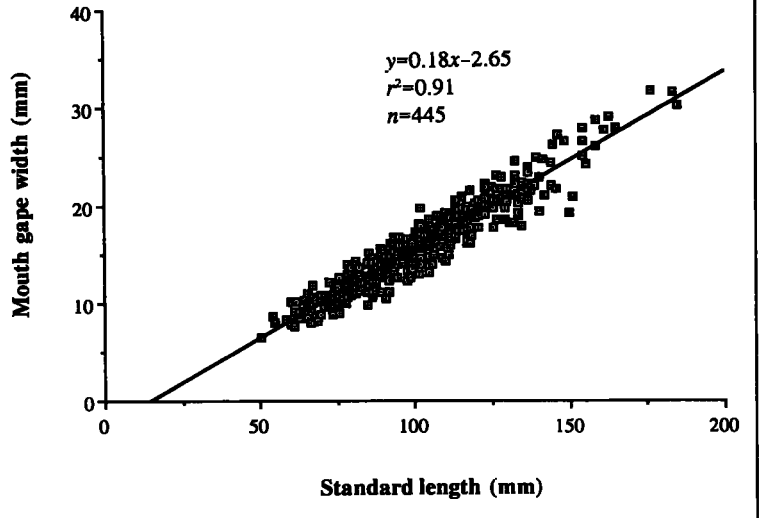

Figure 2

Staghorn sculpin, *Leptocottus armatus*, mouth gape width (y) to standard body length (x) relation based on 445 sculpin from Grays Harbor, Washington, April–August 1989.

In early June, juvenile Dungeness crab recruited to the estuary (Fig. 6) and became the second most important diet category (24% IRI, Fig. 5). The nereid polychaete *N. brandti* was first in dietary importance, accounting for 59% IRI, and *Crangon* spp. shrimp ranked third (10% IRI) in early June. The major pulse of 0+ crab settlement had occurred during late May–early June (after the mid-May sampling; Fig. 6) and thus J1 and J2 crab had become readily available prey by the beginning of summer. Nereid polychaetes continued as the most important prey item through mid-June (88% IRI), whereas *C. magister* juveniles accounted for only 4% IRI and were consumed by 24% of the sculpin examined.

During the mid and later part of summer, decapod crustaceans represented the majority of staghorn sculpin diet. In July and August nereid worms were rarely found in stomach contents, but thalassinid shrimp, *N. californiensis* and *U. pugettensis*, together totalled 70% IRI in July and 54% IRI in August (Fig. 5). Juvenile crab accounted for 15% and 13% IRI of

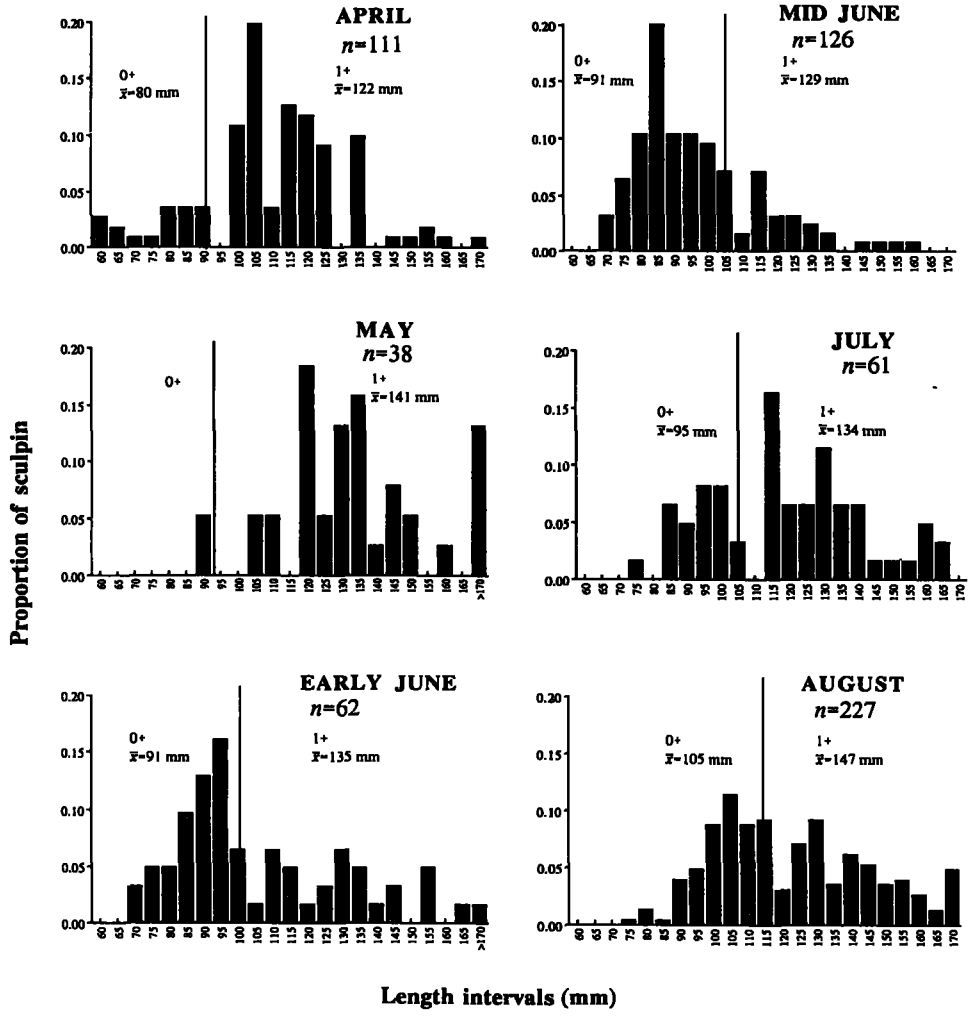

Figure 3

Staghorn sculpin, *Leptocottus armatus*, length-frequency histograms and inferred age classes (0+ and 1+ and older) from Grays Harbor, Washington, April–August 1989. Vertical line indicates upper size cut-off of 0+ from 1+ sculpin. Mean sizes of the age class are given by $\bar{x}$, n = total number of fish examined, both age classes combined.

sculpin diets during these months and *Crangon* spp. for 10% and 11% IRI.

Sculpin age-class and prey composition

Sculpin length-frequency histograms by trip were examined and fish were separated into two age groups based on size (Fig. 3). The diets of 0+ and ≥1+ sculpin were compared to determine whether there were differences in prey composition based on fish size. Both sculpin age groups had the same proportion of empty stomachs (5%) and the same mean number of prey species (3.4) per predator, indicating similar feeding success rates. Small (0+) sculpins primarily consumed *N. brandti* (50% IRI), *N. californiensis* (13% IRI), *Crangon* spp. (11% IRI), *C. magister* (9% IRI), bivalve siphon tips, and miscellaneous or unidentified crustaceans (5% IRI each; Fig. 7). Larger sculpins consumed less *N. brandti* and crangonid shrimp (23% and 5% IRI) but more thalassinid shrimp (*N. californiensis* [31% IRI] and *U. pugettensis* [12% IRI]) and large gammarid amphipods (*E. confervicola* [8% IRI]). Dietary overlap was significant (S_{IO}=0.6). Sculpins over the entire size range sampled (70–215 mm TL) consumed young Dungeness crab (9% of IRI in the summer diet of both

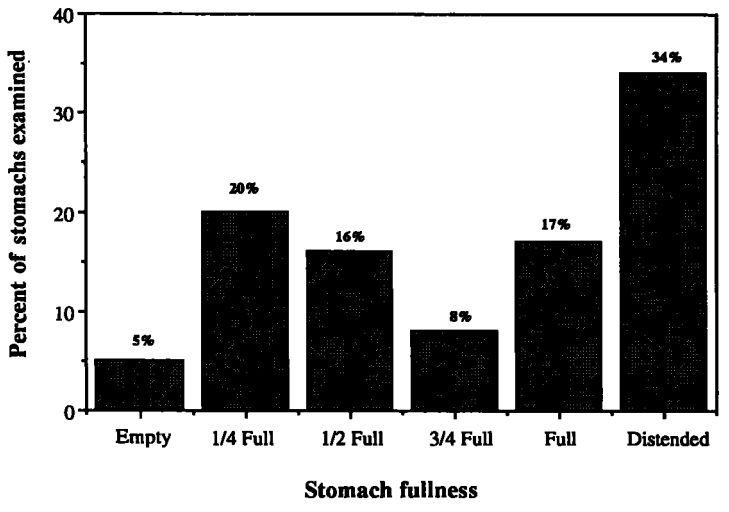

Figure 4

Relative-frequency histogram of staghorn sculpin, *Leptocottus armatus*, stomach fullness. All sculpin (n=482) from Grays Harbor, Washington, April–August 1989.

Table 2

Summer diet composition of staghorn sculpin, *Leptocottus armatus*, from Grays Harbor, Washington, all data combined, April–August 1989. Values are percent composition by number (%NC), weight (%GC), frequency of occurrence (%FO), and percent of total Index of Relative Importance (%IRI) by prey categories. Bold values indicate the five most important prey categories as measured by % total IRI. The total cumulative percentage of the diet comprised by those five categories appears in the bottom line of the table.

Prey category	%NC	%GC	%FO	%IRI
Nereis brandti	9	30	30	**30**
Neotrypaea californiensis	9	27	30	**27**
Crangon spp.	12	7	27	**13**
Cancer magister	9	7	22	**9**
Upogebia pugettensis	3	17	11	**6**
Eogammarus confervicola	13	<1	12	4
Misc./unid. crustacea	9	2	12	3
Fish	4	6	12	3
Bivalve siphon tips	10	<1	10	2
Misc./unid. amphipods	6	<1	7	1
Allochestes spp.	5	<1	5	<1
Corophium salmonis	6	<1	5	<1
Misc./unid. polychaetes	2	<1	5	<1
Algae	3	<1	8	<1
Total cumulative percentage of diet within top 5 categories				**85% IRI**

0+ and 1+ sculpin). Whole bodies of crab instars, J1–J4 (mean CW: 6–21 mm), were found in sculpin stomachs (Fig. 8).

Habitat comparison

Sculpin diets from two intertidal sites dominated by eelgrass and epibenthic shell (Fig. 1; E and S) were compared. At each site two trawls per trip were made at high tide after sculpin had moved from the adjacent subtidal channels up onto the flats to feed. Mean number of individual prey items per predator (about 3) was the same at both sites, but the percentage of empty guts was significantly lower among sculpin caught over the eelgrass compared with the percentage of empty guts among sculpin caught over shell habitat (2% vs. 11%; approximation of Fisher Exact Test, Z=1.98, P=0.024, Zar, 1984). Mean length of sculpin captured at the eelgrass and shell sites were 104 ±24 mm (1 SD) and 123 ±27 mm TL, respectively. The most pronounced difference in sculpin diets between sites was that juvenile *C. magister* composed 77% IRI over shell habitat but only 5% over eelgrass (Fig. 9). Frequency of occurrence of crab in sculpin stomachs was 3.6 times greater over shell habitat than over eelgrass habitat (69% FO vs. 19% FO). In addition to *C. magister*, the other top diet categories at shell habitat were ranked as *N. californiensis* (7% IRI), *U. pugettensis* (6% IRI), *N. brandti* (5% IRI), and unidentified amphipods (2% IRI). In contrast, primary prey at the eelgrass habitat were *N. californiensis* (27% IRI), *N. brandti* (25% IRI), and *Crangon* spp. (24% IRI). *Cancer magister* and bivalve siphons represented 5% and 4% IRI respectively (Fig. 9). There was not significant dietary overlap in sculpin diets between the two habitats (S_{IO}=0.2).

Staghorn sculpin and 0+ crab densities

Relative density at intertidal and subtidal channels To assess the availability of crab as prey for sculpin predators, relative density was calculated for both sculpin and 0+ crab to contrast intertidal and subtidal eelgrass and shell habitats. At either site, relative crab densities were initially higher on the intertidal compared with adjacent subtidal channels during peak crab settlement in June. Intertidal densities in shell habitat at South Channel were about 9,500/ha in early June and declined to 6,000/ha later in the month. However, in the adjacent subtidal channel crab densities were less than 100/

ha where the primary epibenthic cover is allochthonous leaves, branches, and bark. Initial mean crab densities were almost four times higher in the intertidal shell than at the intertidal eelgrass site (Fig. 10; 9,500 crab/ha vs. 2,500 crab/ha, *t*-test, t=2.4, P=0.136). At the eelgrass site, intertidal and subtidal crab densities were comparable by mid-June at about 2,500/ha. As the summer progressed, 0+ crab density declined in the intertidal at both the shell and eelgrass sites to about 900/ha and 320/ha, respectively, but increased in the subtidal channel adjacent to the shell habitat (Fig.10). The subtidal epibenthos at the shell site in South Channel is composed predominately of wood, bark, and leaves, whereas the subtidal benthic cover at the eelgrass site is primarily shell, eelgrass, and algae; these differences probably contribute to the density differences in mid-June between the two locations.

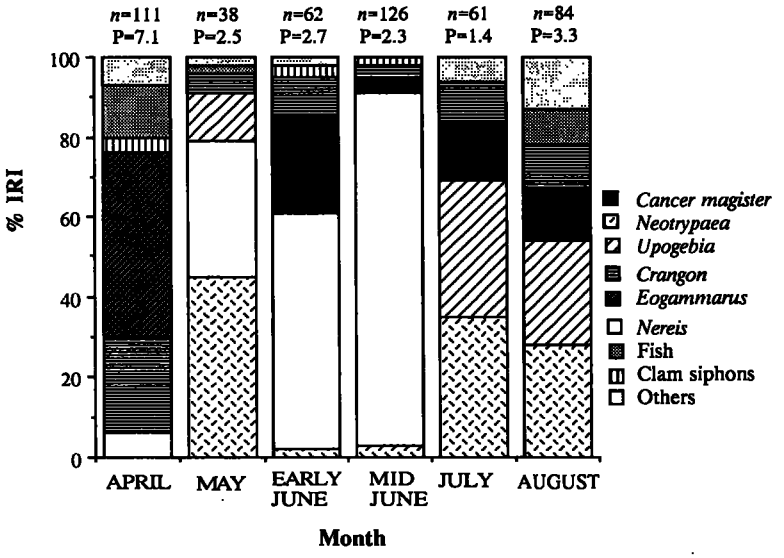

Figure 5

Diet composition of staghorn sculpin, *Leptocottus armatus*, from Grays Harbor, Washington by month, expressed as % IRI. n = number of fish examined and P = mean number prey per predator.

Relative density at shell habitats Sculpin densities at the shell habitat were always higher in the intertidal areas than in the subtidal channel except in mid-June (Fig. 10). In contrast, at the eelgrass site there were higher densities of sculpin in subtidal than in intertidal areas in early June (230 vs. 40 sculpin/ha), but by August higher mean sculpin densities occurred in the intertidal areas (138 vs. 30 sculpin/ha).

Discussion

Importance of crustaceans as prey

Juvenile staghorn sculpins have been reported to feed heavily on small crustaceans including amphipods and isopods. Studies in Tomales Bay, California (Jones, 1962), and the San Juan Islands, Washington (Thornburgh, 1980), have shown that juvenile sculpin primarily consume amphipods, especially *Corophium* spp., mysids, and shrimp. Smith (1980) reported that juvenile staghorn sculpin (20–80 mm TL) in Skagit Bay, Washington, consume the amphipods *Corophium salmonis* and *Anisogammarus confervicolus*, tanaids, and the polychaete *Neanthes limnicola*. Dinnel et al. (1990) showed ontogenetic diet shifts for staghorn sculpin from Padilla Bay, Washington. The smallest sculpin (45–79 mm TL) consumed amphipods and isopods; sculpin 80–119 mm consumed amphipods, isopods, and crabs; and the largest sculpin (≥120 mm) consumed isopods, crabs, and fish. While juvenile sculpin less than 60 mm TL were not sampled in the present study, no significant diet shift was noted for the two size groups (60–119 mm and ≥120 mm) of the Grays Harbor prey assemblage, although relative importance of items differed between the size groups. Smaller fish did consume a relatively higher proportion of polychaetes, whereas larger sculpins consumed more thalassinid shrimp (Fig. 7).

Other studies have shown that adult staghorn sculpins consume crustaceans as a major portion of their diet when they are available. Dinnel et al. (1990) found that amphipods, isopods, and an assemblage of crab species (including *C. magister* and *Pinnixa* spp.) composed a majority (79% IRI) of the August diets of staghorn sculpins from Padilla Bay, Washington. Data presented by Jones (1962) and Boothe (in Tasto, 1975) showed that the majority of staghorn sculpin diet (92% IRI) consisted of decapod crustaceans, including *Crangon* spp., *Upogebia pugettensis*, and a crab assemblage of *Cancer* sp., *Hemigrapsus sp.*, *Pinnixa* sp., and *Scleroplax* sp. Year-round sampling in Anaheim Bay, California, revealed that sculpin consumed primarily decapod crustaceans (78% of the diet by weight) including *N. cali-*

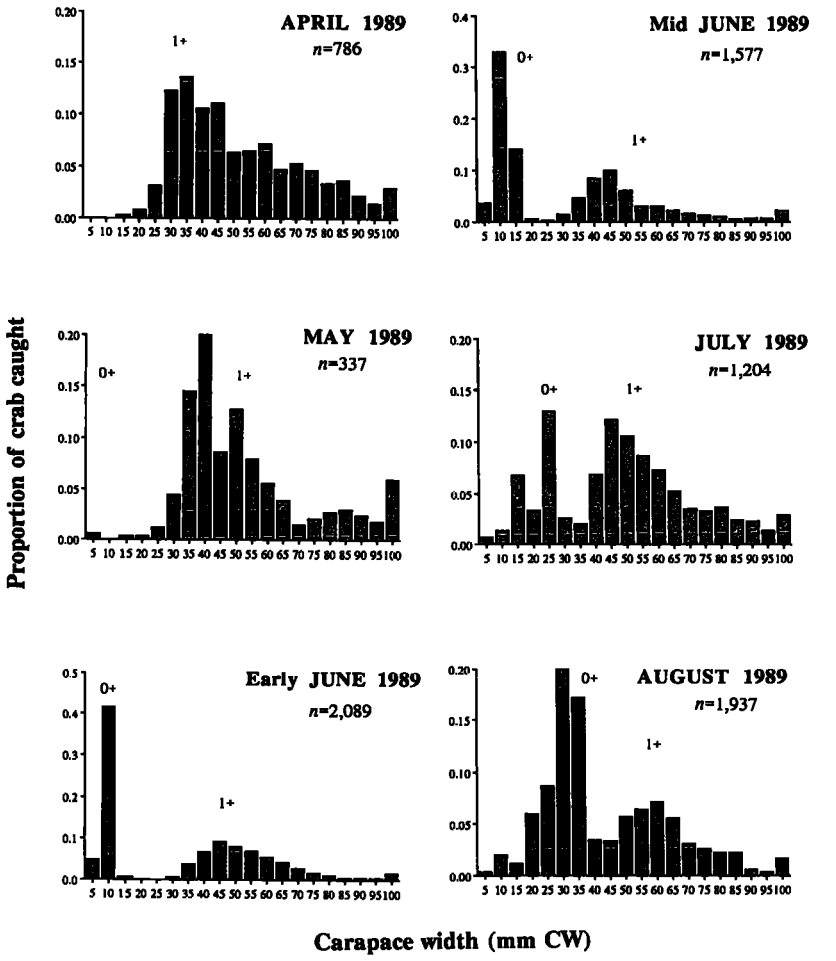

Figure 6

Dungeness crab, *Cancer magister*, length-frequency histograms from Grays Harbor, Washington, April to August 1989. Note first occurrence of 0+ crab in May (6 mm CW) and peak settlement in early June. Summer growth of 0+ crab is evident by 0+ size modes attaining 30–35 mm CW by August.

forniensis, H. oregonensis, and pea crabs, *Pinnixa* spp. (Tasto, 1975). A multi-species assemblage of crab including *Pugettia producta, Cancer productus* and *C. gracilis, Pinnixa* spp., *Scleroplax granulata* (pea crabs), *Hemigrapsus nudus, H. oregonensis,* and *Pagurus* spp. accounted for 25–30% of the spring diet (by volume) of staghorn sculpins >100 mm TL in an estuary of Vancouver Island, British Columbia (Mace, 1983).

The summer diet of staghorn sculpins from Grays Harbor, Washington, corroborates Tasto's (1975) observation that the diet of staghorn sculpin >70 mm TL consists of crustaceans, especially decapods including ghost and mud shrimp (*N. californiensis* and *U. pugettensis*), sand shrimp (*Crangon* spp.), and seasonally abundant 0+ *Cancer magister*. From IRI analysis, it was determined that Dungeness crab represented about 9% of the overall total summer diet of sculpin. Over 30% of all staghorn sculpin collected during June and 23% during July and August had 0+ Dungeness crab in their stomachs. Two other decapods that composed even greater proportions of the overall sculpin summer diet were *Neotrypaea californiensis* and *Crangon* spp. (27% and 13% IRI, respectively).

Other prey

Staghorn sculpin also consume prey species such as nereid polychaetes, fish, and bivalves that are seasonally abundant and readily available (see Gunderson et al., 1990, for list of infaunal and epifaunal prey in Grays Harbor). These sculpin have relatively plastic feeding behavior and their diet changes month to month, fluctuating with relative prey abundance and accessibility. Despite this plasticity, the majority of this species' diet (85–99% IRI) generally consisted of only 4 or 5 prey species (Fig. 5; Table 2). In April, before crab were available, sculpin consumed amphipods, especially *E. confervicola*, and *Crangon* spp. shrimp. Nereid polychaetes and the thallassinid shrimp *Neotrypaea californiensis* were primary prey in May. Dungeness crab were incorporated into the diet as they settled in June and were ranked second in IRI importance after *N. brandti*.

The late spring or early summer predominance of *N. brandti* polychaetes in the diet of sculpin was somewhat unexpected because polychaetes have not often been reported as a major diet item by other researchers from Washington (Smith, 1980; Thornburgh, 1980; Dinnel et al., 1990), or British Columbia (Mace, 1983), although they are mentioned as prey among fish from California (Jones, 1962; Tasto, 1975). The importance of this polychaete during spring and early summer to sculpin in Grays Harbor suggests that adult worm reproductive activity (Bass and Brafield, 1972; Giese and Pearse, 1975; Durchon, 1984) might make them vulnerable to sculpin preda-

tion at this time of year. We examined well-preserved specimens of this polychaete from stomach contents but found all were immature. High predation on immature stages of *N. brandti* may indicate worms are leaving their burrows to disperse as described by Dean (1978). By July and August, the behavior of the polychaetes may have changed, or their abundance may have declined since worms were rarely observed from stomach contents during those months.

Dungeness crab

Predation on 0+ Dungeness crab by sculpin is of interest because of the substantial commercial value of the *C. magister* fishery from northern California through southeast Alaska (Botsford et al., 1989) and because of the ecological implications of this estuarine predator-prey relation that is dependent on the annual arrival of oceanic crab larvae. Estuaries are important nursery grounds for 0+ crab (Cleaver, 1949; Tasto, 1983; Gunderson et al., 1990) and provide refuge by means of several habitats including eelgrass and epibenthic shell (Stevens and Armstrong, 1985; Gunderson et al., 1990; Jamieson and Armstrong, 1991; Dumbauld et al., 1993). Fernandez et al. (1993a) demonstrated that megalopae and newly settled 0+ *C. magister* prefer heavy shell habitat over eelgrass, mud with scattered shell, or bare mud. In addition, field tethering of crab in Grays Harbor showed that shell provided the best protection from predation compared with other habitats and that crab tethered with attached hooks were most often attacked by staghorn sculpin.

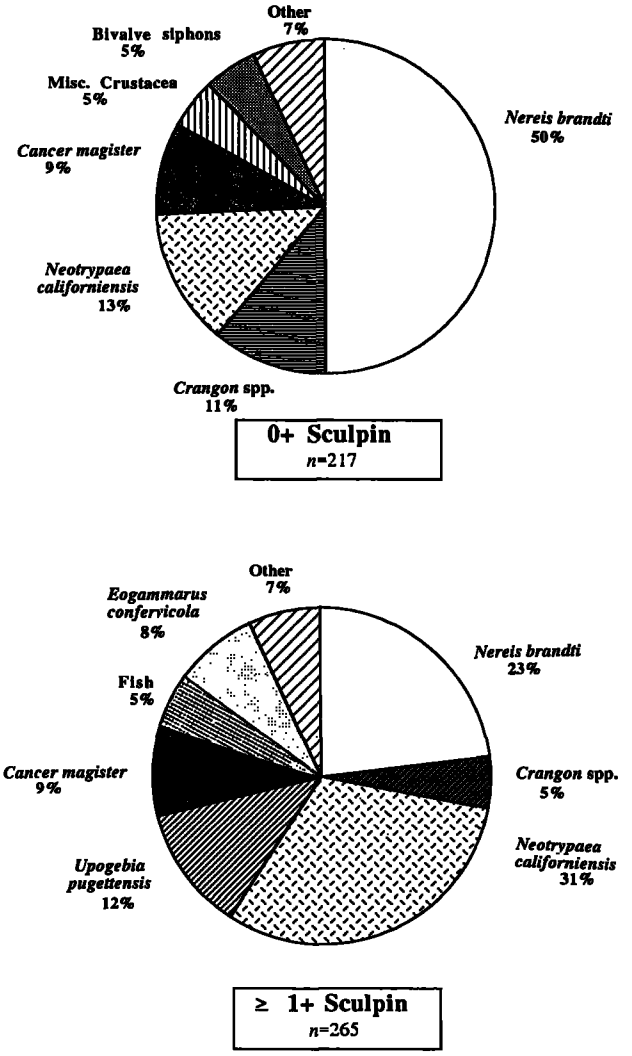

Figure 7

Staghorn sculpin, *Leptocottus armatus*, diet composition from Grays Harbor, Washington, expressed as %IRI, by age class; 0+ and ≥1+ sculpin. All data were combined from April to August 1989.

During peak crab settlement in early June, juvenile crab were found in 42% of the sculpin stomachs examined and represented 10% of the total diet by weight (%GC), or 24% of IRI (Fig. 5). At this time crab are highly vulnerable to predation; the small J1 and J2 instars (6–11 mm CW) are very abundant (over 100/m^2; Fernandez et al., 1993b), compete for limited refuge habitat, and molt frequently (every 2–3 weeks; Wainwright and Armstrong, 1993). The temporal pattern of 0+ intertidal density is consistent with inferences regarding both the rapid predation of much of the 0+ crab population shortly after settlement and with the relative importance of epibenthic shell as a refuge to ensure some survival of the year class. From early June to July, 0+ density decreased an order of magnitude at both the intertidal shell and eelgrass sites as measured by trawl, but density was generally about three times higher over shell habitat compared with eelgrass habitat (Fig. 10). This difference in density between the two habitats is likely much greater than that indicated by the trawl data. Net efficiency is unknown, but the gear was designed to operate on a fairly uniform sand-mud substrate (Gunderson and Ellis, 1986) and, we assume, is less efficient over the shell habitat compared with eelgrass habitat (although much shell is taken in trawls). More importantly, the net "integrates" animals and material along the trawl path and cannot provide distinctions over smaller spatial scales of highly heterogeneous habitat such as intertidal shell. We know from previous intertidal work done in Grays Harbor that

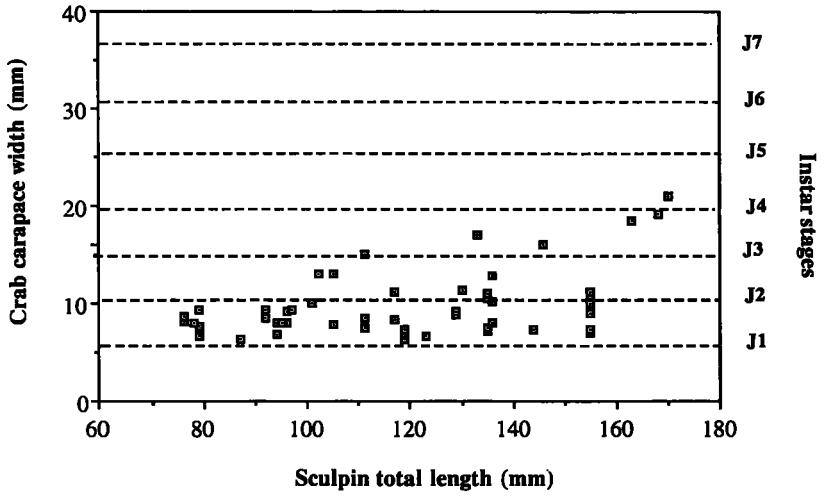

Figure 8

Relationship between body length (TL) of staghorn sculpin, *Leptocottus armatus*, predators and carapace widths of Dungeness crab, *Cancer magister*, instars consumed. Left axis shows mean sizes of instars J1–J7 (dotted lines) from Wainwright and Armstrong (1993).

megalopae settle and that J1 instars occur initially on both open tideflats and in refuge materials (e.g. shell, eelgrass) but are absent from the former within several tidal cycles and are virtually never found on open flats thereafter[9] (Dumbauld et al., 1993). Detailed excavation of shell patches at low tide reveal post-settlement densities of J1 in excess of 100/m^2, but only a few per m^2 in eelgrass (Fernandez et al., 1993a), which suggests that trawl data collected at high tide are likely a substantial underestimate of 0+ crab in shell compared with crab in eelgrass.

These observations reflect a paradox indicated by the data. Higher apparent crab consumption was measured among sculpin collected from the shell habitat (77% IRI) than from the eelgrass (5%) (Fig. 9), inconsistent with the notion that shell provides critical refuge habitat for small crab instars. The mean density of 0+ crab from eelgrass intertidal trawl sites decreased by an order of magnitude from 2,455 crab/ha in early June to 280 crab/ha in mid-July (Fig. 10). During the same period, mean 0+ crab density in shell habitat decreased from 9,452 crab/ha to 874 crab/ha, reflecting migration into the channels (Wainwright, 1994) and the impact of predation including cannibalism (1+ on 0+ instars [Stevens et al., 1982]; early 0+ on later 0+ [Fernandez et al. 1993b] fish on 0+ crab [Fernandez et al. 1993a]). There appears to be a short time period during peak crab settlement when staghorn sculpin eat many small instars, especially those that settle on bare sand or mudflats. In this respect Dungeness crab survival throughout much of the bay is dependent upon the availability of suitable refuge habitat[2,10] (Fernandez et al., 1993a) as has been found for juveniles of other decapod species (Herrnkind and Butler, 1986; Barshaw and Lavalli, 1988; Howard, 1988; Warren, 1990).

This pattern may be explained by the short time scale of settlement and rapid predation on small instar crab (especially J1–J2). A possible explanation for the difference in observed crab consumption by sculpin between the two habitats is that crab settlement in eelgrass or on open tideflats is predated very rapidly and depleted from those areas compared with crab settlement in the shell habitat. Pulses of cohorts could be severely reduced in much less time than the interval between sampling trips and thereafter effectively be unavailable to sculpin in certain areas of the estuary because of virtual removal. Crab that recruit to areas of extensive shell may provide a more stable and persistent prey basis as the dynamics of small instars (agonistic interactions and foraging) make them vulnerable on the exterior of the shell matrix or as they move short distances between shell piles. Predation by sculpin on J1–J4 instars in shell habitats may occur over a longer period, thereby increasing the likelihood that sculpin in our samples contained crab later in the summer, long after they were depleted from less protected areas of open mud and light cover of eelgrass. This would be reflected both in greater numbers of crab consumed and in greater frequency of occurrence

[9] Armstrong, D. A., K. A. McGraw, P. A. Dinnel, R. M. Thom, and O. Iribarni. 1991. Construction dredging impacts on Dungeness crab, *Cancer magister*, in Grays Harbor, Washington, and mitigation losses by development of intertidal shell habitat. Final Rep. FRI-UW-9110 to U.S. Army Corps of Engineers, Seattle District, Seattle, WA, 63 p.

[10] Doty, D., D. A. Armstrong, and B. R. Dumbauld. 1990. Comparison of carbaryl impacts on Dungeness crab (*Cancer magister*) versus benefit of habitats derived from oyster culture in Willapa Bay, Washington. Univ. Washington, Fisheries Res. Inst., Seattle, WA. Rep. FRI-UW-9020, 69 p.

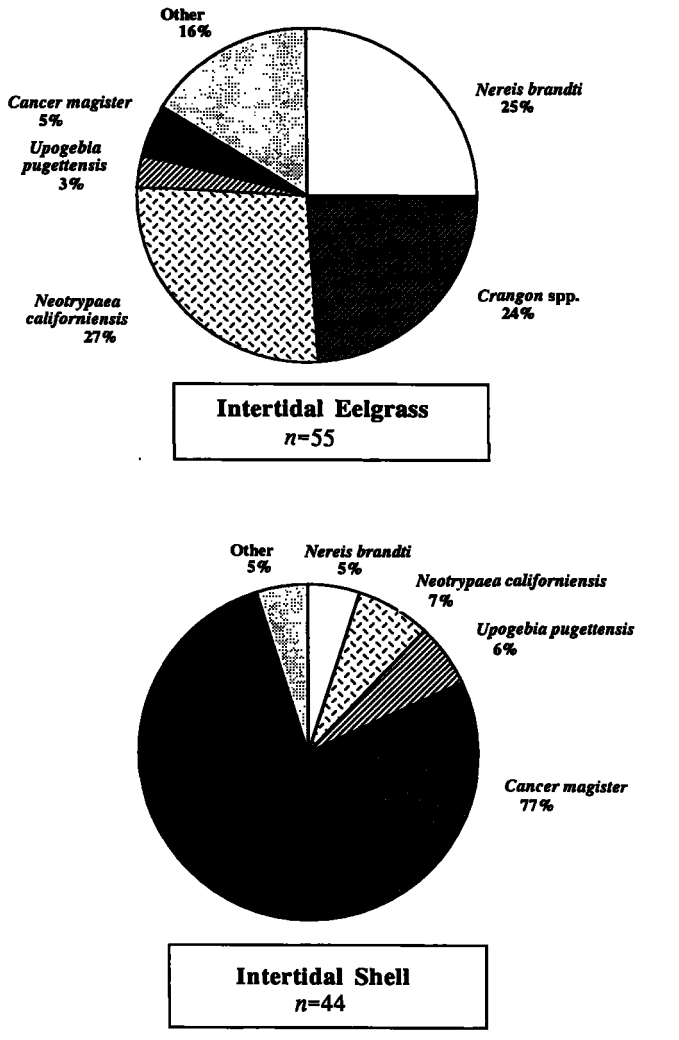

Figure 9

Staghorn sculpin, *Leptocottus armatus*, diets, expressed as % IRI, from intertidal eelgrass and intertidal shell habitats, Grays Harbor, Washington. All data combined, April to August 1989.

in sculpin sampled from the shell habitat (higher %NC and %FO in the IRI calculation).

Size at which 0+ crab were no longer vulnerable to sculpin predation was hypothesized to be about 25 mm CW (about instar J5) (Reilly, 1983) based on mouth gape width of the most prevalent size sculpin (gape limited predation [Zaret, 1980]). Theoretically, small crab newly settled to the estuary would be available and vulnerable to sculpin predation for much of their first full summer (as J1-J6), whereas 1+ crab resident in the estuary during summer would be too large (50–100 mm CW, Fig. 6; Stevens and Armstrong, 1985; Gunderson et al., 1990) for staghorn sculpin to consume. These assumptions were confirmed because only J1–J4 (below 25 mm max. CW) were consumed (Fig. 8). Generally there were relatively few sculpin with an estimated gape width of 25 mm (Fig. 2), thus sculpin were restricted to J1–J4 crab. Carapace width is the larger body dimension of this species of crab, but if attacked from the side (i.e. laterally at the walking legs rather than face-on towards the chelae), then body length (from the posterior of the carapace to the orbit of eyes) could be the limiting dimension with respect to sculpin mouth gape. Based on data of Weymouth and MacKay (1936), the carapace length (CL) of J3, J4, and J5 instars is about 73%, 71%, and 70% of width, respectively. From this perspective, the average size sculpin of this study could possibly consume instars up to J5 with respect to length (approximately 18.8 mm CL). Very few sculpin longer than 175 mm TL were caught; even their estimated gape width was only about 24.6 mm, less than the average carapace width of most 0+ crab by September (Wainwright and Armstrong, 1993).

The six other potential fish predators of 0+ crab found in greatest abundance throughout the summer included juvenile English sole, *Pleuronectes vetulus*, shiner perch, *Cymatogaster aggregata*, snake prickleback, *Lumpenus sagitta*, saddleback gunnels, *Pholis ornata*, sand sole, *Psettichthys melanostictus*, and starry flounder, *Platichthys stellatus*.[2] The first five species have relatively small mouths, are most prevalent as juveniles within the Grays Harbor estuary (English sole) or are not documented as being important crab predators[1] (Williams, 1994). Starry flounder may prey on 0+ Dungeness crab both in Grays Harbor[1] and San Francisco Bay (Reilly, 1983) but are uncommon as adults in the former estuary (Rogers et al., 1989).

The results of this study expand current knowledge of staghorn sculpin's diet composition and feeding behavior, establish the importance of 0+ Dungeness crab as part of the estuarine summer diet of sculpin, and provide a perspective of the potential impact that sculpin predation has on juvenile Dungeness crab survival after settlement. Posey (1986) showed that staghorn sculpin predation limits the distribution of ghost shrimp *N. californiensis* on intertidal sandflats and labeled this fish a keystone predator controlling the depth distribution of newly settled ghost shrimp and the expansion of established beds of adult shrimp. Our data demonstrate that staghorn sculpin are a major predator of small

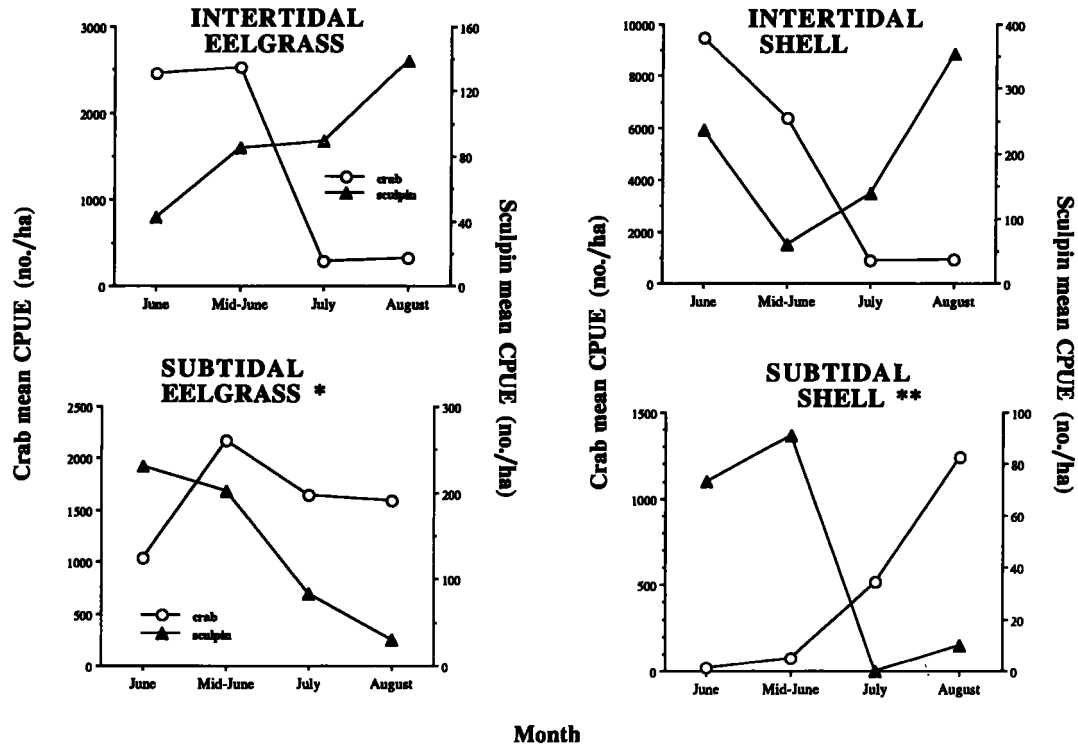

Figure 10

Mean densities of staghorn sculpin, *Leptocottus armatus*, and Dungeness crab, *Cancer magister* (no./ha), from intertidal and subtidal eelgrass and shell habitats, Grays Harbor, Washington, June–August 1989. Note different vertical scales. Each symbol represents the mean CPUE of 2 trawls. * = benthic habitat with shell, ** = benthic habitat with wood and stick material.

0+ Dungeness crab instars during a short period of late spring and early summer settlement and growth and that sculpin may be capable of exerting a pronounced effect on crab year-class strength within coastal estuaries (Armstrong, 1991).

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Larval distribution and transport of penaeoid shrimps during the presence of the Tortugas Gyre in May–June 1991

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Abstract.—As part of the Southeast Florida and Caribbean Recruitment Project (SEFCAR), penaeoid shrimp larvae were collected during the spring and summer cruise of the RV *Longhorn* in the Lower Florida Keys and Dry Tortugas from 29 May to 30 June 1991. Larvae of the pink shrimp, *Penaeus duorarum*, and the rock shrimp, *Sicyonia* sp., were distributed inshore close to the Dry Tortugas Grounds, whereas larvae of the oceanic shrimp *Solenocera* sp. showed mainly an offshore distribution. Significant concentrations of *Solenocera* sp., *Sicyonia* sp., and *P. duorarum* larvae at the Tortugas transect in early June were found within and above the seasonal thermocline while the cold cyclonic Tortugas Gyre was intensively developed. For *Solenocera* sp., which spawn on the outer edge of the gyre, high concentrations of larvae were found at the inshore stations of the Tortugas transect in early June, presumably as a result of the cyclonic circulation of the gyre followed by onshore Ekman transport. *Penaeus duorarum*, which spawn in the shallow Tortugas Grounds, showed a mode of zoea II–III progressing to postlarvae I at the Tortugas Grounds during the 15 days in which the drifter *Halley* recirculated in the interior of the Tortugas Gyre. Retention of *P. duorarum* larvae by the internal circulation of the gyre at the spawning grounds may be an important mechanism for local recruitment of these shrimp to the nursery grounds of Florida Bay.

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Penaeoid shrimps constitute the second most valuable segment of the U.S. fishing industry and are arguably one of the most valuable groups of marine species in the world. Annual stocks fluctuate widely and few spawning stock/recruitment relationships have been demonstrated (Garcia, 1983). The penaeid shrimp *Penaeus duorarum*, or pink shrimp, supports an important commercial fishery in south Florida. Pink shrimp yielded a stable catch of 9.6 million pounds per year from 1960 to 1986 (Klima et al., 1986). However, this catch has declined by more than 50% in the last four years (NMFS[1]). This fishery is directly dependent on young shrimp that migrate from nursery areas onto the fishing grounds (Nance and Patella, 1989). Animals with short life spans (≈2 years), such as pink shrimp, depend almost entirely on one year class being recruited during the year.

The life history of *P. duorarum* of the Dry Tortugas (shallow banks located about 100 km west from Key West) involves one oceanic and one estuarine phase (Garcia and Le Reste, 1981). Adults spawn offshore on the Dry Tortugas, where females lay demersal eggs (Fig. 1). The larvae undergo several changes in feeding habits and morphology including five naupliar stages, three zoeal or protozoeal, and three mysid stages. The last mysis undergoes a moult at which time it transforms into a postlarva. The average time required by *P. duorarum* to reach the first postlarval stage is approximately 20 days at 26°C (Ewald, 1965).

The first postlarval stages are still planktonic whereas those that follow are benthic. Postlarvae migrate inshore, entering the Florida Bay nursery grounds where they metamorphose to juveniles. When they have reached a length of about 10 cm, they return to the Tortugas spawning area (Allen et al., 1980).

Advective processes of *P. duorarum* and their relation to oceanographic and environmental factors are not fully understood. Research on the larval phase was performed in the mid 1960's. Munro et al. (1968) and Jones et al. (1970) studied the abundance and distribution of larvae of *P. duorarum* on the Tortugas Shelf and in the Florida Keys. These authors

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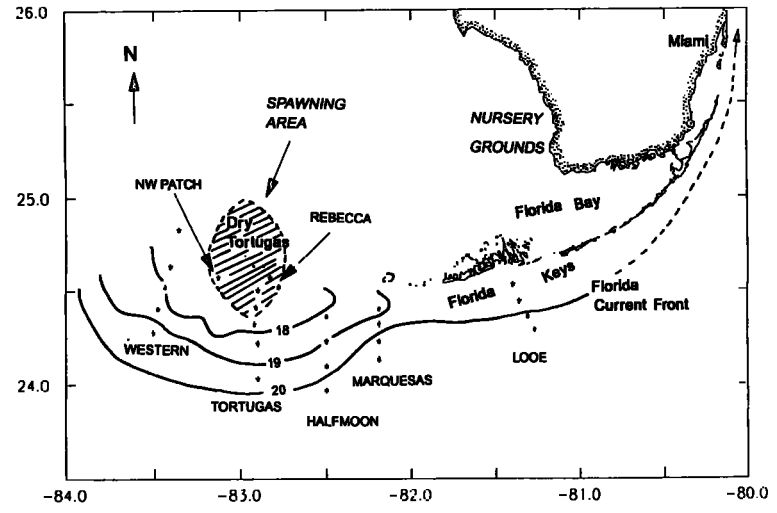

Figure 1

Location of transects and 1-m² MOCNESS sampling stations (*) of the Southeast Florida and Caribbean Recruitment Project (SEFCAR) cruise LH3, 29 May–30 June 1991 at the Dry Tortugas and Lower Florida Keys. Shaded area indicates spawning area of pink shrimp, *Penaeus duorarum*, in southeast Florida. Solid lines are the CTD temperatures at 100 m depth in late May 1991. Dashed line indicates the continuation of the Florida Current.

hypothesized that *P. duorarum* larvae migrate from where they are spawned in the Dry Tortugas by means of the Florida Current and return to Florida Bay through passes in the middle Keys. However, they had difficulty in explaining the exact migratory path in light of inconsistencies between the prevailing currents and the abundance of larvae in the pathway to the coast.

Penaeoid shrimps other than *Penaeus* are abundant in the Dry Tortugas and may occur in commercial catches (Eldred, 1959), but they are of little or no economic value. Such is the case for the rock shrimp, *Sicyonia* spp., the humpback shrimp, *Solenocera* spp., and the roughneck shrimp, *Trachypenaeus* spp. Life histories of these species are poorly known, and larval research in the Gulf of Mexico has focused on trends of seasonal distribution (Eldred et al., 1965; Temple and Fisher, 1967; Subrahmanyam, 1971b).

The Southeast Florida and Caribbean Recruitment Project (SEFCAR) has investigated the effect of oceanographic processes on plankton and regional recruitment of fishes and other reef species along the continental shelf in southeast Florida. The hydrographic conditions in the Straits of Florida are dominated by the strong Florida Current. In the southwestern part of the Florida Keys, the Florida Current is highly variable, often associated with meanders and gyres (Lee et al., 1992). The Dry Tortugas are located near the turning point where the southward-flowing Loop Current swerves abruptly east to enter the Straits of Florida (Gaby and Baig, 1983). A cyclonic gyre over the slope off the Dry Tortugas with horizontal dimensions of approximately 200 km has been described by Lee et al. (1994). The gyre, which persisted for about 100 days from mid-May to late August 1994, was observed to move eastward to the region of the Pourtales Terrace (Lee et al., 1994). Lee et al. (1992) called this gyre the Pourtales Gyre, and its effect on lobster *Scyllarus* sp. and shrimp larvae was demonstrated by the high abundance of larvae nearshore in the path of the westward flow of the gyre (Yeung and McGowan, 1991; Criales and McGowan, 1994).

The objective of this study is to describe the horizontal and vertical distribution patterns of the three most abundant penaeoid shrimp larvae in the Dry Tortugas and lower Florida Keys during the presence of the cyclonic Tortugas Gyre. This work will form a basis for later comparisons with surveys under different hydrographic conditions.

Materials and methods

Plankton and hydrographic sampling

Samples were collected between 29 May and 30 June 1991, as part of the cruise LH3 of the RV *Longhorn*, by using a 1-m² MOCNESS (multiple opening-closing net and environmental sensing system [Wiebe et al., 1976]) with 0.333-mm net mesh size. The nine nets of the MOCNESS were towed in an aperture along an oblique path at a speed of approximately 2 $m \cdot s^{-1}$, and samples from the surface to near the bottom were collected. Net 1 in the set was towed obliquely from the surface down to about 200 m or to the closest multiple of 20 m if the water depth was less than 200 m. Net 2 (deepest) to net 9 (uppermost) sequentially opened or closed at controlled depths of 200–160 m, 160–130 m, 130–100 m, 100–80 m, 80–60 m, 60–40 m, 40–20 m, and 20–0 m for the deeper stations, and 50–40 m, 40–30 m, 30–20 m, 20–10 m, and 10–0 m, or 45–30 m, 30–15 m, and 15–0 m depth intervals for the shallow stations (<50 m). A flowmeter and conductivity-temperature depth (CTD) sensors were attached to the net frame. The volume of water filtered in each layer varied from 130 to 593 m³, depending on the depth strata sampled.

The cruise was divided into four legs (fifty-six stations) from west of the Dry Tortugas to Looe Key in the middle Florida Keys (Fig. 1). The sampling data are summarized in Table 1. Stations of leg 1 were repeated in the other three legs. During leg 2, one transect was added at Marquesas and another at Halfmoon. Leg 3 repeated stations of legs 1 and 2 in addition to an upstream transect (Western transect). Leg 4 included a downstream transect (Looe Key) in addition to the Tortugas, Rebecca, NW Patch, and Marquesas transects (Fig. 1).

Sampling was carried out continuously depending on the time the ship arrived at the station (Table 1). Samples were taken during the day at 35 stations and at night at the remaining 21 stations. Three moon phases were covered during this cruise. Twenty-six stations were sampled during the full moon, eight during the last quarter, and eight during the new moon.

Three ARGOS satellite-tracked surface drifters were deployed on the northern side of the gyre as part of the physical oceanographic survey. Two stations were sampled on the track of drifter *Halley* after a 15-day interval (day 1=30 May, day 15=13 June).

Larval identification and standardization

Plankton samples were preserved in 4% formaldehyde-seawater solution and later transferred to 70% ethanol. Aliquot sampling was performed after the similarity of duplicate samples was statistically evaluated (t-test, t_9=0.04, P<0.05). Each sample was adjusted to a volume of 500 mL, and the penaeoid larvae sorted from five 25-mL aliquots. The mean of the five counts was standardized to the concentration of larvae (no./100 m^3) or to abundance (no./10 m^2 of sea surface). No nauplii were caught because the mesh size of the net was too large to retain them.

Penaeoid shrimp larvae were identified to genus or species by using existing keys and larval descriptions (Heldt, 1938; Pearson, 1939; Gurney, 1943; Dobkin, 1961; Cook, 1966; Heegaard, 1966; Subrahmanyam, 1971a). Postlarvae of *Penaeus* sp. were identified from the keys of Williams (1965) and the morphometric study of Chuensri (1968). Individual stages were separated only for *P. duorarum* because it was the only species of interest for which larval stages have been described (Dobkin, 1961). The remaining penaeoid identifications were made to a generic level.

Statistical analysis

Mean abundance of total larvae caught at day (0631–2000 h; n=35, $\bar{x}$=98.3, SD=111.6) versus night (2001–0630 h; n=21, $\bar{x}$=91.4, SD=115.5) stations was not significantly different (t-test, t_{54}=0.82, P>0.05); therefore day and night data were pooled (Sokal and Rohlf, 1981).

To characterize the vertical distribution of the different larval stages per species, the depth of the center of mass (Z_m) was calculated (Röpke et al., 1993):

$$Z_m = \sum (P_i \times Z_i)$$

$$P_i = C_i \times H_i \Big/ \sum (C_i \times H_i),$$

where P_i is the standardized (no./100 m^3) number of larvae in the ith depth stratum; Z_i is the mean sampling depth of the ith depth stratum; C_i is the concentration of larvae in 100 m^3; and H_i is the width of ith depth interval. Day and night stations were separated to determine any daily vertical larval migration. Differences in Z_m between day and night were not significant for any of the three species (*P. duorarum* t-test, t_{24}=0.63, P>0.05; *Sicyonia* sp. t-test, t_{36}=0.95; *Solenocera* sp. t-test, t_{50}=0.28, P>0.05), suggesting no daily vertical migration of larvae; therefore data were pooled. However, this may be biased by the greater number of day stations (35 day, 21 night).

Results

Horizontal distribution and abundance

Penaeus duorarum These larvae showed an onshore distribution concentrated near the Dry Tortugas (Fig. 2). The density ranged from 1.5 to 57.1 larvae/10 m^2 represented by 60.3% zoeae, 15% myses, and 24.7% postlarvae. Distribution of zoeae was nearshore; 90% were caught no farther than 25 km offshore from the Dry Tortugas. Myses were distributed a little farther offshore and eastward than zoeae but no more than 45 km from the coast. The trend of distribution of postlarvae was also close to shore; 83% of postlarvae I–III were located inshore at the Tortugas, Halfmoon, NW Patch, and Rebecca transects. The other 17% were found at the offshore stations of Marquesas associated with the Florida Current front, and no postlarvae were captured at the Looe Key transect (Fig. 2).

Larval stages in the spawning area at the NW Patch and Tortugas transects showed a progression of ages during the four legs of sampling (Fig. 3). In late May zoeae II–III showed a high concentration (33.8–45.4 larvae/10 m^2) at the spawning area, few myses were found at these stations, and no postlarvae were caught. In early June, 15 days after the first sampling, the abundance of myses and postlarvae increased. Postlarvae II–III reached their peak of con-

Table 1

Station data and abundance (no./10^2) of penaeoid shrimp larvae during the Southeast Florida and Caribbean Recruitment Project (SEFCAR) cruise LH3, 29 May–30, June 1991.

Station	Latitude N	Longitude W	Max-depth (m)	Distance offshore (km)	Date	Local time (h) (EDT)	Moon phases	Transect	*Penaeus duorarum*	*Sicyonia* sp.	*Solenocera* sp.
Leg 1, 29–31 May											
15	24.498	82.904	25	13.28	29 May	1118 day	Full	Tortugas	12.14	36.43	0.00
17	24.408	82.907	60	25.19	29 May	1242 day	Full	Tortugas	0.00	0.00	56.09
19	24.317	82.916	200	37.03	29 May	1418 day	Full	Tortugas	0.00	0.00	3.46
21	24.222	82.902	207	48.65	29 May	1621 day	Full	Tortugas	0.00	0.00	54.01
23	24.032	82.903	201	73.10	29 May	1754 day	Full	Tortugas	0.00	0.00	0.00
26	24.570	83.125	40	21.50	30 May	1947 day	Full	NW Patch	37.87	29.73	20.60
27	24.559	83.141	40	23.99	31 May	2113 night	Full	NW Patch	41.33	69.10	12.87
Leg 2, 4–7 June											
29	24.500	82.916	20	13.28	4 June	1656 day	Full	Tortugas	19.02	22.83	3.80
30	24.406	82.908	60	25.19	4 June	1816 day	Full	Tortugas	19.76	54.01	129.26
31	24.317	82.916	202	37.03	4 June	2036 night	Full	Tortugas	7.05	52.24	191.50
32	24.227	82.912	203	48.65	4 June	2237 night	Full	Tortugas	0.00	4.04	254.62
36	24.567	83.132	40	22.33	5 June	1946 day	L. quarter	NW Patch	0.00	32.85	100.29
37	24.357	82.500	48	40.28	6 June	1121 day	L. quarter	Halfmoon	36.57	200.21	84.40
38	24.229	82.499	167	47.29	6 June	1243 day	L. quarter	Halfmoon	18.96	35.17	16.64
39	24.103	83.501	197	58.03	6 June	1442 day	L. quarter	Halfmoon	2.86	9.71	21.62
40	23.972	82.503	200	71.39	6 June	1644 day	L. quarter	Halfmoon	0.00	10.46	90.89
42	24.226	82.189	198	30.09	6 June	2334 night	L. quarter	Marquesas	5.28	0.00	16.13
43	24.324	81.194	196	17.47	7 June	0209 night	L. quarter	Marquesas	0.00	0.00	43.38
44	24.403	82.191	77	7.31	7 June	0409 night	L. quarter	Marquesas	0.00	0.00	5.12
Leg 3, 12–18 June											
45	24.568	83.120	40	20.17	12 June	0914 day	New	NW Patch	6.45	3.37	24.84
46	24.833	83.359	56	35.80	12 June	1209 day	New	Western	2.45	0.00	145.05
47	24.634	83.408	57	44.96	12 June	1429 day	New	Western	0.00	0.00	103.36
48	25.524	83.445	125	57.06	12 June	1631 day	New	Western	4.27	6.76	564.17
49	24.401	83.483	202	72.29	12 June	1834 day	New	Western	0.00	0.00	67.77
50	24.280	83.522	200	88.52	13 June	2057 night	New	Western	0.00	0.00	93.78
51	24.032	82.903	200	72.76	13 June	0225 night	New	Tortugas	0.00	0.00	428.11
52	24.222	82.902	203	47.84	13 June	0503 night	New	Tortugas	0.00	0.00	37.43
53	24.317	82.916	202	34.46	13 June	0709 day	New	Tortugas	15.64	7.89	153.24
54	24.408	82.907	58	24.93	13 June	0859 day	New	Tortugas	17.74	26.72	95.20
55	24.498	82.904	21	13.58	13 June	0612 day	New	Tortugas	0.00	5.03	10.74
56	24.524	82.784	17	14.75	13 June	1437 day	New	Rebecca	16.72	22.94	13.72
62	24.403	82.191	57	2.02	17 June	1422 day	New	Marquesas	0.00	4.56	5.94
63	24.324	82.194	162	16.29	17 June	1625 day	New	Marquesas	0.00	2.58	23.66
64	24.226	82.189	162	28.28	17 June	1751 day	New	Marquesas	2.72	10.16	11.50
65	24.133	82.186	159	42.05	17 June	1924 day	New	Marquesas	6.95	17.76	6.00
66	23.972	82.503	160	71.39	17 June	2236 night	New	Halfmoon	0.00	1.95	48.16
67	24.103	82.501	163	58.03	18 June	0107 night	New	Halfmoon	0.00	0.00	50.30
68	24.231	82.501	164	47.29	18 June	0314 night	New	Halfmoon	0.00	0.00	41.40
69	24.360	82.501	15	40.28	18 June	0500 night	New	Halfmoon	0.00	15.09	11.05
70	24.524	82.784	15	14.75	18 June	0638 day	New	Rebecca	20.14	16.60	1.95
71	24.559	83.141	30	19.89	18 June	0938 day	New	NW Patch	17.63	0.00	4.64

centration (18.9 larvae/10 m^2) in mid-June. In late June the peak of zoeae II reoccurred (35.8 larvae/10 m^2).

***Sicyonia* sp.** Rock shrimp was the second most abundant species after *Solenocera* sp. The highest densities were located at the NW Patch and Halfmoon transects (Fig. 4A). Zoeae represented 31.3% of the catch and myses 68.7%. Zoeae were highly abundant at the NW Patch stations in early May (78.8 larvae/10 m^2) and early June (91.1 larvae/10 m^2), and myses were distributed in patches with two large peaks, one at the Halfmoon transect (184.8 lar-

Table 1 (continued)

Station	Latitude N	Longitude W	Max-depth (m)	Distance offshore (km)	Date	Local time (h) (EDT)	Moon phases	Transect	*Penaeus duorarum*	*Sicyonia* sp.	*Solenocera* sp.
Leg 4, 28–30 June											
77	24.032	82.903	160	73.10	28 June	1101 day	Full	Tortugas	0.00	6.60	146.53
78	24.222	82.902	160	48.65	28 June	0140 night	Full	Tortugas	0.00	5.03	10.62
79	24.317	82.916	160	36.46	28 June	1540 day	Full	Tortugas	0.00	4.11	14.38
80	24.408	82.907	57	24.93	28 June	1817 day	Full	Tortugas	1.55	8.60	4.66
81	24.498	82.904	20	13.28	28 June	1827 day	Full	Tortugas	41.34	15.64	0.00
82	24.559	83.141	28	21.95	28 June	2031 night	Full	NW Patch	57.12	151.39	0.00
83	24.570	82.832	15	27.75	28 June	2347 night	Full	Rebecca	14.09	7.05	58.13
85	24.133	82.186	160	36.46	29 June	1616 day	Full	Marquesas	1.72	1.72	3.00
86	24.226	82.189	160	24.93	29 June	1800 day	Full	Marquesas	6.85	2.81	37.73
87	24.324	82.194	158	16.28	29 June	2009 night	Full	Marquesas	0.00	5.75	39.50
88	24.403	82.191	53	2.02	29 June	2148 night	Full	Marquesas	0.00	3.10	23.94
89	24.528	81.395	25	2.16	30 June	0414 night	Full	Looe	0.00	0.00	0.00
90	24.444	81.356	160	11.49	30 June	0443 night	Full	Looe	0.00	0.00	23.69
91	24.361	81.312	161	20.82	30 June	0810 day	Full	Looe	0.00	2.42	33.53
92	24.293	81.269	160	28.27	30 June	2213 night	Full	Looe	0.00	17.31	89.51
									434.20	929.70	3531.90

vae/10 m^2) in early June and the other at the stations of NW Patch transect (60.3 larvae/10 m^2) in late June.

***Solenocera* sp.** This species represented the most abundant penaeoid larvae at the Dry Tortugas and lower Florida Keys, accounting for 72% of the total catch (Fig. 4B). The highest densities were located offshore of the Tortugas and Western transects. Abundances were lowest in late May, increased considerably in early June, and reached their peak in mid-June (Table 1). Of the catch, 29.2% was represented by zoeae and 70.8% by myses. Distribution of early zoeae was patchy; two main peaks occurred at the Western (282.9 larvae/10 m^2) and Tortugas transects (135.4 larvae/10 m^2), and mysid stages were very widely distributed throughout the area with the highest abundance at the Tortugas transect (136.6 larvae/10 m^2) (Fig. 4B). Zoeae and myses showed an offshore distribution, except at stations along the Tortugas transect in early June where high concentrations of *Solenocera* sp. larvae were found at the inshore stations while the Tortugas Gyre was well developed (Figs. 4B and 5).

Vertical distribution

Depths of the center of mass (Z_m) were calculated for the different larval stages of each species (Table 2). *Penaeus duorarum* larvae showed a shallow distribution (Z_m=18 m) which was similar among stages. *Sicyonia* sp. showed a mean Z_m of 27 m, though zoeae were distributed deeper than myses. *Solenocera* sp. larvae were widely spread throughout the water column from 0 to 100 m; the peak concentration occurred at about 42 m, and myses occurred deeper than zoeae (Table 2).

Penaeus duorarum larvae were distributed between temperatures of 23° and 29°C, *Sicyonia* sp. larvae between 20° and 28°C, and *Solenocera* sp. larvae between 15° and 29°C. Maximum concentrations were found between 22° and 26°C (Fig. 5).

Penaeus duorarum postlarvae at the offshore stations of the Marquesas transect (n=6, $Z_m \bar{x}$=20.8, SD=14.8) were relatively deeper than those at inshore stations (n=11, $Z_m \bar{x}$=11.6, SD=6.7) restricted to the seasonal thermocline (t-test, t_{15}=0.09, P>0.05).

Effect of the Tortugas Gyre on larval abundance and dispersal

Abundance and vertical distribution at Tortugas transect A general downward slope of the upper seasonal thermocline (23–27°C) toward shore was present during the four legs at the Tortugas transect (Fig. 5). *Solenocera* sp., *Sicyonia* sp., and *P. duorarum* larvae were highly concentrated above or within the seasonal thermocline. The strength of the seasonal thermocline, which is uplifted in the interior of the gyre, appears to have been a limiting factor for vertical migrations of these penaeoid larvae.

Solenocera sp. larvae were very abundant at the inshore stations between 25 and 75 m in depth during leg 2, corresponding with the strongly developed

thermocline (Fig. 5). The inshore distribution of *Solenocera* sp. during this leg was noteworthy because these larvae showed an offshore distribution during the other legs.

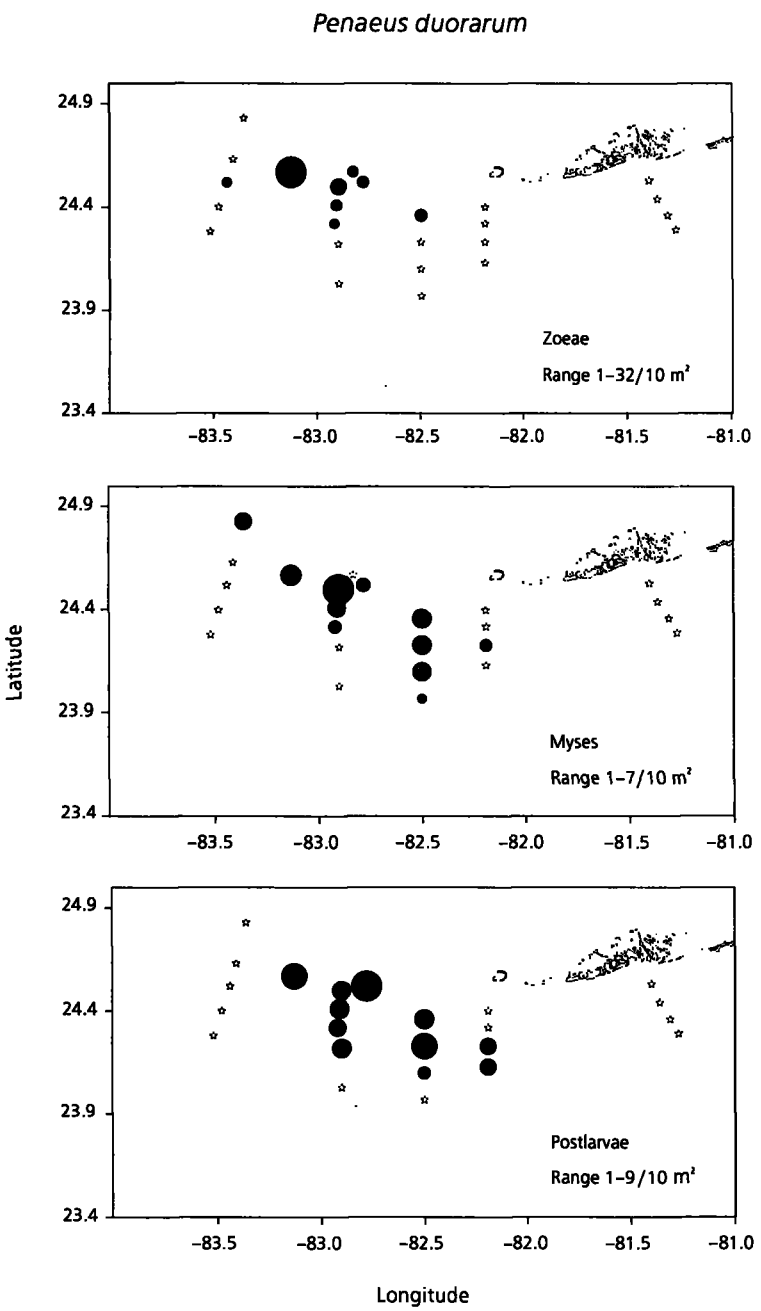

Figure 2

Horizontal distribution and relative abundance (larvae/10 m^2) of the larval stages of pink shrimp, *Penaeus duorarum*, at the sampling stations of the four legs of the LH3 cruise, 29 May–30 June 1991. Symbols are proportional in size to the abundance range and are positioned at the sampling stations. The stars = no catch.

High larval concentrations of the three species (*P. duorarum:* 1–40 larvae/100 m^3; *Sicyonia* sp.: 1–22 larvae/100 m^3; and *Solenocera* sp.: 10–60 larvae/100 m^3) were found at the Tortugas transect during leg 2 in early June within and above the seasonal thermocline between 25 and 75 m in depth (Figs. 5 and 6). Total abundances during leg 2 were much higher than those during any other leg for all three species. The abundance of *Solenocera* sp. was twice as great during leg 2, and there were highly significant differences among legs (ANOVA, $P \leq 0.05$) (Fig. 6).

Drifter circulation Drifter *Halley*, deployed on 30 May on the northern side of the Tortugas Gyre, moved south-southeast for about seven days, then turned back toward the west-northwest for about seven days (Fig. 7). The drifter spent the first 14 days in a tight recirculation in the interior of the gyre. The position of the drifter upon release initially corresponded with the position of stations 26 and 27. On 13 June, when it broke out of the gyral circulation, the drifter was located at Rebecca transect at station 56. At this point the drifter entered the Rebecca Channel between the Dry Tortugas and Rebecca Shoal where it stayed for about 10 days, undergoing tidal excursions of up to 7 km, but with no net through-flow. Relative percentages of the larval stages of *P. duorarum* at the station where the *Halley* drifter was released (Stns. 26 and 27) and at the station where this drifter broke out of the gyre circulation (Stn. 56) are plotted in Figure 7. On 30 May at stations 26 and 27, *P. duorarum* larvae showed one mode of zoeae, mainly II-III (84%). After 15 days, on 13 June, one mode of postlarvae I (67.7%) was present at station 56, a station near the departure point. The trajectory of the drifter *Halley* and the progression of age of *P. duorarum* larvae over the 15 days that the drifter spent recirculating within the gyre may indicate retention of *P. duorarum* larvae at the spawning area.

Abundance and composition of *Sicyonia* sp. larvae at the same two locations, stations 26 and 27, and at station 56 of

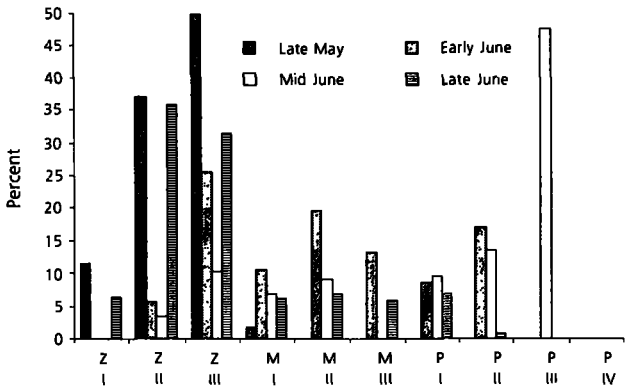

Figure 3

Percentages of the larval stages of pink shrimp, *P. duorarum*, at the Tortugas and NW Patch transects during the four legs of the cruise LH3, 29 May–30 June 1991. Z = zoeae; M = myses; and P = postlarvae.

Rebecca transect showed a similar trend to that described for *P. duorarum*: a high concentration of zoeae at the deployment of the drifter (80% zoeae) and 15 days later a dominance of myses (100% myses).

Discussion

Munro et al. (1968), in an examination of abundance and distribution of *P. duorarum* larvae in southeast Florida, could not reach firm conclusions regarding the path of migration from the Dry Tortugas to Florida Bay because of the inconsistency between the prevailing currents and the abundance of larvae in the pathway to the coast. However, they hypothesized that *P. duorarum* larvae may have been advected from where they were spawned in the Tortugas Grounds by means of the Florida Current and then were carried back into Florida Bay by tidal currents through passes in the middle Keys. The conceptual path of larval advection outlined by Munro et al. (1968) was consistent with the general current pattern known at that time. More recent oceanographic research on the Straits of Florida has shown a high variability in the Florida Current in the lower Keys and Dry Tortugas associated with meanders and gyres (Lee et al., 1992, 1994). Lee et al. (1994) showed from moored current meter data and surface drifter tracks that a cold, cyclonic gyre formed off the Dry Tortugas in mid-May and continued as a weak counterclockwise recirculation about 200 km in diameter until late August. Thus, the presence of the gyre could have acted as a larval retention and recirculation mechanism for the duration of the sampling cruise.

Table 2

Mean and standard deviation of the center of mass ($Z_m \pm$ SD) of the larval stages of three penaeoid shrimps during the SEFCAR cruise LH3, May–June 1991.

	Z (m)	SD	n
Solenocera sp.	42.41	20.97	52
Zoea	35.64	20.08	27
Mysis	42.18	20.69	49
Sicyonia sp.	26.85	17.02	38
Zoea	30.14	20.24	14
Mysis	25.19	13.22	36
P. duorarum	18.42	12.14	26
Zoea	15.00	9.13	15
Mysis	15.07	14.04	15
Postlarvae	16.81	18.67	17

Distributions of zoeae and myses of *P. duorarum* found in this study agree with those of Munro et al. (1968) and Jones et al. (1970) for the Tortugas shelf. However, postlarval distribution in the present study was different; most postlarvae (stages I–III) were located inshore near the area where they were spawned, rather than offshore as was found by Munro et al (1968). Composition of larval stages at the

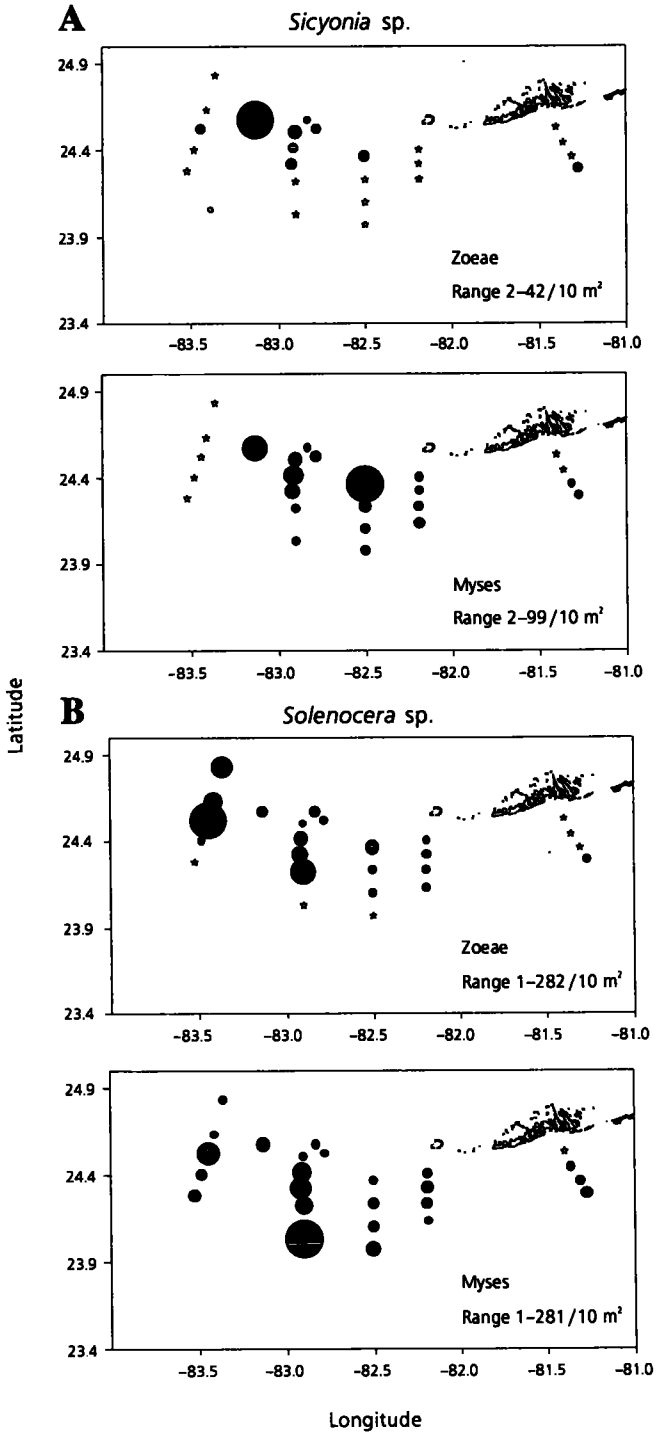

Figure 4

Horizontal distribution and relative abundance (larvae/10 m^2) of zoeal and mysid stages of (**A**) the rock shrimp *Sicyonia* sp. and (**B**) the humpback shrimp *Solenocera* sp. for the four legs of the LH3 cruise, 29 May–30 June 1991. The symbols are proportional in size to the abundance range and are positioned at the sampling stations. The stars = no catch.

Tortugas and NW Patch transects and at the two stations sampled on the track of the drifter *Halley* showed the same modal progression of zoeae to postlarvae within 15 days. This period corresponds to the time reported by Ewald (1965) for zoeae III to become postlarvae I at 26°C. This time period for larval development from zoeae to postlarvae also agrees remarkably well with the trajectory time of the drifter recirculating in the interior of the gyre. The timing of the modal progression of larval stages occurring within those 15 days of gyre recirculation at the spawning area, as shown by the drifter, may indicate that *P. duorarum* larvae were recirculating in the interior of the gyre during development. Interestingly, after the drifter broke out of the gyre circulation it moved toward the east and north toward the Florida Bay shrimp nursery grounds, suggesting a local recruitment pathway for this species.

Retention of *P. duorarum* larvae at the spawning area by the Tortugas Gyre for some days after hatching may enhance the survival of these larvae because food resources are available in the uplifted nutracline where Lee et al. (1994) found maximum concentrations of chlorophyll and copepod nauplii. Furthermore, postlarvae located in the northern (nearshore) portion of the gyre may increase their chance of settling either by escaping the offshore flow on the western side of the gyre entirely or by resisting the offshore flow, thereby drifting to the west rather than being swept offshore (Porch, 1993). Thus, the primary pathway for *P. duorarum* larvae to reach the nursery areas of Florida Bay may include retention at the spawning area by recirculation in the Tortugas Gyre followed by movement onto the Southwest Florida shelf and Florida Bay by wind and tidal currents. Those larvae that are advected eastward by the Florida Current may reach the upper and middle Keys. The latter alternative could explain the great number of postlarvae found in the middle Keys by Munro et al. (1968) and Roessler and Rehrer (1971).

Sicyonia sp. larvae showed a coastal and shallow distribution. Young zoeae were generally restricted to the inshore stations, indicating that this species may spawn near the Dry Tortugas Grounds. Myses showed the highest concentrations inshore, with a maximum concentration at the Marquesas transect. Larval stages at the two stations of the drifter showed a similar trend to that of *P. duorarum*. The time of development of *S. brevirostris* from spawn-

ing to the first postlarval stage is approximately 30 days (Cook and Murphy, 1965). Local retention of larvae at the spawning area followed by recruitment into the coastal region may be the migration mechanism for this coastal and short-lived species as well.

Early-stage zoeae of *Solenocera* sp. were widely distributed offshore; two main peaks were located at the Western and Tortugas transects at a depth of about 35 m. The age of these zoeae was estimated to be 3 to 5 days in accordance with Heldt's description (1938) of the larval development of *S. membranacea*. These data indicate that this species may have spawned somewhere in the Gulf of Mexico in a location corresponding to the outer edge of the Tortugas Gyre. Myses showed an offshore distribution in all but the Tortugas transect during leg 2, where most larvae were found inshore. The great concentration of *Solenocera* larvae at the inshore stations of the Tortugas transect in early June between 25 and 75 m in depth corresponded with the strongly developed

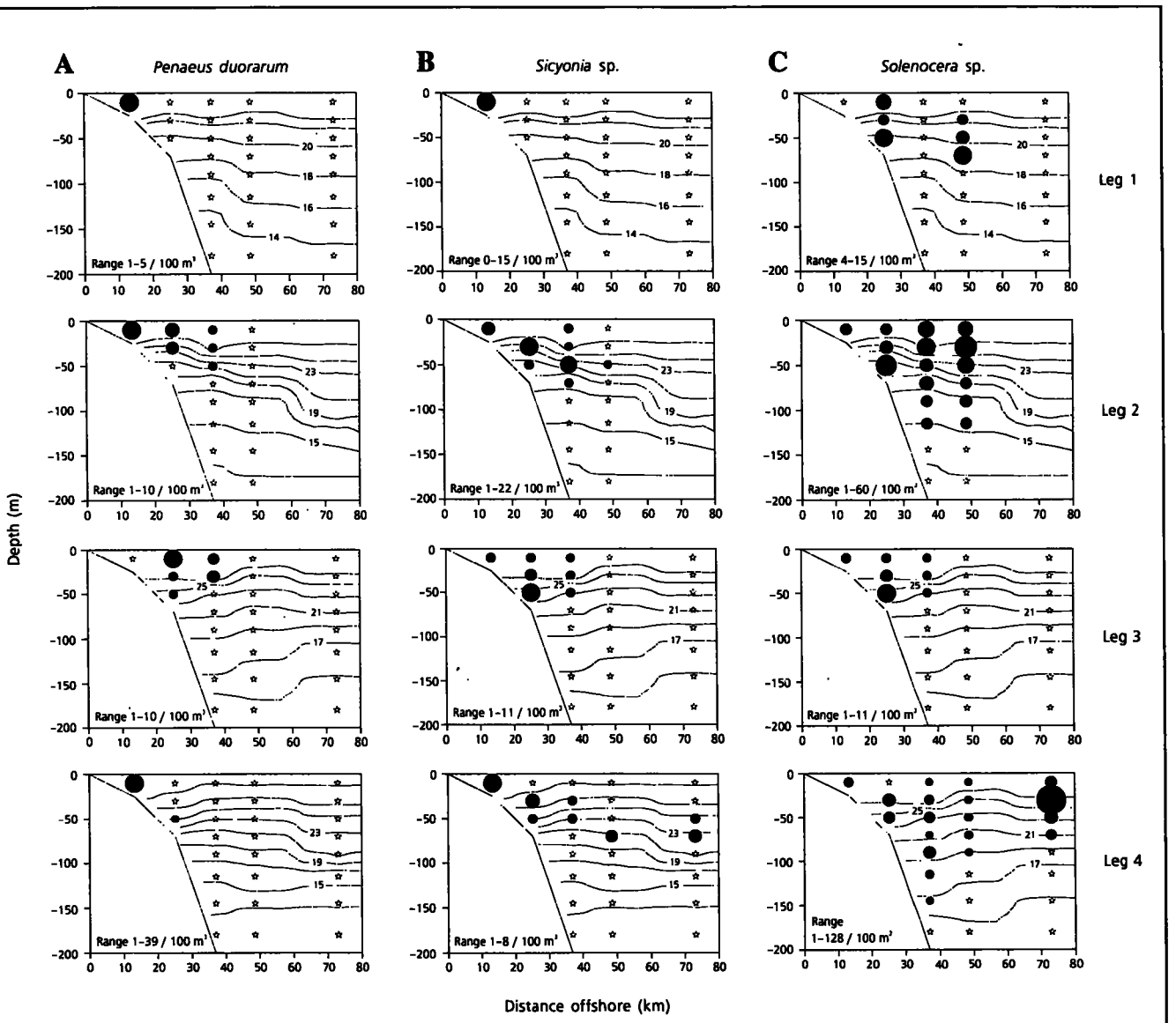

Figure 5

Cross section of Tortugas transect during the four legs showing the vertical distribution and relative concentrations (larvae/100 m^3) of the three penaeoid species: pink shrimp, *Penaeus duorarum* (**A**); the rock shrimp *Sicyonia* sp. (**B**); and the humpback shrimp *Solenocera* sp. (**C**), superimposed over the vertical temperature profiles (°C) from the MOCNESS temperatures. Symbols are proportional in size to the abundance range. The stars = no catch.

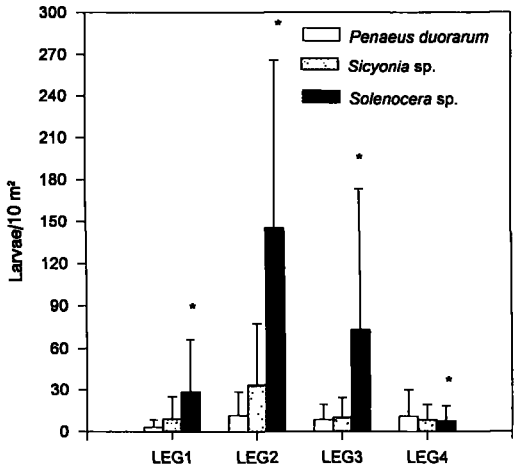

Figure 6

Mean relative abundance (larvae/10 m^2) and standard deviation of the pink shrimp, *Penaeus duorarum*, the rock shrimp *Sicyonia* sp., and the humpback shrimp, *Solenocera sp.*, at the sampling stations of the Tortugas transect during the four legs of the LH3 cruise, 29 May–30 June 1991. (*) = significant differences in mean relative abundance between legs, within species ($P \leq 0.05$).

thermocline as a consequence of the Tortugas Gyre. Criales and McGowan (1994) found *Solenocera* larvae in high abundance (62% of the penaeoid larvae) at an inshore station of Looe Reef transect during the presence of the Pourtales Gyre, whereas few larvae (only 15%) were captured in the absence of the gyre when the Florida Current intruded close to the coast.

The combination of the cyclonic gyre circulation and inshore surface Ekman transport convergence should result in a concentration of larvae in the interior of the gyre and in an onshore transport in the eastern portion. Onshore Ekman transport is expected to be relatively high in the Lower Keys and Dry Tortugas where prevalent southeast winds favor onshore transport toward the east-west oriented coast. The importance of Ekman transport on recruitment has been shown in the Florida Keys for *Scyllarus* larvae (Yeung and McGowan, 1991) and for other decapod larvae particularly brachyuran larvae in other regions (see Hobbs et al., 1992; McConnaughey et al., 1994).

Substantial gaps exist in our knowledge of the life histories of penaeoid shrimps. For example, larval development of *Solenocera* spp. has not been conducted for any of the five western Atlantic species (Perez-Farfante and Bullis, 1973), and larval development of only one of the seven western Atlantic species of *Sicyonia* spp. is known (Cook and Murphy, 1965). As long as our knowledge of the life history and larval development of these species remains limited, further conclusions regarding interactions of recruitment processes with the physical environment will remain uncertain.

This research showed the effects of the Tortugas Gyre circulation on dispersal and abundance of local coastal (*P. duorarum* and *Sicyonia* sp.) and oceanic (*Solenocera* sp.) shrimp species. The modal progression of *P. duorarum* zoeae to postlarvae within the same 15-day period in which the gyre recirculated in the Tortugas region indicates that *P. duorarum* larvae, in addition to the advective process postulated by Munro et al. (1968), may recirculate within the gyre during their development. Retention of larvae by the gyre circulation at the Dry Tortugas, combined with wind driven transport on the southeast Florida shelf, is a plausible recruitment pathway for pink shrimp recruiting to the nursery grounds of Florida Bay.

Acknowledgments

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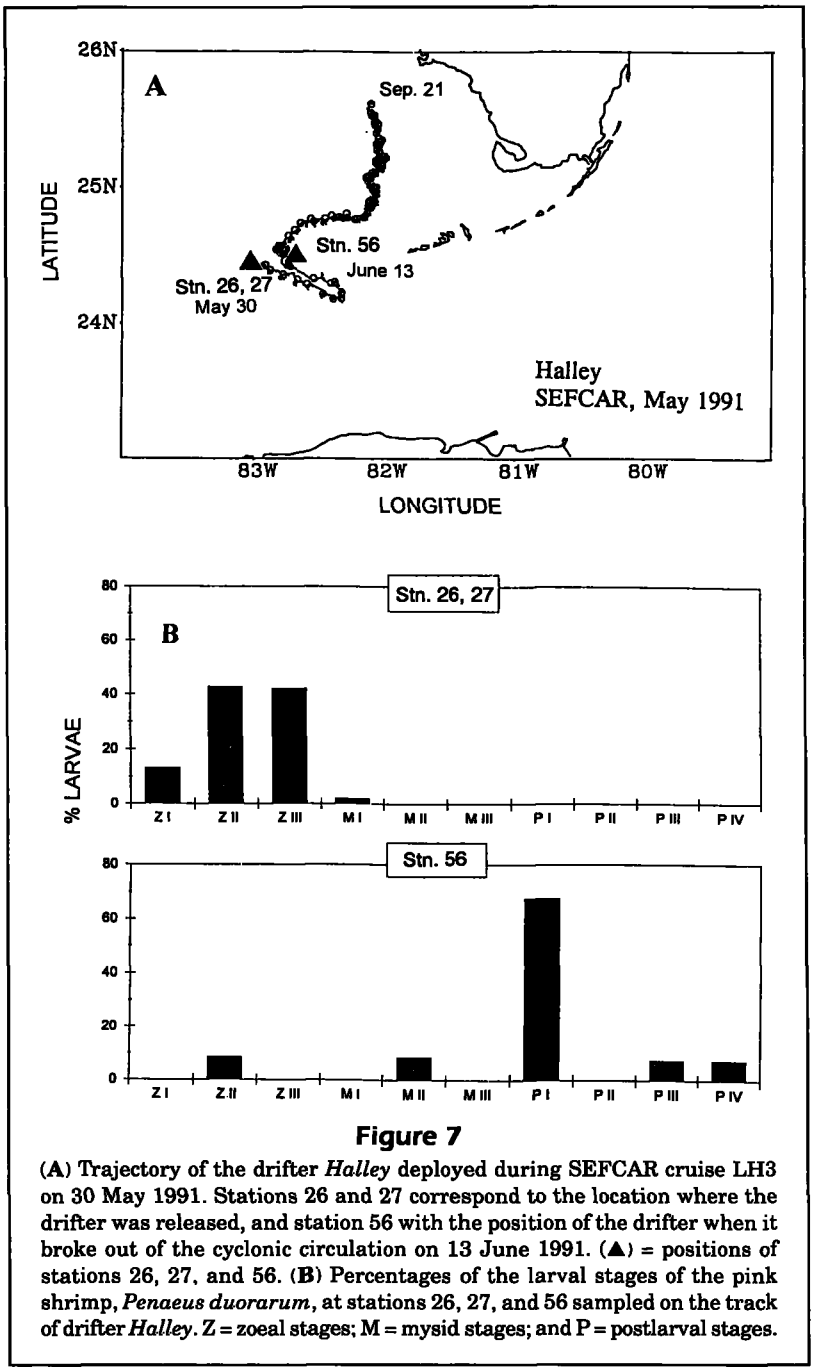

Figure 7

(**A**) Trajectory of the drifter *Halley* deployed during SEFCAR cruise LH3 on 30 May 1991. Stations 26 and 27 correspond to the location where the drifter was released, and station 56 with the position of the drifter when it broke out of the cyclonic circulation on 13 June 1991. (▲) = positions of stations 26, 27, and 56. (**B**) Percentages of the larval stages of the pink shrimp, *Penaeus duorarum*, at stations 26, 27, and 56 sampled on the track of drifter *Halley*. Z = zoeal stages; M = mysid stages; and P = postlarval stages.

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Growth and reproduction of the common dolphin, *Delphinus delphis* Linnaeus, in the offshore waters of the North Pacific Ocean

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Abstract.—A total of 707 common dolphins, *Delphinus delphis* Linnaeus, (376 males and 331 females) taken in Japanese, Korean, and Taiwanese drift nets in the central North Pacific Ocean from February to November 1990 and 1991 were examined. Sex, total length, date, and location of capture were recorded. Biological samples were collected from 152 of the dolphins examined (93 males and 59 females). Ages were determined by counting dentinal layers. Female reproductive status was determined by macroscopic examination of ovaries (n=43). Eight females were mature, two were pregnant, three were resting, two were lactating, and one was of unknown condition. Testes and epididymes were examined for evidence of spermatogenesis (n=70); 21 males were mature. A preliminary estimate of gestation period was 11.1 months. The sex ratio appeared to favor males; segregation during the sampling period may be responsible for differences from 1.0. Male average age at sexual maturation was estimated to be 10.5 years. The largest sexually immature male was 179 cm; the smallest sexually mature was 182 cm. Mature testis weights ranged from 273.2 g to 1,190 g. Females reached sexual maturation at about 8.0 years; estimates of length at sexual maturation were 172.8 and 170.7 cm. Predicted asymptotic lengths for males and females were 188.1 cm and 179.4 cm, respectively. Calving appeared to peak in May and June. Sampling effort moved northward through September; infrequent sampling of parturient females and neonates during the projected calving mode suggests they were segregated outside the fishing area at that time.

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Fishery Bulletin 93:483–494 (1995).

The common dolphin, *Delphinus delphis* Linnaeus, is an oceanic species widely distributed throughout the tropical and temperate seas of the world. In the western North Pacific Ocean, published accounts have dealt almost exclusively with taxonomy, distribution, and seasonal movements (Ogawa, 1937; Nishiwaki, 1967; Kasuya, 1971; Ohsumi, 1972). The common dolphin has been studied most extensively in the eastern North Pacific Ocean where research has focused primarily on species distribution, herd movements, reproductive seasonality, stock differences, and behavior (Norris and Prescott, 1961; Brownell, 1964; Hui, 1979; Evans, 1982; Perrin et al., 1985; Perryman and Lynn, 1993; Heyning and Perrin, 1994; Walker and Cowan[1]; Walker et al.[2]).

Two morphotypes of common dolphin, a short-beaked form and a long-beaked form, differing in rostral length, overall size, and color pattern, have been described from southern California waters (Banks and Brownell, 1969; Evans, 1975). Heyning and Perrin (1994) described two species of *Delphinus* from the eastern North Pacific Ocean, a short-beaked form which is referable to *D. delphis* Linnaeus and a long-beaked form assigned to the nominal species *D. bardaii* Dall, 1893. Recent studies of molecular genetics confirm the morphologic findings and support distinction of these two morphotypes of common dolphin as separate species (Rosel et al., 1994).

Despite the abundance of *D. delphis* in the eastern North Pacific Ocean, little biological information on age, growth, and reproductive condition exists in the literature. Ridgway and Green (1967) and Harrison et al. (1972) present gonadal data for a total of 30 male and 25 female specimens collected over a 16-year period from single strandings or live-capture. Correlations with age were not incorporated in either study. Hui (1979) correlated age, reproductive condition, and flipper bone development and summarized

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[2] Walker, W. A., F. G. Hochberg, and E. S. Hacker. 1984. The potential use of parasites *Crassicauda* (Nematoda) and *Nasitrema* (Platyhelminthes) as biological tags and their role in the natural mortality of common dolphins, *Delphinus delphis*, in the eastern North Pacific. Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038. Admin Rep. LJ-84-08C, 31 p.

data on age and gonadal condition for 35 male and 52 female specimens. Most of the dolphins examined in this study were collected during purse-seine research operations off the southern California coast (Hui, 1973).

In the late 1970's, Japan, Taiwan, and the Republic of Korea initiated high-seas driftnet fisheries for flying squid, *Ommastrephes bartrami*, and large-mesh fisheries for pelagic fish species including albacore tuna, *Thunnus alalunga*. The majority of squid driftnet fisheries operated from June to November in the central North Pacific Ocean between lat. 34°–46°N and long. 171°E–147°W, while large-mesh fisheries operated farther south and west between lat. 29°N–45°N and long. 147°E–150°W from February to November. *Delphinus delphis* was the most frequently killed cetacean in the large-mesh fisheries and was also found regularly entangled in the squid driftnet fisheries (Hobbs and Jones, 1993).

Beginning in 1990, under international cooperative agreements, biological samples were collected from marine mammals killed in the Japanese and Taiwanese squid and large-mesh fisheries and from marine mammals killed in the Korean squid fishery. Combining the 1990 and 1991 biological samples provided an opportunity to estimate growth and reproductive parameters for *D. delphis* from the offshore waters of the North Pacific Ocean.

Materials and methods

Specimen collection

Scientific observers collected biological data from all cetaceans caught in Japanese, Korean, and Taiwanese driftnet operations. Soon after arrival on deck, each cetacean was identified, sexed, measured (total length to nearest 1.0 cm), photographed twice (left lateral and ventral), and given an individual specimen number.

When an animal was dissected, the left lower jaw was tagged and frozen intact. For males, the right testis and epididymis were collected whole, tagged, and preserved in 10% formalin. Females were checked for evidence of lactation by longitudinal incision through the left mammary gland. The ovaries and uteri for most females were collected intact. The left ovary and entire reproductive tract was tagged and preserved in 10% formalin. If the animal was pregnant with a large fetus or was recently postpartum, only the ovaries and a cross section of the left uterine horn were collected. Fetuses were sexed, weighed to the nearest 1.0 g, and measured to the nearest 1.0 cm.

Frozen and preserved samples were shipped to the National Marine Mammal Laboratory in Seattle, Washington, for analyses.

Age determination

Teeth were extracted from the center of the left lower jaw for age determination. Each tooth was decalcified and sectioned (24 μm) longitudinally on a freezing microtome. Tooth-section preparation and dentinal growth-layer group (GLG) counting procedure followed guidelines developed by Myrick et al. (1983) for *Stenella* spp. Six to eight stained sections from the center of each tooth were mounted on a glass slide and examined under a compound microscope at 40× and 100× magnification with transmitted light. Dentinal GLG characteristics have been described for *Delphinus* (Perrin and Myrick, 1981). Annual deposition of dentinal GLG's has been established for tetracycline-marked common dolphins (Gurevitch et al., 1981). We followed these findings and assumed one GLG represented one year of growth.

Each tooth was read independently by two readers. Ages were recorded to the nearest 0.5 layer except for animals with less than one complete GLG. In these cases, we estimated the thickness of the incomplete layer to the nearest 0.2 GLG. Predetermined limits on reader variability were established following those used for *Lissodelphis borealis* in Ferrero and Walker (1993). This procedure allowed for a 0.5-layer difference between readings for estimated ages up to 5 years (measured from the median reading), one layer for estimates between 5 and 10 years, and one additional layer for every 5-year interval thereafter. Within these limits, we averaged the two readers' estimates to obtain the final age. When readings differed by more than these limits, the tooth was reread.

Examination of reproductive organs

Males Right testes with epididymides were weighed to the nearest 0.01 g and measured to the nearest 0.1 cm. A 1-cm^3 block was removed from the center of each testis; a similar section of epididymis was removed at mid-length, and both were prepared for histological analysis. Paraffin-embedded tissues were sectioned at 6 μm, stained with hematoxylin and eosin, and mounted on glass slides. Testes and epididymides were examined for evidence of spermatogenesis by using a compound microscope at 100× with transmitted light. Males were considered mature if sperm were present in testes tubules.

Females Ovaries were weighed to the nearest 0.01 g. Maximum diameter of the left uterine horn was

measured to the nearest millimeter. Each ovary was sliced transversely into serial sections (≈1 mm thick) with a scalpel and examined for the presence of corpora lutea and corpora albicantia. Two measurements of corpus diameter, taken at right angles, were recorded for well-regressed corpora; three diameters were recorded for larger corpora. Total corpus counts included corpora albicantia and corpora lutea from both the right and left ovaries. Females were classified as sexually mature if at least one corpus was present on either ovary.

Corpora were examined externally for indications of regression, including color change (i.e., darkening), reduced size and surface furrowing, and were classified by type following Perrin et al. (1976).

Results

The sample

From February to December 1990 and 1991, a total of 707 *D. delphis* (376 males and 331 females) were examined (see Fig. 1 for approximate collection locations). Sex, length, collection date, and location were recorded for each specimen, and biological samples were collected from 152 of these dolphins (93 males and 59 females).

Postnatal growth patterns and the reproductive parameters, average age and average length at sexual maturation, were measured by using the portion of the dissected sample for which both age and reproductive status were determined (70 males and 43 females). We tested for differences in the length distributions of the total sample and the reproductive sample; no significant differences were detected (Kolmogorov-Smirnov Test, D=0.18, P>0.05) The total sample (n=707) was used to examine sex ratios, gestation period, and reproductive seasonality. The spatial and temporal distribution of the total sample reflects the movement of the driftnet fisheries northward from February to August, then southward in the fall (Gong et al., 1993; Nakano et al., 1993; Yatsu et al., 1993; Yeh and Tung, 1993; Table 1).

Male *D. delphis* ranged from 0.4 to 27 years in age (n=93): 3% were calves <1 year old (n=3), 23% were yearlings (n=21), and the remainder were >2 years old. Female ages ranged from 0 to 26 years (n=59); one newborn was sampled, 5% were calves <1 year old (n=3), and 32% were yearlings (n=19). The age distribution of both sexes (Fig. 2) declined intrinsically except between the two youngest age groupings.

Males ranged in length from 86 to 211 cm. Females ranged from 81 to 199 cm (Figs. 3 and 4).

Stock identification

The two recently described species of common dolphin in the North Pacific Ocean are separable on the basis of cranial morphometrics and color pattern (Heyning and Perrin, 1994). To date five cranial specimens are available from the driftnet fisheries and of these, one is from an adult animal. The rostral length to zygomatic width ratio for the single adult specimen (201 cm, male) was 1.36. The mean ratio for adult male short-beaked common dolphin presented in Heyning and Perrin (1994) was 1.37 (SE=0.046). Preliminary comparison of photographs of common dolphins taken in the driftnet fisheries (color pattern features are described in Heyning and Perrin [1994]) suggests that our sample more closely resembles the short-beaked common dolphin. Furthermore, the currently known distribution of both species of *Delphinus* presented in Heyning and Perrin (1994) indicates that only the short-beaked form of

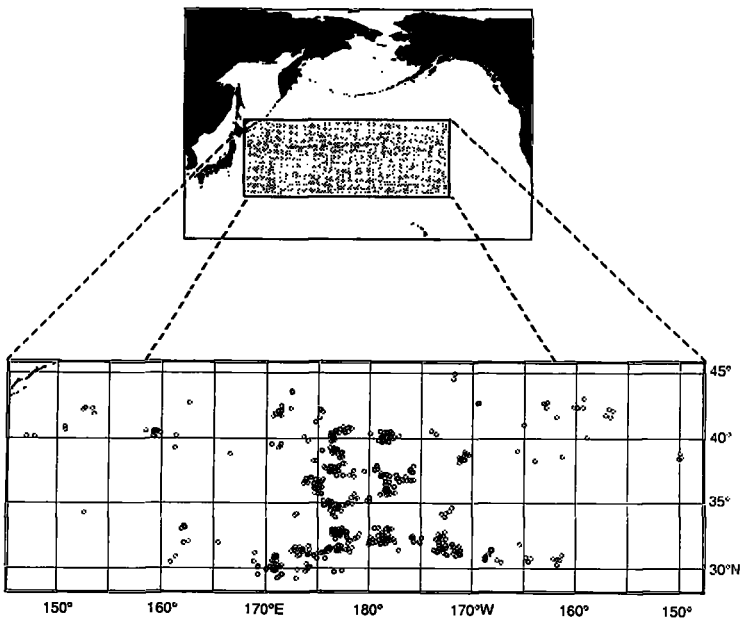

Figure 1

Approximate sampling locations of 376 male and 331 female common dolphin, *Delphinus delphis*, caught in Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991.

Table 1

Number of *Delphinus delphis* specimens examined from February to December, 1990 and 1991, from latitudes 29°N to 44°N in Japanese, Korean, and Taiwanese drift nets.

	Latitude (in degrees)															
Month	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
February	1	9	8	0	0	0	0	0	0	0	0	0	0	0	0	0
March	15	41	92	15	0	0	0	0	0	0	0	0	0	0	0	0
April	0	4	10	103	10	0	0	0	0	0	0	0	0	0	0	0
May	0	0	0	0	0	53	24	0	0	4	0	0	0	0	0	0
June	0	0	0	0	0	0	15	46	59	33	6	8	0	0	0	0
July	0	0	0	0	0	0	0	0	0	2	21	37	2	13	0	0
August	0	0	0	0	0	0	0	0	0	0	1	11	0	5	2	2
September	0	0	0	0	0	0	0	0	0	0	0	0	2	6	0	0
October	0	0	0	0	0	0	0	0	0	0	0	21	12	4	0	0
November	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
December	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

common dolphin extends into the driftnet fisheries area of the central North Pacific Ocean. On the basis of these factors, we provisionally assign the *Delphinus* in our sample to the short-beaked common dolphin *D. delphis*.

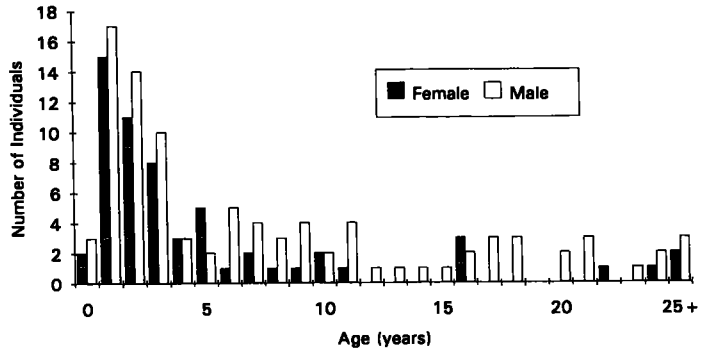

Figure 2

Age-frequency distribution of 93 male and 59 female common dolphin, *Delphinus delphis*, caught in Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

Growth

Length at birth and gestation period

Only two fetuses (65.0 cm and 12.6 cm) and one age-0 neonate (82 cm) were collected; this small sample size limited our ability to calculate a length at birth with the method described by Hohn and Hammond (1985) or the modified DeMaster (1978) approach described by Ferrero and Walker (1993).

The small sample size of newborns and lack of near-term fetuses also limited estimation of the gestation period. However, if we assume that the length of the age-0 neonate approximates the size at birth (82.0 cm) and consider the collection dates and lengths of the two fetuses, then preliminary estimates can be determined. We explored the gestation period parameter in two ways: 1) by using the relationship between fetal length and time described by Hugget and Widdas (1951), and 2) by using the relationship between size at birth and gestation period described for several species of delphinids by Perrin et al. (1977).

Following Hugget and Widdas (1951), we regressed the lengths (y) of our two fetus specimens and the age-0 neonate (we assumed this animal was recently born given the complete absence of postnatal dentine) on time, indexed by day of the year of collection (x), in order to estimate the linear phase of growth (t_g–t_o), where t_g is the gestation period and t_o is the "nonlinear" phase of growth. The regression equation

$$y = -57.04 + 0.264x \quad (1)$$

was significant (r^2=0.996, P<0.001). The linear growth phase was estimated to be 10.5 months. We did not attempt to estimate the nonlinear phase be-

cause an empirical method for doing so is lacking (Perrin and Reilly, 1984).

We also used Perrin et al.'s (1977) regression equation:

$$\mathrm{Log}(y) = 0.1659 + 0.4586\,\mathrm{Log}(x), \quad (2)$$

substituting x with the length of our age-0 neonate. The *D. delphis* length at birth estimate of 82.0 cm approximated the gestation period at 11.1 months.

Postnatal growth Growth curves were fitted separately for males and females by using a nonlinear least-squares method. The Laird/Gompertz formula (Laird, 1969) was used as a base model for both sexes:

$$L(t) = L_0 \exp\{a[1-\exp(-\alpha t)]\}, \quad (3)$$

where $L(t)$ is the length at age t, L_0 is the length at birth, t is the age, a is the specific rate of exponential growth, and α is the rate of decay of exponential growth.

For both sexes, we fit two Laird/Gompertz curves, one for the sexually mature animals and the other for the sexually immature, in order to minimize the number of positive residuals in the upper curve segment. The low sample size prohibited attempts to iteratively fit the two curve segments and locate the intersection point.

Female growth through age 2 was rapid, with a predicted length at age of 146.4 cm. The predicted asymptotic length was 179.4 cm (Fig. 5).

The male growth curve through age 2 was slightly steeper than that portion of the female growth curve, reaching a predicted length at age of 149.8 cm. The predicted asymptotic length was 188.1 cm (Fig. 6).

The mean length of females age 16 and older (i.e. those animals likely to have reached maximum size based on the predicted length at age [16 yr] falling on the asymptotic portion of the upper growth curve) was 179.8 cm (n=5, SE=6.76). The mean length of males age 16 and older was 187.1 cm (n=15, SE=5.57). The difference in mean lengths between sexes was significant (t-test, one-tailed, P=0.04).

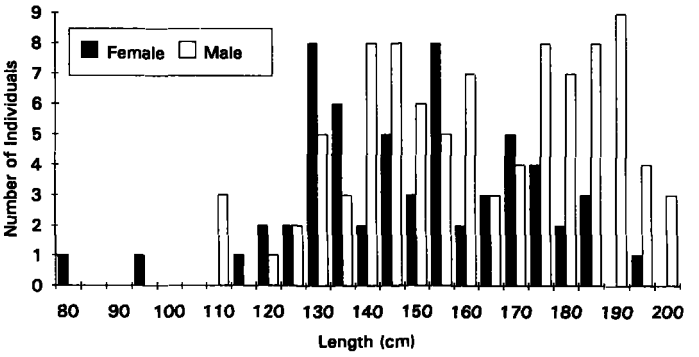

Figure 3

Length-frequency distribution of 93 male and 59 female common dolphin, *Delphinus delphis*, for which ages were determined. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

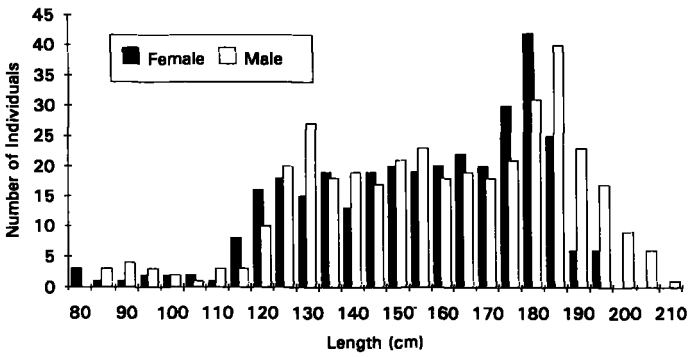

Figure 4

Length-frequency distribution of all common dolphins, *Delphinus delphis*, examined at sea February–November 1990–91 (376 males and 331 females). Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

Reproduction

Sex ratio Sex ratios were estimated for four subsets of the aggregate sample of measured animals (n=707) to represent progressively older age groups. The predicted length at age from our postnatal growth models (Figs. 5 and 6) were used to separate the sample into four approximate age groups (≤1 year, 1 to 10 years, 10 to 15 years, and >15 years) on the basis of length. In addition, we calculated separate sex ratios for the portions of the sample collected north and south of 34°N latitude. The latitudinal break corresponded to a break in the timing of collections, splitting February, March, and April sampling from the remainder of the year (Table 1). We used the empirical logistic transform method (Cox and Snell, 1989) to estimate sex ratio as

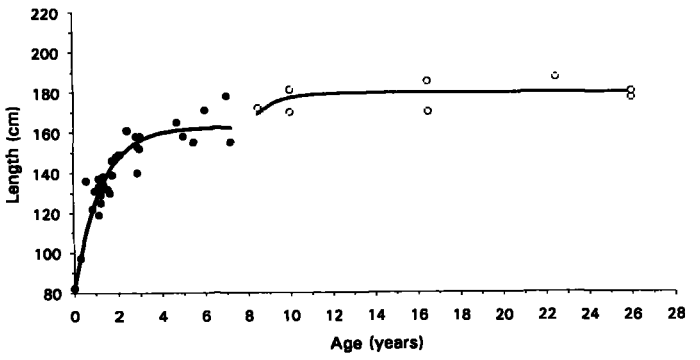

Figure 5

Age at length of female common dolphin, *Delphinus delphis*, with fitted growth curves (Laird/Gompertz model). The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

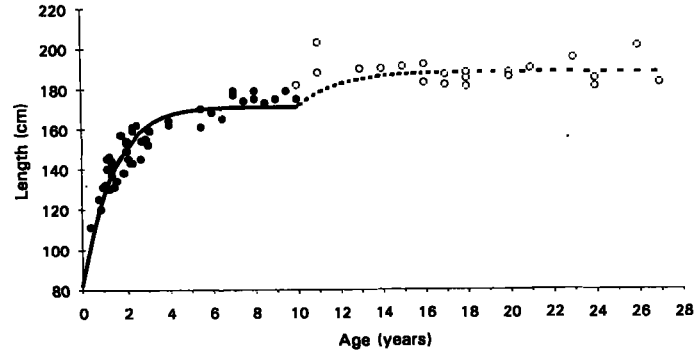

Figure 6

Age at length of male common dolphin, *Delphinus delphis*, with fitted growth curves (Laird/Gompertz model). The open circles are mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

$$r = \frac{m+0.5}{f+0.5}, \quad (4)$$

where r is the ratio of males to females, m is the number of males, and f is the number of females. The natural logarithm of r is normally distributed with variance,

$$\mathrm{var}[\ln(r)] = \frac{(n+1)(n+2)}{n(m+1)(f+1)}, \quad (5)$$

where n is the total number of males and females, m is the number of males, and f is the number of females. Of the sex ratios calculated by using the sample collected from all areas, only the 10 to 15 year-old group ratio (1.792) was significantly different from 1.0 (Exact Binomial Test, $P<0.01$). When only the portion of the sample collected south of 34°N was considered, none of the ratios was significantly different from 1.0 (P-values were all >0.2). The sample collected north of 34°N yielded a sex ratio significantly different from 1.0 (Exact Binomial Test, $P<0.01$) in the 10 to 15 year-old group (2.641) (Table 2).

Average age at sexual maturation Only preliminary estimates of average age at sexual maturation (ASM) could be calculated owing to the insufficient number of indeterminant age classes represented in the sample. No indeterminant age classes were represented in the female sample. For males we used the DeMaster (1978) method which computes the mean age as

$$ASM = \sum_{a=j}^{k} a(f_a - f_{a-1}), \quad (6)$$

where f_a is the fraction of mature animals in the sample aged a, j is the age of the youngest mature animal in the sample, and k is the age of the oldest immature animal in the sample.

Maturity status overlapped one age class in the male sample, where we estimated the variance as

$$\mathrm{var}(ASM) = \sum_{a=j}^{k} \frac{f_a(1-f_a)}{(N_a - 1)}, \quad (7)$$

where N_a is the total number of animals aged a.

Males The preliminary estimate of average age at onset of sexual maturation for males was 10.5 years (SE=0.50). Only at age 10 did both sexually mature and immature specimens appear in the sample.

There was a significant linear correlation between testis weight and age among the immature animals (r^2=0.83, $P<0.01$), but the overall increase in testis weight was small (<50 g over 10 years). A linear relationship between age and testis weight was not apparent among mature animals (r^2=0.15). Testis weight dramatically increased after age 10 (Fig. 7A).

The sample contained 21 sexually mature and 50 sexually immature males. The testis weight of the

youngest sexually mature male (10 years) was 370 g; the testis weight of the oldest immature (10 years) was 34.6 g. Weights of mature testes ranged from 273.2 to 1,190 g.

Females Only a rough approximation of female average age at sexual maturation was determined. The oldest sexually immature female was age 7.2 years, and the youngest sexually mature was 8.5 years. Of the forty-three female reproductive tracts collected, 8 were from mature animals. The youngest sexually mature female had three corpora (Fig. 8A). Of the mature females, three were resting, two were pregnant, two were lactating and had stage-2 corpora, and one was of unknown status (Table 3).

Average length at sexual maturation Calculation of average length at sexual maturation was limited for the male sample because no indeterminant length classes were represented. The female sample was adequate to estimate the parameter. Two methods were used: the DeMaster (1978) method, modified to estimate the average length instead of average age, and a logistic regression method.

The modification of DeMaster's method, applied to females, used lengths grouped into even intervals as

$$LSM = \sum_{i=i_{min}}^{i_{max}} l_i (f_i - f_{i-1}), \quad (8)$$

where i_{min} is the index of the size class with the smallest mature animal, i_{max} is the index of the size class with the largest immature animal, l_i is the lower limit of the ith size class, and f_i is the fraction mature in the ith size class.

The variance estimate on female LSM was obtained by modifying the formula of DeMaster (1978) to account for the interval width (w) so that

Table 2

Sex ratios for four age groups of *Delphinus delphis*. Predicted lengths at age from the Laird/Gompertz growth model were used to determine the upper limits for each group (i.e. 125 cm, both sexes ≤1 year; 171 cm for males and 169 cm for females aged 1 to 10 years; 187 cm for males and 179 cm for females aged 10–15 years). Sex ratios significantly different from 1.0 (α=0.05) are marked with an asterisk. SE = Standard error.

Area and age groups	No. of individuals		Sex ratio	SE
	Male	Female		
All areas				
≤1	32	41	0.7831	0.2342
1–10	182	161	1.1362	0.1079
10–15	90	50	1.7921*	0.1756
>15	71	79	0.8994	0.1630
South of 34°N latitude				
≤1	11	18	0.6216	0.3750
1–10	78	72	1.0828	0.1629
10–15	39	31	1.2540	0.2388
>15	24	35	0.6901	0.2625
North of 34°N latitude				
≤1	21	23	0.9149	0.2985
1–10	105	89	1.1788	0.1437
10–15	51	19	2.6410*	0.2649
>15	47	44	1.0674	0.2086

$$\mathrm{var}(LSM) = w^2 \sum_{i=i_{min}}^{i_{max}} \frac{f_i(1-f_i)}{N_i - 1}, \quad (9)$$

where N_i is number of individuals in the ith size class and the interval width (w) was constant.

The logistic regression (Cox and Snell, 1989) fits a logistic curve, ($\mu(a)$), the probability that a dolphin

Table 3

Age, length, corpus count, and reproductive condition for eight mature female *Delphinus delphis* taken in Japanese, Korean, and Taiwanese drift nets in the central North Pacific Ocean from February to December, 1990 and 1991.

Specimen number	Collection date	Length (cm)	Age (years)	Corpus count	Reproductive condition
RAT 036	23 Sep 90	170	10	1	Pregnant
EJW 037	25 Sep 90	172	8.5	3	Unknown
RAT 050	3 Oct 90	180	26	8	Resting
JAS 045	28 Mar 91	185	16.5	3	Pregnant
JAS 062	4 Jun 91	187	22.5	5	Resting
JAS 071	7 Jun 91	181	10	7	Lactating
JAS 109	26 Jun 91	177	26	6	Lactating
JAS 121	17 Jul 91	170	16.5	2	Resting

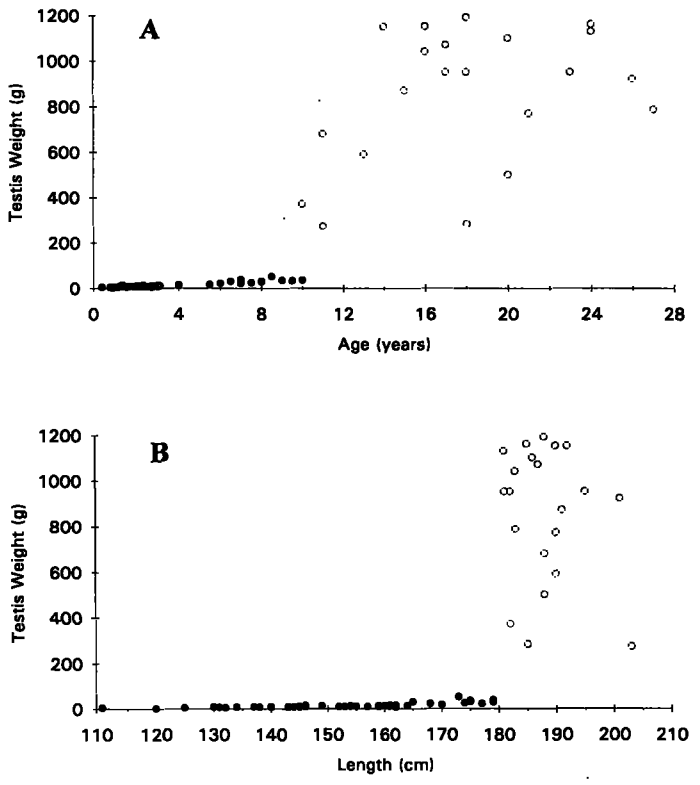

Figure 7

(A) Scatterplot of age (years) and testis weight (g) for 93 male common dolphin, *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean. (B) Scatterplot of length (cm) and testis weight (g) for 93 male *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

of length l is mature, to the distribution of mature and immature animals by age:

$$\mu = \frac{e^{lb+c}}{1+e^{lb+c}}, \qquad (10)$$

where, l is the length of the dolphin and b and c are the slope and intercept of the regression. Average length at sexual maturation is then estimated as the age where $\mu(a) = 0.50$ so that LSM $= -c/b$.

The regression was done by using a maximum likelihood and iteratively reweighted least-squares algorithm (Chambers and Hastie, 1992). The standard error for μ was obtained by transforming the standard error of the linear fit.

Males Length at sexual maturation could only be suggested by the largest immature male, 179 cm, and the smallest mature male, 182 cm. There was a significant linear correlation between length and individual testis weight among immature animals (r^2=0.61, P<0.0001). Testis weights changed little with length up to the onset of sexual maturity when weights increased greatly (Fig. 7B). No correlation between length of mature animals and testis weights was detected (P>0.4).

Females Female average length at sexual maturation based on the DeMaster (1978) method was 172.8 cm (SE=0.56). With the logistic method, female LSM was 170.7 cm (SE=2.74). The smallest sexually mature female measured 170 cm; two corpora were present on the left ovary. The largest sexually immature female was 178 cm (Fig. 8B).

Ovulation rate Calculation of ovulation rate followed methods used for *Stenella attenuata* in Perrin et al. (1976). The average reproductive age ($\bar{A}$) in interval p was calculated as

$$\bar{A}_p = \frac{\left(\sum_i^p a_i b_i\right)}{c}, \qquad (11)$$

where a is the percent maturing in the ith interval, b is the average reproductive age in interval p of females which matured in i, and c is the percent mature in interval p. The average corpus count in each age interval was calculated by dividing the sum of corpora counted in interval i by the number of mature females in interval i. We then regressed the average corpus count on the average reproductive age.

Ovarian scars numbered from 1 to 8 corpora among mature females. A linear model provided the best fit to the corpus count and average reproductive age data (r^2=0.61, P<0.1).

Seasonality Evidence of reproductive seasonality was detected by correlating age and length on collection date. From the aged portion of the sample we regressed ages of specimens ≤0.5 years (n=5) and the day of the year of collection using a linear model that resulted in the equation

$$y = 158.76 + 265.14x, \qquad (12)$$

where x is age and y is the day of the year of collection. At age 0.0, the intercept corresponds to a date in early June, suggesting the calving mode. Both the slope and the intercepts were significant ($P<0.001$ and $P<0.05$, respectively).

We also regressed the lengths of specimens ≤115 cm from the overall sample ($n=30$) with day of the year. The 115-cm length corresponded to ages slightly older than 0.5 year for both sexes according to the predicted length-at-age relationship from the Laird/Gompertz growth model. We obtained the equation

$$y = -133.44 + 3.435x, \qquad (13)$$

where x is the length and y is the day of the year. Substituting 82 cm, our provisional length at birth, for x, the line intercepts a date in mid-May. Both the age- and length-based regressions suggest a seasonal peak in mid-May or early June. The lengths and dates of collection for the two fetuses also support this modal peak. The 65-cm fetus collected 28 March 1991 and the 12.6-cm fetus collected 23 September 1990 were projected to reach full-term in late May to early June.

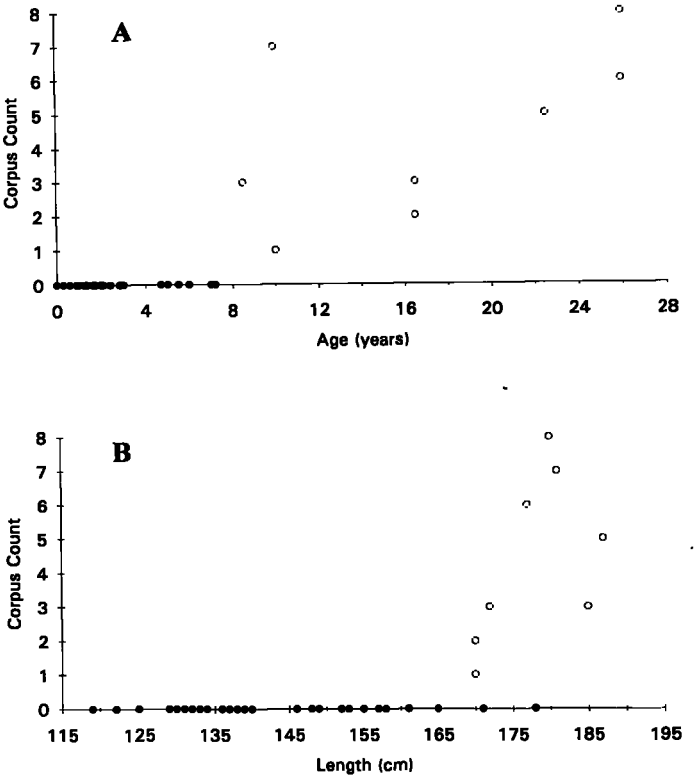

Figure 8

(**A**) Scatterplot of age (years) and total corpus count for 59 female, common dolphin, *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean. (**B**) Scatterplot of length (cm) and total corpus count for 59 female *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

Discussion

The structure of the *D. delphis* sample suggested that it was suitable for preliminary estimation of several basic growth and reproduction parameters, although our values would be improved with larger sample sizes. With uncertain prospects for collecting additional *D. delphis* samples, owing to the discontinuation of the high seas squid driftnet fisheries and thus any associated sampling programs, we attempted to provide as much quantitative analysis as possible; however, we must regard many of our estimates as provisional. In particular, more reliable estimates of ASM and LSM will require more samples in the indeterminant age and length classes. Strong evidence of seasonality in calving made this sample unsuitable for calculation of calving interval, length of lactation, age of weaning, length of resting period, or reproductive rates.

Our application of the double Laird/Gompertz growth model is consistent with methods applied in previous growth studies on small cetaceans (Perrin et al., 1976, 1977), although our sample was not large enough to iteratively fit an intersection point between the upper and lower curves. While our application of the two-stage model suggests a secondary growth surge near the onset of sexual maturation, the magnitude and timing of that event should not be considered reliable without further sampling.

We attempted to fit a single Laird/Gompertz model to both the male and female data sets, but in both cases we encountered a preponderance of positive residuals at predicted lengths at age >10 years. Using the single curve, we predicted asymptotic lengths for both sexes at least 10 cm lower than any of the observed lengths for mature specimens. Our results from the double Laird/Gompertz model provide predicted length-at-age relationships with comparatively smaller residuals, distributed both positively and negatively at older ages.

Very few neonates, pregnant females with near-term fetuses, or lactating females, were collected even though we found strong evidence for a calving mode during the sampling period. We considered three possible factors to explain the inconsistency: 1) differing entanglement rates by various age and sex strata, 2) temporal disproportion in sampling effort, especially during the projected peak of the calving season, and 3) population segregation.

Following the same rationale developed for sampling *L. borealis* in Ferrero and Walker (1993), we did not consider the potential for bias as a result of the sampling method (i.e. incidental take in drift nets) to be a major factor. *Delphinus delphis* entanglements were scattered randomly along the length of the nets. Multiple entanglements were rare. The entanglements, therefore, appear to arise as individual events rather than as whole school encounters. Consequently, the sample likely reflects the composition of the population in the area rather than the composition of an individual school. There is also no evidence to assume that neonates or pregnant females avoid entanglement more than other age or sex strata.

Regarding the second possibility, the temporal distribution of the sample does not reflect low sampling effort during the late spring and early summer months. The peak in sampling effort occurred in June, and over 75% of that effort was accomplished in March–June. Thus, the absence of neonates and parturient females in the sample did not result from inadequate collection effort at that time.

Population segregation appears to be a likely factor in contributing to the small number of neonates and parturient females in our samples, and its effect is reflected in our sampling where collection locations tracked the northerly progress of the fishery. Our only advanced-term fetus was collected at the southern end of the study area in March. As the sampling effort moved northward, the parturient or lactating females and calves probably remained to the south and were unavailable for sampling. The remaining part of the female population appeared to have been represented in the sample.

The age and length distributions also reflect the likelihood that a significant portion of the female population was missing from the sample. The sex ratios calculated for specimens collected in areas south of lat. 34°N were not significantly different from 1.0; however, north of 34°N the ratio significantly differed from 1.0, favoring males in the 10 to 15 year-old age group. Furthermore, in the 15+ age group the sex ratio was not significantly different from 1.0 which is inconsistent with data for other delphinid species characterized by a greater proportion of mature females in the population (see Table 8 in Perrin and Reilly, 1984). Our age and length distributions, which suggest a male-dominated ratio, better describe only the part of the *D. delphis* population inhabiting the northern portion of the study area during the fishing season. These distributions and the sex ratio, therefore, should not be considered indicative of the overall population structure.

Schooling segregation by age, sex, and reproductive status has been demonstrated for numerous species of delphinid cetaceans (Perrin and Reilly, 1984); *Delphinus delphis* is among this group. Schooling segregation of *D. delphis* has been documented in the Black Sea where during calving and early lactation, females occur predominantly in offshore waters (Kleinenberg, 1956; Tomlin, 1957).

Our preliminary estimate of 11.1 months for gestation is similar to published accounts for the common dolphin. Gestation periods ranging from 10 to 11 months have been reported for *D. delphis* (Kleinenberg, 1956; Tomlin, 1957; Harrison, 1969).

Growth curves for North Pacific *D. delphis* have not been published and little definitive information on age and length at the onset of sexual maturation is available. Gurevitch and Stewart[3] reported that male *D. delphis* in the eastern tropical Pacific Ocean (central tropical population) reach sexual maturity around 6–7 GLG's, at a mean length of 200 cm. Hui (1979) presented data on *Delphinus* from southern California where females were reported to attain sexual maturity around 7–14 GLG's, and males between 8 and 12 GLG's. Length at onset of sexual maturation was 165–182 cm for females and 175–190 cm for males. Our preliminary estimates of age and length at sexual maturation for both sexes fall within the ranges presented in Hui (1979).

However, comparisons of our findings on the short-beaked *D. delphis* from the North Pacific transition zone with those from the southern California sample of Hui (1979) are potentially misleading, given recent evidence for the occurrence of two sympatric species of common dolphin in the southern California area (Heyning and Perrin, 1994). These two species, *D. bairdii* and *D. delphis*, are documented to differ markedly in overall size, and it is possible that Hui's (1979) sample contained members of both these species, accounting for the wide ranges in lengths at sexual maturation. In addition, differences in ages at onset of sexual maturation between our sample

[3] Gurevitch, V. S., and B. S. Stewart. 1978. Structure of kill of the common dolphin, *Delphinus delphis*, from the eastern tropical Pacific in 1977. Final Rep. for Contract 03-78-M02-0101, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038, 19 p.

and those presented in Hui (1979) and Gurevitch and Stewart[3] may be due to ageing methods. Both these studies employed an early technique of reading undecalcified, thin sections of formic-acid-etched teeth. This method is now considered imprecise for ageing small cetacean teeth (Perrin and Myrick, 1981).

Perryman and Lynn (1993) documented reproductive seasonality differences between three morphologically distinct common dolphin populations from adjacent but differing habitats in the eastern North Pacific Ocean. Calving season in the tropical region was year-round. In the temperate regions, which are characterized by a wider range of oceanographic conditions, strong evidence of reproductive seasonality was evident.

Our sample suggests evidence for a May–June calving peak as well as for schooling segregation of parturient females in the southern regions of the transition zone, closer to the subtropical domain. Evidence for pronounced reproductive seasonality should be anticipated in this region because the North Pacific transition zone is characterized by extreme oceanographic conditions, particularly in the northern regions adjacent to the subarctic frontal zone (Roden, 1991).

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The feasibility of direct photographic assessment of giant bluefin tuna, *Thunnus thynnus*, in New England waters

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Abstract.—Controversy concerning the validity and accuracy of recent assessment results for giant bluefin tuna, *Thunnus thynnus*, led us to examine alternative methods of estimating their abundance. In collaboration with a New England giant bluefin tuna industry group, we tested the feasibility of using commercial spotter pilots and aerial photography as a means of obtaining tuna counts in the Gulf of Maine and adjacent New England waters. Nine commercial spotter pilots photographed a total of 126 schools of bluefin tuna during the summer of 1993, representing 13,973 fish, with a maximum one-day count of 4,894. Three spotter pilots contributed nearly 70% of the total photographic effort. Differences in photographic ability and commercial involvement in the fishery appeared to influence spotter pilot participation. Aerial photographic surveys may provide a means of obtaining area-specific minimum abundance and distribution data for giant and large-medium bluefin tuna.

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Stock assessments of the highly migratory northern Atlantic bluefin tuna, *Thunnus thynnus*, are primarily based on age-structured and lumped biomass models derived from landings data and various abundance indices (Scott et al., 1993). These production or CPUE (catch per unit of effort) models provide the framework for international management of the commercially valuable bluefin tuna. A problem with CPUE-derived estimates of stock biomass, however, is that they are affected by changes in fishing effort, technology, fish density, and the marketplace (Lo et al., 1992). How accurately recent assessment models portray seasonal bluefin abundance in the west Atlantic, a fishery with a 1993 catch of 1,047.2 metric tons of giant tuna (≥77 inches straight fork length [SFL]) and of large-medium category tuna (between 70 and 77 inches SFL), remains controversial (Clay, 1991; Suzuki and Ishizuka, 1991; Safina, 1993).

Aerial surveys have been used to obtain relative indices of abundance in fisheries worldwide, including northern anchovy (*Engraulis mordax*), jack mackerel (*Trachurus symmetricus*), menhaden (*Brevoortia* spp.), mullet (*Mugil* spp.), and other pelagic fishes (Squire, 1961, 1972, 1993; Williams, 1981; Scott et al., 1989; Lo et al., 1992). Estimates of fish biomass from these surveys are based on appraisals of school size in tonnage per unit of area, or by size of remotely detected signals such as bioluminescence or turbidity fields. Visual biomass estimates from aerial survey data are relatively easy to construct but are difficult to interpret without ground truth or information on surfacing behavior (Lo et al., 1993).

In contrast, direct enumeration of pelagic fish is notoriously difficult. In the 1950's, U.S. fisheries scientists attempted to count giant bluefin tuna migrating along the Bahama Banks (Rivas, 1978) and later undertook direct assessment with photographic and video techniques (NMFS[1]). Despite dedicated search time, very few fish were detected during the survey. More recently, other countries have explored aerial and remote sensing methods as a means of calibrating catch-related indices for tuna species. Since 1990, transect surveys have provided estimates of regional abundance and recruitment indices for southern bluefin tuna, *Thunnus maccoyii*, in

[1] Anonymous. 1975. A study of the application of remote sensing techniques for detection and enumeration of giant bluefin tuna. Rep of Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA. Contrib. No. 437.

the Great Australian Bight (Morgan, 1992; Chen and Polacheck[2]). Aerial surface-detection radar surveys targeting bluefin tuna and other tunas have been explored by the French in the Mediterranean and tropical South Pacific areas (Petit et al., 1992).

Recently, members of the New England commercial giant bluefin tuna industry suggested that spotter pilots might provide a platform to examine the potential applications and limitations of direct visual assessment of giant and large-medium bluefin tuna. In coastal waters off New England, spotter pilots have located surface schools of giant bluefin tuna that are then targeted for capture by harpoon, hook and line, and purse-seine operations. In 1993, the New England Aquarium (NEA) and East Coast Tuna Association (ECTA) initiated a collaborative project involving fish spotter pilots locating and photographing surface schools of bluefin tuna normally targeted by the fishery. Our objective was to determine whether aerial photography could be used to provide information on the relative abundance, schooling characteristics, and spatial distribution of bluefin tuna.

Methods

The present study relied on a simple technical framework involving only voluntary participation by commercial spotters and the use of two cameras, one to photograph tuna schools (for enumeration) and another to document school location. Nine commercial spotter pilots participated in this survey while engaged in the 1993 seasonal fishery. All fish spotters flew single engine aircraft (models Cessna 172 and 182, Citabria, SuperCub) and were based on Cape Cod or in lower Maine. Four pilots spotted for seining operations, five were associated with harpoon or general category fishing (hook and line), and at least two participated in all three categories. Bluefin tuna were photographed from 23 July to 13 September, when participating pilots ceased activities because fishing quotas were filled.

Each pilot was provided with a hand-held 35-mm camera (Nikon N8008s) and an autofocus zoom lens (70–210 mm, F3.5/4.5, SIGMA Corp.) to photograph tuna schools. Synchronized databacks on cameras (Nikon, MF–21) imprinted date and time directly on exposed film. A second viewfinder camera (Shotmaster Ultra Zoom, 38–60 mm, f6.9 lens, Ricoh Corp.) was mounted overhead in the aircraft cabin to document positions from onboard global positioning system (GPS) or LORAN units located in or below the dashboard. Both cameras had auto advance features and were linked via cable so that they were simultaneously triggered when pilots depressed a remote shutter control. A photographic record of position (in TD Loran lines or lat./long.) could then be provided for each photographically documented tuna school. A digital clock synchronized with the 35-mm camera databack was mounted near the LORAN/GPS within range of the viewfinder camera. We could then verify sequence linkage between frames of tuna schools and locations if film advance speeds were not perfectly matched.

Tuna schools were photographed with color slide film (Ektachrome 400 ASA, Kodak), selected for depth of penetration and contrast characteristics (NMFS, 1975; Lockwood et al.[3]). Lenses were fitted with a circular polarizing filter or haze filter for glare reduction. Aircraft positions recorded by the viewfinder camera were read directly from developed black and white film (Tri-X 400 ASA, Kodak).

Pilots were supplied with labelled film canisters and with stamped and coded direct mailers for color processing, and were instructed to mail the film immediately when it was finished. Black and white film was returned directly to us and processed locally.

Analysis

Processed film was logged with an identification code, and a cursory examination was made on a light table with a film eye loupe. Tuna counts were made by projecting selected slides of schools and by visually counting individual fish. Images were enlarged by projection to a standard size (78 × 52 cm) onto a sheet of drafting-quality tracing paper marked with 10 × 10 cm square gridlines. Positions of clearly identifiable fish were marked and the total tallied per grid square and per slide frame. Upon completion of the tally, each sheet was labelled with the film identification code, frame number, time, and total fish count. No attempt was made to estimate the total number of fish in the school.

Since bluefin tuna are fast-swimming, mobile fish, it was possible for pilots to photograph the same school at slightly different locations on a single day. A school might be difficult to distinguish from adjacent, similarly sized schools. When photographed by a spotter in close succession, these schools had to have distinctly different spatial configurations or had

[2] Chen, S. X., and T. Polacheck. Data analysis of the aerial surveys (1991–1994) for juvenile southern bluefin tuna in the Great Austrialian Bight. 1994 SBT Recruitment Monitoring Workshop, Hobart, Tasmania. Available from T. Polacheck, CSIRO, Div. Fisheries, GPO Box 1538, Hobart, Tasmania 7001.

[3] Lockwood, H. E. Technicolor Graphics Services, Inc., Houston, TX 77058.

to be separated by at least one nautical mile (nmi) in order to be tallied independently. Spotters and fishermen reported maximum travel rates of 4–10 knots for bluefin tuna in the study area. With the assumption that swimming speeds were 10 knots, similarly sized schools photographed by different pilots on the same day had to be far enough apart so that it was unlikely that schools could have travelled from one location to the other in a given time period.

Results

The bluefin tuna survey area, fish spotter land bases, and locations of photographed schools are depicted in Figure 1. A total of 126 bluefin tuna schools, representing a cumulative count of 13,973 fish, were successfully photographed by spotter pilots on 17 days out of a 50-day survey period, for a total of 35 pilot-days. Pilots reported that, to the best of their knowledge, they photographed only giant or large-medium bluefin tuna size categories (>70 inches SFL), those targeted by the New England fishery. The position of surveyed schools, indicated by TD values or lat./long. on the pilot's navigational system, was established for 56 schools. Numbers of fish counted in schools ranged from 5 to 1,294 individuals (Fig. 2). Total giant and large-medium tuna counts were >1,000 fish on four survey days, with a maximum count of 4,894 tuna on 8 August (Table 1). A data summary of schools for three high count survey days (8–10 Aug) is given in Table 2.

From one to four spotters participated on high-count days, but no more than four pilots photographed fish on any given survey day. Spotters photographed schools from 0900 to 1803 h, but the greatest effort occurred during midday between 1200 and 1600 h (Table 3). Spotters report that slack tide (estimated to

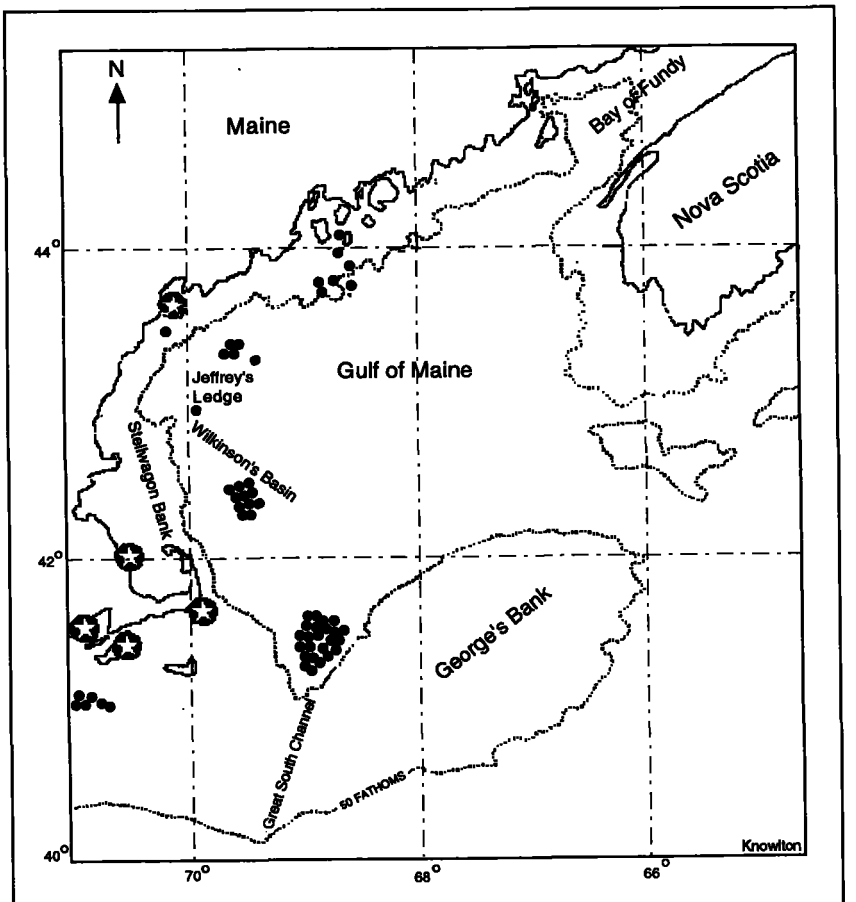

Figure 1

Aerial survey area for giant bluefin tuna, *Thunnus thynnus*, in New England waters, July–September 1993. Land bases of participating spotter pilots are indicated by stars. Filled circles indicate positions of photographed tuna schools.

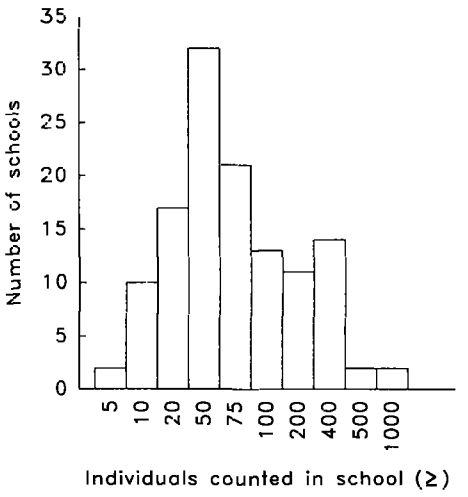

Figure 2

Frequency distribution of counts of giant and large-medium bluefin tuna, *Thunnus thynnus*, schools photographed by spotter pilots in New England waters, July–September 1993.

be within one hour of nearest coastal reference) often provides good conditions for locating fish. There was no discernible relation between lunar cycle or estimated slack tide and timing of greatest survey effort.

Surface schooling configurations of bluefin tuna, documented during the survey, included "soldiers" (small school of giants, fish swimming abreast in a parabola or straightline formation, Fig. 3A), "cartwheels" (spinning wheel-like formations, Fig. 3B), surface sheets (Fig. 3C), and densely packed domes (Fig. 3D). Basking sharks and, less frequently, humpback, fin, and other whales, were also photographed in association with bluefin tuna schools.

Discussion

Spotting and survey effort

Most of the bluefin tuna were photographed over a four-day period in August by only a few of the participating pilots, indicating that survey effort was strongly affected by environmental conditions and pilot effort. Fish spotters flew on less than half the survey period, grounded largely by inclement weather. They photographed all sizes of bluefin tuna schools, but small to medium-sized schools (≥5 counts <200) were located and photographed most frequently. Although initially instructed to document schools of any size, some pilots reported not bothering to photograph very small schools, particularly on "good" fishing days.

Table 1

Highest count days for aerial photography of bluefin tuna, Thunnus thynnus, in New England waters, July–September 1993.

Date[1]	Count	No. of schools	No. of pilots
8 Aug	4,894	24	2
22 Aug	2,517	16	4
9 Aug	1,067	15	2
10 Aug	1,275	7	1

[1] Full moon 2 August; new moon 17 August.

Search and photographic efforts of participating fish spotters varied widely, reflecting differences in commercial involvement in the fishery and in motivation. For example, one pilot photographed a minimum of 6,767 giant and large-medium bluefin tuna over five days under excellent survey conditions. However, his survey effort in hours represented <10% of the estimated 400 total flight hours he expended in the 1993 season. This result suggests that aerial photography of giant bluefin tuna can be accomplished with a small team of motivated pilots. In contrast, a fish spotter in partnership with seining operations photographed far fewer fish (467) because his total survey effort was limited to the few days permitted for his boat to achieve its seasonal quota. If all nine participating pilots had undertaken simultaneous surveys throughout the season, more complete documentation might have been achieved.

Throughout the survey we maintained frequent phone contact with the pilots in an effort to improve the quality of aerial and position photographs. Although we were able to count tuna in the majority of submitted frames, there was clearly a learning curve in the spotters' attempts to take high-resolution pictures. Blurring from aircraft vibration and underexposure were the most frequent problems with tuna school photographs. Unreadable Loran frames more often than not resulted from excessive glare on the digital readout, from improper film advance, or because the pilot had shifted position and had subsequently blocked the camera's view of the Loran. This problem could be eliminated if position were electronically logged each time the spotter photographed bluefin schools.

Enumeration analysis

In general, we assumed that environmental conditions were fairly uniform (low wind and sea states,

Table 2

Summary of photographed bluefin tuna, *Thunnus thynnus*, schools on three highest-count survey days in New England waters, July–September 1993.

Date	Pilot	Count	Time	Latitude (°N)	Longitude (°W)
08 Aug	g	57	12:53	41°25'	68°57'
08 Aug	g	152	12:59	41°25'	68°56'
08 Aug	g	186	13:01	41°25'	68°57'
08 Aug	g	284	13:09	41°25'	68°57'
08 Aug	g	1039	13:15	41°27'	68°55'
08 Aug	g	457	13:17	41°26'	68°57'
08 Aug	g	371	13:57		
08 Aug	f	96	14:09	42°27'	69°30'
08 Aug	g	26	14:27	41°28'	68°55'
08 Aug	g	499	14:28	41°28'	68°55'
08 Aug	g	315	14:37		
08 Aug	g	300	14:58	41°29'	68°55'
08 Aug	g	52	15:03	41°28'	68°56'
08 Aug	g	95	15:06		
08 Aug	g	42	15:09	41°29'	68°56'
08 Aug	g	85	15:17	41°28'	68°56'
08 Aug	g	107	15:31	41°29'	68°55'
08 Aug	f	313	15:34		
08 Aug	g	26	15:35		
08 Aug	f	85	15:45		
08 Aug	g	44	15:46		
08 Aug	g	69	15:54		
08 Aug	g	176	16:09	41°29'	68°55'
08 Aug	g	18	17:37	41°27'	68°57'
09 Aug	g	79	12:53		
09 Aug	g	60	12:58		
09 Aug	c	64	13:04		
09 Aug	g	83	13:12		
09 Aug	g	51	13:19		
09 Aug	c	22	13:20	4137	68°50
09 Aug	g	78	13:23		
09 Aug	g	94	13:40		
09 Aug	c	58	14:06	41°39'	68°44'
09 Aug	g	62	14:23	41°35'	68°45'
09 Aug	g	13	16:00	41°36'	68°47'
09 Aug	c	136	16:10	41°40'	68°42'
09 Aug	c	73	16:28	41°41'	68°41'
09 Aug	c	123	16:31	41°38'	68°40'
09 Aug	c	71	16:42	41°42'	69°03'
10 Aug	g	262	12:52	41°33'	68°48'
10 Aug	g	54	13:04	41°34'	68°48'
10 Aug	g	209	15:50	41°04'	70°51'
10 Aug	g	286	15:58	40°59'	70°47'
10 Aug	g	344	16:07	41°06'	70°56'
10 Aug	g	74	16:09	41°05'	70°56'
10 Aug	g	46	16:26	41°01'	71°02'

[1] Latitude and longitude have been rounded to nearest degree and minute.

good light levels, minimal glare) when schools were photographed. Altitude varied among spotters but seemed to be less important in producing good records than were sea state and light condition. However, spotters photographing large schools at low altitude were occasionally unable to include the entire school within the frame. We enumerated only clearly discernible individuals in schools and in some circumstances were able to count fish in at least one tier below the surface tier. With smaller schools, particularly in "soldier formation" or in surface-oriented groups, we were able to count all members of the school.

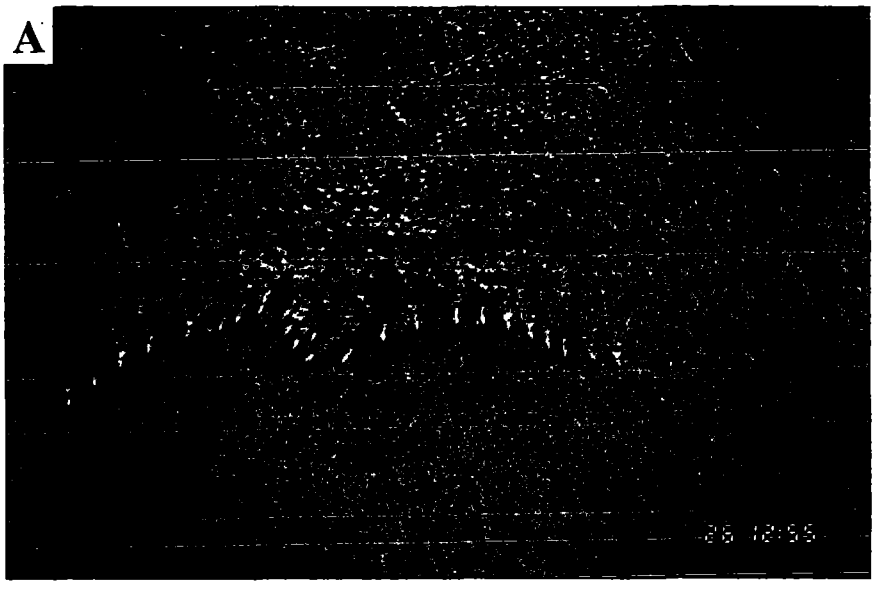

Figure 3

Examples of giant bluefin tuna school configurations photographed by fish spotters in the 1993 New England waters aerial census: (**A**) soldiers; (**B**) cartwheels; (**C**) surface sheet; and (**D**) densely packed dome.

Limitations of the data

Direct enumeration of giant bluefin tuna from aerial survey involves potential sources of error that must be addressed. These include species and size-class identification, differences in surfacing behavior caused by environmental or biological variables, and redundant counts as fish migrate through the study area. In the 1993 feasibility study, we identified and resolved only a few of these issues but nevertheless obtained information vital for improving future aerial surveys.

We observed small differences (<1%) in medium-size and large school totals when three different individuals examined and counted bluefin tuna in

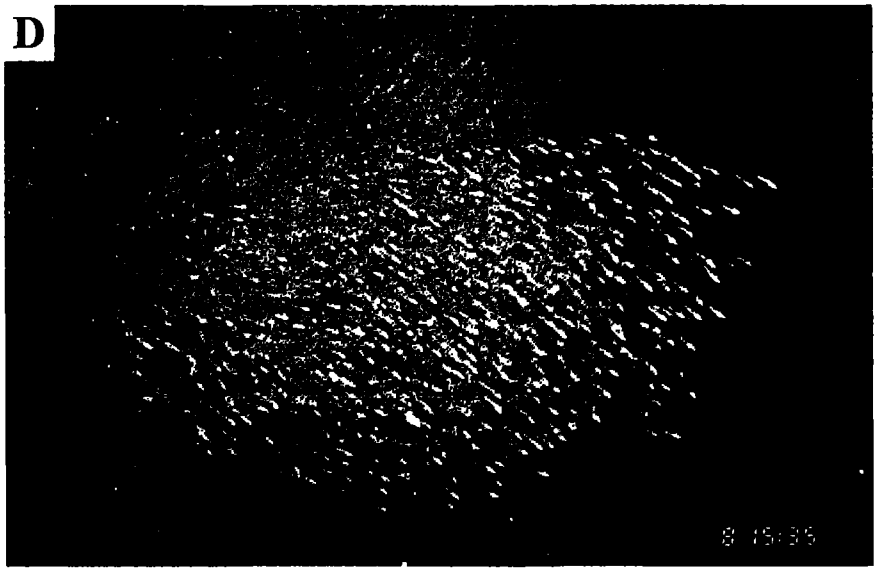

Figure 3 (continued)

projected images. Considering that we could enumerate only an undefined portion of the entire school, this source of error was considered negligible.

Species identification of small tunas by aerial observers can be difficult (Morgan, 1992), but the likelihood that spotters would mistake other species for giant or large-medium bluefin tuna targeted in this New England fishery is very slight. Commercially valuable schools of yellowfin tuna are rare north of Nantucket Shoals (Mather, 1962; Roffer, 1987), and experienced fish spotters would be unlikely to mistake targeted bluefin tuna for the smaller yellowfin tuna.

Marine mammals aggregate in groups of sizes comparable to that of giant bluefin tuna schools. Spotters have reported that they can easily distinguish giant and large-medium bluefin tuna from small marine mammals by body shape, tail orientation, and color, but identification is primarily made from swimming postures and frequency of dorsal flexure.

Table 3

Fish spotter photography effort by time of day in New England waters, July–September 1993.

Time of day (h:min)	No. of schools photographed
09:00–09:55	1
10:00–10:59	3
11:00–11:59	3
12:00–12:59	21
13:00–13:59	30
14:00–14:59	17
15:00–15:59	27
16:00–16:59	17
17:00–17:59	6
18:00–18:59	1

Because we did not have direct altimetry capabilities, size classes of bluefin tuna photographed in this survey could be generally documented only as large-medium or giants from spotter estimates alone. Spotters undoubtedly photographed, and we subsequently counted, some bluefin tuna below commercial size classes (<70 inches SFL). Catch records indicated that lengths of individuals in a school may vary by several inches, but only 10% of a seine catch is allowed to be undersized.[4] Because a spotter's survival in the commercial fishing industry depends upon size judgments being made before seine boats expend effort to capture schools, there is a strong selection for accuracy (Williams, 1981; Squire, 1993).

Despite confidence in spotter estimates (Squire, 1993), adequate documentation and validation of their ability to judge size or biomass are lacking. Research to define the accuracy of New England bluefin tuna spotter estimates, or to explore alternative methods of establishing lengths of photographed bluefin tuna, are clearly needed. Future surveys must obtain more specific information on size classes of photographed fish in order to be used as a point of reference for present CPUE-based models that use total length to assign year class (Anonymous, 1986).

The majority of bluefin tuna schools were photographed in five areas traditionally fished for giant tuna, including Great South Channel, Wilkinson Basin, Platt's Bank, and Jeffreys Ledge. This group of areas may reflect the past experience of the spotters and their unwillingness to search where fish are not usually found; it may also indicate that giant and large-medium-sized tuna exhibit clumped distributions in New England waters, where oceanic frontal systems, bottom topography, and concentration of prey provide favorable feeding and thermal conditions (Laurs et al., 1984; Maul et al., 1984; Roffer, 1987).

Clumped distributions make redundant counts an underlying problem for aerial assessments. Lacking GPS capabilities in 1993, we acknowledge that we may have counted bluefin tuna schools more than once because we had insufficient data to precisely locate all photographed schools. We have learned, however, that a given spotter is unlikely to photograph the same school twice over a period of a few hours. Once a spotter directs a boat onto a school, he moves to other areas because circling by boat is believed to force the fish down, rendering them difficult to catch for some time. In future surveys, an algorithm incorporating maximum swimming speeds and surfacing behavior could be used to limit redundant counts. Minimum counts based on daily rather than pooled totals would also reduce counting problems resulting from residence time and sequential movement of fish through the study area.

Conclusions

In this collaborative study neither we nor the ECTA believe that expended effort was sufficient to derive, on any given day, a minimum count of giant and large-medium bluefin tuna in New England waters. To do so would require not only perfect environmental conditions (noted by pilots and fishers as a "show" day) but also the complete cooperation and coordination of efforts by participating pilots. Given that the feasibility survey started relatively late in the fishing season, the latter was a difficult goal to achieve.

A fundamental limitation of aerial assessment is that only fish at or near the surface are accounted for, providing only a minimum estimate of school size. Surveyed schools subsequently captured by seiners might help define relations between aerial counts and total biomass, but this relation was established for only one set in the 1993 season. In this case (27 Aug), we counted 32 fish at the surface of a tightly domed school that yielded 125 large giants once captured.

Factors that govern schooling behavior and aggregation dynamics are poorly documented in bluefin tuna and the tunas in general (Mather, 1962; Clark and Mangel, 1979; Partridge et al., 1983). Mather (1962) described bluefin tuna behavior patterns of "pushing, milling, and smashing" in New England waters. We have noted spatial configurations (domes, cartwheels, surface sheets) and soldier groups (Partridge et al., 1983) depicted in photographed schools. Understanding the interplay of ecological and environmental factors that govern aggregation of giant bluefin tuna would help to define biases in direct assessment efforts. For example, giant bluefin tuna

[4] Foster, K. Gloucester Laboratory. Natl. Mar. Fish. Serv., NOAA, 30 Emerson Ave., Gloucester, MA 01930. Personal commun., March 1994.

are believed to exhibit the most rigidly defined spatial structures in schooling fishes (Partridge et al., 1983). If relations between the surface structure of schools and total biomass were known, surface counts could be adjusted to include an estimate of biomass.

In future studies, on-board data loggers might be used to give accurate records of search effort and survey tracks and possibly to determine fish size through direct altimetry from phototelemetry and GPS data. Hydroacoustic trials, Lidar, or remotely operated vehicle analysis undertaken alongside seining operations may provide additional groundtruth information that would allow derivation of indices of abundance (Petit et al., 1992).

In spite of limitations faced in the 1993 feasibility study, this preliminary aerial survey provided information on counts, distribution, and schooling characteristics of giant and large-medium bluefin tuna. Direct photographic surveys to obtain minimum counts of giant bluefin tuna may be a practical method of obtaining real-time measures of their relative abundance in New England waters.

Acknowledgments

This research was conducted under an agreement between the New England Aquarium and the East Coast Tuna Association (ECTA). The following pilots participated in data collection, served as the backbone of this survey, and provided valuable advice on fishery operations: Marc Avila, John Betzner, Wayne Davis, Jim Glyman, Roger Hillhouse, Ted Malley, Jonathan Mayhew, Norman St. Pierre, and Trip Wheeler. Richard Ruais, ECTA, and participating boat captains supported and funded the study and contributed organizational support. Grant MacNally served as photo consultant and helicopter pilot for film trials. We thank two anonymous reviewers for helpful comments on the manuscript.

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Egg and larval development of laboratory-reared gulf flounder, *Paralichthys albigutta*, and southern flounder, *P. lethostigma* (Pisces, Paralichthyidae)

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Abstract.—The egg and larval development of *Paralichthys albigutta* (gulf flounder) and *P. lethostigma* (southern flounder) are described from laboratory-reared and field-collected specimens. *Paralichthys albigutta* eggs and oil globules had a mean diameter of 0.87 mm (range: 0.84–0.90 mm) and 0.18 mm (range: 0.17–0.19 mm), respectively. *Paralichthys lethostigma* eggs and oil globules had a mean diameter of 0.91 mm (range: 0.84–0.96 mm) and 0.18 mm (range: 0.16–0.20 mm), respectively. Recently hatched *P. albigutta* larvae ranged from 1.8 to 2.2 mm in notochord length (NL) and *P. lethostigma* from 2.0 to 2.2 mm NL. Pigment on embryos and newly hatched larvae was relatively more developed for *P. albigutta*. Almost-paired and almost-contiguous ventral midline melanophores occurred on preflexion larvae of both species and remained throughout the larval stages. Pigment on the maxillary, vomer, dorsum of the mid-brain, lateral surface of the caudal area, lateral surface of gut, and extent of pigment along the ventral midline of the isthmus were used to separate laboratory-reared *P. albigutta* from *P. lethostigma*. However, this pigment was less useful in separating field-collected material. The number of cranial spines appeared to be diagnostic in separating laboratory-reared early-preflexion larvae. *Paralichthys lethostigma* consistently had three cranial spines, whereas *P. albigutta* had less than three spines. The development of meristic characters was considered the most useful character in separating *P. albigutta* from *P. lethostigma* because at any given size *P. albigutta* was generally more developed than *P. lethostigma*.

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Fishery Bulletin 93:504–515 (1995).

Four species of the genus *Paralichthys* occur in southeastern U.S. coastal waters. *Paralichthys squamilentus* (broad flounder) is not commonly encountered and is of little commercial or recreational value. *Paralichthys dentatus* (summer flounder), *P. lethostigma* (southern flounder), and to a lesser extent *P. albigutta* (gulf flounder) are common and of great commercial and recreational value (N.C. Div. Marine Fisheries[1]). *Paralichthys dentatus* range from Maine to Cape Canaveral, Florida, and *P. albigutta* and *P. lethostigma* range from North Carolina to Texas (Gutherz, 1967). Eggs and larvae of *P. dentatus* have been described (Smith and Fahay, 1970) whereas those of *P. albigutta* and *P. lethostigma* have not. Comparative taxonomic studies of late larvae and early juvenile (fully formed vertebrae, dorsal, and anal rays) *P. dentatus*, *P. lethostigma*, and *P. albigutta* have been reported. Deubler (1958) showed that late-larval–early-juvenile *P. dentatus* can be distinguished from the other two congenera by differences in pigmentation of the dorsal and anal fins and in vertebral number. The only characters useful for separation of *P. lethostigma* and *P. albigutta* were dorsal-ray and anal-ray counts. Woolcott et al. (1968) showed that 100% separation of the three species could be obtained through a combination of anal-ray and vertebral counts. However, these characters must be fully formed in order to be diagnostic. Vertebral counts alone cannot be used to separate *P. albigutta* and *P. lethostigma*.

The objective of this study is to describe the eggs and larvae of laboratory-reared *P. lethostigma* and *P. albigutta* to provide diagnostic characters for identification of these paralichthyids in field-collected material.

[1] North Carolina Division of Marine Fisheries. 1992. Assessment of North Carolina commercial finfisheries. Completion Rep. for Job 2-IJ-16. North Carolina Div. Mar. Fisheries, Morehead City, NC 28557.

Methods

Adult *P. albigutta* and *P. lethostigma* were collected in the early fall during 1991 and 1992 from commercial pound nets in Core Sound, North Carolina. Individual fish were tagged and meristic data (gill-raker and anal-ray counts) were used to confirm identification (Gutherz, 1967). Spawning was induced with the aid of hormones as described by Smigielski (1975). For *P. albigutta* three different females were fertilized by a single male. Females were injected with carp pituitary hormone (2 mg/kg fish) two or three times to promote hydration. Eggs were fertilized on 14 and 19 February 1992. For *P. lethostigma*, a total of four different males and four different females were spawned. Eggs were fertilized on 17 December 1992, 24 February, and 2 March 1993.

Eggs and sperm from both species were manually stripped into 1-L bowls; eggs were fertilized, and embryos incubated in 100-L black-sided tanks. *Paralichthys albigutta* larvae were reared in uncirculated, filtered water at a mean temperature of 19°C (range: 14–24°C) and a mean salinity of 30 ppt (range: 28–30 ppt). *Paralichthys lethostigma* larvae were reared at a mean temperature of 18°C (range: 16–19°C) and a mean salinity of 32 ppt (range: 23–42 ppt). Rotifers and *Artemia* nauplii were provided to young (≤15 days old) and older (>15 days old) larvae, respectively. Only three *P. lethostigma* larvae were alive after approximately 35 days, limiting the amount of material available for this species. Eggs and larvae were preserved in 10% buffered formalin. Counts of meristic characters were obtained from cleared and stained specimens (Potthoff, 1984). All measurements and observations were made with a Wild M5A stereomicroscope equipped with an ocular micrometer.

The larval period was separated into preflexion, flexion, and postflexion stages—the three stages associated with the development of the caudal fin before, during, and after the upward flexion of the notochord tip. During preflexion and flexion, larval body length was measured from the tip of the snout to the tip of the notochord (notochord length, NL). In postflexion larvae (defined when 6 upper + 7 lower principal rays were formed) body length was measured from the tip of the snout to the base of the hypural plate (standard length, SL).

Postflexion larvae and transforming juveniles of *P. albigutta* and *P. lethostigma* captured in Onslow Bay off North Carolina during the winter of 1990 and 1991 were used for 1) comparison with laboratory-reared specimens and 2) illustrations and investigation of pterygiophore patterns. This material also was used to determine the size when meristic characters develop for *P. lethostigma* because material from laboratory-reared specimens was limited for this species. Observations on pterygiophore patterns and meristic characters were made on cleared and stained specimens. Larval material is deposited at the Beaufort Laboratory under the care of the senior author.

Results

Eggs and recently hatched larvae

Paralichthys albigutta Eggs were spherical and had a mean diameter of 0.87 mm (range: 0.84–0.90 mm, n=44). One oil globule was present and had a mean diameter of 0.18 mm (range: 0.17–0.19 mm, n=44). The yolk was homogenous, the chorion smooth, and the perivitelline space (in live eggs) narrow (ca. 0.2 mm). Pigment was first observed in the caudal area of embryos just after blastopore closure (Fig. 1A). On embryos from late-stage eggs (from tail twisting to hatching), pigment occurred on the oil globule, sparsely in the head region, and was most

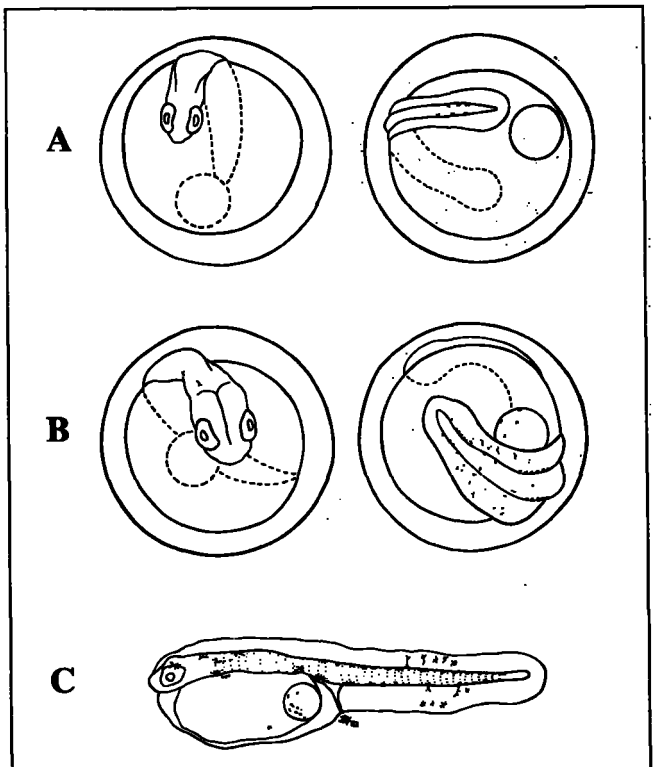

Figure 1

Laboratory-reared eggs and newly hatched larvae of gulf flounder, *Paralichthys albigutta*: (**A**) middle stage: left, anterior view; right, posterior view; (**B**) late stage: left, anterior view; right, posterior view; and (**C**) 2.2-mm-NL newly hatched yolk-sac larva.

developed in the caudal area. In the caudal area, melanophores occurred in the dorsal- and anal-fin folds, dorsal and ventral midlines, and sparsely on the lateral surface (Fig. 1B). Recently hatched *P. albigutta* larvae ranged from 1.8 to 2.2 mm NL. The oil globule was located in the posterior portion of the yolk sac (Fig. 1C).

Paralichthys lethostigma *P. lethostigma* eggs had a mean diameter of 0.91 mm (range: 0.84–0.96 mm, n=154), and the oil globule had a mean diameter of 0.18 mm (range: 0.16–0.20 mm, n=154). Pigment on embryos from middle-stage eggs (just after blastopore closure) was less developed than that observed for *P. albigutta* (Fig. 2A). Like *P. albigutta*, pigment on *P. lethostigma* embryos was only observed in the caudal area. Pigment on embryos from late-stage eggs was less developed than that observed for *P. albigutta* (Fig. 2B). Pigment was observed only in the caudal area on *P. lethostigma* embryos. Recently hatched *P. lethostigma* larvae were similar in size to *P. albigutta* (range: 2.0–2.2 mm NL). Like *P. albigutta*, the oil globule was located in the posterior portion of the yolk sac (Fig. 2C).

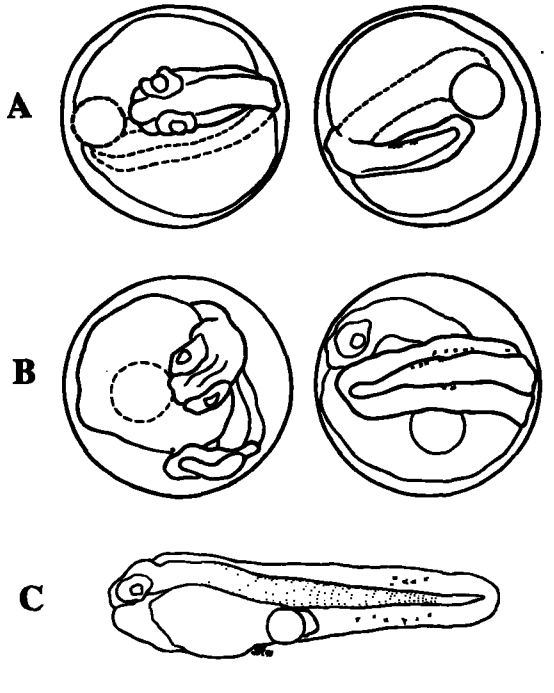

Figure 2

Laboratory-reared eggs and newly hatched larvae of southern flounder, *Paralichthys lethostigma*: (**A**) middle stage: left, anterior view; right, posterior view; (**B**) late stage: left, anterior view; right, posterior view; and (**C**) 2.1-mm-NL recently hatched yolk-sac larva.

Fin development

Paralichthys albigutta Fins began to develop in the following sequence: dorsal and caudal, anal, pelvic, and pectoral (Table 1). The adult complement of rays (Gutherz, 1967; Woolcott et al., 1968; Fahay, 1983) was attained in the following sequence: principal caudal rays (10 upper + 8 lower), dorsal fin (71–85), anal fin (53–63) and pelvic fin (6), and pectoral fin (10–12) (Table 1).

The development of the caudal fin, indicated by a thickening of tissue on the ventral side, began at 5.2 mm NL. Caudal-fin rays (2 upper + 2 lower) were first observed at 5.5 mm NL, indicating the beginning of the flexion stage. The rays began to form at the middle of the fin and developed dorsally and ventrally almost simultaneously. The adult complement of principal caudal rays (10 upper + 8 lower) was attained at 6.9 mm SL.

Dorsal rays were first observed during early flexion (5.5 mm NL, Table 1). Dorsal rays first formed in the head region anterior to the first neural spine. They were accompanied by an extension of the dorsal-fin fold that appeared as a flap (Fig. 3B). Dorsal-fin development proceeded slowly during the flexion stage and more rapidly during postflexion (Table 1). Development proceeded posteriorly; however, the anteriormost ray was not observed until 6.1 mm SL. The anterior rays in the head region, especially the third ray, were elongated (Fig. 3D). The adult complement of dorsal-fin rays consistently was attained at 7.8 mm SL (Table 1).

Anal-fin rays began to form on postflexion larvae at approximately 6.1 mm SL (Table 1). Formation began in the vicinity of the first haemal spine and development proceeded anteriorly and posteriorly simultaneously. Anal-fin-ray development was rapid, and by 7.7 mm SL the adult complement of anal-fin rays consistently was observed (Table 1).

Pelvic-fin rays were first observed on postflexion *P. albigutta* larvae at 6.9 mm SL (Table 1). All specimens ≥8.5 mm SL had a completed pelvic fin.

The pectoral fin persisted as a large rayless blade throughout flexion and early postflexion (Table 1). Rays began to form at 7.1 mm SL at the dorsal position of the blade and developed ventrally (Fig. 4). All specimens ≥8.5 mm SL had the adult complement (10–12 rays) of pectoral fin rays (Table 1).

Paralichthys lethostigma Fins began to develop in the following sequence: dorsal, caudal, anal, pelvic and pectoral (Table 2). The adult complement of rays (Gutherz, 1967; Wolcott et al., 1968; Fahay, 1983) was attained in the following sequence: caudal fin (10 upper + 8 lower), dorsal fin (80–95) and anal fin (63–74), pelvic fin (6), and pectoral fin (11–13) (Table 2).

Table 1

Meristic data from cleared and stained laboratory-reared gulf flounder, *Paralichthys albigutta*. Dashed lines separate preflexion, flexion, and postflexion stage larvae. Postflexion was defined as the stage when 6 upper + 7 lower caudal rays were observed. NL = notochord length; SL = standard length.

Body length (mm)	Days after hatching	Dorsal-fin rays	Anal-fin rays	Pelvic-fin rays	Pectoral-fin rays	Principal caudal rays (upper + lower)
4.5 NL	18	0	0	0	0	0
5.2 NL	19	0	0	0	0	0
5.5 NL	19	3	0	0	0	2+2
5.7 NL	19	2	0	0	0	2+2
5.7 NL	19	2	0	0	0	2+2
5.8 NL	19	3	0	0	0	3+3
5.8 NL	24	5	0	0	0	6+5
6.1 NL	19	2	0	0	0	3+3
6.4 NL	31	4	0	0	0	5+5
5.9 SL	24	9	0	0	0	7+7
6.1 SL	26	15	4	0	0	9+8
6.3 SL	26	16	14	0	0	9+8
6.8 SL	31	55	34	0	0	9+8
6.9 SL	36	72	54	3	0	10+8
7.0 SL	36	68	50	4	0	10+8
7.1 SL	36	68	50	5	1	10+8
7.2 SL	31	62	43	0	0	10+8
7.7 SL	36	74	57	5	3	10+8
7.8 SL	36	69	54	5	5	10+8
7.8 SL	44	75	54	5	9	10+8
8.0 SL	36	72	55	5	5	10+8
8.2 SL	44	72	51	5	5	10+8
8.5 SL	44	71	54	6	10	10+8
8.6 SL	44	74	56	6	10	10+8
10.2 SL	59	74	58	6	11	10+8
10.7 SL	52	73	54	6	13	10+8

The development of the caudal fin began at 5.4 mm NL and was similar to that of *P. albigutta*, but caudal rays were not observed until 6.5 mm NL. The adult complement of principal caudal rays (10 + 8) was attained at 8.2 mm SL (Table 2).

Dorsal rays were first observed on a preflexion specimen but were not consistently observed till early flexion (6.5 mm NL, Table 2). The development of dorsal rays was similar to that observed for *P. albigutta*. Complete development of the dorsal-fin rays occurred at approximately 8.4 mm SL.

Anal-fin rays began to form on postflexion larvae at approximately 7.3 mm SL. Development was similar to that observed for *P. albigutta*. Like *P. albigutta*, anal-fin-ray development was rapid and the anal fin appeared to be completely formed by approximately 8.4 mm SL (Table 2).

Pelvic-fin rays were first observed on postflexion larvae (8.2 mm SL, Table 2). All specimens >9.7 mm SL consistently had a completed pelvic fin.

Pectoral-fin rays began to form at 8.4 mm SL at the dorsal position of the blade and developed ventrally. The largest specimen (11.0 mm SL) still had not attained a completed (11–13 rays) pectoral fin (Table 2).

Pigmentation of laboratory-reared specimens

Paralichthys albigutta Newly hatched *P. albigutta* larvae had dendritic melanophores on the dorsal and anal finfolds midway between the anus and notochord tip (Fig. 1C). Dorsal and anal midline pigment posterior to the anus was well developed. Melanophores occurred on the trunk and head, on the oil globule, and on the yolk sac (Fig. 1C). Melanophores were observed on the snout on a one-day old larva (2.8 mm NL) but not on newly hatched larvae.

Characteristic pigment on preflexion larvae was almost-paired and almost-contiguous dorsal and ventral midline melanophores that remained character-

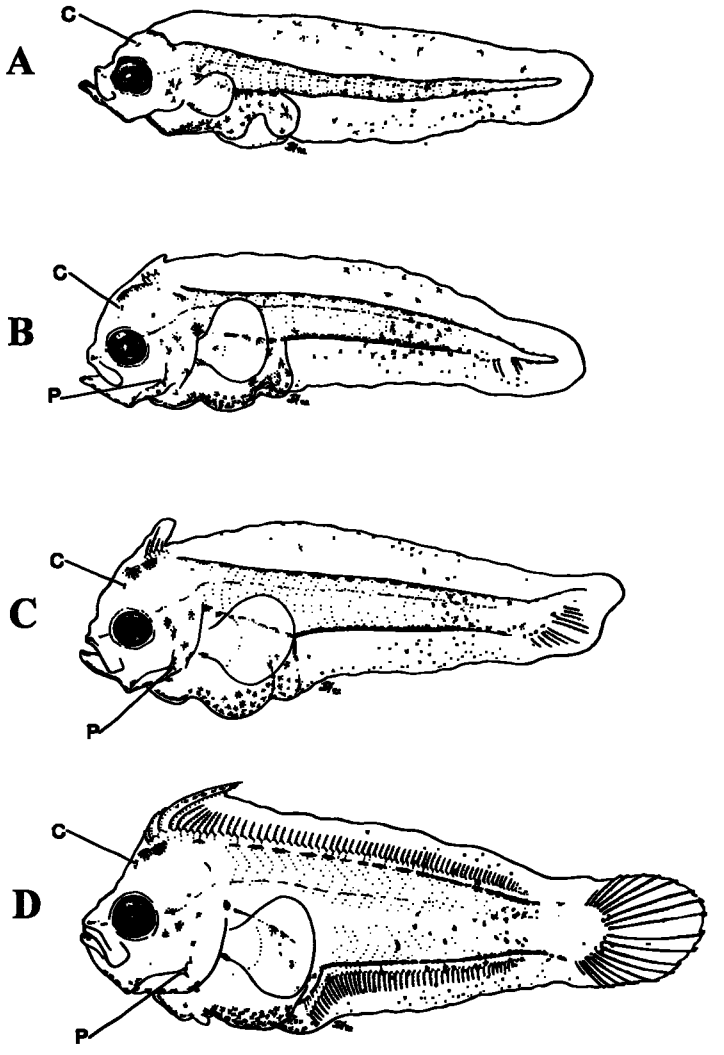

Figure 3

Developmental stages of laboratory-reared gulf flounder, *Paralichthys albigutta* (C=cranial spines, P=preopercular spines). (**A**) 3.5-mm-NL preflexion larva, 10 days old; (**B**) 5.8-mm-NL early flexion larva, 25 days old; (**C**) 6.2-mm-NL late flexion larva, 21 days old; and (**D**) 7.1-mm-SL postflexion larva, 31 days old.

istic throughout the larval stages (Fig. 3A). The almost-paired dorsal and ventral midline melanophores merged into one row of dorsal and ventral punctate melanophores in the future caudal-fin region. The most posterior melanophores generally were opposite each other. The dorsal midline pigmentation extended anteriorly to the forebrain. Melanophores were first observed on the lateral portion of the caudal region at approximately 3.5 mm NL (Fig. 3A). Embedded notochord pigment extended anteriorly ventral to the brain and continued through the eye, giving the appearance of a stripe through the eye. Pigment occurred over most of the ventral finfold and more prevalently in the middle one-third of the dorsal finfold. In the gut region of preflexion larvae, melanophores occurred along the ventral midline, extending anterior of the cleithral symphysis and along the lateral surface of the gut. Melanophores occurred along the dorsal surface of the gut as a continuation of ventral midline pigment and generally terminated in a distinct melanophore at the junction of the operculum (Fig. 3A). In most specimens a distinct melanophore occurred on the ventral area of the base of the pectoral-fin blade. In the head region, melanophores occurred on the operculum and on the dorsum of the midbrain (cranial bump). Pigment was first observed on the dorsum of the cranial bump during early preflexion (2.9 mm NL), but only 20% of the specimens examined (n=10) had a melanophore here at this time. With increasing size the cranial-bump melanophore occurred at a greater frequency, and by 4.0 mm NL all specimens had a melanophore in this region. In the lower-jaw region, melanophores occurred both along the lower-jaw rami and at the lower-jaw angle (Fig. 3A). A punctate melanophore was observed on both sides of the premaxilla or maxilla, or both. This pair of melanophores was first observed on early preflexion larvae (2.9 mm NL) and was observed on every laboratory-reared specimen examined. Vomerine pigment was first observed on 3.2-mm-NL preflexion larvae and occurred thereafter on all specimens examined.

Pigment on flexion larvae was similar to that observed on late preflexion larvae (Fig. 3, B and C). Melanophores occurred on the lateral surface of the body in the caudal area on all specimens. The most anterior melanophore on the dorsal surface of the gut at the junction of the operculum was stellate and was seemingly isolated from the other gut pigmentation (Fig. 3, B and C). Pigment occurred along the proximal base of the developing caudal-fin rays. In the late flexion stage (6.4 mm NL), pigment first appeared on the third elongated dorsal ray. Most of the lateral surface of the hind gut was pigmented. The ventro-lateral surface of the mid- and foregut was pigmented (Fig. 3, B and C).

On early postflexion larvae (Fig. 3D), pigment was observed on the base of the caudal fin and on the

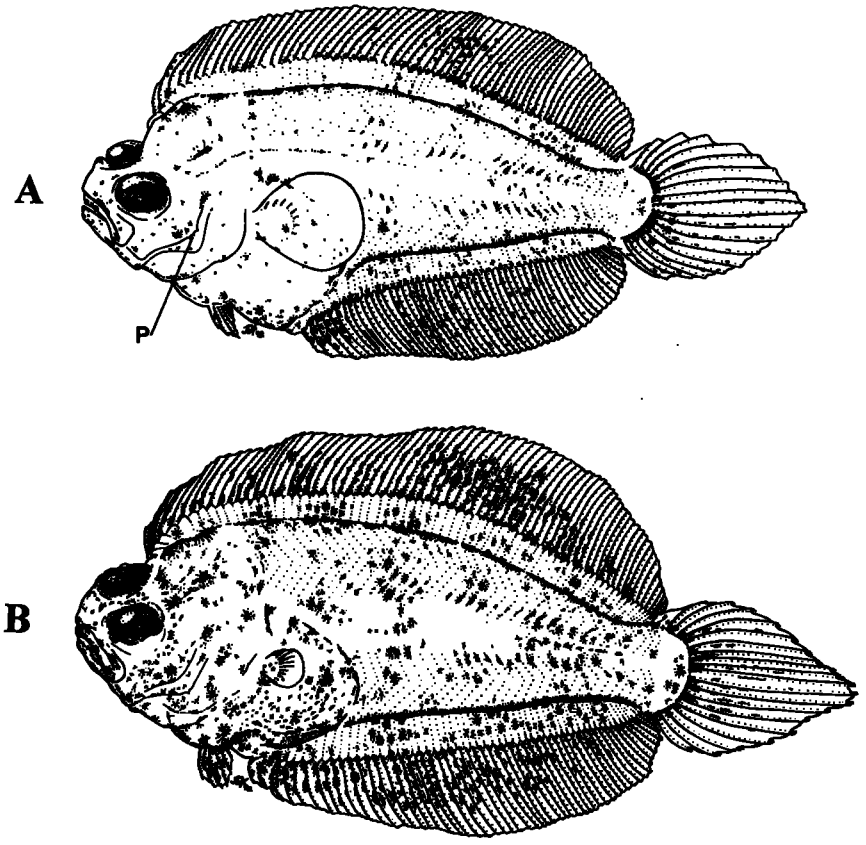

Figure 4

Developmental stages of transforming, postflexion laboratory-reared gulf flounder, *Paralichthys albigutta* (P=preopercular spines). (A) 8.2-mm-SL larva, 34 days old; (B) 9.0-mm-SL larva, 45 days old.

pelvic fin. Melanophores on the lateral surface of the body in the caudal area began to align with the myosepta. Pigment on the lateral surface of the body increased with increasing size (Fig. 4). The extended third dorsal ray was pigmented, and pigment was scattered on the developing dorsal- and anal-fin rays. This pigment increased in area during development (Fig. 4). Pigment was scattered in no apparent pattern medially on the dorsal- and anal-fin pterygiophores. The anal-fin pterygiophores were relatively more pigmented than those on the dorsal fin. Pigment increased in these areas during development (Fig. 4). The characteristic almost-paired, almost-contiguous dorsal and ventral midline pigment was located at the proximal edge (base) of the dorsal- and anal-fin pterygiophores. Pigment in the head region of early postflexion larvae was similar to that of flexion larvae (Fig. 3D) but increased in intensity during development (Fig. 4).

During transformation, *P. albigutta* larval body pigment increased in intensity (e.g. compare Fig. 4, A and B). Melanophores occurred along the entire base of the caudal fin, but most of the fin was not pigmented. A blotchy pigment pattern was observed on the pterygiophores, caudal peduncle, and lateral line from mid-body anterior to the cleithrum. Melanophores along the lateral line from mid-body to the caudal peduncle formed a streak of pigment in later transforming larvae (ca. 8.7 mm SL). Numerous melanophores on the lateral surface of the caudal area were aligned with the myosepta. This pigment occurred mainly in the posterior two-thirds of the caudal area and extended more anteriorly in the dorsolateral area (Fig. 4). The dorsal and anal fins were pigmented along the entire length of their base (i.e. proximally). On the medial portion of the dorsal- and anal-fin rays on earlier (ca. 7.8 mm SL) transforming larvae, pigment appeared as blotches on the

Table 2

Meristic data from cleared and stained laboratory-reared and field-collected southern flounder, *Paralichthys lethostigma*. Dashed lines separate preflexion, flexion, and postflexion stage larvae. Postflexion was defined as the stage when 6 upper + 7 lower caudal rays were observed. An asterisk indicates field-collected material. NL = notochord length; SL = standard length.

Body length (mm)	Days after hatching	Dorsal-fin rays	Anal-fin rays	Pelvic-fin rays	Pectoral-fin rays	Principal caudal rays (upper+lower)
4.7 NL	20	0	0	0	0	0
4.9 NL	20	0	0	0	0	0
5.4 NL	20	0	0	0	0	0
6.2 NL	31	2	0	0	0	0
6.4 NL	24	0	0	0	0	0
6.5 NL	31	6	0	0	0	5+5
6.6 NL	31	5	0	0	0	4+4
6.8 NL	31	4	0	0	0	4+3
6.9 NL	31	5	0	0	0	6+6
6.9 NL	35	6	0	0	0	6+6
7.0 NL	40	5	0	0	0	5+5
7.1 NL	35	6	0	0	0	6+6
6.7 SL	39	13	0	0	0	7+8
6.7 SL	*	13	0	0	0	9+8
6.7 SL	*	10	0	0	0	9+8
7.3 SL	*	14	13	0	0	7+6
7.3 SL	48	9	0	0	0	7+8
7.8 SL	*	68	41	0	0	9+8
8.2 SL	*	84	65	5	0	10+8
8.4 SL	*	90	71	5	2	10+8
8.7 SL	*	90	70	5	2	10+8
9.2 SL	40	82	62	6	0	10+8
9.2 SL	*	83	64	6	5	10+8
9.7 SL	*	85	67	5	1	10+8
9.8 SL	*	87	63	6	2	10+8
9.8 SL	*	87	65	6	4	10+8
10.2 SL	*	85	64	6	6	10+8
11.0 SL	*	86	63	6	9	10+8

anterior and midbody surfaces of the fins and gradually expanded over the medial portion with development (Fig. 4).

Paralichthys lethostigma Newly hatched *P. lethostigma* larvae had melanophores on the dorsal and anal finfolds that were concentrated in the middle of the body (Fig. 2C). Dorsal midline pigment was well developed and generally occurred from the anterior portion of the caudal region to the head and snout. There were fewer melanophores on the dorsal and ventral midline posterior to the anus (i.e. in the caudal region). Pigment was observed on the oil globule.

Like *P. albigutta*, characteristic pigment on *P. lethostigma* preflexion larvae was almost-paired and almost-contiguous dorsal and ventral midline melanophores that merged into one row of dorsal and ventral melanophores in the future caudal-fin region (Fig. 5A). On very early preflexion larvae (2.8–3.0 mm NL) that still contained vestiges of yolk and oil, the dorsal midline melanophores were continuous over the brain and snout, and the ventral midline melanophores were continuous over the gut. Melanophores on the lateral portion of the caudal region were not observed on early preflexion larvae (ca. <3.6 mm NL) and were not as well developed on later preflexion larvae compared with *P. albigutta* larvae (Figs. 3A and 5A). In the gut region of preflexion *P. lethostigma*, the lateral portion of the gut was typically devoid of pigment (Fig. 5A) and was never as well developed as that observed for *P. albigutta* (Fig. 3A). Usually, ventral melanophores in the gut region

were not continuous because a gap appeared just anterior to the anus. Regularly, we observed a pair of melanophores located ventrally on each side of the hindgut. The pectoral-fin-ray blade was pigmented. Pigmentation of preflexion *P. lethostigma* at the base of the pectoral fin and in the head region was similar to that observed for *P. albigutta* (Figs. 3A and 5A). Pigment on the maxillary and the dorsum of the midbrain (cranial bump) was less frequently observed in preflexion *P. lethostigma* larvae compared with preflexion *P. albigutta* larvae. Cranial bump pigment was observed on 36% of the specimens and maxillary pigment on 64% of the specimens (n=25). Pigment on the vomer of preflexion *P. lethostigma* also occurred less frequently (36% of the specimens had this pigment; n=15); however, this pigment was difficult to discern. It was most effectively seen on fresh, cleared and stained material. Ventral pigment on the isthmus, anterior to the cleithrum, did not extend the full length of the isthmus as was observed on preflexion *P. albigutta* (Figs. 3A and 5A). The number of melanophores observed on the operculum (commonly one) was less than that observed for *P. albigutta*.

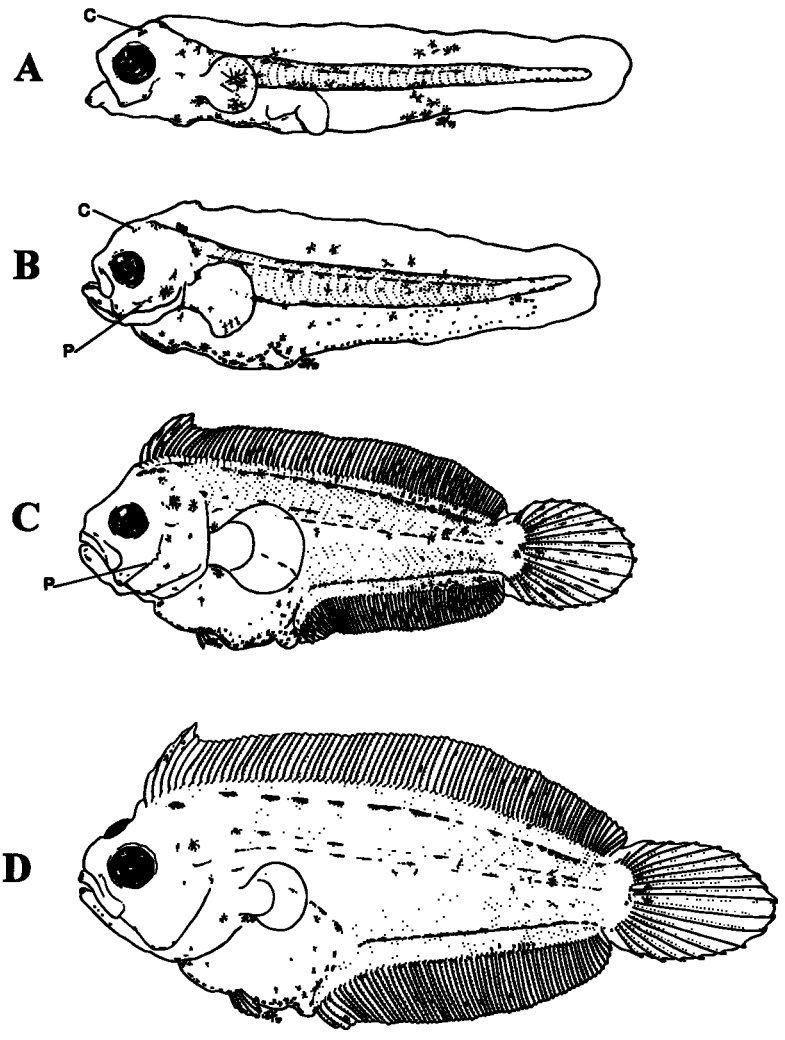

Figure 5

Developmental stages of laboratory-reared southern flounder, *Paralichthys lethostigma* (C=cranial spines, P=preopercular spines). (**A**) 3.3-mm-NL early preflexion larva, 9 days old; (**B**) 6.4-mm-NL late preflexion larva, 24 days old; (**C**) 7.7-mm-SL postflexion larva, 45 days old; and (**D**) 9.1-mm-SL transforming postflexion larva, 40 days old.

Pigment on flexion *P. lethostigma* larvae was similar to that observed on later preflexion larvae (Fig. 5B). Melanophores were observed on the lateral side of the caudal region; however, they were less organized than those observed for *P. albigutta*, which appeared to be more banded in appearance. During flexion, pigmentation increased on the lateral surface of the hindgut. Dorsal finfold pigmentation was sparse and located at midbody. Ventral finfold melanophores occurred along the distal margin and on the finfold surface at midbody. A melanophore was observed at the ventral edge of the pectoral-fin blade, and a distinct melanophore was observed at the junction of the dorsalmost portion of the opercle and the anteriodorsal portion of the gut. This characteristic pigmentation was observed for both species. Pigmentation along the ventral midline of the isthmus increased to cover the entire isthmus. Like *P. albigutta*, melanophores were typically observed on the maxillary and the dorsum of the midbrain, but vomerine pigment was irregularly observed on flexion *P. lethostigma* larvae. Pigmentation (1–4 melanophores) occurred on the opercular region posterior to the eye. Melanophores along the edge of the interopercle and subopercle were first observed on flexion larvae.

On postflexion larvae (6.4–9.3 mm SL), pigment was observed at the base of the caudal fin and on the pelvic fin (Fig. 5, C and D). Melanophores occurred on the lateral surface of the body, but they were never

aligned with the myosepta as was observed for *P. albigutta* (Figs. 3D, 4, and 5).

Other structures and size at transformation

Dorsal and anal fin supports The arrangement of pterygiophores in relation to neural and haemal spines may be valuable for separating *P. albigutta* and *P. lethostigma* larvae because they share similar vertebral counts (hence similar haemal and neural spine counts), but different dorsal and anal fin-ray counts.

The cumulative number of anal-fin-ray pterygiophores between the first haemal spine (which is associated with the first caudal vertebrae) and haemal spines posterior to the fourth haemal spine appeared to be diagnostic (Table 3). Although there was overlap in counts, there is a fair degree of separation in the cumulative number of anal-fin pterygiophores. For example, between haemal spines 1 and 13, from 28 to 31 pterygiophores would aid in identifying *P. albigutta*, whereas ≥28 pterygiophores would aid in identifying *P. lethostigma*. As expected, there was a lesser cumulative number of pterygiophores for *P. albigutta* compared with *P. lethostigma* (Table 3).

The cumulative number of dorsal-fin pterygiophores between the first neural spine (which is associated with the first caudal vertebrae) and following spines appeared less valuable (Table 3). There was considerable overlap between species. The cumulative number of pterygiophores was most valuable when a considerable number were developed. For example, between neural spines 1 and 27, from 46 to 52 pterygiophores would aid in identifying *P. albigutta*, whereas ≥58 pterygiophores would aid in identifying *P. lethostigma* (Table 3).

Cranial spines and preopercle spines Weak, fleshy preopercle spines were observed on both species at all stages, and they decreased in number with increasing size (Figs. 3–5). On both species the exact arrangement and number of preopercle spines generally were difficult to discern but were more readily observed in cleared and stained material. Generally, there were four to five minute spines on the inner shelf of the preopercle, a larger spine at the angle of the outer shelf, and one dorsal to the latter on the outer shelf. Preopercle spines were not observed for specimens of either species ≥ approximately 8.5 mm SL.

Cranial spines may be diagnostic for separating *P. albigutta* and *P. lethostigma* preflexion larvae. We consistently observed three cranial spines on *P. lethostigma* preflexion larvae (2.9–5.4 mm NL). We never observed more than two (zero to two) on *P. albigutta* preflexion larvae of similar size. However, in most instances spines could be discerned only on cleared and stained material. Cranial spines generally were never observed on postflexion larvae of either species.

Paralichthys albigutta began transformation at a smaller size than did *P. lethostigma*. For *P. albigutta*, the migrating eye first appeared at the dorsal midline at 7.8 mm SL. On all specimens >7.8 mm SL, the eye had migrated at least to the dorsal midline. For *P. lethostigma*, the migrating eye first appeared at the dorsal midline at 8.7 mm SL. With one exception, the eye had migrated to at least the dorsal midline on all larvae >8.7 mm SL. On one field-collected larva of 11.2 mm SL, the eye had barely reached the dorsal midline as described for *P. dentatus* (Fahay, 1983). Pigmentation and meristic characters clearly identified this specimen as *P. lethostigma*.

Table 3

The cumulative number (range) of pterygiophores between the first neural and haemal spines and other spines (up to neural and haemal spine number 30 and 20, respectively) for gulf flounder, *Paralichthys albigutta* (n=15 laboratory-reared and 14 field-collected specimens) and southern flounder, *P. lethostigma* (n=1 laboratory-reared and 13 field-collected specimens).

Spine numbers	*P. albigutta*		*P. lethostigma*	
	Dorsal fin	Anal fin	Dorsal fin	Anal fin
1–2	2–3	1–3	2–3	2–3
1–3	4–6	3–5	5–6	4–5
1–4	5–8	5–7	7–9	6–8
1–5	6–9	7–9	8–9	9–10
1–6	8–10	9–11	8–10	11–13
1–7	9–12	10–13	10–12	13–16
1–8	11–13	12–15	12–14	15–18
1–9	13–16	14–17	14–16	17–21
1–10	15–18	16–20	16–18	19–23
1–11	16–21	17–22	18–21	22–26
1–12	18–23	19–25	20–23	24–29
1–13	20–25	21–27	23–26	26–31
1–14	22–28	23–29	25–29	28–34
1–15	24–30	25–31	27–31	30–37
1–16	26–33	27–33	30–34	33–39
1–17	28–35	29–36	32–36	34–42
1–18	30–37	31–38	34–38	37–45
1–19	32–40	33–40	36–41	39–48
1–20	34–42	36–42	38–43	43–51
1–21	36–44		40–45	
1–22	38–46		42–48	
1–23	39–49		44–50	
1–24	41–51		46–53	
1–25	43–53		48–55	
1–26	45–55		51–58	
1–27	46–57		53–61	
1–28	48–60		55–64	
1–29	51–62		58–67	
1–30	53–65		60–70	

Identification of field-collected material Material collected from Onslow Bay off North Carolina was examined to determine the reliability of pigment patterns established from laboratory-reared material (Table 4). We examined the extent of pigment along the isthmus, lateral pigment in the caudal area, vomer and maxillary pigment, and the extent of pigment on the lateral surface of the gut of field-collected material. On the basis of our observations, caution must be used when relating pigmentation of laboratory-reared material to field-collected material. Generally, field-collected specimens had less intense pigmentation than those reared in the laboratory (Figs. 3–6). Our observations of vomer pigment, maxillary pigment, and lateral pigment on the surface of the gut on laboratory-reared larvae were not consistently observed on field-collected larvae (Table 4). Pigment on the lateral surface of the caudal area that aligned with the myosepta and ventral midline pigment that appeared to migrate dorsally on the lateral surface was observed only on *P. albigutta* larvae (laboratory-reared and field-collected). The presence of this pattern might aid in the separation of *P. albigutta* from *P. lethostigma*. However, the absence of this pattern has little value because field-collected *P. albigutta* may lack lateral caudal pigment (Table 4) and when present may not always be aligned with myosepta. On preflexion and flexion field-collected *Paralichthys* larvae, we were unable to define two distinct pigment types but were limited in the number of larvae available. Eight early preflexion larvae (approximately 2.6 mm NL) from Onslow Bay were examined for cranial spines, and only two spines or less were observed. We considered these to be *P. albigutta* on the basis of observations of laboratory-reared material. A collection of material that included early flexion larvae with three cranial spines would be useful 1) to verify the presence of three cranial spines in field-collected material and 2) to categorize larvae into two types (i.e. three cranial spines vs. ≤ two cranial spines) for a detailed examination of pigment patterns. In addition, the use of otolith characteristics produced during the early larval period may be useful in facilitating separation of *P. albigutta* and *P. lethostigma* (Laidig and Ralston, 1995).

Identification of field-collected specimens was based on stage of development of meristic characters (Gutherz, 1967) (Tables 1 and 2). Unless field-collected material is cleared and stained and then measured, the stage of development of meristic characters may not be a valid diagnostic character. The bodies of field-collected material generally are bent, and measurements taken before and after clearing and staining, which tend to straighten the bodies, may vary by 1 mm (Table 4). This is especially pertinent when attempting to identify flexion and early postflexion larvae by size at a developmental stage.

Two specimens of *Paralichthys squamilentus* postflexion larvae were tentatively identified from February collections in Onslow Bay. Pigment at the dorsal and ventral midline resembled *P. dentatus* (Fahay, 1983). One specimen (5.9 mm SL) had 10 postanal melanophores along the ventral midline. Lateral pigment in the caudal area was absent. The

Table 4

Selected field-collected specimens used to examine the effectiveness of pigmentation to identify gulf flounder, *Paralichthys albigutta*, and southern flounder, *P. lethostigma*, larvae. Species identification was determined by relating body length (measured on cleared and stained material) and ray formation. Presence of pigment indicated by a plus sign (+), absence by a minus sign (—).

Specimen number	Body length (mm) preserved	Body length (mm) cleared and stained	Caudal rays	Dorsal rays	Anal rays	Lateral gut pigment	Vomer pigment	Maxillary pigment	Pigment along entire length of isthmus	Lateral caudal pigment	Species identification
1	5.4 NL	6.2 NL	10	8	0	—	—	—	—	—	*P. albigutta*
2	5.2 NL	5.7 NL	8	5–6	0	—	—	—	—	—	*P. albigutta*
3	6.4 NL	7.3 SL	13	13–14	13	—	+	—	—	+	*P. lethostigma*
4	5.4 NL	6.0 SL	12	8	0	+	—	+	+	+	*P. albigutta*
5	5.6 NL	5.7 NL	11	6–7	0	+	+	+	+	+	*P. albigutta*
6	5.0 NL	5.2 NL	0	3	0	—	+	—	—	+	*P. albigutta*
7	5.5 NL	6.5 NL	10	8	0	—	—	—	—	+	Unknown
8	5.0 NL	5.7 NL	4	3	0	+	+	—	—	+	*P. albigutta*
9	5.4 NL	5.9 NL	6	3	0	—	—	—	—	—	*P. albigutta*
10	5.1 NL	5.7 NL	4–5	3	0	—	—	—	—	—	*P. albigutta*
11	7.8 SL	7.8 SL	17	68	41	—	—	—	—	—	*P. lethostigma*
12	6.7 SL	6.7 SL	17	10	0	—	—	—	—	—	*P. lethostigma*

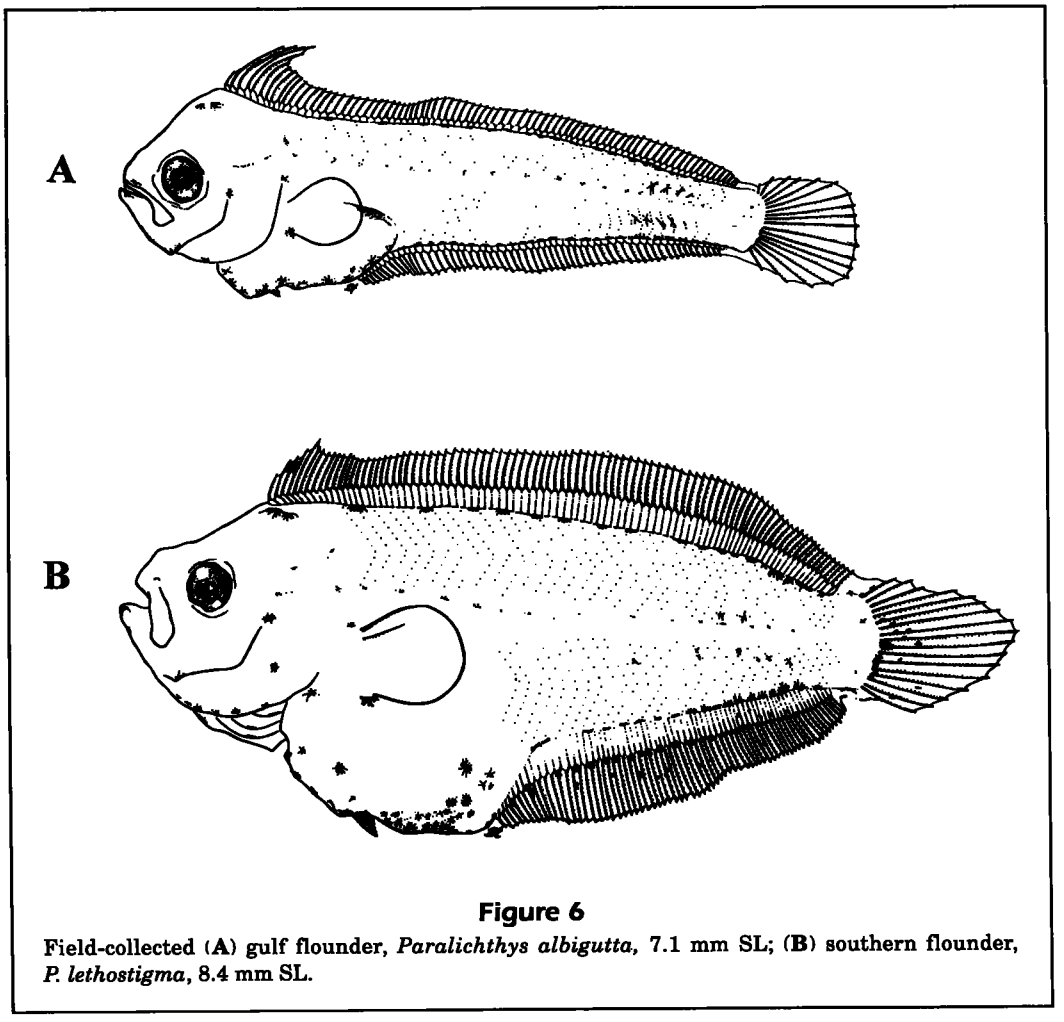

Figure 6
Field-collected (**A**) gulf flounder, *Paralichthys albigutta*, 7.1 mm SL; (**B**) southern flounder, *P. lethostigma*, 8.4 mm SL.

other specimen (6.2 mm SL), had 12 postanal melanophores along the ventral midline. One melanophore occurred on the lateral portion of the caudal area. We considered these specimens to be *P. squamilentus* because they were well developed for their size compared with *P. dentatus* (Fahay, 1983). Approximately 64 dorsal rays and 55 anal rays were formed. Neither the dorsal nor anal fins were completely formed. One specimen had four well-defined cranial spines and five preopercle spines. The other specimen had three cranial spines and five preopercle spines. Both specimens had 40 vertebrae.

Discussion

Paralichthys larvae can be separated from other bothid larvae by ventral midline pigment and the caudal formula when the principal caudal rays are formed (Fahay, 1983). *Paralichthys dentatus* and, tentatively, *P. squamilentus* larvae can be separated from *P. albigutta* and *P. lethostigma* larvae by differences in postanal ventral midline pigment (Fig. 7) and in size at development. *Paralichthys dentatus* has a maximum of 13 postanal melanophores along the ventral midline that are not uniform in size or spacing (Smith and Fahay, 1970). Tentatively, *P. squamilentus* has ventral midline pigment similar to *P. dentatus*. *Paralichthys albigutta* and *P. lethostigma* have approximately 19–31 postanal ventral midline melanophores that are uniform in size and spacing (Fig. 7). Larval *P. dentatus* can tentatively be separated from larval *P. squamilentus* by differences in development. At any given size, *P. squamilentus* appears to be significantly more developed than the other three *Paralichthys* species. However, early preflexion larvae might be difficult to separate from *P. dentatus* because *P. squamilentus* has only been tentatively described from two postflexion specimens (this study). On the other hand, at any given

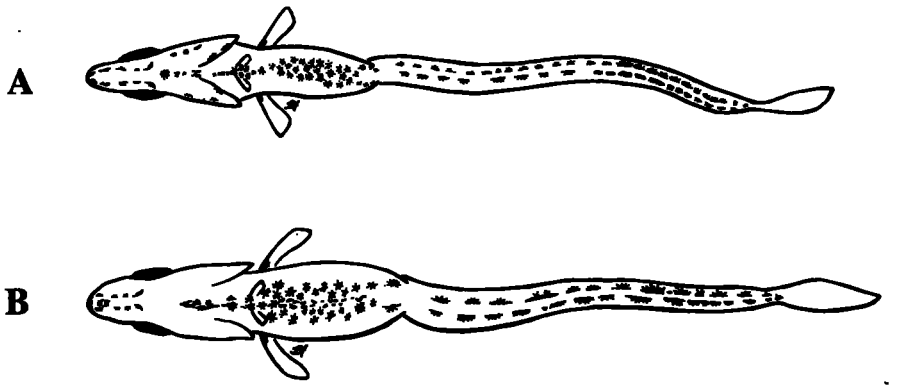

Figure 7

Pigmentation on the ventral side of field-collected, postflexion (**A**) gulf flounder, *Paralichthys albigutta* (9.1 mm SL), and (**B**) summer flounder, *P. dentatus* (9.7 mm SL).

size *P. dentatus* is the least developed of the four paralichthids (Fahay, 1983).

The best diagnostic character for separating *P. albigutta* from *P. lethostigma* is the development of meristic characters, but field-caught specimens must be cleared and stained prior to identification. At any given size, *P. albigutta* is more developed than *P. lethostigma* (Tables 1 and 2). The number of cranial spines could be useful in separating preflexion *P. albigutta* (zero to two spines) from preflexion *P. lethostigma* (three spines) if field-collected specimens are in concordance with those reared in the laboratory. Pigmentation on the lateral surface of the hindgut and caudal area are more developed in *P. albigutta* compared with *P. lethostigma*, but these characters may not be as consistent on wild specimens (e.g. Table 6). Caution should be used when extrapolating pigment patterns on laboratory-reared material to field-collected materials.

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Distribution of pelagic metamorphic-stage sanddabs *Citharichthys sordidus* and *C. stigmaeus* within areas of upwelling off central California

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Abstract.—Upwelling and its associated offshore advection of surface waters can affect the recruitment of nearshore organisms. Late-stage pelagic Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, were collected with a midwater trawl off central California during the spring and summer upwelling season. In both species, otolith size increased linearly with metamorphic development; standard length, however, increased asymptotically. Earlier stages of both species occurred shallower in the water column, whereas later stages occurred deeper. The deeper distribution of later stages may have been due to decreased buoyancy as a result of increased otolith size and ossification of bony structures coincident with metamorphosis. Earlier stages of both species were more abundant offshore and less abundant in areas of upwelling, whereas later stages were more abundant nearshore regardless of upwelling. The difference in the horizontal distributions of early and late stages may have been passively driven by different current patterns as a result of the difference in vertical distributions between early and late stages.

Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, are abundant along the Pacific coast of North America (Miller and Lea, 1976). In both species, spawning peaks during the summer months but also occurs at lower levels during the remainder of the year; individuals may spawn more than once during a given season (Arora, 1951; Ford, 1965; Goldberg and Pham, 1987; Matarese et al., 1989; Rackowski and Pikitch, 1989). Sanddabs have a long pelagic stage, which may exceed 324 days in speckled sanddabs and 271 days in Pacific sanddabs (Kendall, 1992; Brothers[1]), and settle at a relatively large size (20 to greater than 39 mm standard length (SL) for Pacific sanddabs and 24 to greater than 36 mm for speckled sanddabs) (Ahlstrom et al., 1984; Matarese et al., 1989). Kramer (1990) noted that flatfish with nearshore nurseries had brief pelagic stages and settled at small sizes, whereas those with less restricted coastal nurseries had longer pelagic stages and settled at larger sizes. Kramer (1990) placed sanddabs in the latter category; however, speckled sanddabs, in particular, have a somewhat restricted bathymetric distribution as settled individuals (usually found at depths of 40 m and less)(Rackowski and Pikitch, 1989; Kramer, 1990). Both species are widely distributed as pelagic larvae (as far as 724 km offshore for Pacific sanddabs and 320 km offshore for speckled sanddabs) (Rackowski and Pikitch, 1989), but settled individuals occur within a somewhat more restricted coastal region.

The existence of late-stage Pacific and speckled sanddabs in midwater trawls conducted off central California by the National Marine Fisheries Service (NMFS) Tiburon Laboratory (Wyllie-Echeverria et al., 1990) provided an opportunity to examine ontogenetic changes in distribution associated with metamorphosis and settlement of these two sanddabs. In this paper we investigated the vertical and horizontal distribution of pelagic-stage sanddabs, with the general purpose of elucidating the changes that take place at metamorphosis and settlement. Because the NMFS collections were made during the spring

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and summer upwelling season, when the associated offshore advection of surface waters can adversely affect marine organisms with pelagic life stages (Parrish et al., 1981; Bailey and Francis, 1985; Roughgarden et al., 1988), the effect of upwelling on pelagic-stage sanddabs was also investigated.

Methods

Data collection

Pelagic Pacific and speckled sanddabs were collected in conjunction with the annual juvenile rockfish surveys conducted by NMFS Tiburon Laboratory scientists aboard the National Oceanic and Atmospheric Administration (NOAA) research vessel *David Starr Jordan*. Standard stations extending from Point Reyes to Cypress Point (Fig. 1) were sampled with a 26 × 26 m modified Stauffer midwater trawl with a codend liner of 9.5-mm stretched mesh (Wyllie Echeverria et al., 1990). Standard trawling depth was 30 m except at shallow-water stations where trawls were conducted at 10 m. At certain standard stations a series of three depth-stratified trawls (depths=10 m, 30 m, and 110 m) were conducted to determine bathymetric distributional patterns (Fig. 1). As time permitted, additional trawls, both standard depth and depth-stratified, were conducted at nonstandard stations. All trawls were 15 minutes in duration and were completed between the hours of 2100 and 0600. Stations were sampled during a 10-day "sweep" of the survey area. Three replicate sweeps were completed from mid-May to mid-June of each year; in some years one additional sweep was completed in early April.

CTD (conductivity, temperature, and depth) casts were made at each trawl station to obtain temperature and salinity information at depth. Additional CTD casts were made during the day along tracklines interspersed between the trawl station lines (Schwing et al., 1990). Surface temperature and salinity were also recorded continuously by a thermosalinometer aboard the vessel. CTD and thermosalinometer data were used to determine the relation between upwelling and the spatial distributions of the different pelagic stages of both sanddabs.

Although the annual juvenile rockfish surveys began in 1983, sanddabs were not identified to species before 1987. Therefore, data were analyzed only from the 1987 through 1991 surveys. In addition to the May–June surveys in each year, sampling was carried out in April of 1987, 1988, and 1990. Sanddabs were identified and enumerated on board the research vessel at sea. In 1990 and 1991, samples were frozen after identification and enumeration and brought back to the laboratory where standard length (SL) and stage of metamorphosis were additionally recorded for each specimen collected. Five metamorphic stages, based on the staging system used by Pearcy et al. (1977), were defined as follows:

Stage 1 = left and right eyes positioned symmetrically on both sides of head;
Stage 2 = right eye has begun to move dorsally;
Stage 3 = upper edge of right eye within close proximity to the top of the right side of the head;
Stage 4 = right eye has begun to cross over to the left side of the head;
Stage 5 = right eye completely crossed over to left side of the head.

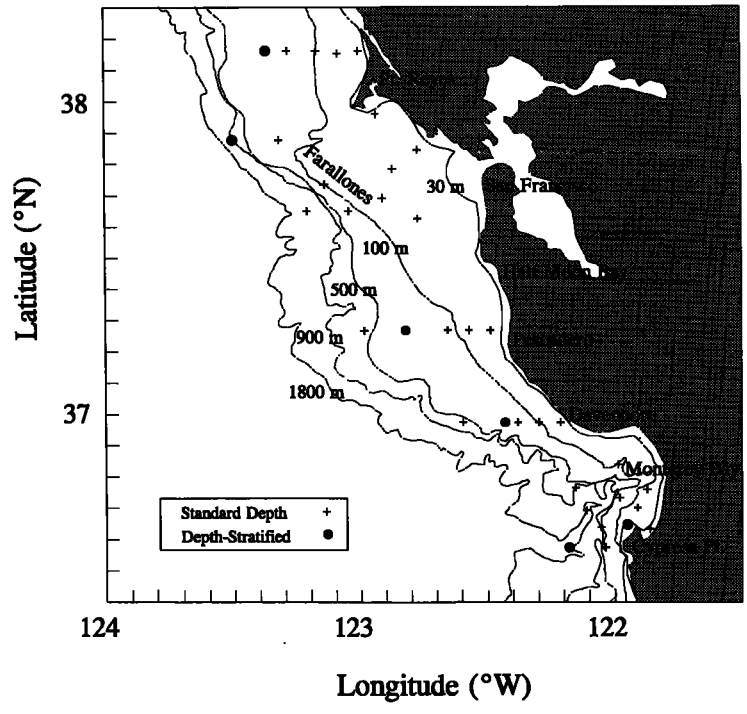

Figure 1
Location of standard trawling stations for Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected during 1987–91.

No stage-1 individuals were collected, probably because their small size allowed them to pass through the net.

To determine if metamorphic stage was a more useful character than SL in resolving spatial patterns, twenty individuals from each metamorphic stage of each species were randomly selected from the May to June survey of 1991, and their otoliths were removed. The diameter of the largest otolith, the sagitta, was measured with a compound microscope connected to a video camera, monitor, digitizer, and computer.

Data analysis

Statistical analyses were performed by using the program SAS (SAS Institute, Inc., 1988). Abundances were transformed by $\ln(x+1)$ to normalize the data. Mean abundances from the April surveys and for each sweep of the May–June surveys were then calculated for all standard stations successfully sampled to describe temporal differences in abundance.

Means and ranges of SL's of the metamorphic stages of both sanddab species were calculated by using specimens measured from the April and May–June surveys of 1990 and from the May–June survey of 1991. Mean SL's were calculated separately for the specimens randomly selected for otolith removal in order to compare the observed changes in otolith size relative to metamorphic stage with SL. Tukey's studentized range tests were performed to determine if there were significant differences in SL and otolith diameter with metamorphic development.

Owing to changes in the width of the net mouth with depth (width=8 m at 10 m depth, 11 m at 30 m depth, and 13.5 m at 110 m depth), abundances for the depth-stratified trawls were adjusted prior to analysis (Lenarz et al., 1991). Abundances for 10-m depth trawls were multiplied by 11/8, abundances for 30-m depth trawls were not adjusted, and abundances for 110-m depth trawls were multiplied by 11/13.5. Because of the large spatial variability in abundances and the fact that not all depth-stratified trawls sampled every depth (i.e. because of time constraints only the 10 m and 30 m depths were sampled at some stations, and only the 30 m and 110 m depths were sampled at others), differences in abundance with depth were evaluated by paired comparison t-tests. Pairing was by station; each depth pair available was considered (10 m versus 30 m, 30 m versus 110 m, and 10 m versus 110 m). When both observations of a pair were equal to 0, that pair was deleted from the analysis. To determine if there was a seasonal change in depth distribution, analyses were performed on all the surveys from 1987 to 1991, the April surveys alone, and the May–June surveys alone. To determine changes in vertical distribution with development, the paired comparisons were also carried out on each of the metamorphic stages, by using data from the April and May–June surveys of 1990 and from the May–June survey of 1991.

To determine the similarity of horizontal distributions among metamorphic stages, Spearman rank correlation coefficients were calculated for the abundances of different stages over standard stations during the 1990 and 1991 surveys.

CTD salinity at the surface (average salinity at 3–5 m depth) and at the standard mid-depth of 30 m (average salinity at 28–32 m) from each sweep of the May–June surveys of 1990 and 1991 was contoured by using the Kriging option in the program SURFER (Golden Software, Inc., 1990). Owing to problems with the CTD during the second sweep of the May–June survey of 1991, thermosalinometer data were incorporated into the available CTD data to generate the surface contours. The log-transformed abundances of metamorphic stages 2 and 5 were overlaid onto the salinity contours to observe the relation (if any) between the abundances of these two metamorphic stages and salinity features indicative of coastal upwelling. These two stages had the greatest potential for differences in spatial relations with salinity features, given that stage-2 individuals were not competent for settlement, whereas stage-5 individuals were relatively close to settlement.

Thermosalinometer data were used to determine trawls conducted in areas of recent upwelling. Schwing et al. (1991) designated recently upwelled water as having surface temperatures less than 10.5°C and surface salinities greater than 33.6 ppt. We used surface salinities greater than 33.6 ppt but surface temperatures less than 11.0°C to allow for marginal surface layer warming during the daylight hours prior to the nighttime trawls. Log-transformed abundances obtained at standard stations from the May–June surveys of 1990 and 1991 were converted to standard scores (log-transformed abundances rescaled for each year so that mean=0 and standard deviation=1) to adjust for year effects, allowing the data from both years to be combined. T-tests were used to compare the mean standard scores of metamorphic stages in upwelling and non-upwelling areas. Separate analyses were performed for shallow-depth (10-m) trawls and standard mid-depth (30-m) trawls because of the possibility of a depth effect due to metamorphic stage and the fact that upwelling typically affects only the upper 20 m of the water column (Parrish et al., 1981). To increase sample size, trawls at nonstandard stations were included in the analysis.

Results

Overall abundances and seasonal abundance patterns of the two sanddab species were variable (Fig. 2). In 1991, the abundance of both species increased monotonically during the May–June sampling period, whereas in 1987 and 1988, catches were relatively high in April but showed a marked decrease by the end of May–June, suggesting that pelagic sanddab abundance frequently declines during the April–June period (Fig. 2). However, catches of Pacific sanddabs in April of 1990 were low relative to May–June, and the May–June catches in 1988 and 1989 did not change monotonically, suggesting interannual variation in seasonal patterns (Fig. 2). Although April–June abundances were variable (Fig. 2), the interannual variation in year-class strength of pelagic sanddabs could not be determined without complete seasonal data.

In both species, SL increased asymptotically with metamorphic stage (Fig. 3). In addition, the range of lengths within each stage was quite large (Fig. 3). Pacific sanddabs were generally larger than speckled sanddabs at each metamorphic stage (Fig. 3). Although stage-2 individuals were significantly smaller than individuals of subsequent stages, the mean SL's did not differ significantly among the three later stages (α=0.05, df=76 for Pacific sanddabs and df=75 for speckled sanddabs). Whereas SL increased asymptotically with metamorphic development in both sanddabs, otolith diameter showed a linear increase (Fig. 4). In addition, otolith diameter increased dramatically with SL (Fig. 5), and mean otolith diameter increased significantly with each successive stage (α=0.05, df=76 for Pacific sanddabs and df=75 for speckled sanddabs). It appears that metamorphosis in sanddabs is possible at a range of sizes (30 mm to >50 mm SL in Pacific sanddabs and 25 to 40 mm SL in speckled sanddabs) and that once initiated, there is little growth in length but continued otolith growth (Figs. 3–5).

In general, Pacific sanddabs were relatively evenly distributed throughout the water column; there was a slight decrease in abundance with increasing depth (Table 1). Separate analyses of the April and May–June surveys showed similar results (Table 1).

In contrast to Pacific sanddabs, speckled sanddabs were significantly more abundant in shallow and mid-depth trawls than in deep trawls (Table 2). Analyzed separately, the May–June surveys showed a similar pattern to the overall analysis, but the April surveys showed less distinct differences in depth distribution (Table 2). The April surveys showed a trend of decreased abundance in deep trawls relative to shallow and mid-depth trawls, but the differences were not significant (Table 2).

Depth distributions differed among the metamorphic stages of both sanddab species: Stage-2 individuals of Pacific sanddabs were significantly more abundant in mid-depth trawls than in deep trawls, with a trend for increased abundance in shallow trawls versus deep trawls (Table 3; Fig. 6). Although both stage-3 and stage-4 sanddabs showed a relatively even distribution throughout the water column (with no significant differences among depths), stage-3 individuals tended to be less abundant with increased depth, whereas stage-4 individuals tended to be more abundant with increased depth (Table 3; Fig. 6). Stage-5 individuals were generally less abundant in shallow trawls and showed a tendency toward increased abundance with increased depth (Table 3; Fig. 6).

In speckled sanddabs, stage-2 individuals were significantly more abundant in mid-depth trawls

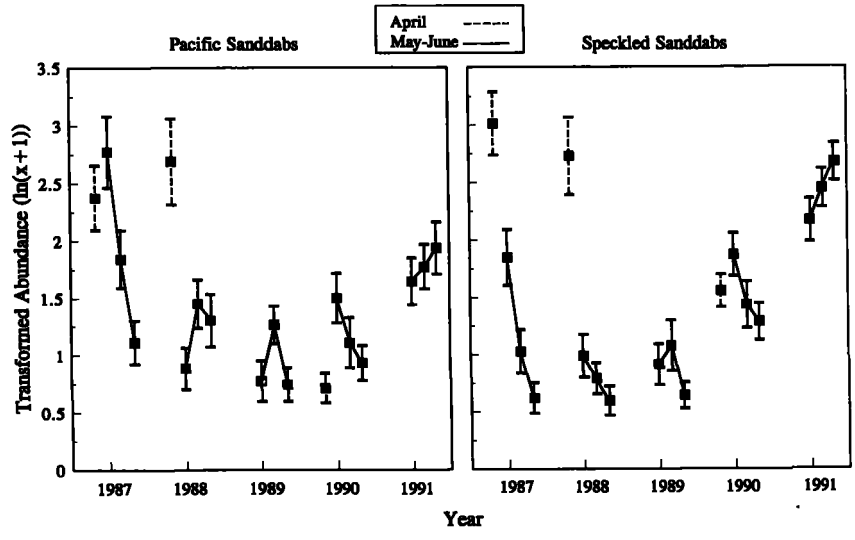

Figure 2

Means and standard errors of the log-transformed abundances of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected at standard stations during April and May–June 1987–91 (means of the three sweeps for the May–June surveys are connected by a line).

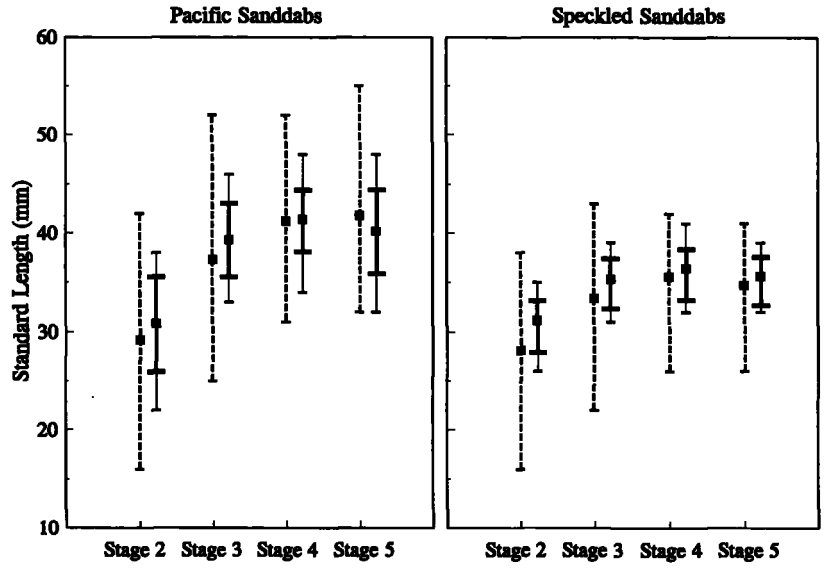

Figure 3

Means and ranges of standard lengths of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus,* in 1990 and 1991 as a function of metamorphic stage. All specimens measured are represented by dotted lines; those subsampled for otolith removal are represented by solid lines. Standard deviations for the specimens selected for otolith removal are shown with thick lines; ranges are shown with thin lines.

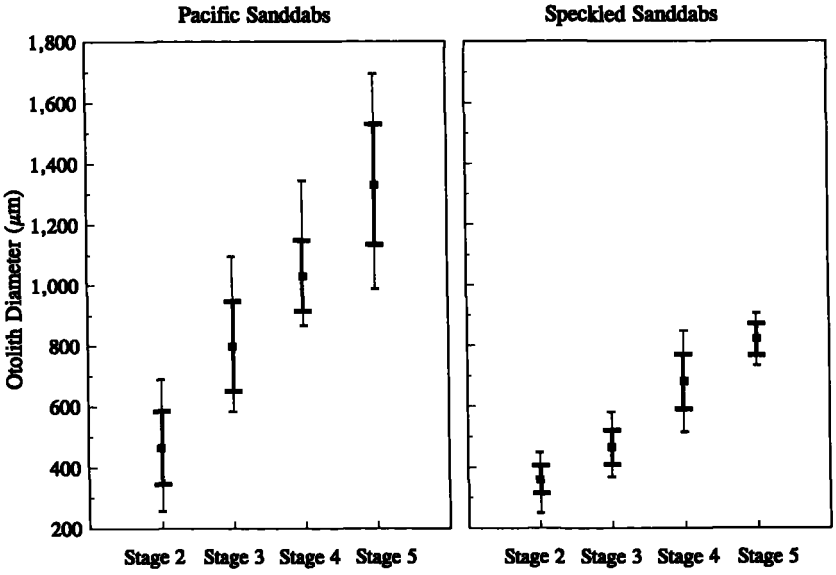

Figure 4

Means, standard deviations, and ranges of otolith diameters of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in 1990 and 1991. Standard deviations are shown with thick lines; ranges are shown with thin lines.

Table 1

Paired comparison *t*-tests of log-transformed abundance ($\ln(x+1)$) of Pacific sanddabs, *Citharichthys sordidus*, from 1987 to 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	*n*	Mean diff.	SE	*t*	*P*
All surveys					
10 m – 30 m	57	0.07	0.1723	0.4047	0.6872
30 m – 110 m	63	0.03	0.1358	0.2075	0.8363
10 m – 110 m	39	0.43	0.2122	2.0419	0.0482
April surveys					
10 m – 30 m	15	0.11	0.4375	0.2515	0.8051
30 m – 110 m	11	–0.35	0.3193	–1.0889	0.3018
10 m – 110 m	8	0.53	0.5727	0.9192	0.3886
May–June surveys					
10 m – 30 m	42	0.06	0.1779	0.3109	0.7574
30 m – 110 m	52	0.11	0.1491	0.7223	0.4734
10 m – 110 m	31	0.41	0.2278	1.7962	0.0825

Table 2

Paired comparison *t*-tests of log-transformed abundance ($\ln(x+1)$) of speckled sanddabs, *Citharichthys stigmaeus*, from 1987 to 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	*n*	Mean diff.	SE	*t*	*P*
All surveys					
10 m – 30 m	54	–0.01	0.1379	–0.1024	0.9188
30 m – 110 m	51	0.62	0.1395	4.4494	0.0001
10 m – 110 m	37	0.69	0.1555	4.4301	0.0001
April surveys					
10 m – 30 m	14	0.02	0.3319	0.0499	0.9610
30 m – 110 m	13	0.59	0.3488	1.7036	0.1142
10 m – 110 m	8	0.75	0.3479	2.1487	0.0687
May–June surveys					
10 m – 30 m	40	–0.02	0.1484	–0.1675	0.8678
30 m – 110 m	38	0.63	0.1476	4.2666	0.0001
10 m – 110 m	29	0.67	0.1768	3.8038	0.0001

than in deep trawls with a trend for increased abundance in shallow trawls versus deep trawls (Table 4; Fig. 6). Stage-3 and stage-4 individuals were most abundant in mid-depth trawls; stage-3 individuals showed a tendency for decreased abundance in shallow trawls versus mid-depth trawls (Table 4; Fig. 6). Stage-5 individuals were distributed relatively evenly throughout the water column, with a tendency toward increased abundance with increased depth (Table 4; Fig. 6). In contrast to Pacific sanddabs, of the four metamorphic stages, only stage-5 individuals of speckled sanddabs were abundant in the deep trawls (Table 4; Fig. 6). Thus, speckled sanddabs generally occurred shallower in the water column than did Pacific sanddabs (Fig. 6).

Within each species of sanddab, abundances of adjacent metamorphic stages were correlated over stations (Table 5). However, the correlations decreased among more dissimilar stages, indicating changes in distribution with advancing metamorphosis (Table 5). The only two stages in either species that were not significantly correlated with each other were stages 2 and 5 (Table 5). Results of the correlation analysis provided a substantial basis for overlaying only stage-2 and stage-5 abundances onto the salinity contours in Figures 8 and 9.

CTD salinity contours showed that many of the patterns at the surface were still noticeable at 30 m (Fig. 7; and Sakuma, 1992). Therefore, only the surface salinity contours were used because they provided the widest horizontal spatial coverage (salinity at 30 m was not available for nearshore stations because of the shallow bottom depth).

Table 3

Paired comparison *t*-tests of log-transformed abundance ($\ln(x+1)$) of each metamorphic stage of Pacific sanddabs, *Citharichthys sordidus*, from 1990 and 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	*n*	Mean diff.	SE	*t*	*P*
Stage 2					
10 m – 30 m	16	0.08	0.3686	0.2217	0.8276
30 m – 110 m	15	0.53	0.2073	2.5674	0.0224
10 m – 110 m	14	0.65	0.3890	1.6758	0.1176
Stage 3					
10 m – 30 m	14	0.09	0.4787	0.1846	0.8564
30 m – 110 m	17	0.25	0.2058	1.2234	0.2389
10 m – 110 m	16	0.34	0.3987	0.8649	0.4007
Stage 4					
10 m – 30 m	10	–0.55	0.4237	–1.3017	0.2254
30 m – 110 m	12	–0.05	0.3156	–0.1684	0.8693
10 m – 110 m	13	–0.51	0.3946	–1.2940	0.2247
Stage 5					
10 m – 30 m	15	–0.77	0.3505	–2.1952	0.0455
30 m – 110 m	16	–0.35	0.2927	–1.1901	0.2525
10 m – 110 m	13	–0.70	0.3931	–1.7859	0.0994

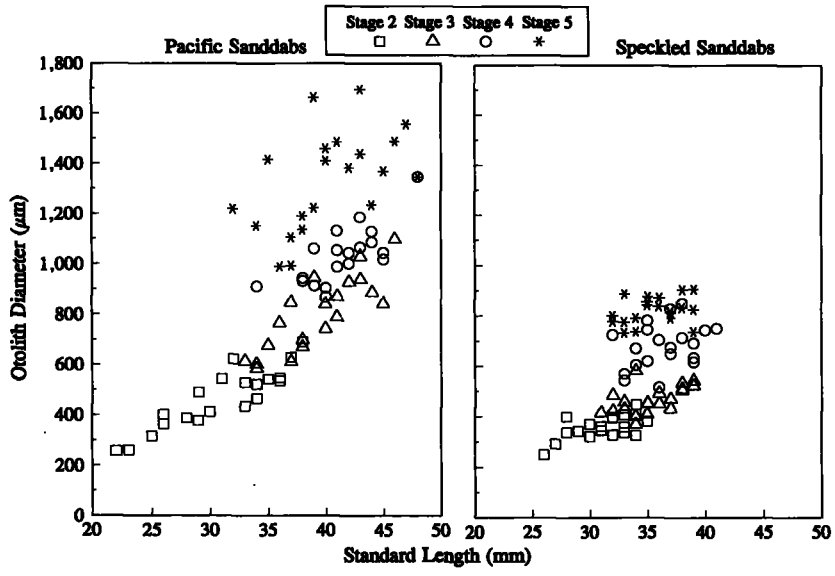

Figure 5

Otolith diameter versus standard length of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in 1990 and 1991.

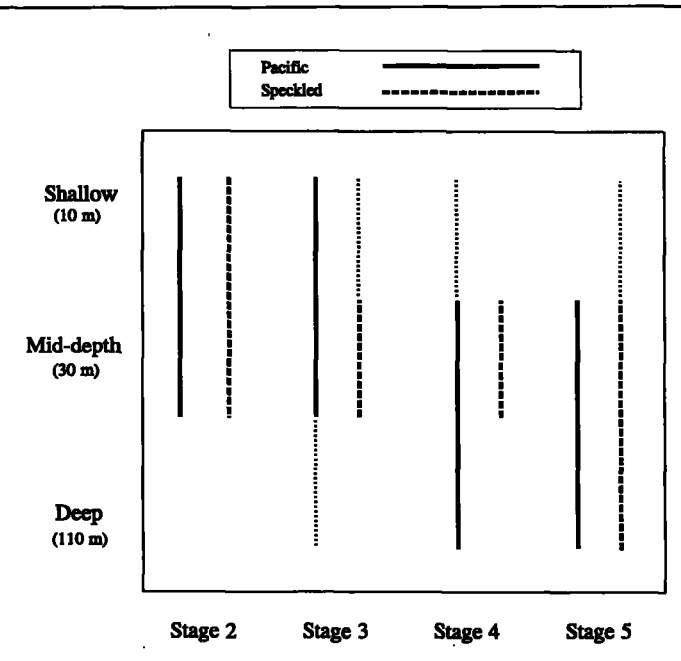

Figure 6

Depth distributions of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in 1990 and 1991, based on paired comparisons of abundance at different depths (Tables 3 and 4). Small dotted lines indicate nonsignificant ($P>0.05$) trends of decreased abundance at the given depth.

Contours for sweep 1 of the May–June survey of 1990 showed a pattern of recent or ongoing upwelling occurring off Point Reyes and the Davenport area (see Fig. 1 for place names) as evidenced by the filaments of higher salinity water projecting seaward and shoreward impingement of lower salinity, more oceanic water (Simpson, 1987) at the surface north of Point Reyes (Fig. 8). The contours for sweep 2 indicated a reduction in offshore transport due to upwelling, with lower salinities closer to shore (Fig. 8). The contours for sweep 3 showed upwelling activity occurring off Point Reyes but not off Davenport (Fig. 8).

The contours for the May–June survey of 1991 showed pronounced seaward filaments off Point Reyes and Davenport during sweep 1, which indicated recent or ongoing upwelling (Fig. 9). During sweep 2, upwelling was still evident off Davenport, but owing to problems with the CTD, patterns off Point Reyes were not easily discernible (Fig. 9). During sweep 3, there was a relaxation of upwelling as evidenced by the lack of seaward-projecting filaments of higher salinity water (Fig. 9).

The overlaid abundances of stages 2 and 5 showed that large abundances of stage-5 individuals of both species generally occurred nearshore and could be found within centers of upwelling (Figs. 8 and 9 off Davenport and Monterey Bay; Fig. 9 off Point Reyes). In contrast, large numbers of stage-2 individuals of both species were relatively more abundant in the offshore transitional zone between coastal water (nearshore, high salinity due to upwelling) and oceanic water (offshore, low salinity) (Figs. 8 and 9). In addition, large numbers of stage-2 individuals were observed nearshore in the area north of Point Reyes during sweep 1 of 1990 associated with the shoreward impingement of oceanic water (Fig. 8).

Although the effects of upwelling would be expected to be most intense near the surface, no significant differences in the abundances of the metamorphic stages of either sanddab species were observed between upwelling and nonupwelling areas at the shallow trawl depth of

Table 4

Paired comparison *t*-tests of log-transformed abundance ($\ln(x+1)$) of each metamorphic stage of speckled sanddabs, *Citharichthys stigmaeus*, from 1990 and 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	*n*	Mean diff.	SE	*t*	*P*
Stage 2					
10m – 30 m	21	–0.08	0.2339	–0.3240	0.7493
30m – 110 m	18	0.49	0.2408	2.0436	0.0568
10m – 110 m	14	0.52	0.3199	1.6392	0.1251
Stage 3					
10m – 30 m	23	–0.46	0.2438	–1.8982	0.0709
30m – 110 m	17	0.51	0.2350	2.1629	0.0460
10m – 110 m	16	0.44	0.2647	1.6492	0.1199
Stage 4					
10m – 30 m	17	–0.79	0.2212	–3.5700	0.0026
30m – 110 m	14	0.67	0.2532	2.6485	0.0201
10m – 110 m	10	0.05	0.2604	0.1739	0.8658
Stage 5					
10m – 30 m	10	–0.72	0.4615	–1.5548	0.1544
30m – 110 m	4	–0.27	0.3705	–0.7186	0.5243
10m – 110 m	5	0.11	0.4416	0.2584	0.8088

Table 5

Spearman rank correlations of log-transformed abundance ($\ln(x+1)$) of each metamorphic stage of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected at standard stations during 1990 and 1991 (significance probabilities of each correlation are listed in bold type under the coefficients).

	Pacific sanddabs (n = 257)			
	Stage 2	Stage 3	Stage 4	Stage 5
Stage 2		0.58	0.31	0.06
		0.0001	**0.0001**	**0.3559**
Stage 3	0.62		0.47	0.13
	0.0001		**0.0001**	**0.0316**
Stage 4	0.15	0.37		0.38
	0.0181	**0.0001**		**0.0001**
Stage 5	0.04	0.13	0.53	
	0.4827	**0.0346**	**0.0001**	
	Stage 2	Stage 3	Stage 4	Stage 5

Speckled sanddabs (n = 257)

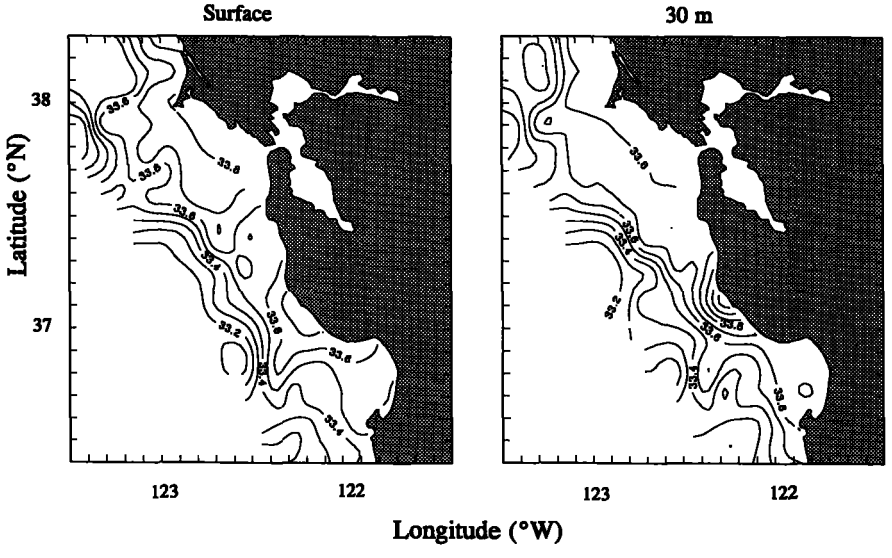

Figure 7

Salinity contours at the surface compared with salinity contours at 30 m depth during 1990 sweep 1.

10 m (Table 6; Fig. 10). However, at the mid-depth of 30 m, stages 2 and 3 of Pacific sanddabs were significantly less abundant in upwelling areas than in non-upwelling areas, and stages 2 and 3 of speckled sanddabs showed a strong tendency for decreased abundance in upwelling areas (Table 6; Fig. 10). In contrast, stage 5 in each species tended to be more abundant in upwelling areas than in non-upwelling areas (Table 6; Fig. 10).

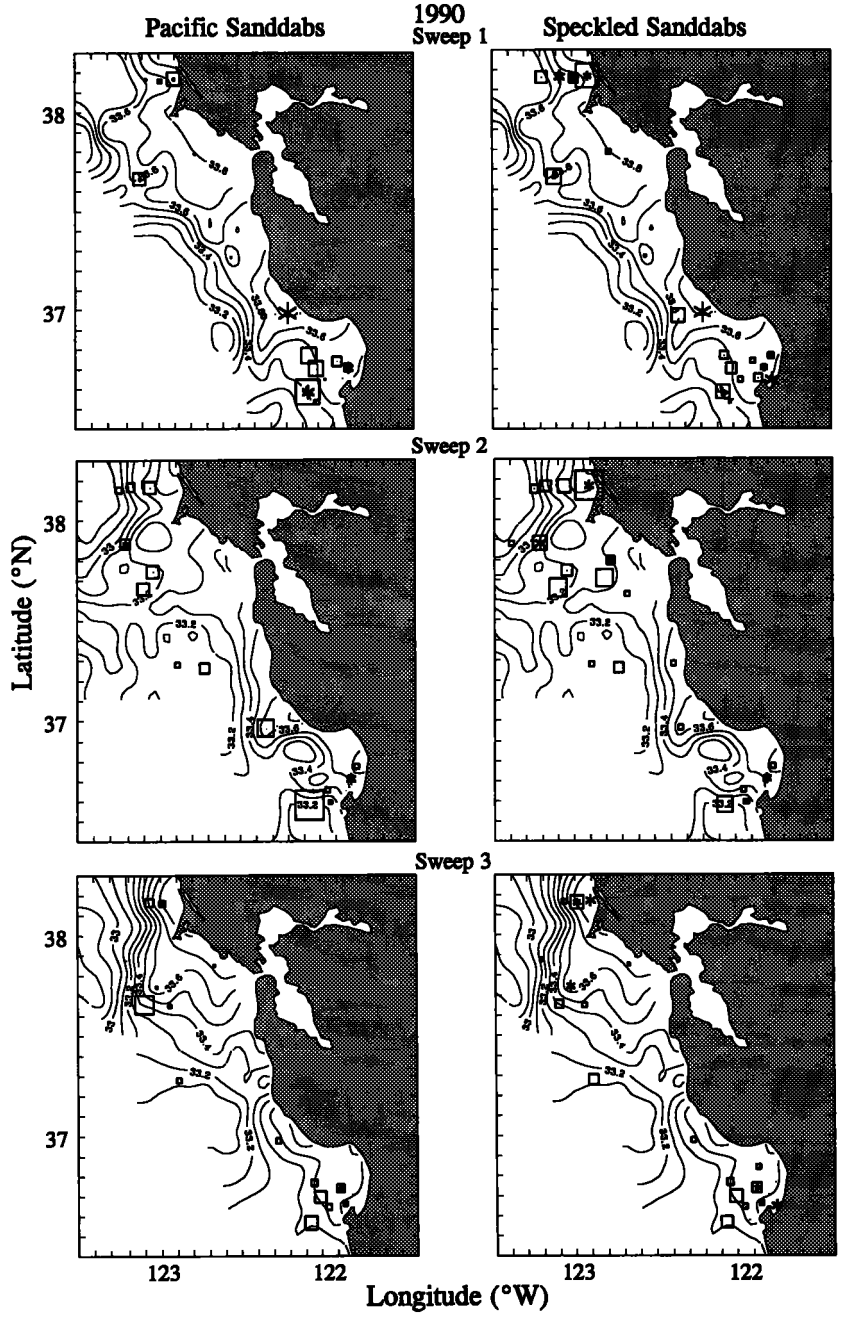

Figure 8

Salinity contours at the surface during the May–June survey of 1990 with overlaid abundances of stages 2 (represented by squares) and 5 (represented by asterisks) of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*. Size of each symbol is proportional to the abundance.

Discussion

During the springtime series covered by this study, metamorphosis in both sanddab species occurred at a wide range of sizes, indicating little growth in body size during metamorphosis (Figs. 3 and 5). Later metamorphic stages tended to occur in deeper water than did earlier stages; Pacific sanddabs shifted to deeper water at earlier stages than speckled sanddabs (Tables 3 and 4; Fig. 6). Later metamorphic stages of both sanddabs occurred nearer to shore than earlier stages, despite the upwelling-associated offshore advection of surface waters (Table 6; Figs. 8–10).

Given the reported variability of size at metamorphosis in both sanddab species (Ahlstrom et al., 1984; Matarese et al., 1989), it was not surprising to observe a large amount of overlap in the SL's of the different metamorphic stages (Fig. 3). Kendall (1992) reported that speckled sanddabs settled at ages ranging from 113 to 324 days. In general, she found that larger, recently settled individuals had spent more time in the plankton than smaller recently settled ones (Kendall, 1992). Kendall (1992) also reported that settlement marks on the otoliths of speckled sanddabs were generally observed at an otolith radius of 400–450 μm. This corresponds to the otolith diameters observed in stage-5 individuals, indicating that these individuals were prepared to settle (Figs. 4 and 5).

An important aspect of metamorphosis in flatfishes is the

ossification of bony structures (Ahlstrom et al., 1984). The large increase in otolith size observed in later metamorphic stages of both sanddab species may be attributable to the transition from a planktonic form to a benthic form. Jenkins (1987) observed accelerated otolith growth in relation to growth in length at the beginning of metamorphosis for the flatfish *Rhombosolea tapirina*, which resulted in significant alterations in otolith increment morphology. One alteration in otolith morphology observed in pelagic stage Pacific sanddabs was the formation of accessory growth primordia. Accessory growth primordia first occurred in stage-3 individuals and completely enclosed the otolith by stage 5 (Brothers[1]). Toole et al. (1993) found that the initiation of accessory primordia formation was coincident with the onset of eye migration in Dover sole, *Microstomus pacificus*, and that the completion of accessory primordia formation occurred either during the final stages of eye migration in pelagic individuals or shortly after settlement.

Metamorphosis in some flatfish can take place in as little as five hours, as in *Cynoglossus macrostomus* (Ahlstrom et al., 1984), or up to nine months, as in *Microstomus pacificus* (Markle et al., 1992). The small increase in length seen in metamorphosing sanddabs (Figs. 3 and 5) suggests a relatively rapid metamorphosis relative to growth. However, if metamorphosis occurred very rapidly, then the probability of collecting metamorphosing specimens would be small (Laroche et al., 1982; Ahlstrom et al., 1984). The large numbers of later stages collected in 1991 and the large otolith sizes in later stages suggest that metamorphosis in both sanddab species occurs over a more prolonged period of time (Figs. 5, 8, and 9). Preliminary results from Pacific sanddab otoliths indicate that the transition from stage 3 to stage 5 takes approximately three weeks (Brothers[1]). Kendall's (1992) data on otolith radius at age indicate that the transition from individuals with otolith radii correspond-

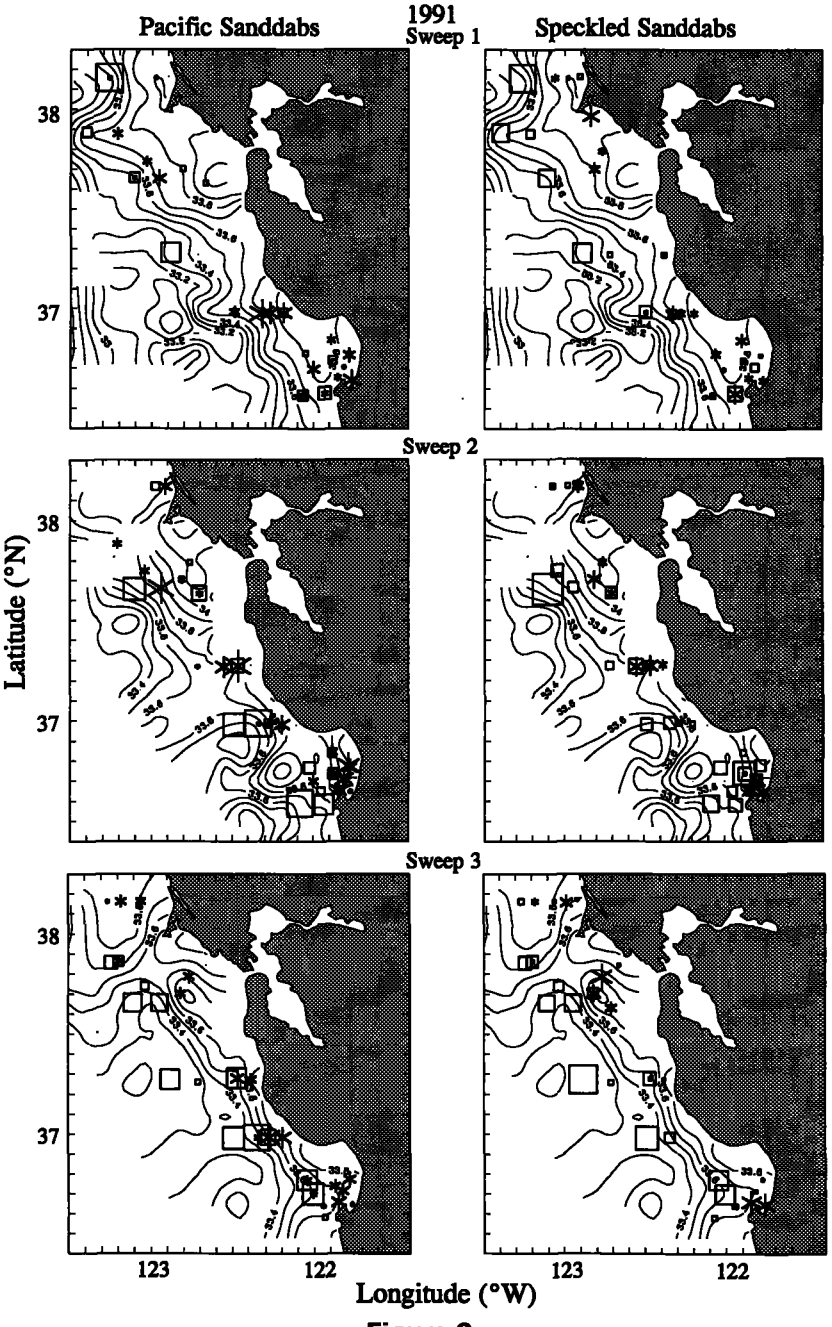

Figure 9

Salinity contours at the surface during the May–June survey of 1991 with overlaid abundances of stages 2 (represented by squares) and 5 (represented by asterisks) of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*. Size of each symbol is proportional to the abundance.

Table 6

Comparison of standard scores of log-transformed abundance ($\ln(x+1)$) of each metamorphic stage of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, in upwelling and non-upwelling areas during 1990 and 1991 (upwelling areas were defined as having surface salinities >33.6 ppt and surface temperatures <11.0°C). Means and standard errors are shown in Figure 10. Degrees of freedom less than $(n_1-1)+(n_2-1)$ indicate cases with unequal variances.

Pacific sanddabs				Speckled sanddabs			
Stage	*t*	df	*P*	Stage	*t*	df	*P*
Shallow trawls (upwelling *n*=36, non-upwelling *n*=44)							
2	0.6797	78.0	0.4987	2	–0.4730	76.2	0.6375
3	0.6911	76.4	0.4916	3	0.6346	78.0	0.5275
4	0.1171	78.0	0.9071	4	0.4846	78.0	0.6293
5	–0.4135	77.0	0.6804	5	–0.3190	78.0	0.7506
Mid-depth trawls (upwelling *n*=63, non-upwelling *n*=99)							
2	–2.3877	159.9	0.0181	2	–1.7268	160.0	0.0861
3	–3.0253	160.0	0.0029	3	–1.7147	160.0	0.0883
4	–0.5325	160.0	0.5951	4	0.7201	160.0	0.4275
5	0.9655	160.0	0.3259	5	1.5650	100.4	0.1207

ing to stage 3 to those corresponding to stage 5 takes approximately five weeks.

Morphological changes associated with metamorphosis probably decrease the buoyancy of pelagic sanddabs. Laroche et al. (1982) found an increase in otolith growth relative to growth in length at metamorphosis for *Parophrys vetulus*, which was similar to that observed for the two sanddab species in this study and for *Rhombosolea tapirina* (Jenkins, 1987). Reared *Parophrys vetulus* that were close to settlement frequently rested on their sides on the bottom and swam with their bodies at an angle (Laroche et al., 1982). This behavior may be related to decreased buoyancy as a result of the ossification of bony structures and to the large increase in otolith size (Laroche et al., 1982). In addition, the gas bladder is lost during metamorphosis in some species of flatfish, including the related Atlantic species *Citharichthys arctifrons* (Richardson and Joseph, 1973; Ahlstrom et al., 1984). Laidig[2] observed that the gas bladder was reduced in stage-4 Pacific sanddabs and absent in 90% of stage-5 specimens.

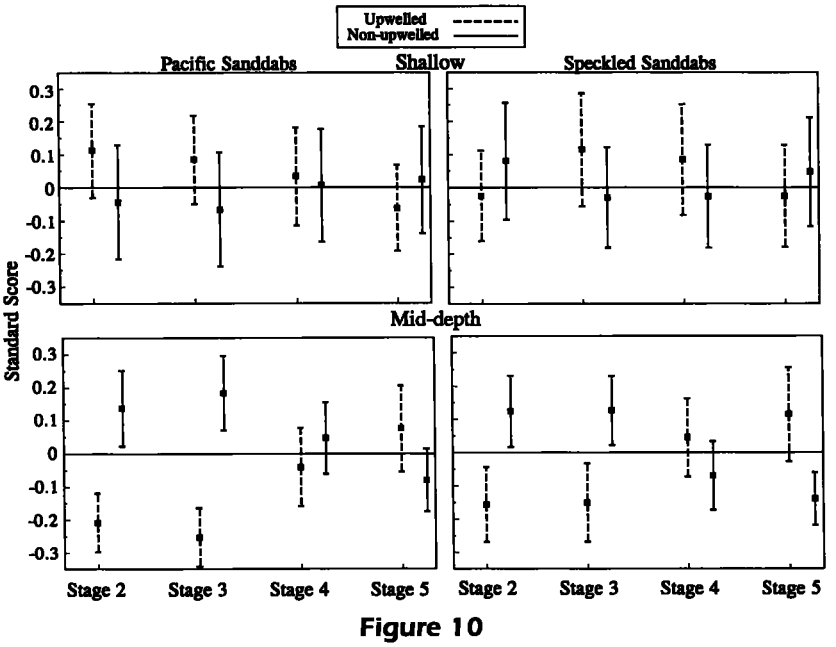

Figure 10

Mean standard scores and standard errors of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in shallow and mid-depth trawls during 1990 and 1991 in upwelling and non-upwelling areas (upwelling=surface salinity >33.6 ppt and surface temperature <11°C).

[2] Laidig, T. E. Tiburon Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Drive, Tiburon, CA 94920. Personal commun., 1994.

The decrease in buoyancy due to increased otolith size, the ossification of other bony structures, and the loss of the gas bladder may account for the deeper bathymetric distribution of later metamorphic stages in both sanddab species (Tables 3 and 4; Fig. 6). The greater water density at deeper depths may reduce the energy expenditure required for less buoyant fish to remain pelagic; however, beyond a given range of SL and otolith size, individuals may sink more rapidly. Therefore, the decrease in buoyancy may account directly for the deeper bathymetric distribution of later-stage pelagic sanddabs, although fish may behaviorally seek deeper water as well.

Lenarz et al. (1991) reported that younger, smaller juveniles of the shortbelly rockfish, *Sebastes jordani*, were found deeper in the water column than larger individuals during May–June. It was suggested that the smaller individuals were adapted to seeking deeper water as a method of avoiding offshore advection due to upwelling (Lenarz et al., 1991). In contrast, the early stages of both sanddab species showed a shallower distribution than the later stages (Tables 3 and 4; Fig. 6). The shallow distribution of early stages may explain the comparisons of abundance in upwelling and non-upwelling areas for the 30-m depth trawls, which suggest that early stages are subject to offshore advection due to coastal upwelling (Table 6; Figs. 6, 8, 9, and 10). The offshore advection of early stages may also explain their predominantly offshore distribution (Figs. 8 and 9).

The lack of significant differences in abundance between upwelling and non-upwelling areas for the shallow depth trawls observed in both sanddab species might be explained by the fact that the majority of these trawls were conducted nearshore where early stages were generally less abundant and that later stages were generally less abundant at the shallow trawl depth (Tables 3, 4, and 6; Figs. 6, 8, 9, and 10). In contrast, the 30-m mid-depth trawls, in which most metamorphic stages occurred, were more widely distributed and probably indicated better the relation between upwelling and the distribution of metamorphic stages (Tables 3, 4, and 6; Fig. 6). Figure 10 shows a change in distribution of metamorphic stages in the 30-m mid-depth trawls; earlier stages tended to be more abundant in water that had not been upwelled recently, whereas later stages were more abundant in recently upwelled water.

The reduction in abundance of early stages in trawls within upwelling areas may have been due to the fact that these stages were present predominantly offshore while upwelling events occurred nearshore (Figs. 8 and 9). However, the large abundances of stage-2 individuals of both species observed nearshore north of Point Reyes during sweep 1 of 1990 associated with an extension of oceanic waters toward shore (Fig. 8) and the large abundances of stage-2 individuals occurring within the transitional areas between offshore oceanic waters and nearshore coastal waters (Figs. 8 and 9) suggest that these early stages were subject to transport by ocean currents. Analysis of California Cooperative Oceanic Fisheries Investigations (CalCOFI) data by Ahlstrom and Moser (1975) and Loeb et al. (1983) indicated that the larvae of both sanddab species were collected both nearshore and well offshore. Therefore, sanddabs of both species are probably passive drifters during their early life history stages as evidenced by the predominantly offshore distribution of their early metamorphic stages (Figs. 8 and 9) and the somewhat dispersed distribution of their larvae (Ahlstrom and Moser, 1975; Loeb et al., 1983).

In contrast to the distributional patterns of early stage metamorphic sanddabs, the tendency for later stages of both species to be more abundant in upwelling areas was probably due to the fact that later stage individuals occurred predominantly nearshore (Figs. 8 and 9). Although large numbers of stage-5 individuals of both species occurred within upwelling plumes (Figs. 8 and 9), large abundances of stage-5 individuals could also be found nearshore in areas outside of the upwelling plumes (Figs. 8 and 9). Because later-stage individuals were more abundant at deeper depths, they were probably less susceptible to offshore advection by upwelling. The deeper and more shoreward distribution of later-stage sanddabs parallels the observations of Barnett et al. (1984) on later stages of northern anchovy, *Engraulis mordax*, white croaker, *Genyonemus lineatus*, and queenfish, *Seriphus politus*, off southern California. Larson et al. (1994) also found that late-stage pelagic juvenile rockfish (*Sebastes* spp.) off central California had a more shoreward distribution, although there was no evidence that later-stage fish were distributed at greater depths (Lenarz et al., 1991).

In summary, it appears that physical changes in metamorphosing sanddabs are correlated with changes in their depth distributions; more developed, less buoyant individuals occur deeper in the water column (Fig. 6). This may influence the horizontal distributions of pelagic sanddabs in the upwelling regions off central California. Early-stage sanddabs present within the upper mixed layer would be subject to offshore advection associated with coastal upwelling or to onshore advection associated with downwelling (Table 6; Figs. 8–10). In contrast, the deeper distribution of later-stage sanddabs decreases their susceptibility to upwelling-associated offshore advection and could potentially lead to onshore advection facilitated by the shoreward movement of

deeper water (Tables 3 and 4; Fig. 6). In addition, the vertical and horizontal distributions of both early and late-stage sanddabs may have a substantial behavioral component; however, the means to resolve such behavioral patterns is beyond the scope of this study.

Acknowledgments

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Abstract.—Nine new species of hagfishes (Myxinidae, *Myxine*) from the Pacific and Atlantic coasts of North and South America are described and a key is offered to the new world hagfishes. New data are presented for *Myxine circifrons* from the eastern Pacific Ocean, *M. limosa* from the northwestern Atlantic Ocean, and *M. affinis* and *M. australis* from in and near the Straits of Magellan. *Myxine limosa* is removed from the synonymy of *M. glutinosa*. The nine new species occur as follows: *M. hubbsi* along the Pacific coast from San Francisco, California, to Valparaiso, Chile; *M. hubbsoides* and *M. pequenoi* near Valdivia, Chile; *M. mccoskeri* and *M. robinsi* in the southern portion of the Caribbean Sea; *M. fernholmi, M. knappi,* and *M. dorsum* near the Falkland Islands, and *M. debueni* in the Straits of Magellan. *Myxine mccoskeri* and *M. pequenoi* are regarded as dwarfed, containing nearly mature eggs or testes at total lengths of 230 and 175 mm, respectively. Hermaphroditism is often found in individuals of *M. hubbsi, M. limosa,* and *M. affinis.*

Review of new world hagfishes of the genus *Myxine* (Agnatha, Myxinidae) with descriptions of nine new species

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Hagfishes (slime eels) are cartilaginous, eel-like, abundant bottom-dwelling scavengers occurring at depths ranging from a few to at least 2,400 meters. *Myxine* is one of the six recognized genera in the "agnathan" family Myxinidae (Nelson, 1994). In the new world it comprises eight species in the Atlantic Ocean and six in the Pacific (references in this study); species occurring in the Straits of Magellan also may occur in either ocean. The genus *Myxine,* which presently contains 19 species including those in this study, is characterized principally by all the efferent gill pouch ducts discharging into a single aperture on each side, the left being confluent with the pharyngocutaneous duct. This character is shared by the genera *Neomyxine* Richardson, 1953, and *Nemamyxine* Richardson, 1958. *Neomyxine* is further characterized by having paired lateral finfolds in the prebranchial region, as well as the usual ventral finfold posterior to the gill apertures. In *Nemamyxine,* the body is extremely slender and the ventral finfold extends far forward nearly to the anteriormost prebranchial slime pores. In all other myxinids the ventral finfold does not extend anterior to the pharyngocutaneous duct. Head grooves ("lateral lines" of earlier authors) are lacking in genus *Myxine* as are the external eyespots common in genus *Eptatretus* (McMillan and Wisner, 1984). Hermaphroditism does not occur in our material of *M. circifrons* but is not uncommon in *M. limosa, M. affinis, M. australis, and M. hubbsi* and occurs in two of the three specimens of *M. hubbsoides.* The remaining new species have too few specimens to state with certainty whether or not hermaphroditism occurs among them. Great variation in developmental stages of eggs occurs among specimens of the same length and possibly age, which supports a widely held belief that hagfishes spawn throughout the year. As eggs mature, the polar caps enlarge into dome-like structures containing anchor filaments that are connected to the eggs when they are extruded. With one exception (a female *M. limosa* discussed below), eggs of all specimens examined here were not fully mature; polar caps were not visible, nor were they still encapsulated.

This study of new world hagfishes, the latest by us in a series on the family Myxinidae begun by Carl L. Hubbs (deceased), includes all 14 known species of *Myxine* from the Pacific and Atlantic coasts of North and South America. We have added old world *M. glutinosa* to all tables for comparison with the closely related *M. limosa.* Of the other four

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known species, *M. ios* from the eastern Atlantic and *M. capensis* from South Africa are compared briefly with the new world species *M. pequenoi.* Both *M. garmani,* and *M. paucidens* Regan, 1913 are known only from Japan and are not closely related to any new world species. The number of new species (nine) from near the coasts only, suggests a need for further and more intensive collecting throughout the world.

Methods

Methods of counting and measuring generally follow those of Fernholm and Hubbs (1981) and McMillan and Wisner (1984). All measurements are in mm, and body proportions (Table 1) are in percent of total length. Features used in measuring and counting are shown in Figures 1 and 2, and geographic distribution in Figure 3. Counts of slime pores (Tables 2–5) and unicusps (Table 6) represent the left side only because we have found no significant differences between the left and right sides. Occasionally one extra gill pouch occurs, usually on one side only and much smaller than normal; one less pouch rarely occurs on either side. The one to three slime pores which may occur over the pharyngocutaneous duct are included in the prebranchial pore count. In all species of *Myxine* only two fused cusps (a multicusp) occur on the posterior set of cusps (inner row of Fernholm and Hubbs, 1981) in contrast to either two or three on the anterior set. This latter character is used to group species (Tables 1–7). Some terms have appeared previously in myxinid accounts without clear definition. We offer precise definition of these and some new terms used in this study: **rostrum**, rounded to pointed, fleshy extension lying over the nasal orifice between the anteriormost pairs of barbels; **head**, from tip of rostrum to a vertical from wrinkled tissue below the mouth; **face**, ventral aspect of head; **mouth**, the elongate slit in face which opens to permit extrusion of cusps for feeding (Fig. 2A); **multicusp**, a unit of two or three cusps (teeth of other authors), fused together at bases (Fig. 2B); **unicusp**, a single unfused cusp (Fig. 2C); **pores** (slime pores), the small openings along the ventral aspect of body which emit mucus; **gill aperture** (GA), the opening through which water discharges to the exterior after passing through the gill pouches; **PCD**, the external opening of the pharyngocutaneous duct, always on the left side and usually confluent with the left gill aperture in *Myxine* (or posteriormost GA in *Eptatretus*); **ventral finfold** (VFF), a band of thin, fleshy tissue extending along ventral midline of body between PCD and origin of cloaca (Fig. 1); **cloaca**, the slit-like ventral opening anterior to tail through which body wastes and sexual products discharge; and **caudal finfold** (CFF), the band of thin fleshy tissue extending around tail, ending dorsally about over origin of cloaca (Fig. 1).

Colors are determined after scraping away the coating of coagulated slime (mucus). Although given in the descriptions, color is subjective and may change greatly with preservation; therefore, the use of counts is preferred as a more distinguishing character. Because eggs are similar in all species, we have not used them as a species character. They vary widely in length and diameter and in developmental stages, ranging from tiny to nearly mature in females of the same length. Accurate measurement of diameter is hindered in eggs deformed because of crowding in life or during preservation; many are somewhat flattened and diameters may vary as much as 1.5 mm in the same specimen. We have not provided photographs or drawings of individual species since

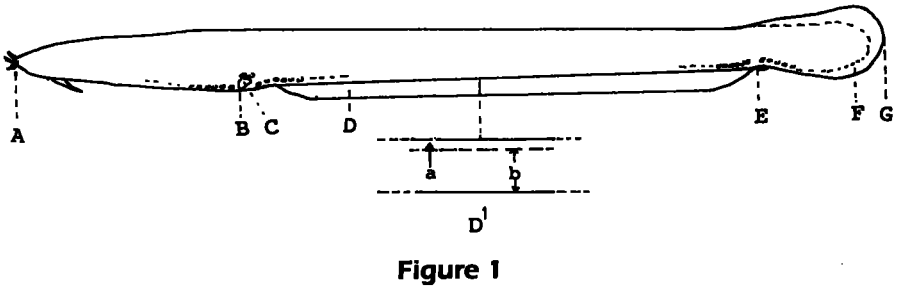

Figure 1

Sketch of a *Myxine* showing features used in measuring and counting: A–G = total length (TL); A–B = prebranchial length; C = opening of the pharyngocutaneous duct (PCD); D = ventral finfold (VFF), D'= enlarged portion of VFF with dashed line indicating the approximate difference between a well and a weakly developed VFF; E = origin of cloaca; E–G = tail length; F = caudal finfold (CFF). The many slime pores along the sides are indicated by a few small circles near PCD and cloaca.

there are no distinguishing external features other than those characters given in the key. A list of the materials examined and of the collections where these materials were obtained follows the Acknowledgment section. Institutional abbreviations are listed as in Leviton, et al. (1985).

Key to new world hagfishes (Genus *Myxine*)

1a A 3-cusp multicusp on anterior set, a 2-cusp multicusp on posterior set of cusps **2**
1b A 2-cusp multicusp on both the anterior and posterior sets of cusps **6**

2a Gill pouches 6, rarely 7 ..... **3**
2b Gill pouches 5 ..... **4**

3a VFF well developed, 3–7 mm high, mounted on thick triangular base extending from the ventral surface; last few prebranchial pores in an uneven line, resembling the letter W; total pores 112–121 ..... ***M. fernholmi***
3b VFF vestigial, not mounted on triangular fleshy base; last few prebranchial pores in a straight line; total pores 103- 104 ..... ***M. debueni***

4a Anterior unicusps 6–9; total cusps 36–48; total pores 77–92; color light brown, often lighter dorsally than ventrally ..... ***M. mccoskeri***
4b Anterior unicusps more than 9 each side **5**

5a Anterior unicusps 11–13; total cusps 56–58; total pores 92–100; VFF usually low (3–6 mm); head and barbels pale ..... ***M. robinsi***
5b Anterior unicusps 7–13; total cusps 43–56; total pores 80–102; VFF usually prominent, averaging 5 mm (1–12 mm); head and barbels usually pale ..... ***M. circifrons***

6a Gill pouches 7; anterior unicusps 4; posterior unicusps 5–6; total cusps 26–28 ..... ***M. pequenoi***
6b Gill pouches 6, rarely 7 ..... **7**

7a CFF extending forward dorsally 2–3 times tail length; total pores 108–109; VFF low, (3–5 mm) ..... ***M. dorsum***
7b CFF not extending forward dorsally much beyond a vertical above cloacal origin **8**

8a Prominent whitish band on ventral surface; VFF usually well developed **9**
8b No prominent ventral whitish band **10**

9a Ventral whitish band not extending above line of trunk pores, but often extending to face; color dark reddish-brown; total cusps 38–46 ..... ***M. affinis***
9b Ventral whitish band extending above line of trunk pores, often increasing as wide blotches between GA and face; body brown to purplish; total cusps 29–38 ..... ***M. australis***

10a VFF moderately to well developed **11**
10b VFF vestigial, or nearly so **12**

11a Color bluish gray to brownish, head pale; whitish mid-dorsal narrow stripe extending forward a variable distance; total cusps 42–48; total pores 101–119 ..... ***M. mcmillanae***
11b Color pinkish-brown to various shades of purple, often dark; head usually pale; narrow whitish streak of variable length extending along dorsal midline from CFF; total cusps 30–49; total pores 89–118 ..... ***M. limosa***

12a VFF nearly vestigial, 1–3 mm high; color pinkish to bluish; head pale; prebranchial pores 31–32; trunk pores 61–65; total pores 108–110 ..... ***M. knappi***
12b VFF vestigial; color brown to purplish-black; prebranchial pores 18–31; trunk pores 58–72; total pores 91–116 ..... **13**

13a Color light to dark purplish-brown; occasional pale blotches ventrally; total pores 101–109; VFF variably vestigial to 8 mm high ..... ***M. hubbsi***
13b Color dark brown to blackish; no pale blotches ventrally; head only slightly pale; total pores 111–116; VFF vestigial, intermittently absent ..... ***M. hubbsoides***

Systematics

Myxine circifrons Garman, 1899

Myxine circifrons Garman, 1899: 344 "Albatross Station 3395; 7°30'36"N, 78°W; 730 fm (1,336 m) temperature 38.5°F; bottom rocky."

Diagnosis A 3-cusp multicusp on anterior sets of cusps; five gill pouches each side; color blackish to dark reddish-brown, anteriormost portion of head pale.

Description Counts and proportions are given in Tables 1–7. Body robust, slightly deeper than wide; snout bluntly pointed, rostrum short, variably triangular to bluntly rounded; cusps short, stout; anterior multicusps bulbous at bases, the free tips about equal in length to bulbous portion; tail length about 13% of TL, its depth about 40% of its length; VFF usually well developed, but may be vestigial, ranging in height from 1 to 12 mm, averaging about 5 mm; CFF high, extending around tail to about over cloaca, thickened dorsally; body color dark, grayish-black to reddish-brown; anterior portion of head paler, often whitish to near vertical from margin of face, occasionally extending into the prebranchial region; barbels color of head; VFF and CFF same color as body, without pale margins; GA and slime pores often with narrow pale margins; total cusps 43–56; total slime pores 80–102; numbers of large eggs (20 mm and longer) range from 15 to 18 in females of 435 mm TL, largest egg 28 × 7 mm.

Distribution From near San Francisco, California, to north-central Chile at depths of about 700 to 1,860 m (Fig. 3). We find no significant differences in counts or proportions throughout this extensive range of about 11,000 kilometers.

Comments Sex ratios in our material are equal off southern California (n=220) but unequal near the mouth of the Gulf of California (n=136), 66% female to 34% male, and Costa Rica to northern Chile (n=54), 59% female to 41% male. We find no hermaphrodit-

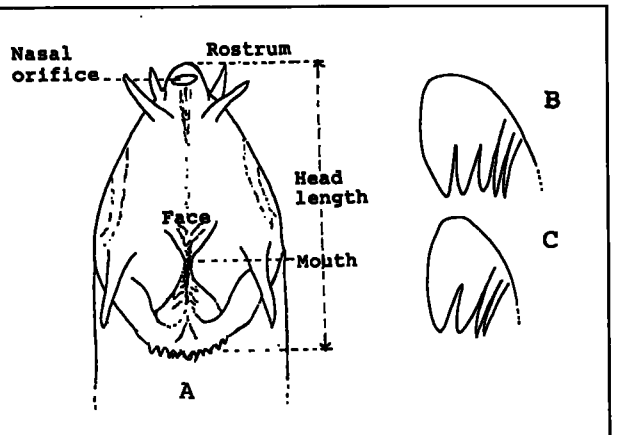

Figure 2

(A) sketch of ventral aspect of a myxinid head, identifying the terms used in the text: (B) and (C), sketches of a 3-cusp and a 2-cusp multicusp, with two adjacent unicusps.

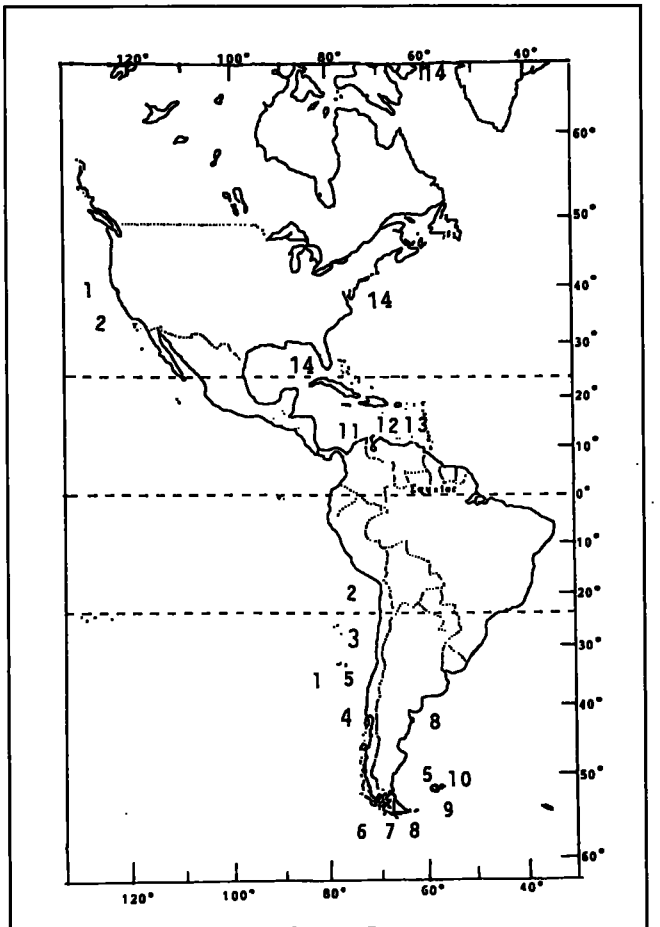

Figure 3

Areas of occurrence of new world species of Myxine: 1 = *M. circifrons*, from near San Francisco, California, to north-central Chile; 2 = *M. hubbsi*, from near San Francisco, California, to near Valparaiso, Chile; 3 = *M. hubbsoides* and 4 = *M. pequenoi*, off south-central Chile; 5 = *M. fernholmi*, from near Valdivia, Chile to Falkland Islands, S.E. Atlantic Ocean; 6 = *M. dorsum* and 7 = *M. debueni*, Straits of Magellan; 8 = *M. australis*, principally in Straits of Magellan; two collections off Chile, and one near Pta. Nuevo, Argentina; 9 = *M. affinis*, Straits of Magellan; 10 = *M. knappi*, near the Falkland Islands; 11 = *M. mccoskeri*, 12 = *M. robinsi*, and 13 = *M. mcmillanae*, southern Caribbean Sea; 14 = *M. limosa*, Davis Strait, Greenland, southerly to eastern portion of the Gulf of Mexico.

ism in 320 specimens exceeding 350 mm TL, a minimum length arbitrarily chosen as offering reliable sex determination.

Myxine mccoskeri new species

Holotype SIO70-363, female, 201 mm, taken at 09°39'N, 78°60'W, 530–560 m, 1 October 1970.

Paratypes SIO70-363, 2 (117, 170 mm), taken with the holotype; SIO90-117, 1 (235 mm), 11°46'N, 67°05'W, 1, 100–1,174 m (formerly UMML 29269); USNM 325212, 2 (170, 235 mm), 11°30'N, 72°26'W, 530–567 m (formerly UMML 28722); CAS 79537, 2 (170, 235 mm), 12°13'N, 75°50'W, depth unknown (formerly UMML 29884); MCZ 48809, 2 (218, 264 mm), 11°35'N, 62°52'W, 512–547 m; MCZ 41634, 1 (254 mm), 11°35'N, 62°59'N, 439–476 m.

Diagnosis A 3-cusp multicusp on anterior sets of cusps; five gill pouches each side; VFF weakly developed, often nearly vestigial, 0–5 mm high; color dark brown, often lighter dorsally than ventrally; a dwarf species, mature at about 300 mm TL.

Description Counts and proportions are given in Tables 1–7. Body slender, slightly deeper than wide, its width about 75% of its depth; tail narrow, its length about 15% of TL, its depth about 33% of its length. VFF usually low, ranging in height from 0–5 mm, average 2 mm; CFF prominent, its margins thin, the internal supporting rays visible; snout rather sharply pointed, rostrum elongate, bluntly pointed; cusps long, slender, sharp, the bases of multicusps slightly bulbous; body variably pale to medium or dark brown, the head and ventral aspects anterior to GA lighter than body; posterior to GA the ventral aspect is notably darker toward end of tail, a pale band extends dorsally to over the cloaca, the general aspect being reverse countershading; VFF and CFF color of body, usually without, or with faintly expressed, pale margins; barbels very slightly or not at all pigmented; GA with narrow pale margins, slime pores without; total slime pores 77–92; total cusps 36–48. A 264-mm-TL paratype (MCZ 48809) contains only four large eggs, each about 18×7 mm; in addition, two other females (218, 222 mm) contain four and five eggs, about 15×5 mm. We consider this species dwarfed because of the short length of females with such large eggs.

Etymology We name this species for John E. McCosker, Director, Steinhart Aquarium, San Francisco, for his work on Caribbean and Panamanian fishes, and for making the first specimens of this species available to us.

Distribution Known only from the southern Caribbean Sea (Fig. 3).

Comments Shimizu (1983) reported as *Myxine* sp. three specimens (273–320 mm TL) from off Suriname at 310 m, with 3-cusp multicusps on anterior sets of cusps, 38 total cusps, and 87–90 total slime pores; number of gill pouches and sexual maturity not stated. Color was described as "Body color white on snout, gradually becoming blackish, and uniformly black behind posterior half of head." The cusp and slime pore counts agree well with *M. mccoskeri*; however, the white snout as described and shown in the color photo from Shimizu, is whiter than those on our specimens of *M. mccoskeri*. This feature and the blackish body are more like those of *M. robinsi* (described below); however, the latter has more total cusps (56–58) and total pores (94–104).

Myxine robinsi new species

Holotype SIO90-149, ripe female, 475 mm TL, taken at 11°37'N, 60°50'W, in a 40-ft otter trawl between 783 and 1281 m (formerly UMML 29270, date of capture not recorded).

Paratypes SIO90-149, 1 (510 mm) taken with the holotype; USNM 325213, 1 (540 mm); 11°37'N, 60°59'W (formerly UMML 29877); MCZ 101239, 1 (460 mm), 10°03'N, 7620'W, (formerly UMML 22807), 675–966 fm [1,235–1,768 m].

Diagnosis A 3-cusp multicusp on anterior set of cusps; five gill pouches each side; whitish on head and continuing to first few prebranchial pores, and light dorsally to about over GA; body light to medium brown.

Description Counts and proportions are given in Tables 1–7. Body rather robust, slightly deeper than wide; tail length about 13% of TL, its depth about 38% of its length; VFF moderately well developed, 3–6 mm high; CFF prominent, extending around tail to about over cloacal origin, thickening dorsally; rostrum variably rounded to bluntly conical; anterior unicusps long, slender, sharp, curved near tips; bases of anterior multicusps slightly bulbous; color light to medium brown; head whitish continuing to first few prebranchial pores; a decreasingly paler area, often blotchy, extends posteriorly along dorsal surface and often laterally to near GA; slime pores and GA with no or very pale margins; VFF and CFF color of body, without pale margins. One female 475 mm TL contains six large eggs, 29–31 mm long by 11–12 mm wide, arranged in a single row.

Etymology We name this new species for both C. Richard and Catherine Robins, University of Miami Rosenstiel School of Marine and Atmospheric Sciences, for their works on the marine fauna of the tropical western Atlantic, particularly the Caribbean area.

Distribution Known only from the type material from the southern Caribbean Sea (Fig. 3).

Discussion *Myxine circifrons, M. mccoskeri,* and *M. robinsi* may be closely related. Each has a 3-cusp multicusp on the anterior sets of cusps and are the only species of *Myxine* known to have only five gill pouches each side. Counts and most body proportions overlap, which invites speculation that prior to the permanent establishment of the Panamanian land barrier, *M. circifrons* may have occupied the Caribbean area. If true, *M. robinsi* evolved primarily to a lighter color and *M. mccoskeri* to a dwarfed state, with fewer anterior unicusps, trunk and total slime pores, as well as a strikingly different color pattern. All counts for *M. robinsi* are similar to those for *M. circifrons.* However, despite these similarities, we hold *M. mccoskeri* and *M. robinsi* to be specifically distinct from *M. circifrons.* Although *Myxine mcmillanae* is also from the same area (see below), we do not consider it related because it has a 2-cusp multicusp on both anterior and posterior sets of cusps and six gill pouches rather than five. One other species with 3-cusp multicusps on anterior row is *M. garmani,* known only from Japan and distinct from the three species described above that have six gill pouches rather than five and a wide geographical separation.

Myxine fernholmi new species

Holotype ISH 257-1978, female, 555 mm TL, taken at 49°29'S, 58°56'W, 200-ft bottom trawl, 400 m, 6 June 1968.

Paratypes SIO90-138, 1 (790 mm), 53°00'S, 64°00'W (formerly ISH 108–1971); SIO90-139, 1 (575 mm), 33°39'S, 72°09'W, 1,170–1,480 m; ZIL 791–966, 1 (665 mm), 54°35'S, 57°30'W, 135–145 m.

Diagnosis A 3-cusp multicusp on anterior sets of cusps, total cusps 34–37; six gill pouches each side; tail length 10% or less of TL; last four prebranchial pores forming an irregular line which resembles the letter *W.*

Description Counts and proportions are given in Tables 1–7. Body moderately robust, slightly deeper than wide; tail short, 8–10% of TL, its depth about half its length; VFF extending 3–7 mm, and mounted on a prominent fleshy triangular extension along the ventral surface; CFF thin, high, extending around tail to about over cloacal origin; reddish supporting rays visible on most specimens; rostrum triangular, the tip slightly rounded; unicusps long, slender, sharp, slightly curved at tips; bases on anterior multicusps bulbous, posterior multicusps not bulbous; last four prebranchial slime pores anterior to GA in an irregular line forming a pattern resembling the letter *W*; all slime pores tiny; tail pores 7–9, total slime pores 112–121; color variably pale, yellowish, or light bluish-pink; GA with prominent pale margins, slime pores with less prominent; females with only immature eggs, 2–8 mm long.

Etymology We name this species for Bo Fernholm, Museum of Natural History, Stockholm, for his work on the physiology, anatomy, and systematics of Myxinidae.

Distribution Known only from the type material taken off south- central Chile and near the Falkland Islands, southwestern Atlantic Ocean (Fig. 3).

Myxine debueni new species

Holotype SIO90-140, male, 570 mm TL, taken at 53°39'S, 70°14'W, 300 m, 27 April 1970, Straits of Magellan.

Paratype SIO90-140, male 545 mm TL, taken with the holotype.

Diagnosis A 3-cusp multicusp on anterior sets of cusps; six gill pouches each side; VFF absent; tail short, 8–9% of TL; rostrum triangular, the tip pointed; prebranchial slime pores in a straight line anterior to GA.

Description Counts and proportions are given in Tables 1–7. Body slender, nearly cylindrical; tail short, 8–9% of TL; depth about 40% of length; VFF absent; CFF prominent, thickened at margin, extending around tail to over cloacal origin; head narrow, pointed, rostrum triangular, the tip pointed; unicusps long, slender, sharp, slightly curved; bases of multicusps not bulbous; prebranchial slime pores in a straight line anterior to GA. The two specimens appear to have been "dry-burned" from insufficient preservative, causing the skin to harden and become a dark reddish-brown color on damaged portion, mostly dorsally. Undamaged part of body is pale bluish-gray anterior to GA; posteriorly a pale pinkish color continues to tail; CFF with narrow pale margins, slime pores with very narrow ones.

Etymology We name this species for Fernando DeBuen in recognition of his extensive work on fishes of South America.

Distribution Known only from the two specimens from the Straits of Magellan (Fig. 3).

Comments This species and *M. fernholmi* (described above) are similar in that each has a tail length of 10% or less of TL and a somewhat longer trunk length than other species treated here. Each has a 3-cusp multicusp on the anterior sets of cusps; they differ primarily in *M. debueni* lacking a VFF (prominent in *M. fernholmi*); also, the last four prebranchial pores lie in a straight line not forming the letter *W*.

Myxine hubbsi new species.

Synonymy *Myxine circifrons* Chirichigno, 1968:383 (description; a 2-cusp multicusp on anterior set of cusps; northern Peru to Gulf of Panama).

Holotype SIO65-452, female, 515 mm TL, taken at 32°38'N, 118°08°4'W, 25 September 1965, bottom trap, 2,009 m.

Paratypes SIO65-452, 82 (209–522 mm), taken with the holotype; SIO68-60, 36 (120–484 mm), 23°07'N, 109°16'W, 1,830 m; SIO68-61, 2 (350, 400 mm), 23°06'N, 109°13'W, 2,196 m; SIO73-293, 16 (230–480 mm), 09°24'N, 85°06'W, 1,107 m; SIO92-114, 7 (260–450 mm), 03°41'S, 81°36'W, 2,440 m; SIO92-115, 7 (290–420 mm), 08°26'S, 80°36'W, 1,830–1,930 m; SIO72-176, 8 (326–473 mm), 21°37'S, 70°55'W, 2,114 m; CAS 79536, 10 (280–445 mm), taken with the holotype, CAS 77360, 3 (322–410 mm), 31°00'N, 118°06'W, 1,739 m (formerly SIO65-451); LACM 45786-1, 18 (222–456 mm), 32°40'N, 118°12'W, 1,742 m (formerly SIO65-451); USNM 325214, 16 (258–486 mm), 32°39'N, 118°11'W, 1,830 m, (formerly SIO68-676); MCZ 101240, 6 (275–460 mm), 32°41'N, 118°12'W, 1,823 m.

Diagnosis A 2-cusp multicusp on both anterior and posterior sets of cusps; six gill pouches each side (very rarely 5 or 7); body nearly cylindrical; VFF low to vestigial; rostrum rounded; color light to dark brownish-purple to nearly black; head and barbels pale.

Description Counts and proportions are given in Tables 1–7. Body nearly cylindrical, its width narrowing posteriorly; tail length about 10% of TL, its depth about 38% of its length; VFF weakly developed, often vestigial or absent. Of 205 specimens, 155 (75%), VFF ranges in height between 3 and 4 mm, and between 6 and 8 mm in only 4 specimens; CFF well developed, often thick at margin, ending over cloacal origin; head bluntly pointed, rostrum short, rounded; multicusps small, short, bulbous at bases; unicusps slender, sharp; body color variably light to dark purplish-black, rarely with pale blotches; head usually pale anteriorly; all barbels pale; VFF and CFF color of body; GA with narrow pale margins; slime pores only occasionally with pale margins. From 7 to 15 large eggs, ranging between 17×6 and 24×8 mm, occur in eight females (415–450 mm TL); all other females have small eggs. The largest number of eggs (15) occur in a female of 440 mm TL.

Etymology We name this species for our deceased friend and mentor Carl L. Hubbs, primarily for his foresight in instigating the worldwide study on hagfishes.

Distribution Known from 33°N to 34°S, at depths from about 1,100 to 2,440 m (Fig. 3). As in *M. circifrons* (discussed above), we find no significant differences in counts or proportions over this range of about 9,000 km.

Comments The sex ratio in our material is extremely unbalanced; of 150 specimens, 114 (76%) are female, 35 (23%) hermaphroditic, and 6 (0.4%) male. Although there were few large eggs (7–15), no eggs were lost since no specimens were opened prior to our examination. Bichromatism is rare; only five of 36 specimens from near Cape San Lucas, Baja California, Mexico (SIO68-60), are notably bichromatic with colors generally bluish-purple ventrally and laterally, the dorsal areas pinkish. Most bodies are pale anterior to GA, with occasional small to large bluish blotches; similar bichromatism occurs in five of nine specimens off San Diego, California.

Myxine hubbsoides new species

Holotype SIO90-143, hermaphroditic female, 826 mm TL, taken at 34°00'S, 72°14'W, 880 m, formerly MNHMC 80047).

Paratypes SIO90-141, hermaphroditic female, 702 mm TL, 34°21'S, 78°18'W, 820 m (formerly MNHMC 80043); SIO90-142, female, 651 mm TL, 34°14'S, 72°21'W, 735 m (formerly MNHMC 80044).

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; VFF vestigial or nearly so, often absent; total pores 111–116.

Description Counts and proportions are given in Tables 1–7. Body slender, cylindrical; tail length about 12% of TL, its depth about 35% of its length; VFF very low, portions intermittently absent; CFF variably well developed, ranging between thick at cloaca and around tail to thin dorsally, ending about over cloaca; rostrum broadly rounded at tip; all cusps in anterior sets bulbous at bases, those of posterior sets not bulbous; all unicusps straight or only slightly curved; body color blackish-brown with no pale areas or spots; head only slightly paler; face pale to slightly past mouth; barbels almost entirely pale; GA and slime pores with very narrow pale margins. The 702-mm paratype (SIO90–141) has 49 dark brown eggs as large as 17×5 mm, with many tiny round eggs scattered among them; the holotype has many eggs to about 11 mm, but was not opened fully for count; well-developed testicular tissue present posterior to eggs; the 651-mm paratype is spent or immature and has very few tiny eggs present.

Etymology The name *hubbsoides* refers to the similarity to *Myxine hubbsi* described above.

Distribution Known only from off central Chile between Coquimbo and Punta Topocalma (Fig. 3).

Myxine pequenoi new species.

Holotype SIO90-145, 183 mm TL, maturing female, taken at 41°29'S, 74°09'W, 185 m.

Paratype SIO90-146, 175 mm TL, mature male, taken at 40°44'S, 74°14'W, 215 m.

Diagnosis A 2-cusp multicusp on both anterior and posterior sets of cusps; total cusps 26–28; seven gill pouches each side; VFF nearly vestigial; total slime pores 81–85; a dwarfed species.

Description Counts and proportions are given in Tables 1–7. Body slender, slightly deeper than wide; tail about 12% of TL, its depth about 30% of its length; VFF very low; CFF thick at margin, thinner around tail, ending well behind a vertical from origin of cloaca; rostrum short, sharply pointed; barbels small, pale; all cusps have bulbous bases, with sharp, slender points; seven gill pouches; head and body medium brown, lighter ventrally; GA and slime pores with narrow pale margins; VFF and CFF with pale margins; holotype with 10 maturing eggs to 10×4 mm; most eggs in a single row; paratype with well-developed testes. We regard this species as dwarfed because of the advanced sexual development of these two small specimens, 175 and 183 mm TL (even smaller than *M. mccoskeri* described above).

Etymology We name this species for German Pequeño R., Instituto de Zoologia, Universidad Austral de Chile, Valdivia, for his work on the fishes of Chile and for making specimens available to us.

Distribution Known only from the type specimens taken south of Valdivia, Chile, about 41°S, 74°W (Fig. 3).

Discussion Within the genus *Myxine,* only three species have seven gill pouches (except rarely in *M. hubbsi* and *M. mcmillanae*). These three are *M. capensis* Regan, 1913, from off South Africa (22° to 25°S, 16°17°W), *M. ios* Fernholm, 1981, from southwest of Ireland (40° to 41°N, 12° to 13°W) and *M. pequenoi* (described above) from off Chile. Proportions of the three species are quite similar despite the dwarfed condition of *M. pequenoi*, but significant differences occur in certain counts. Those for *M. pequenoi* are given first followed in parentheses by those for *M. capensis* and *M. ios*. Total cusps 26–28 (36–43, 44–49); prebranchial slime pores 22–23 (26-28–28–36); total slime pores 81–88 (92–110, 103–117). Body colors are similar in all three species except that *M. ios* from near Ireland has a white head; the others do not. *Myxine paucidens* (known only from Japan) has the same number of unicusps as *M. pequenoi* (4 on anterior and 5 on posterior sets of cusps) but is distinctly different with six gill pouches, as well as having wide geographical separation.

Myxine dorsum new species

Holotype ISH 99-1971, 440 mm female, taken at 54°25'S, 59°42'W, 140-ft bottom trawl, 112 m.

Paratype SIO92-21 (formerly ZIN 722–966), 490 mm female, taken at 49°16'S, 57°02'W, bottom trawl, 630–650 m.

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches; VFF low, 2.0 mm high; CFF extending forward dorsally as a ridge beyond a vertical from cloacal origin three to four times the length of tail; total slime pores 108–113; color light pinkish-brown.

Description Counts and proportions are given in Tables 1–7. Body moderately slender, slightly deeper than wide; tail about 13% of TL, its depth 40% of its length; VFF low, 2.0 mm, mounted on a prominent fleshy narrow triangular base extending 4–7 mm from body and defined by an intermittent suture-like line below the rows of pores; a structure similar to that of *M. fernholmi* (described above) but much less strongly developed; CFF wide, thick ventrally, thin-

ning around tail and dorsally; prominent dorsal ridge extending anteriorly as a finfold to 4.3 times tail length in holotype and 3.2 times in paratype; body light pinkish-brown, the original label states "life-long color pink"; VFF and CFF pale; GA and slime pores with narrow pale margins; holotype with 9 well-developed eggs to 19×5 mm; paratype with 8 similar eggs to 18×6 mm; eggs widely and irregularly spaced; only a few paired.

Etymology The name *dorsum,* from Latin meaning "ridge," refers to the far forward extension of the CFF dorsally as a ridge to three or four times length of tail.

Distribution Southwestern Atlantic Ocean between 112 and 650 m (Fig. 3).

Discussion Although the two specimens are slightly wrinkled and hardened, the integuments cannot be stretched laterally and down far enough to eliminate the dorsal ridges. In addition, a suture-like line parallels the base of these ridges, ending at the point where downward stretching fails to eliminate them. This feature is not previously reported in species of *Myxine;* in all others, CFF extends dorsally little more than half a tail length forward of a vertical from cloacal origin.

Myxine knappi new species

Holotype SIO90-144, 565-mm female, taken at 49°16'S, 57°02'W, 24 March 1965, 630–650 m.

Paratypes SIO90-144, 2 (510,560 mm TL) taken with the holotype.

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; tail slime pores 11–14; rostrum broadly rounded; VFF nearly vestigial; color pinkish-blue, head and barbels slightly paler than body; total slime pores 116–123.

Description Counts and proportions are given in Tables 1–7. Body slender, slightly deeper than wide; tail length about 13% of TL, its depth about 33% of its length; VFF low and variably developed; in the holotype it is 2.5 to 3.5 mm high; in a paratype (510 mm TL) it is less than 1.0 mm high to about 60 mm anterior to cloaca where it increases to 3.0 mm high, continuing to cloaca; CFF prominent around tail, thickened ventrally; in the 510 mm paratype CFF extends forward of a vertical from cloacal origin about half the tail length; rostrum broadly rounded at tip; cusps robust, bluntly pointed, bases of multicusps slightly bulbous; 1–2 slime pores over GA; body color pinkish to bluish, one paratype more pink than blue; head pale to about over mouth; barbels pale; VFF entirely pale; CFF color of body, without pale margin; GA and slime pores with narrow pale margins; a label in the package containing the bluish specimen states "life-long color blue." The pinkish specimen was packaged separately with label stating "life-long color pink"; holotype with 15 large eggs to 26×7 mm; pink paratype with 12 eggs as large as 18×6 mm.

Etymology We name this species for Leslie W. Knapp, Director, Department of Fishes, Smithsonian Sorting Center, primarily for supplying us with study material.

Discussion This species and *M. dorsum* appear to be closely related, differing primarily in far forward extension of CFF in *M. dorsum;* this feature is weakly expressed in a paratype of *M. knappi* by an extension of about half the tail length.

Distribution Known only from near the Falkland Islands (Fig. 3).

Comments A discrepancy exists in recorded dates of capture. The "life-long pink" specimen has a label stating the date of capture as "March 24, 1935"; the label with the two "life-long blue" specimens (packaged separately) states "March 24, 1965." All other data, handwriting, and label paper are identical; therefore we assume the date of 1935 to be in error because we know of no Russian research vessel collecting near the Falkland Islands in 1935. Because of the poor condition of one of the paratypes, it was not possible to obtain accurate body measurements or slime pore counts; however, we were able to count the cusps.

Myxine australis Jenyns, 1842

Myxine australis Jenyns, 1842:159 (description: "colored like an earthworm but more leaden, beneath yellowish, head purplish; Tierra del Fuego").

Synonymy *Myxine acutifrons* Garman, 1899:347 (from original description: rostrum acute, resembling a barbel; color dark brown, lighter ventrally; anterior two teeth of each series confluent to bases).

Diagnosis 2-cusp multicusp on both anterior and posterior sets of cusps; six gill pouches each side; head pointed, rostrum variably acute to rounded at tip; VFF low, averaging less than 2 mm; CFF narrow; a

wide yellow ventral band extends slightly above rows of slime pores, continuing in a variably wide band to the yellow face.

Description Counts and proportions are given in Tables 1–7. Body slightly deeper than wide; tail slender, width about 33% of its length, its length 15% of TL; head narrow, pointed; tip of rostrum variably acute to rounded; a 2-cusp multicusp on both the anterior and posterior sets of cusps; VFF usually low, 0–6 mm, averaging 1.6 mm; CFF thin and wide around slender tail; body color reddish to dark brown, top of head dark; prominent yellow band ventrally extending slightly above rows of slime pores, continuing forward and widening into large blotches anterior to GA and to yellow face; large eggs range in numbers and sizes between 9 (24×8 mm) in a 330 mm female, and 16 (21×7 mm) in one of 345 mm TL.

Distribution Principally in and near the Straits of Magellan; however, three collections are from farther north (two off Argentina: 48°18'S, 65°06'W, and 50°00'S, 68°30'W, and one off Chile at 48°29'S, 78°46'W). Frequently taken with *M. affinis* (Fig. 3).

Comments The sex ratio of our material is unbalanced: of 86 specimens, 71 are female, 12 male, and 3 hermaphroditic. Although the multicusp pattern and number of gill pouches is the same as *M. affinis*, *M. australis* may be distinguished by fewer unicusps, fewer trunk and total pores, and shorter TL of mature specimens.

Myxine affinis Günther, 1870

Synonymy *Muraenoblenny olivacea* Lacépède, 1803: 6524 ("olive without spots, ventral surface whitish; no pectoral fins, no appearance of other fins; copious slime production"); presumably from the Straits of Magellan [nomen dubium].

Myxine affinis Günther, 1870, Catalog 8:511 ("Eleven rather stout teeth in each of two series, the foremost strongest and more confluent at the base than the others. Hab._____? Twelve inches long") Norman, 1937:2–8 (examination of type; 11 teeth in each series; body too dried and hardened for slime pore counts).

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; VFF variably developed; color reddish-brown to purple.

Description Counts and body proportions are given in Tables 1–7. Body slightly deeper than wide; rostrum triangular, tip rounded; barbels dark at base, pale distally; VFF yellowish , usually low, averaging 3 mm, but ranging from 0.5 to 13 mm, only 3 specimens with VFF between 8 and 13 mm; CFF wide, rarely with pale margin; tail about 15% of TL, its depth about 38% of its length; body reddish-brown to purple, head region somewhat lighter; narrow yellow band ventrally limited to below the lines of pores, often extending as intermittent patches to the yellowish face; GA and slime pores with narrow pale margins; numbers and sizes of large eggs range from 36 (20×6 mm) in a female of 550 mm TL to 17 (26×9 mm) in one of 475 mm TL.

Distribution Within or closely adjacent to the Straits of Magellan (Fig. 3).

Comments Frequently taken with *M. australis* but distinguished by higher unicusp and trunk slime pore count, as well as by generally larger eggs and a longer body. Sex ratio of our material is unbalanced; of 256 specimens sexed, 171 (67%) are female, 48 (19%) male and 37 (14%) hermaphroditic.

Myxine mcmillanae Hensley, 1991

Myxine mcmillanae Hensley, 1991:1040–1043.

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches (rarely seven) each side; color dark bluish-gray to brown; head whitish to first slime pores.

Description Counts and proportions are given in Tables 1–7. Body slightly deeper than wide; tail length 13% of TL, its depth 40% of its length; of 43 specimens two have seven pouches on the left side, one has seven on right side; VFF 3–6 mm high; body dark bluish-gray to brown; head pale to first slime pores; rostrum triangular, rounded at tip; VFF, CFF and margins of PCD, GA and slime pores pale; 7 to 11 large eggs (27–36 by 8–9 mm); the polar caps weakly developed.

Distribution Known only from the Caribbean Sea, west and southwest of Puerto Rico and from St Croix, U.S. Virgin Islands (Fig. 3).

Comment Hensley (1991) did not report on the sex of his material. The 10 specimens available to us (SI090-21) were all females. No hermaphroditism was noted.

Myxine limosa Girard, 1858

Myxine limosa Girard, 1858:223–224. (abundance: Grand Manan Isle; Bay of Fundy; 50 fm).

Synonymy *Myxine atlanticus* Regan, 1913:398 (Western North Atlantic, 44°27'N, 58°10'W; 120 fm; counts, proportions).

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; head rather pointed, rostrum triangular, bluntly pointed; color reddish-brown to dark purple; head often pale; occasional ventral blotches; VFF variably low to high; a narrow pale streak on dorsal midline usually present.

Description Counts and body proportions are given in Tables 1–7. Body slender, nearly cylindrical; tail slender, 12–17% of TL, its depth about 30% of its length; VFF low, 0–4 mm (average 1.6 mm); CFF prominent, thin, thickening dorsally; head pointed, rostrum bluntly triangular; body color varying shades of reddish-brown to blackish-purple; head only slightly pale; occasional pale blotches ventrally; VFF and CFF usually with pale margins; GA and slime pores with prominent pale margins; a narrow pale streak of variable length usually present on dorsal midline; females (368–385 mm TL) contain 12 to 20 large eggs, 17×5 to 27×8 mm; a 385 mm female contains 14 fully developed eggs, 16×6 to 17×8 mm, all linked by anchor filaments.

Distribution Between Davis Strait (66°N) and south to Florida, between 75 and 1,006 m; one specimen (383 mm TL) from Campeche Bank, Gulf of Mexico, at 24°25'N, 87°38'W.

Discussion Since its description, *M. limosa* has often been identified as *M. glutinosa* L. (1758) from the eastern North Atlantic (ENA), but we find two characters involving coloration that distinguish the two. All descriptions and our findings on ENA material indicate a grayish-pink color; in contrast, all our western North Atlantic (WNA) material is reddish-brown to blackish-purple. Girard (1858) indicated reddish to dark brown or black. In addition to the much darker coloration, most WNA specimens have a narrow pale streak along the dorsal midline extending forward from CFF an average of 46% (18–80% of TL). This pale streak is not mentioned by any author offering color descriptions of WNA material, and it is not present in ENA material available to us (180 from Skagerrak, Denmark; SIO59–50). This streak appears to result from white connective tissue binding skin to the dorsal midline in conjunction with an overlying unpigmented streak in the skin. Removal of the overlying skin and examination with the aid of strong backlighting shows this band to be present only in WNA material. Also, a difference in maximum lengths exists between mature specimens of *M. limosa* and *M. glutinosa*. Of 250 specimens of the former, the longest is 510 mm TL, and 133 exceed 400 mm, averaging 445 mm TL. Tambs-Lyche (1969:283) reported "maximum 450 mm" for ENA material. Conel (1917:78) recorded a maximum length of 79 cm from off South Harpswell, Maine, and stated that of 20 specimens, only three were between 31 and 36 cm; all others were from 50 to 79 cm. We have not seen any that large, and no further description of the 20 specimens was given.

Comments Apparently all previous authors have assumed that *M. glutinosa* occurs across the North Atlantic Ocean, but Saemundsson (1949) did not include it in his list of fishes from Iceland. However, Konstantinov and Shchegelov (1958:1745) stated "On June 16, 1956, near the eastern coast of Iceland, at the depth of 940 m, a *M. glutinosa* L., 28.5 cm long, was caught in a Sigsbee trawl." We consider these two species closely related, and have included *M.glutinosa* in all the tables for comparison with *M. limosa*.

Discussion

Owing to the absence of a fossil record, we are unable to state with certainty whether or not the new world species treated herein are monophyletic or polyphyletic. However, monophyly is assumed, based on the synapomorphic character of having all branchial ducts on either side combined into one single external opening posterior to the gill pouches. Also, monophyly of *Myxine* is supported by allozyme studies of hagfish from three continents.[1]

Relationships among these 14 species are in general somewhat obscure on the basis of body proportions and most counts. Although some means differ (Tables 1–7), considerable overlap in ranges of counts tends to mask significance. Only two species (both new) differ notably in body proportions (Table 1); all 12 others are very similar. *M. fernholmi* has a shorter prebranchial length and a correspondingly longer trunk length and shorter tail. *Myxine debueni* also has somewhat shorter prebranchial and tail lengths, but the trunk length is similar to that of other species, except for *M. fernholmi*. The few specimens available (2 to 4) in 7 of the 14 species inhibits speculation as to relationships, geographical separation notwithstanding. Most counts are similar for most

[1] Fernhom, B. Swedish Museum of Natural History, Section for Vertebrate Zoology, P.O. Box 50007, 5-110405, Stockholm, Sweden. Personal commun., May 1994.

Table 1

Body proportions (mean and range in % of TL) for new world species of *Myxine*.

	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
No. of specimens examined	572	20	4	4	2	136	3	2	2	3	131	271	43	78	143
Size range (mm)	125–650	165–286	460–540	540–846	540–570	209–522	655–820	175–183	440–490	510–565	91–394	141–659	271–473	117–501	227–387
Prebranchial length	29	31	30	22	—	26	27	—	—	27	27	28	29	28	27
	29–30	27–34	29–32	20–25	24–25	25–28	27–28	24–26	28–29	27–28	26–32	26–31	26–31	23–30	24–30
Trunk length	57	51	59	70	—	61	61	—	—	61	58	59	59	58	58
	55–58	52–56	57–60	67–72	66–69	58–65	61–62	57–59	58–60	59–62	53–60	56–62	56–61	55–62	54–62
Tail length	13	15	12	9	—	11	12	—	—	13	15	13	13	11	15
	10–15	13–17	11–14	8–10	8–10	10–12	12–12	11–12	13–13	12–13	11–19	11–15	11–14	12–17	13–17
Body width	5	4	4	4	—	4	3	—	—	4	4	4	4	4	5
	4–6	3–5	3–5	3–5	4–5	3–5	2–4	4–4	4–4	4–4	2–5	3–5	4–6	2–5	3–6
Body depths															
Including ventral finfold	7	6	6	5	—	5	4	—	—	4	6	5	6	6	7
	6–8	5–9	5–7	4–7	5–6	4–6	4–4	4–6	6–6	4–5	4–8	4–7	4–8	4–7	5–9
Excluding ventral finfold	5	5	5	5	—	5	4	—	—	4	5	5	5	7	5
	4–7	4–7	4–6	4–6	5–6	4–5	4–4	3–6	4–5	4–4	5–7	3–7	4–7	3–7	5–8
Over cloaca	5	5	4	4	—	4	4	—	—	4	5	4	5	4	5
	3–5	4–7	4–5	3–5	4–4	3–5	3–4	4–4	3–5	4–4	4–6	4–5	4–6	3–5	4–6
Tail	5	6	5	4	—	4	4	—	—	4	5	5	5	4	5
	5–6	4–7	4–5	4–6	4–4	3–5	4–4	4–5	5–6	4–5	4–7	4–6	4–6	3–6	4–6

Table 2

Numbers of prebranchial slime pores for new world species of *Myxine*.

No. of prebranchial slime pores	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
18	1					2									
19	8					4									
20	26					3									1
21	58				2	24									1
22	76	1				45		1			3			1	2
23	90	3		2		39		1						2	6
24	75	5				35					2				15
25	56	5	1	1		23					3			1	17
26	25	4		1		13					4	1	1	8	16
27	14	2				7					9	6		10	25
28	10		1			5					14	13	3	6	13
29	1										10	29	5	10	15
30	2		1				1				7	35	7	10	13
31							2		1	1	12	39	10	7	8
32	2		1						1	1	5	30	8	9	8
33	1										6	39	6	6	1
34											7	22	1	7	
35											1	19	2	5	1
36											6	16		2	1
37											3	12		2	
38											2	8		1	
39											7	9			
40											1	5		1	
41											3	3			
42											1	2			
n=	445	20	4	4	2	200	3	2	2	2	106	288	43	88	143
$\bar{x}$=	23.24	24.70				23.23					31.25	36.62	31.00	29.88	28.85

Table 3

Numbers of trunk slime pores for new world species of *Myxine*.

No. of Trunk slime pores	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
43		1													
44															
45		1													
46		2													
47		4													
48	1	2													
49	2	1													
50	2	4													2
51	5	4									1				4
52	22							1			2			1	5
53	51	1						1			5				14
54	83										4			1	17
55	86										7			4	14
56	79										7			8	20
57	51					1					14	1		10	12
58	29					2					14			6	26
59	19		1			2					9	2		10	12
60	4		1			5					13	7	1	8	9
61	3		2			5				1	8	7	5	7	3
62	1					16					4	17	4	5	3
63						21					1	20	5	3	2
64						31					3	35	5	5	
65						34			2	1		56	7	4	
66						34					1	43	5	3	
67						17					2	30	6	6	
68						13	1				3	34	2	6	
69						10						21	1	1	
70						5	1					13	2		
71						1	1					4			
72						2									
73						2						2			
74												1			
75					1										
76					1										
77												1			
78															
79												1			
80				2											
81															
82															
83				1											
84															
85															
86															
87				1											
n=	438	20	4	4	2	201	3	2	2	2	98	295	43	88	143
$\bar{x}$=	55.20	48.50				65.14					58.46	65.75	64.65	60.74	56.29

Table 4

Numbers of tail pores for new world species of *Myxine*.

No. of Tail slime pores	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
7	7		1	1	2										
8	48			2		4		1			1			1	1
9	108	1	9	1		17		1			2	7	3	3	2
10	127	5	1			59					23	29	22		16
11	116	8	1			70			2	1	34	93	15	25	22
12	33	5				40	2				22	102	3	20	47
13	2					9	1			1	5	38		25	37
14		1				1					1	11		10	16
15															2
16														4	
n=	441	20	4	4	2	200	3	2	2	2	88	280	43	88	143
$\bar{x}$=	10.00	11.05				10.78					11.06	11.67	10.50	12.26	11.50

Table 5

Total numbers of slime pores for new world species of *Myxine*.

No. of Total slime pores	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
77		1													
78															
79		2													
80	3	1													
81	2	1													
82	14	1						1							
83	19	4													
84	25	1													
85	28							1							2
86	45	1									1				
87	56	4													1
88	52	1													2
89	44	1									1			1	2
90	39	1				2					2			2	9
91	38					2									8
92	18	1				2					2			2	9
93	15										1			1	9
94	21		1			17					3			4	11
95	5		1			12					3			2	10
96	10					14					4			7	11
97	3					20					7			5	6
98	1					26					6			3	14
99						17					11	2		8	9
100	3		1			16					4	1		6	7
101						27					3	4	3	3	9
102	1					12					6	6	5	3	10
103					1	6					3	8	1	8	5
104			1		1	5					2	5	3	3	5
105						7					4	8	8	6	1
106						2					8	10	3	2	
107						4					3	15	1	1	1
108						6			1	1	3	23	5	1	2
109						2			1		1	26		2	
110										1	4	22	8	4	
111						2	1				2	24	2	1	
112											1	22	2	3	
113				1								18	2	3	
114				1			1				1	31		2	
115				1									12	4	
116							1				1	10			
117												6		2	
118											1	5		2	
119												4			
120												5			
121				1								4			
122												3			
123												1			
124												4			
n=	442	20	4	4	2	200	3	2	2	2	88	279	43	91	143
$\bar{x}$=	89.69	84.46				100.40					102.00	111.50	106.83	103.50	96.54

Table 6

Numbers of anterior and posterior unicusps for new world species of *Myxine*.

	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
No. of anterior unicusps															
4						1		2			1				1
5						2					21			2	28
6		4		2		15	1			2	92			25	184
7	1	5		2	2	115	2		1		11	31		40	11
8	5	9				65			1	1		294	7	8	
9	122	2				2						180	55		
10	269											7	27		
11	106		1												
12	11		1												
13	2		2												
n=	516	20	4	4	2	200	3	2	2	3	125	512	89	75	224
$\bar{x}$=	10.00	7.50				6.50					5.50	8.50	9.00	6.50	5.50
No. of posterior unicusps															
5						3		1			1			1	2
6				1		28		1			26			10	66
7		3		3	2	135	3			1	90	4		38	151
8	39	4				34			2	1	8	297	4	26	5
9	283	7								1		203	49		
10	175	6										8	33		
11	18		1										1		
12	1		3												
n=	516	20	4	4	2	200	3	2	2	3	125	512	87	75	224
$\bar{x}$=	10.00	8.50				6.50					6.50	8.50	9.50	6.50	6.50

Table 7

Numbers of total cusps for new world species of *Myxine*.

	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
Total cusps	*M. circifrons*	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
26								1							
27															
28								1							
29											1				2
30											6			2	3
31											9			6	7
32						3					11			10	
33						3					19			5	12
34					1	19	1		1		56			24	63
35						18					11			17	3
36			1		2	1	54	3		3	1	12			29	1
37			1		1		46					4			14	1
38			1			1	25				1	2	11		19	1
39			2				14				1		10		5	
40			1				14						68		4	
41			2				3						46		1	
42			2				1						55	3	1	
43	4												25	4		
44	9	2											34	9		
45	14	3											5	10		
46	60	4											2	9		
47	60													6		
48	107	1												3		
49	77															
50	85															
51	49															
52	30															
53	6															
54	10															
55	4															
56	1			2												
57				1												
58				1												
n=	516	20	4	4	2	200	4	2	4	3	131	256	43	137	93	
$\bar{x}$=	49.50	41.45				36.00					33.68	42.00	45.00	36.00	33.67	

species; numbers of trunk and total slime pores differ more widely, but there is frequent overlap. The total numbers of cusps (Table 7) show the greatest differences between species. The height of VFF shows considerable intraspecific variation; for example, in *Myxine circifrons* it varies between 1 and 12 mm. Both the numbers of fused cusps and the number of gill pouches are constant with only rare or aberrant variation and are extremely useful in separating the 14 species into groups. Five species have a 3-cusp multicusp on the anterior set of cusps. Of these five, *M. circifrons, M. mccoskeri,* and *M. robinsi* have 5 gill pouches and *M. fernholmi* and *M. debueni* have 6; the only new world species with 7 gill pouches is *M. pequenoi.* The remaining eight species have 6 gill pouches and a 2-cusp multicusp in both anterior and posterior sets of cusps. An additional, possibly diagnostic character is that *Myxine mccoskeri* and *M. pequenoi* mature at much smaller sizes than do the other species, and are here regarded as dwarfed. Prior to the permanent Panamanian land bridge, *M. circifrons* of the tropical Pacific, and *M. mccoskeri* and *M. robinsi* of the southern Caribbean Sea, may have represented the same species. Only these three species have five gill pouches; they also have in common the 3-cusp multicusp on the anterior row, and the anterior portions of the heads of *M. circifrons* and *M. robinsi* are notably and consistently whiter than in any of the other species. *M. mccoskeri* may have independently developed a dwarfed condition as well as a unique color pattern of reverse countershading, fewer trunk pores, and anterior unicusps. Hermaphroditism occurs frequently in all the large collections except in *Myxine circifrons.* The fact that in such a large number of hagfishes examined, only one specimen was found with fully developed filaments suggests that eggs are extruded very soon after becoming fully mature, regardless of time of year. We have found no indications of sexual dimorphism in color, body proportions, TL, or slime pore counts.

Acknowledgments

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Material examined

Myxine circifrons

SIO67-118 (51), 38°00'N, 123°31'W, 732 m; SIO64-449 (38), 32°54'N, 117°38'W, 961 m; SIO59-257 (13), 32°35'N, 117°28'W, 1,208 m; SIO74-611 (65), San Diego Trough, 1,201 m; SIO66-7 (34), 32°32'N, 117°27'W, 1,190 m; SIO68-119 (34), 32°27'N, 117°27'W, 1,244 m; SIO69-227 (15), 31°35'N, 116°05'W, 1,202 m; SIO68-118 (110), 25°37'N, 109°43'W, 1,244 m; SIO68-59 (14), 23°07'N, 109°19'W, 1,281 m; SIO68-60 (6), 23°07'N, 109°11'W, 1,830 m; SIO68-119 (25), 25°36'N, 109°45'W, 1,491 m; SIO73-290 (4), 09°48'N, 85°42'W, 994 m; SIO73-293 (3), 09°23'N, 85°00'W, 1,107 m; SIO73-294 (17), 09°24'N, 85°06'W, 900 m; SIO69-148 (7), 02°02'S, 81°10'W, 1,000 m; SIO90-26 (1), 03°15'S, 80°53'W, 960 m; SIO90-27, (1), 03°15'S, 80°55'W, 960 m; SIO90-25, (2), 04°10'S, 81°27'W, 1,860 m; MCZ 49585 (1), 33°17'S, 77°05'W, 1,510 m. Twelve specimens from IMARPE, with incomplete data, taken between 08°S and 17°S, 71° and 81°W, between 800 and 1,500 m.

Myxine hubbsi

SIO92-127 (223), 32°40'N, 118°12'W, 1,830 m; SIO65-451 (19), 32°40'N, 118°12'W, 1,742 m; SIO65-452 (82), 32°38'N, 118°08'W, 2,009 m; SIO68-676 (16), 32°39'N, 118°11'W, 1,830 m; SIO71-116 (1), 28°52'N 115°50'W, 2,004 m; SIO68-60 (37), 23°08'N, 109°16'W, 1,830 m; SIO68-61 (2), 23°06'N, 109°13'W, 2,196 m; SIO73-293 (16), 09°24'N, 85°06'W, 1,107 m; SIO83-288 (1), 09°44'N, 85°00'W, 2,181 m; SIO73-293 (1), 09°24'N, 85°00'W, 1,102 m; SIO92-114 (11), 03°41'S, 81°36'W, 2,440 m; SIO92-115 (7), 08°26'S, 80°37'W, 1,930 m; SIO72-176 (8), 21°37'S, 70°55'W, 2,114 m; MCZ-44897 (2), 34°12'S, 72°76'W, 1,475 m. Examined, but not listed, are numerous collections of few specimens each from off southern California.

Myxine australis

SIO78-39 (8), 45°36'S, 74°11'W, 120 m; SIO78-40 (80), 50°30'S, 75°20'W, 80 m; SIO78-41 (2), 54°15'S, 70°58'W, 4 m; SIO78-43 (1), 55°03'S, 68°10'W, 30 m; SIO78-44 (3), 55°49'S, 67°30'W; SIO78-45 (2), 55°10'S, 65°30'W, 146 m; SIO78-49 (3), 54°46'S, 64°03'W, 23 m; SIO78-51 (18), 54°45'S, 64°10'W, 14 m; USNM 3939 (20), 42°29'S, 78°46'W; AMNH 4098 (2), 51°10'S, 69°30'W; FURG-? (4), 48°18'S, 65°06'W; the following collections lack stated depths but were taken in the area of the Straits of Magellan: MCZ 32518 (1); MCZ 8351 (6); MCZ 3836 (16); MCZ 3836 (16);

MCZ 8837 (22); MCZ 8839 (30); MCZ 8842 (10); MCZ 24972 (19); MCZ 35198 (1); USNM 103769 (1); USNM 117329 (1); USNM 153595 (1); USNM 267750 (1); AMNH 4098 (2); SU 22678 (1); IU 2124 (1); IU 4293 (1).

Myxine affinis

SIO78-39 (8), 45°36'S, 74°11'W, 120 m; SIO78-40 (39), Isla Madre de Dios, Chile, 80 m; SIO78-41 (62), 54°14'S, 70°06'W, 4 m; SIO78-42 (7), 54°52'S, 70°58'W, 60 m; SIO78-43 (21), 55°03'S, 68°10'W, 30 m; SIO 78-44 (15), 54°45'S, 64°09'W; SIO78-45 (4) Bahia Windhond, Chile, 146 m; SIO78-50 (3), 54°54'S, 64°10'W, 14 m; SIO78-51 (31), 54°45'S, 64°10'W, 14 m; SIO83-121 (2), 54°22'S, 71°22'W. The following collections lack stated depths and coordinates but were taken in the area of the Straits of Magellan: MCZ 35198 (12); MCZ 8836 (3); MCZ 8837 (7); MCZ 8839 (1); MCZ 8840 (6); MCZ 8841 (11); MCZ 24972 (1); USNM 77377 (1);USNM 26715 (1); USNM 39039 (2); USNM 39140 (1); USNM 17418 (1); FMNH 9820 (3); SU 22678 (1).

Myxine limosa

SIO74-181 (28), 36°43.2'N, 74°38'W, 300 m; SIO74-185 (3), 37°05'N, 74°39'W, 280-360 m; SIO74-187 (4), 36°36'N, 79°42'W, 316 m; SIO74-188 (1), 38°18'N, 73°35'W, 215-250 m; SIO74-189 (4), 37°27'N, 74°30'W, 120-320 m; SIO74-190 (5), 36°19'N, 74°47'W, 310-400 m; SIO75-677 (5), 41°54'N, 69°50'W, 75 m; SIO75-678 (1), 41°53'N, 68°07'W, 183 m; SIO75-679 (2), 49°09'N, 66°56'W; SIO75-680 (5), 42°30'N, 66°04'W; SIO75-681 (3), 43°02'N, 64°32'W; SIO75-682 (1), 42°33'N,66°58'W, 293 m; SIO75-683 (6), 42°26'N, 68°44'W; SIO75-684 (1), 42°30'N, 69°20'W; SIO75-685 (2), 42°31'N, 69°42'W, 275 m; SIO75-686 (4), 42°33'N, 69°48'W, 275 m; SIO75-689 (3), 37°05'N, 74°40'W, 280-360 m; SIO77-101 (1), 39°35'N, 72°04'W, 201 m; SIO77-102 (1), 39°32'N, 72°22'W, 375-512 m; SIO77-103 (1), 41°32'N, 68°29'W, 86 m; SIO77-104 (1), 41°51'N, 68°05'W, 88 m; SIO77-105 (3), 39°12'N, 72°29'W, 302 m; SIO77-106 (1), 39°05'N, 72°43'W, 234 m; SIO77-107 (4), 38°30'N, 73°19'W, 220 m; SIO77-108 (1), 37°28'N, 74°24'W, 191 m; SIO77-119 (2), 37°54'N, 74°00'W, 261 m; ISH6-1965 (1), 45°06'N, 54°46'W; ISH42-1970 (1), 40°25'N, 68°10'W, 220-230 m; ISH-1987 (3), 66°38.6'N, 56°38.2'W, 540 m; ISH-7238-1982 (2), 66°04'N, 56°13.9'W, 323 m; ISH63-1987 (1), 63°05'N, 52°13'W, 127-155 m; ISH431-1986 (1), 57°38'N, 18°13'W, 1,006 m; ISH5-1965 (1), 45°06'N, 54°48'W, 180-260 m; ISH2-1970 (1), 45°00'N, 54°47'W, 175 m; ISH23-1961 (33), 44°19'N, 54°27'W, 175 m; ISH42-1970 (1), 40°25'N, 68°10'W, 230 m; ISH3653-1979 (1), 33°45.8'N, 76°05.6'W, 608 m.

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Abstract.—Growth of the blacklip abalone, *Haliotis rubra*, was estimated from 1,464 individuals that were tagged and left at large for up to five years at seven sites in New South Wales, Australia. Both the shape of the fitted growth curves and the average growth rates differed significantly among sites, separated by only 1–20 km. There was also significant variation in the growth of individual abalone within sites and this variation differed among sites. Abalone at sites where they grew quickly reached larger lengths and were morphologically different from those at sites where they grew slowly. For example, the shells of abalone from sites where they grew slowly were wider and heavier at a given length than those from sites where they grew quickly. The implication that rates of growth in width are less variable than growth in length suggests that a minimum legal width limit may be more appropriate than the present size limit that is based on length. A minimum legal width limit would redistribute fishing effort away from sites where abalone grow in length quickly towards sites where they grow slowly, including sites which are presently unfished because few individuals reach the minimum legal length. If this were possible, it would reduce the differences in exploitation among sites which, at present, have the potential to seriously deplete populations at sites where individuals grow quickly.

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Covariation between growth and morphology suggests alternative size limits for the blacklip abalone, *Haliotis rubra*, in New South Wales, Australia

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Legal restrictions on the minimum size of individuals allowed to be harvested are used to manage many fisheries. The theory behind their use asserts that by delaying the harvest of individuals until they have grown to a certain size, both yield and egg production can be increased (Beverton and Holt, 1957). Appropriate minimum size limits have traditionally been estimated by considering average rates of growth, mortality, and reproduction (Goodyear, 1993). Spatial variation in demography can complicate the use of a single size limit for a stock by making different size limits appropriate in different areas. Enforcement of different size limits over large spatial scales is possible (e.g. Guzmán del Próo, 1992), but if demography varies over small distances, appropriate size limits are difficult to enforce.

A common finding of studies on the growth of abalone has been that individuals at different sites can grow at markedly different rates (Sainsbury, 1982; Breen, 1986; Tegner et al., 1989). Despite this, there have been few systematic attempts to determine the spatial scale over which differences in growth occur (see Day and Fleming, 1992, for a review). Nonetheless, it is apparent that growth can vary among regions separated by hundreds of kilometers (Nash, 1992) and among sites separated by tens of kilometers (Breen, 1986). As well as differing in their rate of growth, abalone that grow quickly will, in general, reach larger sizes than abalone that grow slowly (e.g. McShane, 1992; Nash, 1992). Consequently, many abalone fisheries contain populations with individuals that grow very slowly to only small sizes (Sloan and Breen, 1988; Tegner et al., 1989; Nash, 1992). Because minimum legal sizes are, in general, enforced over areas larger than those over which such variation in growth can occur, these sites often remain unfished.

Commercial fishing of abalone *Haliotis rubra* in New South Wales (NSW), Australia began in the early 1960's. Initially, divers harvested abalone of any size, but in 1973 a minimum legal length limit of 100 mm was introduced. This length limit was chosen to ensure that abalone recruiting to the fishery had reproduced at least once after reaching sexual maturity at approximately 80–90 mm. As fishing pressure increased through the 1970's and 1980's, it became apparent that the length limit of 100 mm

was not conserving enough egg production (Hamer, 1983). In response, the minimum legal length limit was increased in a series of increments from 100 mm in 1979 to 115 mm in 1987. An unfortunate consequence of these increases was the concentration of fishing effort at sites where abalone grew quickly and to large sizes (see also McShane, 1992). Because of this high level of effort and the limited dispersal of larval abalone (Prince et al., 1987), such sites were often overexploited, whereas in other areas where abalone grew more slowly to smaller sizes the populations were underexploited.

In this study, we describe a tagging study of variation in the growth of *Haliotis rubra* at seven sites along the NSW coast. These sites were grouped into four locations encompassing most of the geographical range of the fishery. This provides an indication of the variability in growth of the species at three spatial scales: among locations separated by hundreds of km, among sites separated by 1–20 km, and among individual abalone within the sites. In addition we describe morphological differences among the abalone that appear to be related to their rate of growth. This link between growth and morphology suggests that a minimum legal width limit may be more appropriate than the present size limit based on length.

Materials and methods

Sites and tags used

Abalone were tagged at seven sites, spanning almost 1,000 km of coastline, that were chosen because they were commonly used by commercial divers in the NSW abalone fishery (Fig. 1). Six of the sites were grouped into three locations (Broughton Island, Sydney, and Eden) each with two sites (referred to as I and II) separated by between 1 and 20 km. The single site at Merrys Beach was approximately midway between those at Sydney and Eden (Fig. 1). Supplementary tagging was also done at Bittangabee Bay near Eden (Fig. 1). This site was not commonly used by commercial fishermen because few individuals reached lengths above the 115-mm minimum legal limit. Estimates of growth parameters for Bittangabee Bay were not calculated separately because only 20 individuals were recaptured. These abalone were, however, used in the estimation of a growth curve for all recaptured individuals and in the relationship among morphological variables (see below).

Small (≈2 × 10 mm), numbered plastic tags were attached to abalone with a cyano-acrylate glue between 20 May 1975 and 3 October 1981. This procedure required that abalone be removed from the water and their shells dried with compressed air before tagging. Individuals were chosen to make the size range at tagging representative of the population at each site. The maximum diameter (i.e. length) of each shell was measured to the nearest 0.5 mm, and the abalone were then replaced in the area near where they were collected. Samples of these tagged abalone were recaptured at opportunistic times between 11 December 1975 and 18 May 1982.

Patterns in growth

Estimates of growth were obtained by using procedures based on a mark-recapture analogue of Schnute's (1981) general growth model (see Francis, in press). Schnute's model relates size to age by several parameters, including two (a and b) which combine to describe a range of traditional growth curves including the von Bertalanffy ($a > 0, b = 1$), Richards

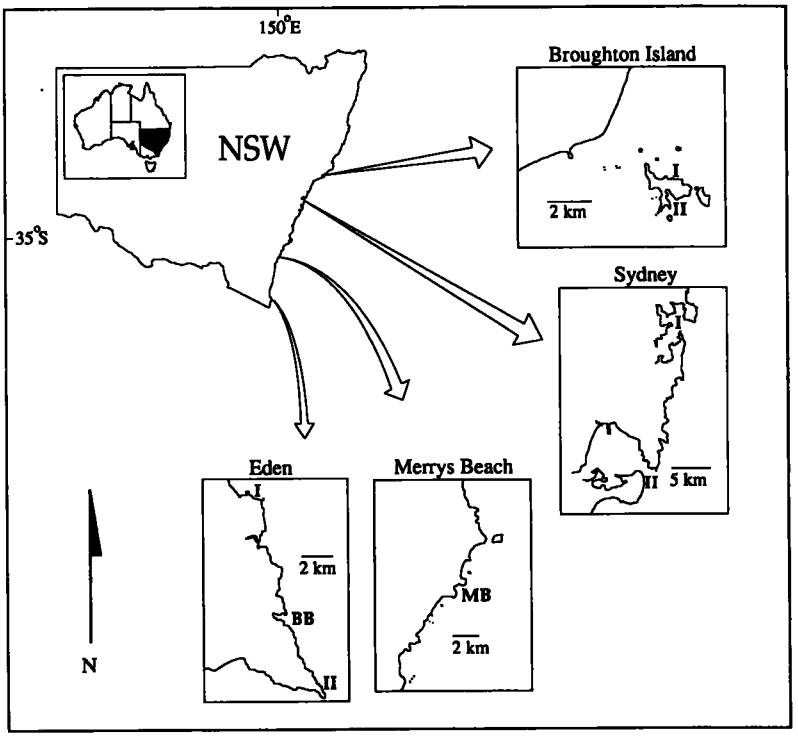

Figure 1

Map of Australia (inset) and New South Wales (NSW), showing the position of eight sites within four locations where blacklip abalone, *Haliotis rubra*, were tagged. Sites I and II within each location are as indicated on the maps; BB = Bittangabee Bay, MB = Merrys Beach.

($a > 0$, $b < 0$), logistic ($a > 0$, $b = -1$), and Gompertz ($a > 0$, $b = 0$) models (Schnute, 1981). Francis (in press) reparameterized this model to express observed increments in length during tagging (ΔY) as a function of the observed length at tagging (Y_t) and time at liberty (Δt). The model can be reparameterized further, so that growth can be described in terms of average annual growth for individuals of a given size (see Francis, 1988a). The general model where both $a \neq 0$ and $b \neq 0$, was

$$\Delta Y = -Y_t + \left[Y_t^b e^{-a\Delta t} + c(1 - e^{-a\Delta t})\right]^{\frac{1}{b}},$$

where $$a = \ln\left[\frac{y_2^b - y_1^b}{\lambda_2^b - \lambda_1^b}\right],$$

$$c = \frac{y_2^b \lambda_1^b - y_1^b \lambda_2^b}{\lambda_1^b - y_1^b + y_2^b - \lambda_2^b}, \text{ and}$$

$$\lambda_1 = y_1 + g_1 \text{ and } \lambda_2 = y_2 + g_2.$$

The model was fitted to the observed increments by using maximum likelihood (Francis, 1988b). Parameters estimated during this process include the mean annual growth rates (g_1 and g_2) at two sizes (y_1 and y_2) and the parameter b. These parameters together combine to define the parameter a, and hence the shape of the fitted growth curve.

Several other parameters were also considered, and were included in the model if they significantly improved the fit (see Francis, 1988b). Two parameters describing seasonal variation in growth were examined by replacing Δt above with $\Delta t + (\phi_{t_r} - \phi_{t_t})$ where for any time (t_i)

$$\phi_{t_i} = \frac{u(\sin(2\pi[t_i - w]))}{2\pi}$$

and t_t and t_r are the times at tagging and recapture. The parameters u and w then describe the amplitude and phase of seasonality in growth, respectively. A parameter describing variation in growth among individuals was also examined, where the mean (μ_g) and standard deviation (σ_g) of the expected increment in length were related by

$$\sigma_g = v\mu_g,$$

where v is the coefficient of variation in growth. A parameter describing contamination by outliers was also examined, but it never added significantly to the model (see Francis 1988b).

The error model used considered errors due to variation in growth and measurement by

$$\Delta Y_{obs} = \Delta Y \varepsilon_g + \varepsilon_m,$$

where the observed increment in length (ΔY_{obs}) was a function of that predicted by the growth model (ΔY) and errors due to variation in growth (ε_g) and measurement (ε_m), assuming $\varepsilon_g \sim N(1, \sigma_g)$ and $\varepsilon_m \sim N(\mu_m, \sigma_m)$. As such, μ_m represents measurement bias (i.e. consistent difference in measurement between marking and recapture) and σ_m represents random error in measurement. Since better estimates of the growth parameters can be achieved when both μ_m and σ_m are known (Francis, in press), they were estimated by repeatedly measuring the same set of shells (n=50) after the tagging program had finished. Measurement bias was disregarded (μ_m=0) because the same people used identical techniques to measure abalone at tagging and recapture. Random errors in measurement among replicate readings and among readers were similar in size, and as a consequence σ_m was set to 0.65 for all analyses. Following fitting of the model, plots of residuals against length at tagging and time at liberty were investigated for any systematic lack of fit.

The parameters y_1 and y_2 should be chosen to span the lengths at tagging and to enable reliable estimates of g_1 and g_2 (Francis, 1988b). Because of differences in the length of abalone tagged among the sites, appropriate sizes for y_1 and y_2 also differed among sites. To facilitate comparison, y_1 and y_2 for each site were chosen from three standard lengths: 65, 90, and 115 mm. At sites where few small abalone were tagged, annual growth rates were estimated at 90 and 115 mm. Alternatively, at sites where few large abalone were tagged, annual growth rates were estimated at 65 and 90 mm. Once fitting of the model was completed, the annual growth rate at the third standard length was also calculated. This growth rate is defined by the parameters chosen during fitting of the model. Comparisons among estimated parameters were made by using t-tests.

To facilitate the comparison of our estimates of growth with those previously published, we also fitted the traditional von Bertalanffy growth model. This was done within the framework described above (see Francis, 1988b). To further aid the comparison of growth rates among studies, we converted the traditional von Bertalanffy parameters estimated from tagging data (k and L_∞) to parameters describing estimates of annual growth at the standard sizes used in this study. This was also done for previously pub-

lished estimates of growth derived from tagging studies in which similar tagging methods were used.

Relation of growth to morphology

The shells of 390 recaptured abalone were retained for further measurement. This allowed us to relate present morphology of the shells to past growth rates. Few shells were retained from Broughton Island I or Eden I because the abalone were used in separate experiments to estimate fishing mortality. Measurements taken included the maximum and minimum diameters (length and width), the width of the ventral ridge of the shell at the aboral margin (ridge), and the dry weight of the shell. Relationships among these variables were investigated by correlation. To relate present morphology to past growth, the length of all shells was related to their width, weight (log transformed), and ridge by using multiple linear regression. The residuals from this relationship then indicate whether a shell is longer or shorter than expected given the other morphological variables. In a similar way, all the tagging data were combined into one growth model. The residuals from this growth model then indicate whether an abalone has grown faster or slower than expected. By averaging the residuals from the morphological relationship and the growth curve across all individuals at a site, any relationship between rates of growth and shell morphology among sites should be apparent.

Results

A total of 1,464 abalone were recovered from the seven sites. At tagging, these individuals ranged in size from 15 to 152 mm, with a mean size of 91.1 mm (SE=0.7). The size of recaptured abalone at tagging differed among sites. Few of the individuals recaptured at Broughton Island II and Eden I were small when tagged (Fig. 2A). In contrast, few large abalone were recaptured from Merrys Beach, both sites in Sydney, and from Eden II.

Tagged abalone were at large for a period between 8 and 1,736 days, although most (98%) of the individuals were recaptured within two years of release. The range of times between tagging and recapture of abalone differed among sites (Fig. 2B). There were generally shorter times between tagging and recapture in Broughton Island I and Sydney I, and longer times at Merrys Beach (Fig. 2B). During the tagging period increments in size ranged from –8 mm to 84 mm, with an average of 11.8 mm (SE=0.4). Negative growth may have been caused by erosion of the shell.

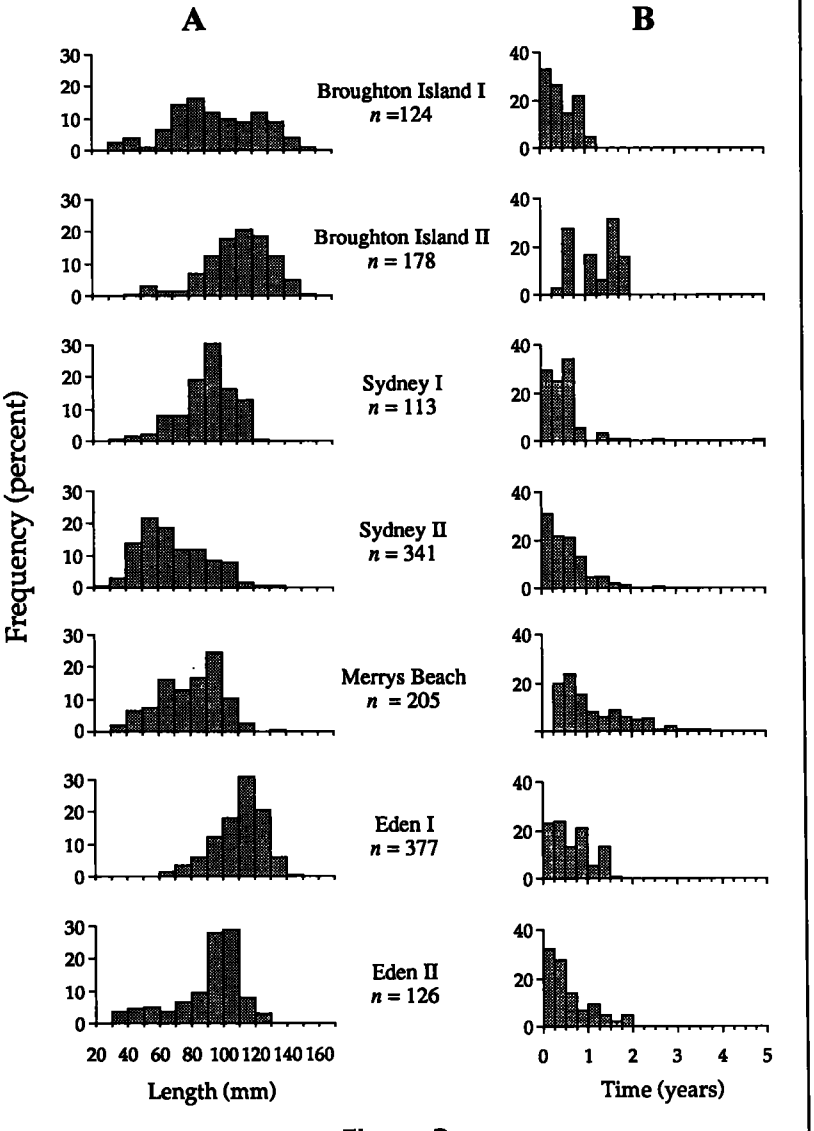

Figure 2

Distribution of (A) length at marking (Y_t) and (B) time at liberty (Δt) for recaptured blacklip abalone, *Haliotis rubra*, at seven sites.

Patterns in growth

The shape of the fitted growth curve differed significantly among sites (t-tests, $P<0.05$; Table 1). At Broughton Island I and Sydney I, the fitted growth curve was similar to a traditional von Bertalanffy shape ($a > 0$, $b \approx 1$ in Table 1), whereas at Eden II it was more similar to a Gompertz shape ($a > 0$, $b \approx 0$ in Table 1), and at Merrys Beach more similar to a logistic shape ($a > 0$, $b \approx -1$ in Table 1). All curves were asymptotic and expected growth approached zero (Fig. 3B). The size at which expected growth equalled zero differed among sites and ranged from 118 mm at Merrys Beach to 151 mm at Broughton Island II (Fig. 3B; Table 1).

Estimates of average annual growth rates differed significantly among the seven sites (Table 1). Abalone at the two sites on Broughton Island had faster rates of growth than all other sites. At Broughton Island II a 65-mm abalone was expected to grow to the 115-mm length limit in approximately 18 months (Fig. 3A). Above 115 mm, growth declined rapidly so that in the next year expected growth was less than 10 mm. The rate of decline in growth rate then slowed, and growth was expected to continue until 151 mm (Fig. 3; Table 1). In contrast, growth at Sydney I was much slower; a 65-mm individual was expected to take almost 9 years to grow to 115 mm (Fig. 3A). Growth rate declined at an approximately constant rate throughout life (i.e. approximating a von Bertalanffy growth curve) until individuals were expected to have no growth at 126 mm (Fig. 3; Table 1). At Merrys Beach, abalone were expected to grow from 65 mm to 90 mm within a year, but then growth declined rapidly and individuals were expected to grow only just above the minimum length limit of 115 mm (Fig. 3A). Growth rates at Sydney II and Eden II were not significantly different at any of the standard sizes (Table 1).

There was significant variation in growth among individual abalone within all sites (Table 1). Variation in growth among abalone at Merrys Beach was significantly less than that at all other sites and significantly greater at Broughton Island II, Sydney I, and Eden I (t-tests, $P<0.05$). The standard deviation of the observed growth increment ranged from 0.29 times the expected increment at Merrys Beach to 0.87 times the expected increment at Eden I (Table 1). This range implies that two-thirds of the abalone at Merrys Beach will grow between 0.71 and 1.29 times the expected increment, whereas at Eden I, two-thirds of the abalone will grow between 0.13 and 1.87 times the expected increment (Fig. 4).

Parameters representing seasonal variation in rates of growth significantly improved the fit of the model at three of the seven sites (Table 1). At Broughton Island II, peak growth rates occurred during late October at 1.9 times the minimum growth rate in late April. In contrast, peak growth rates at both Sydney II and Eden I occurred in December at a rate 2.0 and 2.9 times the minimum, respectively

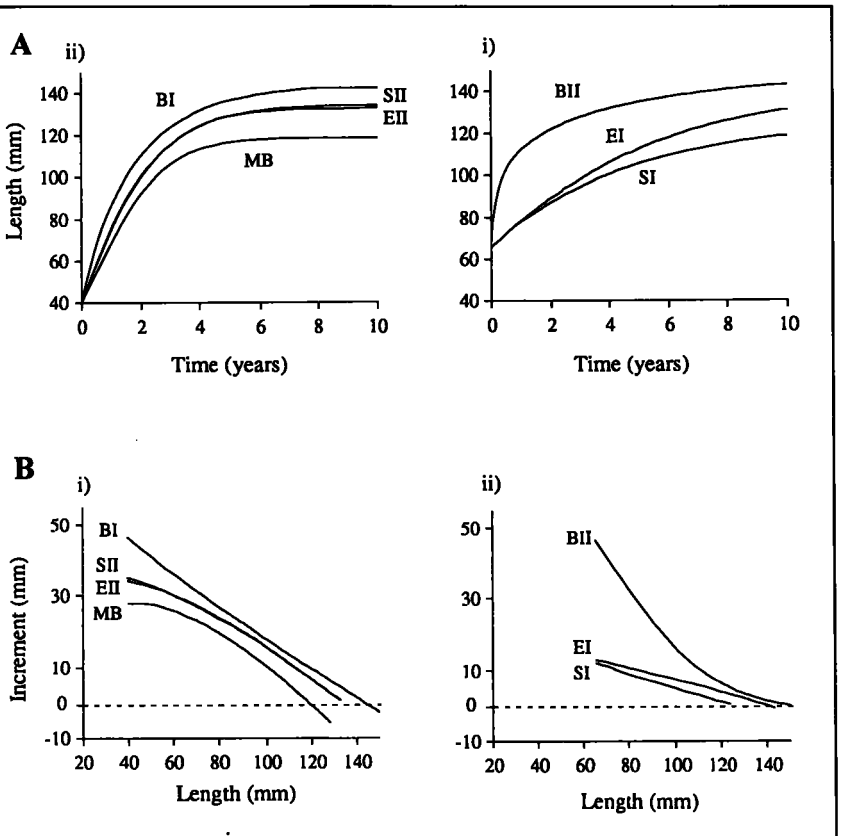

Figure 3

Predicted mean growth of blacklip abalone, *Haliotis rubra*; (**A**) over 10 years for individuals of a given size and (**B**) over 1 year for individuals of a range of sizes. Growth is shown from (i) 40 mm at sites where many small abalone were tagged and (ii) 65 mm at sites where few small abalone were tagged up to the size of the largest abalone. Sites are abbreviated as follows: BI and BII = Broughton Island I and II; SI and SII = Sydney I and II; MB = Merrys Beach; EI and EII = Eden I and II.

Table 1

Estimates of growth parameters and their standard errors (in brackets) for blacklip abalone, *Haliotis rubra*, from tag returns at seven sites. Parameters estimated during fitting are shown in light type; those defined by the fitted parameters are shown in bold. Expected annual growth rate at 65, 90, and 115 mm is shown as g_{65}, g_{90} and g_{115}, respectively. See Materials and Methods section for a description of other parameters. Blanks occur where parameters did not add significantly to the fitted model.

	Site						
	Broughton Island		Sydney			Eden	
Parameter	I	II	I	II	Merrys Beach	I	II
Curve shape parameters							
b	1.33 (0.30)	7.58 (1.13)	1.33 (0.41)	0.25 (0.09)	–0.74 (0.12)	0.50 (0.37)	0.04 (0.10)
a	**0.59 (0.13)**	**0.11 (0.05)**	**0.20 (0.06)**	**0.66 (0.08)**	**0.89 (0.08)**	**0.22 (0.04)**	**0.71 (0.14)**
Growth rate parameters							
g_{65} (mm·year^{-1})	**33.68 (1.52)**	46.93 (2.78)	12.25 (0.77)	28.66 (0.78)	24.63 (0.60)	**12.71 (0.92)**	28.80 (0.96)
g_{90} (mm·year^{-1})	22.24 (0.95)	24.11 (1.39)	6.91 (0.52)	19.58 (0.67)	15.22 (0.34)	9.14 (0.49)	19.87 (0.69)
g_{115} (mm·year^{-1})	11.52 (0.62)	8.36 (0.62)	**2.06 (0.91)**	**8.87 (0.77)**	**2.21 (0.42)**	4.86 (0.28)	**8.85 (1.40)**
Seasonal parameters							
u (year)		0.31 (0.08)		0.48 (0.05)		0.33 (0.07)	
w (year)		–0.19 (0.01)		0.00 (0.01)		–0.01 (0.03)	
Growth variability parameter							
v	0.54 (0.04)	0.73 (0.05)	0.76 (0.06)	0.48 (0.02)	0.29 (0.01)	0.87 (0.05)	0.39 (0.02)
Asymptote (mm)	143	151	126	133	118	140	133
Largest abalone (mm)	151	152	124	132	130	143	129
n	124	178	113	341	205	377	126

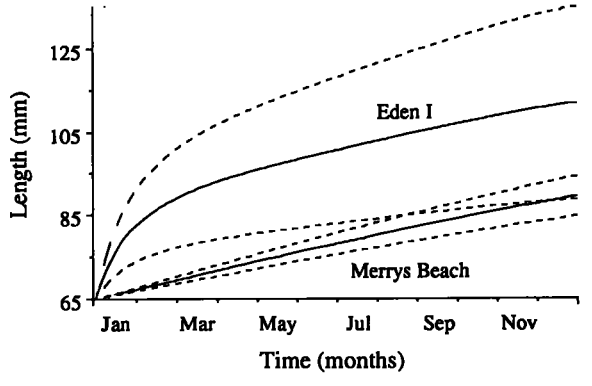

Figure 4

Predicted mean growth (solid line) and 50% confidence intervals (dashed line) of 65-mm blacklip abalone, *Haliotis rubra*, over one calender year at two sites.

(Fig. 4). At Broughton Island I, Sydney I, Merrys Beach, and Eden II there was no evidence of any significant seasonal variation in growth rates (Table 1).

Relation of growth to morphology

There were differences in the morphology of abalone among sites. For example, the shells of abalone recaptured from Merrys Beach were, on average, wider, heavier, and had a larger ridge than individuals of the same length from Sydney II (Fig. 5). There was a significant difference among sites in the slope of each of the relationships (*t*-tests, $P<0.05$), suggesting that the difference in morphology of individuals among sites changed with length. The shell of a 100-mm abalone from Merrys Beach was, on average, approximately 5 mm wider, 8.3 g heavier, and had a 1.7 mm larger ridge than the shell of a 100-mm abalone from Sydney II (Fig. 5). Differences in the width and ridge of shells among the sites increased with length, whereas differences in the weight of shells decreased with length (Fig. 5). The width, weight, and ridge of all shells were each significantly correlated with the other variables (width vs. weight $r=0.76$; width vs. ridge $r=0.58$; weight vs. ridge $r=0.68$; $n=390$ for all correlations).

Abalone from sites where their average growth was faster were morphologically different from those

where their average growth was slower (Fig. 6). The residuals of the general growth model were significantly higher at sites such as those at Broughton Island, Sydney II, and Eden II than at Eden I, which was, in turn, significantly higher than Merrys Beach and Sydney I, or Bittangabee Bay (*t*-tests, $P<0.05$; Fig. 6). This ranking corresponds closely with the estimates of average growth rates in Table 1. The residuals of the relation between length and the independent variables width, weight, and ridge were generally higher at sites where growth was also high (Fig. 6). That is, given their width, weight, and ridge, abalone at sites where they grew quickly were longer than those where they grew slowly. Alternatively, shells of abalone of a given length at sites where they grew quickly were thinner, lighter, and had a smaller ridge than those at sites where they grew slowly.

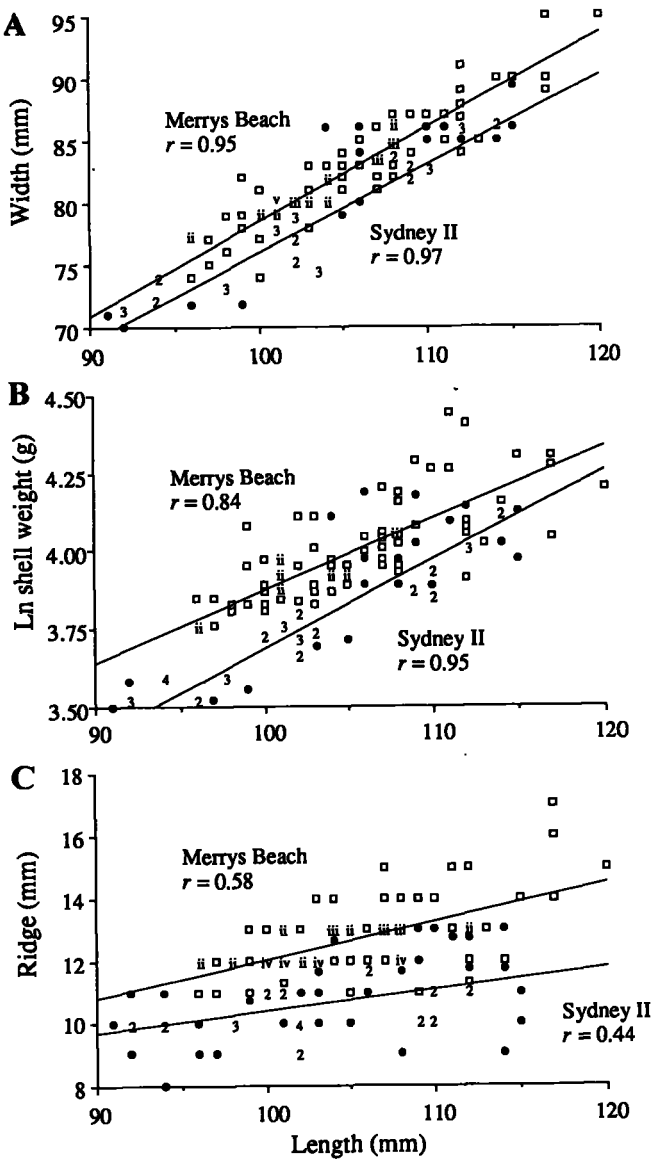

Figure 5

Relationshjp between shell length and (**A**) shell width, (**B**) shell weight, and (**C**) shell ridge for blacklip abalone, *Haliotis rubra*, recaptured from two sites. Filled circles and arabic numerals denote abalone from Sydney II, and open squares and roman numerals denote abalone from Merrys Beach. Numerals denote the number of coincident points, and the lines were fitted by least-squares.

Discussion

Patterns in growth

The intense spatial variation in growth that we observed for *Haliotis rubra* in NSW appears to be characteristic of abalone populations worldwide (Day and Fleming, 1992). At the smallest spatial scale, there was significant variation in the growth rate of abalone within sites. At a larger scale, both average rates of growth and the magnitude of within-site variation differed among sites separated by only 1–20 km. Perhaps the most likely explanation for variation in growth over these smaller spatial scales involves variation in the supply of food, related to local habitat and hydrographic conditions (Day and Fleming, 1992). At the largest spatial scale, average growth rates at the two sites on Broughton Island were significantly higher than all others. Broughton Island is approximately 300 km farther north than any of the other sites, and abalone around the island are likely to be exposed to higher water temperatures than abalone farther south. Water temperature is known to affect the growth rate of abalone (Day and Fleming, 1992), but the trend in NSW stands in contrast to that found for *H. rubra* in Tasmania, where abalone grow more slowly in the warmer, northern areas (Nash, 1992).

Several previous studies have found a relation between the rate of growth and maximum size of abalone at a site (Shepherd and Hearn, 1983; McShane et al., 1988; Sloan and Breen, 1988; Nash, 1992). In general, abalone at sites where they grow quickly reach larger sizes than those at sites where they grow slowly. A similar situation appears to exist in NSW where abalone from the two sites on Broughton Island had the fastest average growth rates and reached the largest shell lengths (i.e. >150 mm, Table 1). In comparison, the slowest average growth rates

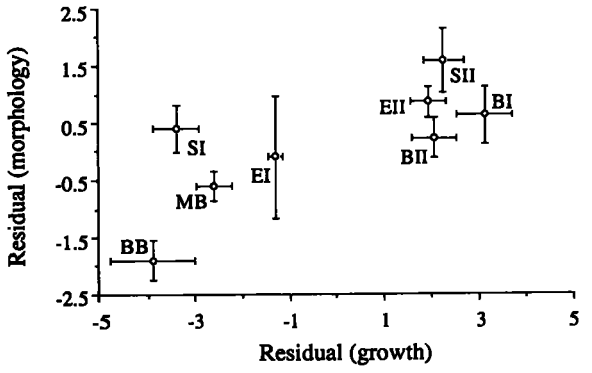

Figure 6

Average residual from growth and morphological relationships for blacklip abalone, *Haliotis rubra*, recaptured from eight sites. Vertical and horizontal bars are standard errors. Sites are abbrieviated as follows: BI and BII = Broughton Island I and II; SI and SII = Sydney I and II; MB = Merrys Beach; EI and EII = Eden I and II; BB = Bittangabee Bay.

were recorded at Sydney I where the largest abalone was smaller than those at all other sites (i.e. 124 mm, Table 1). Despite this general relationship, slow rates of growth were recorded at Eden I, but growth was expected to continue until 140 mm, and many abalone were found over 130 mm in length.

Direct comparison of growth rates estimated by different studies are complicated by the variety of methods used for tagging and analysis. For example, tags attached by wire through an abalone's respiratory pore can affect growth (McShane et al., 1988), and growth parameters estimated from tagging and age-length data need to be interpreted differently (Francis, 1988a). Any comparison of growth rates among studies can also be confounded by the growth model used to fit the observed increments (e.g. compare estimates of growth from the different models used in Tables 1 and 2). When fitted with a similar growth model to past studies, our estimates of the growth of abalone in NSW span almost the entire range of those from similar studies in other states of Australia (Table 2). In addition, estimates of growth at the two sites on Broughton Island are consistently higher than any previously reported natural growth rates for the species.

Relation of growth to morphology

Differences in the morphology of individuals among populations have been reported for a range of gastropod species including abalone (see review by Vermeij, 1980). Despite the significance of variation in the morphology of *Haliotis rubra* in NSW, differences among sites were not large (e.g. compare with those of Breen and Adkins, 1982). There was also substantial variation in the morphology of individuals within sites. Despite little evidence, explanations for the variation in morphology of abalone usually concentrate on environmental rather than on genetic factors (McShane et al., 1988). As for other gastropods, it is likely that all aspects of shell growth that result in morphological differences are influenced by a variety of factors including exposure to wave action, diet, and water temperature (Tissot, 1992; Belda et al., 1993). Although we only present evidence to suggest that differences in morphology of the shell exist among populations of *Haliotis rubra*, there is also evidence for related morphological variation in the soft tissues (McShane et al., 1988).

Differences in the morphology of *Haliotis rubra* among sites were related to differences in growth. At sites where they grew slowly, the shells of abalone were wider, heavier, and had a broader ridge than those at sites where they grew quickly. These observations are similar to those made on other species of abalone (e.g. Breen and Adkins, 1982; Shepherd and Hearn, 1983; Tissot, 1988) and perhaps are not surprising considering that the processes proposed to influence both growth and morphology are similar. Inclusion of the slow-growing population at Bittangabee Bay strengthened the relation between growth and morphology that was evident among the seven sites where extensive tagging was done. Extensive tagging was not done at Bittangabee Bay because few animals grow above the present 115-mm legal length limit and hence the site is rarely fished by commercial divers. Because of the relationship between the maximum size reached by abalone at a site and their growth rate, very slow growing sites are rarely visited by commercial divers and, consequently, were not chosen for tagging in this study. As a result, our estimates of growth represent the higher end of the range of growth rates for abalone in NSW.

The increased width and weight of shells from abalone that grew slowly in length imply that rates of shell growth in width and weight are more consistent among sites than growth in length. This might be explained by increased synthesis of the organic matrix of the shell when energy is plentiful (Palmer, 1992) and can be devoted to expansion of the mantle at the growing edge and hence to rapid growth in length (Belda et al., 1993). Alternatively, when less energy is available, reduced synthesis of the organic matrix may result in a slower expansion of the growing edge of the mantle, causing slower growth in length and proportionally more growth in width and weight (Vermeij, 1980). Such an explanation would

not require any variation in the rate of incorporation of calcium-carbonate, which may continue regardless of the rate of synthesis of the organic matrix (see similar arguments for fish otoliths in Gauldie and Radtke, 1990). Because calcium-carbonate dominates a shell by weight (Palmer, 1992), if the rate of incorporation of calcium-carbonate was similar among different populations, the total weight of the shell might be a reliable indicator of the age of the abalone (see the literature on use of the weight of otoliths to age fish, e.g. Worthington et al., in press). The ability to age abalone is obviously desirable, but much doubt exists about present techniques of ageing, particularly for *Haliotis rubra* (McShane and Smith, 1992). This uncertainty emphasizes the need to investigate alternative methods to age abalone, one of which may be shell weight (Worthington et al., unpubl. data).

Table 2

Comparison of estimates of growth for blacklip abalone, *Haliotis rubra*. Note the estimated growth of abalone below 80 mm from Prince et al. (1988) was determined by analysis of size-frequency distributions; all other estimates were derived from tags glued to the external surface of the shell. Expected annual growth rate at 65, 90, and 115 mm is shown as g_{65}, g_{90}, and g_{115}, respectively.

Study and location	g_{65}	g_{90}	g_{115}	L_∞	k
	(mm·year^{-1})			(mm)	(year^{-1})
Shepherd and Hearn, 1983					
South Australia	21.3	14.1	6.9	139	0.34
	21.3	14.4	7.6	143	0.32
	26.4	18.0	9.7	144	0.41
McShane et al., 1988					
Victoria	13.1	6.8	0.5	117	0.29
	16.5	9.2	1.8	121	0.35
	16.1	10.2	4.3	133	0.27
Prince et al., 1988					
Tasmania	21.0	12.6	6.3	140	0.29
McShane and Smith, 1992					
Victoria	26.9	19.2	11.5	152	0.37
	16.5	9.2	1.8	121	0.35
	7.8	4.3	0.8	121	0.15
This study, NSW					
Broughton Island					
I	38.0	25.7	13.3	142	0.68
II	28.0	19.8	11.5	150	0.40
Sydney					
I	16.3	9.3	2.3	123	0.33
II	32.1	21.1	10.1	138	0.58
Merrys Beach	22.6	11.7	0.9	117	0.57
Eden					
I	18.0	12.1	6.2	141	0.27
II	30.4	17.9	5.5	126	0.69

Potential for alternative size limits

The present 115-mm minimum legal length limit is enforced along the entire coast of NSW for both the commercial and recreational fisheries. This size limit was chosen by considering average rates of growth, mortality, and reproduction in an attempt to maximize yield from the entire stock. The intense spatial variation in growth that we have described creates several problems which combine to restrict the effectiveness of the length limit. For example, because the 115-mm length limit was chosen by considering average rates of growth, it is less appropriate for sites where abalone grow faster or slower than average. At sites where they grow quickly, abalone rapidly reach the minimum legal length and may be harvested before contributing significantly to levels of egg production. Because of the limited dispersal of larval abalone (Prince et al., 1987), such sites have a limited capability to recover after fishing and hence may easily become overexploited. In contrast, at sites where they grow slowly, abalone take a longer time to reach the minimum legal length limit, and few are removed by divers. Consequently, rates of egg production may be high but they do not contribute significantly to other populations because of the restricted dispersal of larvae (see also Tegner, 1993). In addition, because of the link between growth rate and the maximum length of abalone at a site, as the maximum length of abalone at the site is below the minimum length limit, many populations can never be fished. Different length limits related to the growth of abalone at a site would be desirable, but considering the small spatial scales over which significant differences in growth can occur, their enforcement would be impractical.

An alternative approach to applying different length limits would be to enforce a size limit based on shell width. Because of the differences in morphology of abalone among sites with different growth rates, a width limit would allow individuals from sites where they grow slowly to be removed at shorter lengths than those where they grow quickly. This

would have two potentially desirable consequences. First, it would distribute effort more evenly across sites with the entire range of growth rates. This would occur because more abalone could be collected from sites where they grow slowly, and less would be available at sites where they grow quickly. Following the progressive increase in length limit during the 1980's, most fishing became concentrated at sites where abalone grew quickly (see also McShane, 1992). As described above, the length limit at these sites was also lower than appropriate, which in combination with the intense fishing effort, so that populations at sites where growth was fast were exploited at considerably higher rates than those for other populations.

The second desirable consequence of enforcing a width limit would be to allow the collection of abalone from sites that are presently unfished because abalone grow very slowly and few reach the minimum legal length (i.e. as stunted abalone). If an appropriate width could be chosen, more abalone would be available for collection at sites where they grow slowly, making it viable for divers to visit such sites. There is some evidence to suggest that growth rates of individuals at sites where they appear stunted are limited by a lack of available food (Shepherd and Hearn, 1983). By removing individuals, more food may be available to those that remain and their growth rates may, in turn, increase.

Considering the frequency of studies reporting covariation in growth and morphology of abalone, we suggest that alternative size limits appear to have the potential to improve the management of many abalone fisheries. The intense spatial variation in growth and related differences in morphology of *Haliotis rubra* in NSW, and the ease with which shell width can be measured, make a size limit based on width a potential alternative to the present length limit. The application of a width limit would allow abalone that have grown at different rates to be harvested at different lengths, essentially enforcing different length limits over very small spatial scales. As a consequence, the potentially damaging imbalance in exploitation rates among sites with different rates of growth in length would be avoided.

Acknowledgments

DGW and NLA would like to acknowledge the foresight of GH in the initiation of the tagging program and in the subsequent retention of recaptured shells. Others who helped tag and recapture abalone include T. Butcher and J. Matthews. R. I. C. C. Francis provided us with Grotag, and G. Gordon and M. Krogh helped with programming. N. Bentley, P. Brett, P. Fairweather, D. Ferrell, R. I. C. C. Francis, and W. Nash helped improve various drafts of the manuscript.

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An analysis of weekly fluctuations in catchability coefficients*

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Analyses of time series of commercial catch statistics are usually made with an implied assumption that catchability remains constant. Although the annual catchability from year to year may remain fairly constant, this assumption is rarely, if ever, valid for catchability within a season. Changes in catchability, abundance, and fishing all contribute to fluctuations in the catch from a fish stock (Clark and Marr, 1956; Pope and Garrod, 1975). Behavioral changes due to size or age may cause variations in catchability (Morrissy and Caputi, 1981). By examining the within-season changes in catchability, it may be possible to discern properties of a stock that are not apparent when only annual time intervals are examined.

The objective of this study was to develop a means to estimate weekly within-season catchability coefficients of a stock and to demonstrate how examination of these short-term fluctuations might be useful in a stock analysis. Atlantic menhaden, *Brevoortia tyrannus*, was selected as a model because of the availability of a time series of weekly catch-at-age data for this species.

Methods

Data

Weekly menhaden catch-at-age (in numbers) and vessel-landings data from 1968 to 1982 were made available by the Beaufort Laboratory, National Marine Fisheries Service (NMFS), Beaufort, North Carolina. Migrating menhaden stratify by age and size (Nicholson, 1971b); therefore, the stock was divided into age groups to eliminate differences in catchability due to age-specific (and size-specific) migration patterns.

Calculation of weekly abundances

Abundance estimates with constant time intervals of one week were needed to allow between-year comparisons of weekly catchability and to conform to the Beaufort Laboratory's system of reporting catches. Such short time intervals usually resulted in consecutive intervals of zero catches commonly occurring near the beginning and end of a sequence of weekly landings data for a given year and age group.

Murphy (1965) developed a method for estimating abundance and fishing mortality rates on a cohort of fish when catches are known within time intervals and when an estimate of instantaneous fishing mortality for one time interval and natural mortality for all time intervals are available. A restriction on this method is that the time intervals must be of equal duration and that each time interval must contain catches. Tomlinson (1970) presented a generalization of Murphy's method, which allowed for variable time intervals and zero catches, provided that the first and last time intervals each contain catches and that two or more consecutive zeros do not occur.

The normal method for ensuring that consecutive zero's do not occur in the catch data is to pool time intervals containing zero catches with adjacent nonzero intervals. In this study it was desirable to keep the time intervals fixed, even if it results in consecutive zeros in the catch data. A modification of Tomlinson's method was used, which allows for any number of consecutive zeros, provided that the first and last time intervals contain catches.

Extension to Tomlinson's model

A catch ratio, R_i, can be constructed between catch in the current and subsequent time interval. The ratio for interval i is given by (Eq. 4 in Tomlinson, 1970)

$$R_i = \frac{C_{i+1}}{C_i} = \frac{e^{-t_i(F_i+M_i)}E_{i+1}}{E_i}, \quad (1)$$

where C_i, C_{i+1} = number of fish caught in time intervals i, $i+1$;
F_i = instantaneous fishing mortality in time interval i;
M_i = instantaneous natural mortality in time interval i;
E_i, E_{i+1} = exploitation rate in time intervals i, $i+1$.

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If catch in time interval $i+1$ is zero, then the ratio R_i is zero and the subsequent ratio R_{i+1} is undefined. In this case, the ratio can be constructed between the current time interval and the second subsequent interval. This ratio (R_{i+1}) is given by Equation 5 in Tomlinson, 1970, as

$$R_{i+1} = \frac{C_{i+2}}{C_i} = \frac{e^{(-t_i(F_i+M_i)-t_{i+1}M_{i+1})}E_{i+2}}{E_i}. \quad (2)$$

The above equation is Tomlinson's extension to Murphy's catch equation. This can be further extended to include any number of intermediate time intervals with zero catch. A generalized form of the catch ratio between any two time intervals i and $i+k$, where the catches for all intermediate time intervals is zero, is

$$\frac{C_{i+k}}{C_i} = \frac{E_{i+k}e^{-t_i(F_i+M_i)-(t_{i+1}M_{i+1})-\cdots-(t_{i+k-1}M_{i+k-1})}}{E_i}. \quad (3)$$

Given an estimate of natural mortality rate and fishing mortality rate for the final time interval, F_i's for the previous time intervals can be solved by estimating $E_i \times \exp[t_i(F_i+M_i)]$. This can be estimated from E_{i+k} by rearranging Equation 3 as

$$E_i e^{t_i(F_i+M_i)} = \frac{C_i E_{i+k} e^{-(t_{i+1}M_{i+1})-\cdots-(t_{i+k-1}M_{i+k-1})}}{C_{i+k}}, \quad (4)$$

where C_i is nonzero, and all catches between t_i and t_{i+k} are zero. F_i may be found by iteration after inserting the result of Equation 4 in the following equation (Equation 9 in Tomlinson, 1970)

$$E_i e^{t_i(F_i+M_i)} = \frac{F_i(e^{t_i(F_i+M_i)}-1)}{F_i+M_i}. \quad (5)$$

Once the F_i's have been estimated, the E_i's can be estimated by inserting the value of the above equation into the following:

$$E_i = \frac{(\text{the value of Equation 5})}{e^{t_i(F_i+M_i)}}. \quad (6)$$

After calculating the E_i's and F_i's, the population size at the start of each time interval (N_i) can be estimated from

$$N_i = \frac{C_i}{E_i}, \text{ where } E_i <> 0. \quad (7)$$

To demonstrate the use of this extension to Tomlinson's method for solving the catch equation, the computer program MURPHY (Abramson, 1971), which implements Tomlinson's model, was modified to incorporate the extension for consecutive zeros to estimate weekly abundance and fishing mortalities for the Atlantic menhaden purse-seine fishery. The catch data were broken up into weeks and into age groups within a week.

Constant parameters used

In addition to catch-at-age data, virtual population analysis (VPA) requires estimates of instantaneous natural mortality for all time intervals and an estimate of instantaneous fishing mortality for one time interval. Natural mortality was assumed constant and a weekly value of 0.0087 (annual M=0.45) was adopted on the recommendation of the Beaufort Laboratory. Estimates of fishing mortality for the final week of landings data in each year were obtained from Table 13 of Broadhead et al.[1] for the years 1968–76 and for age groups 0–5. For age groups 6–8 the values for age 5 were used. For the years 1977–82, the average values for the years 1968–76 for each age group were used (1968–75 for age group 0). In each case, the annual value of F from the table was divided by the number of weeks in the year that had landings data to obtain a weekly F. Instantaneous fishing mortality values were probably overestimated because catch generally declined at the end of the season. However, in the backward solution to the catch equation, the value for F tends to converge toward its true value for a given M. Therefore, the error in abundance estimates due to this overestimation of F should be minor at the beginning of each year's landing data, although it may result in the underestimation of abundance toward the end.

Defining effort

An index of fishing effort was needed to calculate a catchability coefficient. The number of vessels with landings in a given week (vessel-week) is commonly used as the unit of fishing effort in studies of the menhaden purse-seine fishery and was the unit used in this study. Menhaden vessels generally operate continuously throughout all or part of the fishing season, fishing every day, as weather permits, un-

[1] Broadhead, G., C. Grimes, J. Loesch, W. Nelson, G. Sakagawa, and K. West. 1980. Report of the Atlantic menhaden population dynamics subcommittee to the Atlantic menhaden scientific and statistical committee on the status of the Atlantic menhaden stock and fishery. Unpubl. manuscr., 68 p.

less they are in port for repairs. Any time period that assumes continuous fishing and accounts for unproductive fishing days should be a satisfactory unit of fishing effort (Nicholson, 1971a). Number of landings as a unit of effort assumes continuous fishing. Although the number of days that a given vessel was fishing in a week was unknown it was assumed that variations were randomly and normally distributed.

Calculation of weekly catchability coefficients

The catchability coefficient is defined as the fraction of a fish stock that is caught by a defined unit of fishing effort (Ricker, 1975). The relation between catch, effort, abundance, and catchability is

$$\left(\frac{C}{f}\right)_t = q_t N_t, \tag{8}$$

where $(C/f)_t$ = average catch per unit of effort over period t; N_t = average abundance during period t; and q_t = catchability during period t.

The VPA estimates of abundance are for the beginning of a time period. For the short, one-week time periods used in this study, average abundance in a period is assumed to approximate $(N_t + N_{t+1})/2$. Average catch per unit of effort in a time period can be calculated as total catch divided by total effort for that period. The above equation can thus be rearranged to define the catchability coefficient as

$$q_t = \frac{\left(\frac{C_t}{f_t}\right)}{\left(\frac{N_t+N_{t+1}}{2}\right)}. \tag{9}$$

This equation was used to calculate initial weekly catchability coefficients for each age group. No catchability estimate was made for weeks in which there was no catch landed for the age group considered. Also, no catchability estimate was made if abundance estimates were not made for both the week being considered and the following week, because the average abundance during the week $(N_t+N_{t+1}/2)$ was used to estimate catchability.

Statistical analysis

Weekly abundance estimates at age were made in each year from the first week in which a catch was landed until the last. Catchability coefficients by age were estimated for each week for which there were abundance estimates for the current and subsequent weeks. Friedman's method for randomized blocks (Sokal and Rohlf, 1981) was used to test for significant differences in annual patterns of weekly catchability coefficients for each age group between years. This is the nonparametric analog to the parametric analysis of variance (ANOVA) randomized complete block design, but the rankings of the variates within each block are used rather than the actual measurements. A nonparametric test was used because the relative degree of weekly fluctuations from year to year may vary owing to biotic or abiotic factors. Thus, heterogeneity of variance between years may be expected, making a parametric model inappropriate.

Results

The Friedman's test indicated that at least one year was significantly different from the others at the 0.05 alpha level for age groups 1, 2, 3, and 4 but not significant for the remaining age groups. Subsequent multiple comparisons for these age groups with Friedman's rank sums (Hollander and Wolfe, 1973) failed to show temporal differences. These differences were therefore considered to be random variations about a mean, allowing the annual variations for each week to be averaged to determine the underlying pattern.

Plots of high, low, and mean weekly catchability were created for each age group (Fig. 1). For most age groups the range of catchability coefficients was greater at the beginning and end of the season than in the middle. The plots were examined visually for signs of fluctuation within a season. The graphs of weekly catchability showed the following pattern: the first part of the catchability curve features an initial peak followed by a rapid decline. This decline is followed by a gradual increase in catchability as the season progresses, then by a second sharp peak near the end of the season. The height of the initial peak relative to the rest of the plot is most pronounced in age-1 and age-2 fish. It becomes less pronounced and disappears altogether as the fish become older. This first peak does not occur for age-0 menhaden, which are subject to a fishery that is largely directed against catching them in the fall.

The catchability graph of age-0 menhaden differs from the other age groups. This age group is not targeted during most of the year but becomes subjected to a directed fishery off North Carolina in the fall. Catchability for this age group remains at or near zero for most of the season because no age-0 fish are being caught. Near the end of the season, it rapidly rises from zero to a peak and then quickly drops back to zero as the fishery ends.

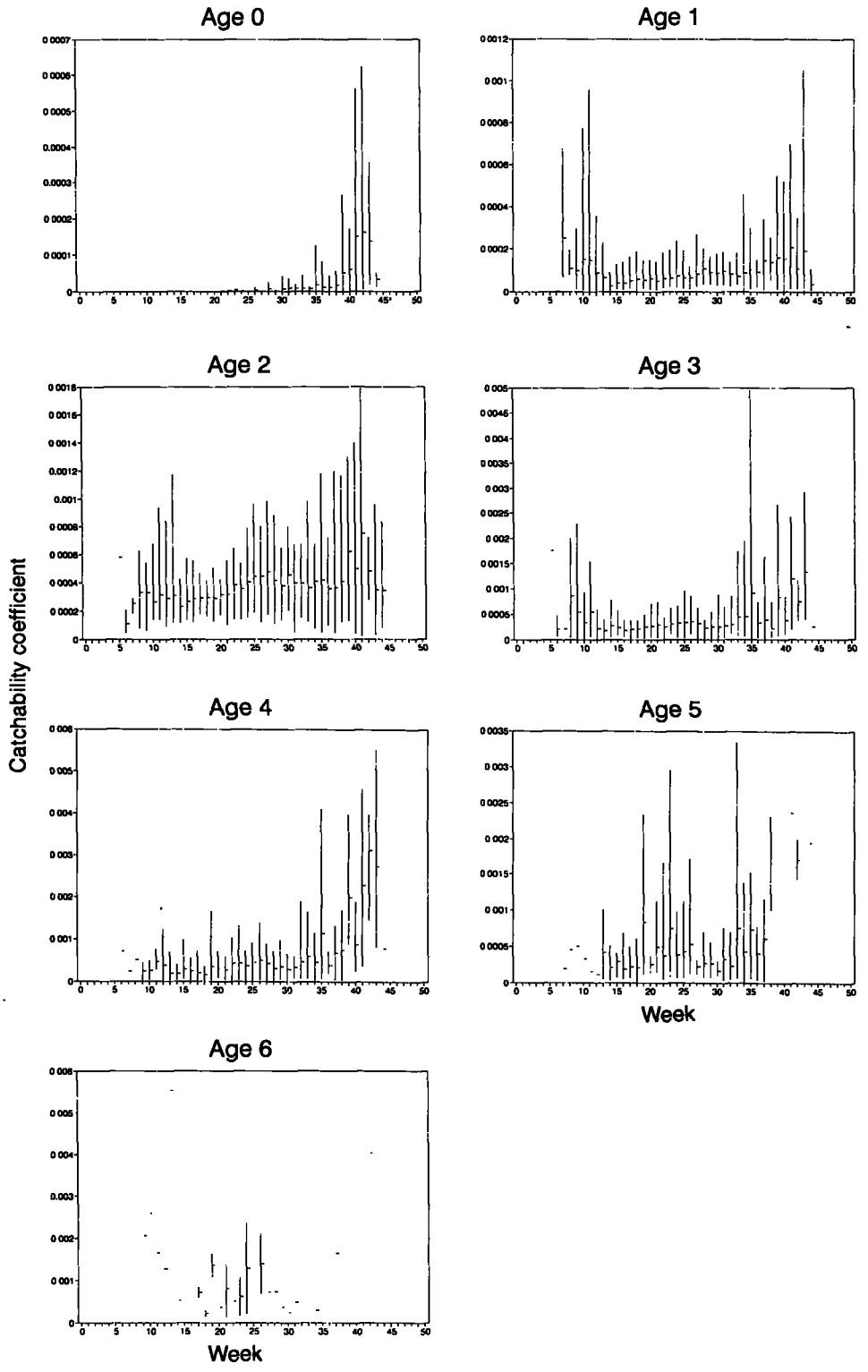

Figure 1

Mean and range of weekly catchability coefficients for Atlantic menhaden, *Brevoortia tyrannus*, from 1968 to 1982.

Discussion

Virtual population analysis assumes that there is complete recruitment for a set of age classes and that availability remains constant for all recruited age classes. The existence of sharp initial and ending seasonal catchability peaks is probably due to underestimation of abundance at the beginning and end of the season from the VPA method. This indicates that VPA can be biased when availability fluctuates. Virtual population analysis measures the "virtual" abundance, that which appears to the fishery to be there, rather than absolute abundance. Early in the season, when the menhaden are migrating into the fishing area from their wintering grounds, only part of the stock is available for exploitation. Changes in availability, or accessibility, can affect the catchability coefficient (Cushing, 1968). Marr (1951) showed that catchability is directly related to availability. However, because VPA assumes that there is full availability, abundance is underestimated. If the abundance is underestimated, then the catchability coefficient will be overestimated (Shardlow and Hilborn, 1985).

Theoretically, this first peak should extend to infinity prior to the start of the season when VPA is used to estimate abundance, because availability at this point in time is zero. If abundance had been measured with a method independent of the fishery catch statistics, such as mark-recapture, catchability estimates would have been based on absolute rather than on virtual abundance and there would not have been an early season peak. The rise from zero or near-zero catchability which occurs in many of the plots, particularly with older age groups, may be due to an earlier or faster migration of these age groups into the fishing area or to more complete recruitment of the age group at the start of the season. Younger age groups are not completely recruited into the fishery, but by age 2, the menhaden are fully recruited into the Atlantic coast purse-seine fishery (Atlantic Menhaden Management Board, 1981). If availability is at or near maximum by the time of the first catch, VPA will not underestimate abundance, and consequently catchability will not be overestimated. One advantage of examining within-season fluctuations of catchability, therefore, may be to assess when the stock becomes available to the fishery.

After the initial peak, a gradual rise in catchability can be seen as the season progresses, most likely due to a decrease in abundance during a period of full availability. This observation is consistent with Schaaf (1975), who reported a logarithmic inverse relation between annual values of catchability and abundance of menhaden. An increase in this rate might result if stock abundance during the season were decreasing faster than normal, and it would then be an indicator of overfishing.

The pattern of catchability for age-0 menhaden differs from that of the other age groups in that there is no initial peak and landings begin much later in the season (Fig. 1). Age-0 menhaden are fished extensively in the North Carolina fall fishery which is largely directed toward these fish. Paloheimo and Dickie (1964) stated that when fishermen selectively apply their effort toward some schools, the result is variance in the catchability coefficient depending on age, species, and relative abundance. This effect is apparent in the plot of average weekly catchability coefficient for age-0 menhaden. When the age-0 menhaden, commonly referred to as "peanuts," migrate out of Virginia and North Carolina estuaries, they become readily available close to shore where they dominate the landings, usually in December and January.

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Temperature influence on postovulatory follicle degeneration in Atlantic menhaden, *Brevoortia tyrannus*

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The occurrence of postovulatory follicles within the ovaries of fish is a positive indication of spawning, because they are the evacuated follicles following ovulation. Therefore, their frequency of occurrence may be used to test factors influencing reproduction. For example, postovulatory follicles can be used to estimate spawning frequency, which in turn is used to estimate spawning biomass (Hunter and Macewicz, 1985). Their state of degeneration can be assessed from histological sections of the ovary to estimate the time elapsed since spawning for females sampled in the wild. In addition, the occurrence of postovulatory follicles might be useful to test hypotheses about events that may trigger spawning and benefit larval transport (see Taylor, 1984; Checkley et al., 1988).

A requisite for applying this histological method of determining spawning frequency is validation of the duration that postovulatory follicles can be detected in field samples. This has been done through closely timed observations of spawning in the field and by laboratory-induced spawning and subsequent sampling of female gonads (Hunter and Macewicz, 1985). Laboratory spawning offers more certainty in determining the time of spawning and facilitates more precise measurement of the degeneration time of postovulatory follicles. Uncertainty regarding the duration of postovulatory follicles has led to questions about estimates of spawning frequency (Brown-Peterson et al., 1988; Fitzhugh et al., 1993; and Goldberg et al., 1984). Variation in the duration of postovulatory follicles may be largely due to the particular species involved and its preferred spawning temperature (Hunter and Macewicz, 1985).

Atlantic menhaden spawn across a wide geographic range of U.S. coastal Atlantic waters (Cape Canaveral, Florida, to Martha's Vineyard, Massachusetts) and probably over a wide range of temperature as well (Judy and Lewis, 1983). Eggs have been collected between the 15° and 20°C surface isotherms in the mid-Atlantic Bight (Kendall and Reintjes, 1974). We wished to examine differences in postovulatory follicle duration and age at stage due to temperature in Atlantic menhaden. As a preliminary step to future estimation of spawning frequencies, our objective was to characterize postovulatory follicle degeneration and validate postovulatory follicle duration for Atlantic menhaden induced to spawn at different temperatures in the laboratory.

Materials and methods

Adult menhaden were collected near Harker's Island, North Carolina, between mid-August and mid-September 1988, 1990, 1991, and 1992. During each period, menhaden were maintained in outside tanks under ambient flow-through conditions until mid-October to mid-November when they were moved to inside tanks to begin conditioning for spawning. We induced spawning in either December (1990) or March (1988, 1991, 1992) with methods reported by Hettler (1981). Menhaden of both sexes were conditioned to spawn by means of intraperitoneal injections of human chorionic gonadotropin (HCG) and carp pituitary extract (CP). We gave injections between 0800 and 1000 hours on successive days, and spawning usually occurred the night following the second (CP) injection.

Spawning was induced under three temperature regimes; 14.8–15.7°C for one group in December 1990; 17.9–18.2°C for one group in March 1992; and 19–20°C for groups in March 1988, December 1990, and March 1991. Groups of menhaden ranged from 22 to 31

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individuals and the male to female ratio was about equal. In December 1990, only 12 individuals were induced to spawn at the coldest temperature regime (7 were subsequently identified as females). For each group, acclimation and holding temperatures were held constant prior to spawning and for the week following spawning.

The time of spawning was estimated the following morning when eggs were collected and identified to stage (Ferraro, 1980). Males were identified by the presence of free-flowing milt just prior to the CP injection and were marked by clipping the left pectoral fin. Females (identified as not having a fin clip) were sampled up to 4 days following spawning and killed in a solution of MS-222. We excised a tissue section from the middle right ovarian lobe from each female and fixed it in 10% neutral buffered formalin. Tissue samples were dehydrated, embedded in paraffin, sectioned, stained with Gill's hematoxylin and eosin for histological observation. Our interpretation of the histological states of the postovulatory follicles follows Hunter and Macewicz (1985), and the prominent features we observed are summarized in Table 1.

Results and discussion

The postovulatory follicle, which is the evacuated follicle remaining in the ovary following ovulation of the hydrated oocyte, is characterized by an outer thecal layer and an inner epithelial granulosa layer (Fig. 1). Many species show similar features in postovulatory follicle degeneration (Hunter and Macewicz, 1985) to those that we noted for Atlantic menhaden. Onset of degeneration was evident when vacuoles and eosinophils were detected within the postovulatory follicle (Fig. 1A). The granulosa layer appeared contorted or folded but the granulosa cells and their nuclei imparted a linear or cordlike appearance (Fig. 1A). Initially, the lumen was apparent but narrowed and became less distinct with time (Fig. 1, B and C). We also noted that the linear arrangement of the granulosa cell nuclei became less distinct with time (Fig. 1B). Vacuolization of the follicle increased (Fig. 1C), and a point was reached when the lumen was no longer evident. The postovulatory follicle became reduced in size but the folded appearance of the granulosa layer remained evident and aided in identifying the postovulatory follicle (Fig. 1C). We used this point in degeneration to define the postovulatory follicle duration because as the postovulatory follicle aged further (e.g. Fig. 1D), there were no exact features that could distinguish it from old atretic follicles (preovulatory follicles) that remain after an intact oocyte undergoes atresia (Goldberg et al., 1984; Hunter and Macewicz, 1985). While atresia of oocytes occurs predominately at the end of a spawning season, it is common to observe some oocytes undergoing atresia throughout the spawning season (Hunter and Macewicz, 1985). We also observed some atresia of vitellogenic oocytes in our samples. Since preovulatory follicles can be present and at some point are not distinguishable from postovulatory follicles, we can only estimate the duration that the postovulatory follicles may be identified.

The 54 females sampled after spawning from the three temperature regimes ranged in size from 200 to 250 mm fork length which is typical of 2 to 3 year-olds (Nicholson and Higham, 1964). All females (n=35) from the warm regime (19–20°C) that were sampled within about 40 hours of spawning (determined from the collection and identification of stages of fertilized eggs) displayed detectable postovulatory follicles (100% spawned). Eleven of the twelve females sampled from the 17.9–18.2°C series displayed postovulatory follicles (92% spawned). Six females from the cold series (14.8–17.7°C) contained vitellogenic oocytes, indicating an advanced reproductive state; one female possessed cortical alveolar stage oocytes—an immediate precursor to the vitellogenic stage (deVlamming, 1983). However, only 4 of 7 females from the cold series possessed detectable postovulatory follicles (57% spawned). The reduced temperatures appeared to diminish our ability to induce spawning.

Table 1

Distinguishing features for the stages of postovulatory follicle degeneration[1] in Atlantic menhaden, *Brevoortia tyrannus*.

Stage	Characteristics of postovulatory follicles
1	Granulosa cells are aligned and granulosa-layer nuclei appear linear in orientation. Some lymphocytes and vacuoles may appear in the postovulatory follicle, signaling initial degeneration.
2	Loss of linear arrangement of granulosa layer nuclei; cell membranes and columnar/cuboidal shape of granulosa layer is no longer distinct. Lumen is still clearly visible.
3	Although irregular postovulatory follicle shape is still detectable, fewer folds are apparent as the lumen becomes reduced and is no longer distinct.
4	Linear appearance of the granulosa layer is no longer distinct; postovulatory follicle not readily distinguished from atretic oocytes.

[1] Adapted from Hunter and Macewicz, 1985.

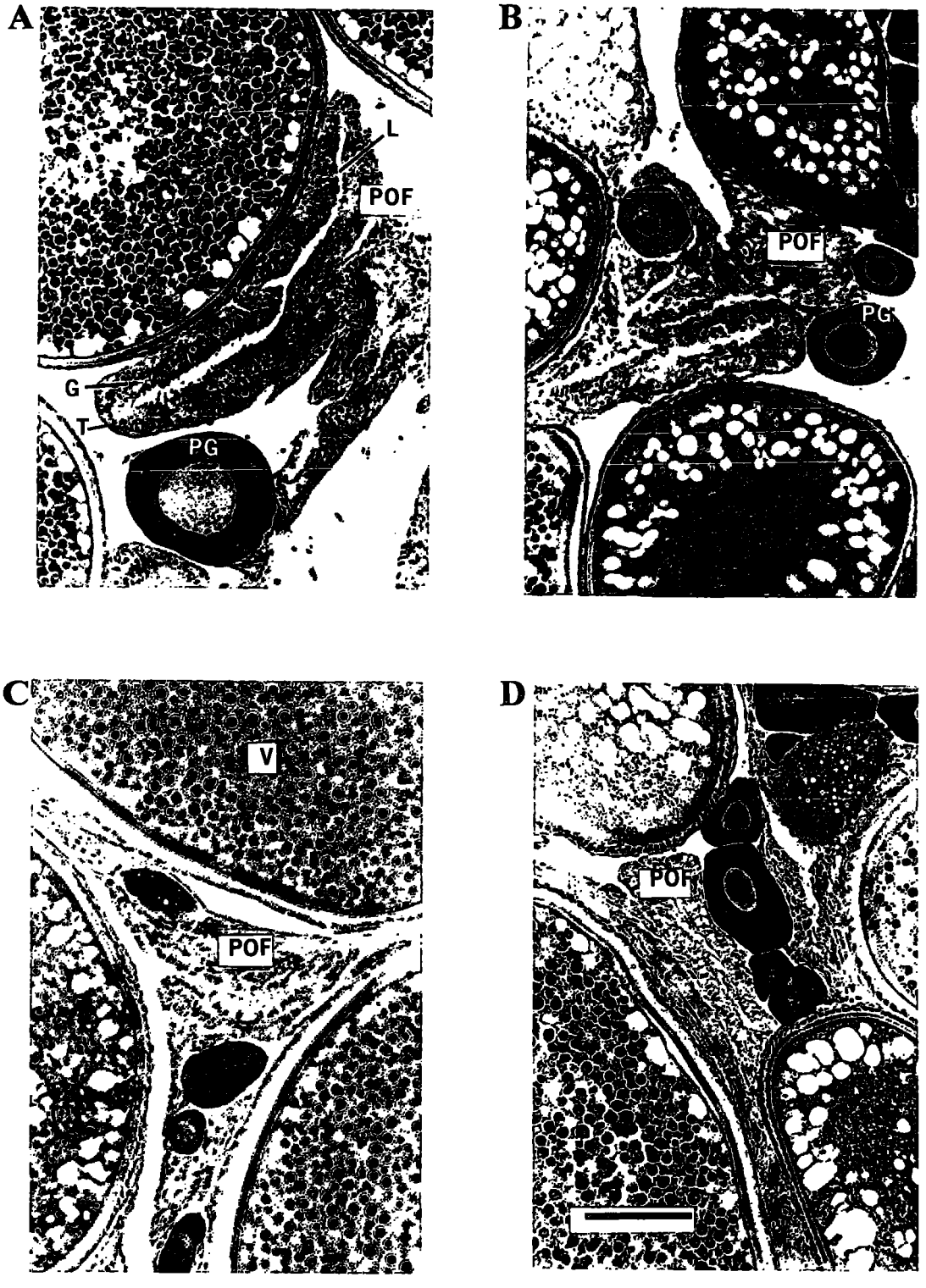

Figure 1

Postovulatory follicles (POF's) from female Atlantic menhaden held at 20°C. Elapsed time from estimated spawning is (**A**) 11 hours, (**B**) 21 hours, (**C**) 38 hours, and (**D**) 45 hours. Features characterizing postovulatory follicles are as follows: L = the lumen; G = the granulosa layer; and T = the outer thecal layer. Vitellogenic oocytes are denoted by (V) and primary growth oocytes are denoted as (PG). The scale bar represents 0.1 mm.

All spawning was estimated to have occurred between 2100 and 0200 hours and time from spawning was recorded at each sampling period. We compared histological states associated with these sampling periods by standardizing the time of spawning (midnight, hour-0; Fig. 2). In general, events associated with induction of spawning slowed down in the cold temperature regime. Spawning at 14.8–15.7°C occurred about 63 hours after HCG injection and about 39 hours after CP injection. However, within the warmest series, spawning occurred about 34 and 11 hours, respectively, after HCG and CP injections.

We saw characteristics of initial follicle degeneration about 6 to 12 hours after spawning for all three temperature regimes (Fig. 2, Table 1). There was an apparent difference in overall duration of postovulatory follicles between the high and low temperature regimes. Filling of the lumen (stage 3) was evident at the warm regime by about 21 to 46 hours (Fig. 2). At 19–20°C, postovulatory follicles were difficult to distinguish (stage 4) as early as 36 hours, but at the two colder regimes, postovulatory follicle degeneration was not as advanced even at 58 hours (e.g. stage 3, Fig. 2). Postovulatory follicle duration at 15°C is probably longer than 60 hours after spawning.

Transition to successive atretic stages was apparently faster at the warmest temperature and there was some overlap of atretic stages at a given time following spawning. For example, stages 1, 2, and 3 were observed at 20 hours from females held at 19–20°C (Fig. 2). This overlap may be due to variation in degeneration rates among females, the subjectivity of stage classification across a continuum of follicle degeneration, or to variation in the exact time of ovulation among females (because time from spawning was estimated for all the females in a group from a sample of fertilized eggs). A more precise analysis of the durations for the various stages of atresia would have been facilitated by sampling each group at constant intervals after the spawning of eggs and by using a larger sample size—particularly for the coldest treatment.

Observations of postovulatory follicle duration vary for species that spawn at different temperatures. We observed durations ranging from about 36 to over 60 hours for Atlantic menhaden spawning from 15 to 20°C. At similar temperatures (13 to 19°C), northern anchovy, *Engraulis mordax*, Peruvian anchovy, *Engraulis ringens*, and Pacific sardine, *Sardinops sagax*, have postovulatory follicles that last about 48 hours (Hunter and Macewicz, 1985). Skipjack tuna, *Katsuwonus pelamis*, and Hawaiian anchovy, *Encrasicholina purpurea*, spawn at approximately 25°C and have postovulatory follicles that last about 24 hours (Hunter et al., 1986; Clarke, 1987). The

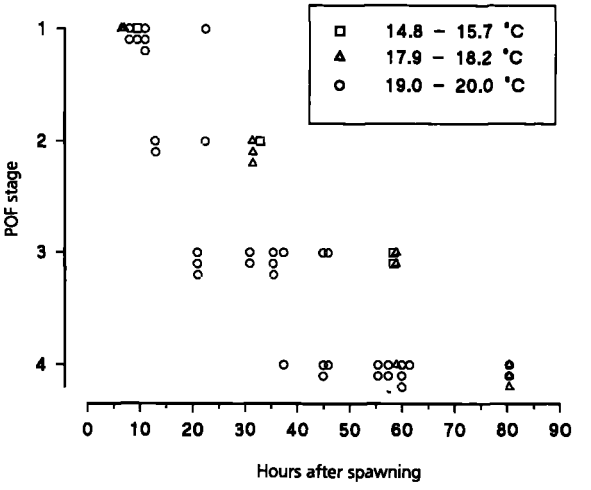

Figure 2

Chronology of spawning and postovulatory follicle (POF) degeneration for three temperature series (14.8–15.7°C, 17.9–18.2°C, and 19.0–20.0°C). Postovulatory follicle stages (1–4) are described in Table 1. All spawning times are set to midnight (hour-0) in order to make contrasts across temperature series (see text). Symbols slightly offset along the y-axis at each stage of degeneration correspond to multiple fish sampled at the same time.

dragonet *Callionymus enneactis* spawns at 28–30°C and has a postovulatory follicle duration less than 15 hours (Takita et al., 1983). Collectively, these observations confirm that increasing temperatures decrease the time that postovulatory follicles can be detected in fishes.

The ability to identify the stage of postovulatory follicles in order to determine spawning frequencies becomes more important as their duration increases. If postovulatory follicles are known to last less than 24 hours, females possessing them can be defined with certainty as having day-0 postspawning ovaries for purposes of estimating spawning frequency. Hunter and Goldberg (1980) and Hunter and Macewicz (1985) developed this approach on the basis of the appearance of various features and assigned day-0 and day-1 classifications to fish known to have postovulatory follicle durations of about 48 hours. However, if durations are known to be longer, knowledge of the age of particular features of postovulatory follicles becomes more critical in classifying postspawning ovaries. We focused on the alignment of the granulosa layer (and nuclei), on the presence of vacuoles, and the appearance of the lumen for identifying stages because these features were easily recognizable in Atlantic menhaden postovulatory follicles and could be used to classify fairly discrete

stages (Table 1). In Atlantic menhaden spawning at about 20°C, disappearance of the lumen of the postovulatory follicle after loss of alignment of the granulosa layer (transition from stage 2 to 3) distinguished day-0 from day-1 postspawning ovaries. However, in several other species, features such as pycnotic nuclei, thickness of the thecal layer, and separation of the thecal and granulosa layers are diagnostic for classification of postspawning ovaries (Goldberg et al., 1984; Hunter and Macewicz, 1985; Agarwal et al., 1992).

Postovulatory follicle durations in *Engraulis* species spawning naturally or in those induced pharmacologically to spawn at similar temperatures are equivalent (Hunter and Goldberg, 1980; Goldberg et al., 1984) suggesting that laboratory observations can be used to access spawning frequencies of fish in the wild. Our estimates of the durations of particular features of postovulatory follicles must be considered preliminary on the basis of our small sample size, particularly for the 14.8–15.7°C treatment fish. However, our general finding that postovulatory follicle duration within Atlantic menhaden can vary from 36 to probably more than 60 hours corresponding to a 5°C range in temperature, supports the view that temperature should be an important consideration affecting spawning-frequency estimation in field surveys.

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Size structure of mutton snapper, *Lutjanus analis*, associated with unexploited artificial patch reefs in the central Bahamas

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The mutton snapper, *Lutjanus analis* (Cuvier, 1828) (Pisces: Lutjanidae), is an important component of shallow water reef fisheries in the tropical western Atlantic (Bortone and Williams, 1986). However, overfishing of shelf-edge spawning aggregations has contributed to a major decline in landings and, in some locations off Florida and Cuba, to a total collapse of the fishery (Brownell and Rainey, 1971; Gulf of Mexico Fishery Management Council, 1992). Much of what we know about *L. analis* (i.e. age and growth, reproductive, and trophic biology) is based on samples from commercial and recreational catches (Rojas, 1960; Erhardt and Meinel, 1977; Erhardt, 1978; Pozo, 1979; Claro, 1981, 1983; Mason and Manooch, 1985; Palazón and González, 1986). Quantitative behavioral studies are few (Mueller, 1994; Mueller et al., 1994), and field investigations concerning the population structure of *L. analis* under natural conditions are lacking.

Visual censuses are useful for comparison of temporal changes in the size structure of fish populations on exploited reefs with those of fish populations on unexploited reefs (Craik, 1981; Russ, 1985). However, such methods have several inherent biases. At best, visual censuses provide reasonably precise records of the fish fauna that are not greatly influenced by conditions of water clarity (Sale and Douglas, 1981). Because counting all the fish in a given area is nearly impossible, size frequencies derived from visual censuses should be used for relative comparisons between populations (Craik, 1981). Using visual census techniques, I describe a preliminary study of seasonal variation in the size structure of *L. analis* on unfished reefs for the purpose of making comparisons with fish of this species that are subjected to fishing pressure.

Materials and methods

Size frequencies of *L. analis* associated with two artificial patch reefs off Lee Stocking Island, Exuma Cays, Bahamas (23°46.21'N, 76°06.59'W), were monitored during snorkeling excursions between 22 May 1991 to 14 December 1992. The primary reef (reef 1, area=491 m^2) was located in a shallow (2.7 m), moderately dense *Thalassia testudinum* Koenig meadow (biomass=40–80 g dry wt·m^{-2}, Stoner and Sandt, 1991), whereas a smaller reef (reef 2, area=78 m^2) was located in deeper water (4 m), 107 m west of reef 1. A distinct, gently sloping contour in the seagrass bed was evident between the two reefs. Both reefs were composed of man-made materials and had a sparse cover of the living corals *Millepora alcicornis* Linnaeus and *Porites porites* (Pallas). The position of and distance between the reefs were determined by using a Magellan™ global positioning system unit. Reef areas were determined by using a waterproof measuring tape during SCUBA dives. Although natural patch reefs occurred in the area, this site was selected because it was unexploited and had a large number of *L. analis* associated with the reefs.

Data were collected every 4–11 weeks, only during the flood tide (greatest water clarity) between 0600–1900 h (daylight hours) to maximize visibility. By comparing my position with the known distance between reef structures at reef 1, I inferred that the maximum limit of my visibility during flood tide was approximately 20 m. Current directions of the flood and ebb tides at the study site were west (180°) and east (0°), respectively. During flood tide, I was able to drift (>30 cm per second) from reef 2 to reef 1 in five minutes or less. Using the natural water flow and bottom topography as references, I followed the same path between the two reefs during each census. All fish observed within 20 m (the approximate limit of my visibility) to either side or end of this quasi-transect (total search area including reefs ≈5,600 m^2) were counted and measured. Fork lengths (FL) were estimated visually within 5 m of fish by comparing subjects to a known scale, the 30-cm length of a hand-held underwater slate. Fish were placed into one of three size classes relative to my slate: 20, 30, and ≥40 cm FL (shorter than, equal to, and longer than the slate, respectively). *Lutjanus analis* swam into the current (positive rheotaxis); therefore once I had passed

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a fish, I did not encounter that fish again during the drift. To confirm the accuracy of my underwater FL estimates, I compared markings on my slate (1-cm increments) with structural relief that *L. analis* rested on or passed by at reef 1. I repeated this practice until I could discern between the three size classes ±5 cm from distances up to 5 m away.

On each sampling date, I performed three replicate drifts from reef 2 to reef 1. Size frequencies were derived from the largest number of fish counted in each of three size classes, irrespective of replicate, because the number of fish in each size class was at least equal to the greatest number of that size class seen during a single drift (Sale and Douglas, 1981).

Results and discussion

Four individual *L. analis* were recognized from census to census for periods up to one year. Fish were identified by body size, scars, fin anomalies, or shape of the black upper-body spot. However, owing to the wary nature of *L. analis*, it was difficult to remain within close proximity of subjects to identify adequately all fish by this method. Although individuals were considered resident, it is possible that others were transient or wandering fish. Still, my observations are consistent with a previous study (Beaumariage, 1969) that indicated little movement in adult *L. analis*.

On each sampling date, up to 56 *L. analis* were counted and measured at the study site. Fish ranged in size from 15 cm FL (half the length of my underwater slate) to 65 cm FL (>twice the length of my slate). Small (20-cm-FL), medium (30-cm-FL), and large (≥40-cm-FL) *L. analis* were aged 1+ yr, 2+ yr, and 3+ yr, respectively (sensu Claro, 1981; Mason and Manooch, 1985). The number of small and medium-size fish observed varied from 6 to 24 and 12 to 25, respectively. The number of large fish never exceeded 13 (Table 1). From April to July, fish sizes were normally distributed; however, during August, fish sizes became negatively skewed. On 23 February 1992, water clarity was extremely poor (<5 m), which may account for the low number of small fish recorded on this date (Table 1).

The causes for seasonal variation in the size structure of *L. analis* are difficult to isolate from my observations; however, some inferences can be drawn from previous studies. For example, the increase of small fish in late August (Table 1) corresponds well with the peak recruitment to seagrass beds reported for juvenile *L. analis* (<7 cm FL) during August (Springer and McErlean, 1962) and September (García-Arteaga et al., 1990). Jones (1990) described a similar pattern in ambon damselfish, *Pomacentrus amboinensis*, Bleeker, 1868, and showed that adult densities increased in proportion to juvenile recruitment success after a two-year period (=maturation time).

The simultaneous decrease in medium-size fish during August (Table 1) is not easily explained. The population structure of unexploited reef fish is determined by a complex sequence of events that includes recruitment, demographic changes (i.e. mortality, migration, and growth), and ecological processes such as habitat structure, resource availability, and intraspecific competition (Jones, 1991). For instance, variable patterns in growth can have a major and direct influence on the size structure of a population (Jones, 1991). Individuals that grow faster may subordinate conspecifics and establish a dominance hierarchy (Forrester, 1990). Once established, hierarchies are often extremely stable (Morse, 1980). For example, where individually recognized recruits were followed over time, juvenile humbug, *Dascyllus aruanus* (Linnaeus, 1758), never outgrew other group members in size during an eight-month period (Forrester, 1990).

Lutjanus analis exhibits much variation in length for a specific age (Mason and Manooch, 1985) but matures sexually at fork lengths above 38 cm (Claro, 1981). In the central Bahamas, *L. analis* form groups of variable-size fish that occupy seagrass meadows

Table 1

Size frequencies of mutton snapper, *Lutjanus analis*, sampled from a population associated with two artificial patch reefs located off Lee Stocking Island, Exuma Cays, Bahamas. Fork lengths were estimated visually by comparing fish to a known scale (30-cm length of a hand-held underwater slate) and are ±5 cm.

	Fork length (cm)			
Sample date	20	30	≥40	Total no. sampled
22 May 91	6	21	8	35
1 July 91	16	25	5	46
29 July 91	11	24	11	46
24 August 91	23	12	6	41
5 October 91	16	12	10	38
7 December 91	22	13	6	41
23 February 92	6	20	10	36
20 March 92	23	18	7	48
19 April 92	8	23	13	44
18 May 92	10	22	6	38
17 June 92	12	22	5	39
16 August 92	24	18	9	51
26 October 92	19	17	9	45
14 December 92	18	25	13	56

near inlets and patch reefs (Dennis[1]). Size-specific asymmetries in both social and foraging behaviors suggest that these groups form dominance hierarchies (Mueller, 1994; Mueller et al., 1994). Assuming that large *L. analis* did not migrate from the study site (Beaumariage, 1969; author's personal observ.) and given that higher proportions of aggressive encounters occur among medium-size and large fish compared with small fish (Mueller et al., 1994), it is possible that the few large, dominant *L. analis* limited the number of medium-size fish on site through social interactions (sensu Doherty, 1983; Jones, 1987; Forrester, 1990). However, because empirical evidence is not available to support this conclusion, experiments should be designed to test whether large *L. analis* are a limiting factor.

Changes in the size structure of *L. analis* between 1991 and 1992 (i.e. the shift from small towards medium-size fish; Table 1) may also be related to growth. For example, small *L. analis* (1+ yr) feed proportionally more often than medium-size or large fish during daylight hours (0600–1730) and are involved in very few intraspecific encounters (Mueller et al., 1994). By limiting their interactions with conspecifics, small fish ostensibly have more time and energy available for growth (≥0.8 cm/mo during years 1 and 2; Claro, 1981; Mason and Manooch, 1985). Further studies may be designed to test this hypothesis.

In conclusion, managers of reef fisheries are challenged with determining whether shifts in the size structure of populations are due to normal recruitment and postrecruitment events or to fishing pressure. For example, low abundance of a certain size class may be due to intraspecific competition (Doherty, 1983; Jones, 1987; Forrester, 1990) or growth rather than to the effects of fishing. However, previous studies also indicate lower average size and abundance of fish captured on exploited reefs as opposed to unexploited reefs (see review by Russ, 1991). I have provided evidence of seasonal variation in the size structure of *L. analis* associated with unfished reefs. Although potential biases exist, this information should be useful for making relative comparisons with analogous populations subjected to fishing pressure.

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Occurrence and group characteristics of minke whales, *Balaenoptera acutorostrata*, in Massachusetts Bay and Cape Cod Bay

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The minke whale, *Balaenoptera acutorostrata*, is one of the smallest of the baleen whales. Despite exploitation by the whaling industry in recent years, comparatively little is known about the biology and behavior of this species. The minke has a cosmopolitan distribution, although recent biochemical studies suggesting large genetic differences between oceanic populations (Amos and Dover, 1991; Hoelzel and Dover, 1991; van Pijlen et al., 1991; Wada and Numachi, 1991; Wada et al., 1991) have cast some doubt on the long-held belief that all populations constitute a single species. As is the case for most baleen whales, minke whales appear to migrate to high latitudes in the summer for feeding and to travel to tropical waters in the winter for birthing (Horwood, 1989; Mitchell, 1991). However, specific breeding grounds have yet to be unequivocally identified, and it is unknown whether both sexes and all age classes in a population undertake the migration to low latitudes. In some temperate, subtropical, and tropical areas, minke whales are observed throughout the year (Ivashin and Votrogov, 1981; Best, 1982; Gong, 1987; Stern, 1990), although it is unclear whether these sightings represent year-round residency on the part of particular individuals or a more general movement through the area by members of one or more populations.

In recent years, much has been learned about other mysticetes through long-term studies based on the identification of individual whales (see Hammond et al., 1990). Unfortunately, minke whales lack the great variability in natural markings that have facilitated detailed investigations of larger confamilials (such as humpback whales, *Megaptera novaeangliae*). This, together with the difficulty of photographing them owing to their small size and great speed, has hindered studies based on photographic identification, although studies of small localized populations have been possible (Dorsey, 1983; Dorsey et al., 1990; Stern et al., 1990). In general, however, studies of free-ranging minke whales have been few, and their population structure, social organization, and migratory movements remain poorly understood.

Minke whales are commonly observed in the waters of Massachusetts Bay and Cape Cod Bay in New England, and since 1979, sightings of this species have been routinely recorded from both commercial whalewatching vessels and dedicated surveys. In this paper, sighting records are examined in an effort to describe the temporal distribution, seasonal abundance, and feeding behavior of minke whales in this region. These data are then compared with information reported for this species from other areas, notably within the North Atlantic.

Methods

Study area

The study area includes the coastal region dominated by Cape Cod Bay and Massachusetts Bay along the northeastern coast of the United States (Fig. 1). Cape Cod Bay is a semi-enclosed sandy basin with a maximum depth of 60 m. Massachusetts Bay lies north of Cape Cod; depths range from 40 m to 100 m except on Stellwagen Bank, an elongated glacial feature of sand and gravel approximately 25 km in length, which has a minimum depth of 18 m.

Effort

Data were collected between 1979 and 1992. The total number of cruises conducted during this period was 10,249 (this figure excludes those made in certain weather conditions, as noted below); of these, 9,728 (94.9%) were made from 30-m commercial whalewatching vessels operating between April and October of each year from Provincetown, Massachusetts. Additional cruises (n=374) were made from a 12-m diesel-powered research vessel beginning in the autumn of 1983, and 77 cruises were made from a 14-m auxiliary ketch beginning in the autumn of 1985. The remaining non-whalewatch cruises were made primarily from a 5-m inflatable boat. Because virtually all of the whalewatching trips were approximately four hours in length,

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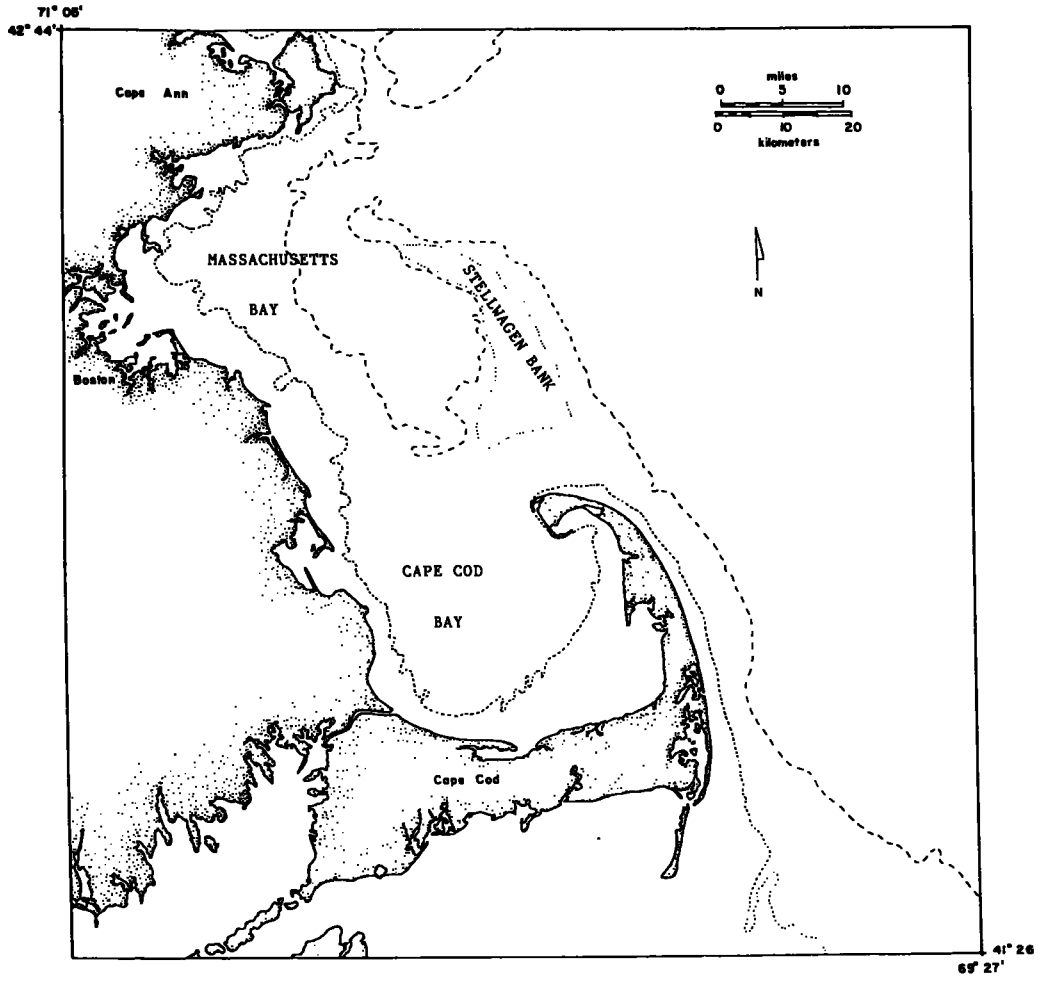

Figure 1

Map of minke whale, *Balaenoptera acutorostrata*, study area: Massachusetts Bay and Cape Cod Bay are located off the northeastern coast of the United States.

all cruises of eight hours or more were broken into separate four-hour blocks in an attempt to standardize temporal effort.

Cruises aboard the 12-m research vessel ran four fixed tracks in Cape Cod Bay between January and May each year. The tracks ranged from six to nine nautical miles in length and were approximately four nautical miles apart. These cruises searched specifically for North Atlantic right whales, *Eubalaena glacialis*; however, all marine mammal sightings were recorded. Owing to frequent unfavorable weather, the tracks were not surveyed equally; effort was concentrated mainly in the more sheltered eastern portion of the Bay. Cruises aboard the 14-m ketch occurred throughout the year and ran either four fixed tracks on Stellwagen Bank or directed searches in areas where large concentrations of whales had been recently reported or were known to have occurred in the past. The fixed tracks covered the southern portion of Stellwagen Bank, although two of the tracks extended northward to include the northwest corner of the Bank. The tracks on the southern portion of the Bank ranged from six to nine nautical miles in length, all tracks being approximately three nautical miles apart from one another. Again, all cetacean sightings were noted, although the majority of these cruises were directed primarily toward humpback whales. The remaining nonwhalewatch cruises were nonrandom, searching areas where large numbers of whales had been recently

reported. All whalewatching cruises were nonrandom and search tracks for these cruises were generally decided by the captain of the vessel.

Search effort was based on four-hour trips. It was not possible to quantify precisely observer effort; time spent searching inevitably varied somewhat between trips. However, because at least one observer was searching for whales constantly for the duration of each cruise (both on the whalewatching cruises and dedicated surveys), it is unlikely that significant differences existed in effort between months or years. Furthermore, because all trips were primarily focused on larger mysticetes, virtually all sightings of minke whales were opportunistic; consequently, search effort towards this species was effectively even throughout the study period. To minimize the possibility that minke whales were present but not sighted owing to bad weather conditions, all cruises conducted in fog or in sea states above Beaufort 4 were excluded from analysis. The total number of cruises for each month of all years is summarized in Table 1.

The following information was routinely collected: date, time, location (by using LORAN-C) and, where determinable, group size and behavior. Although photographs were occasionally taken during this study, the resulting data are not discussed here.

The following terms are used in this paper: **singleton** refers to a lone animal, **group** refers to two or more animals that were considered associated if they were swimming side by side and were generally coordinating their speed and direction of movement during their surfacing and diving behavior. Animals that were farther apart and did not show such coordination of movement were not considered associated. It is possible that two or more minke whales that were not side by side were in acoustic contact and therefore associating; however, such associations are impossible to identify in the field and were not considered in this study. **Feeding** refers to a whale observed with its mouth open or lunging at the surface where prey was visible in the water. It is highly likely that there were other instances in this study when feeding occurred below the surface but could not be observed; consequently, the feeding rates reported here should be considered minimum values. **Calf** refers to an animal considered to be a first-year calf if it was observed in close association with a large whale and was not more than half the apparent length of the latter (presumed to be the mother).

Results

Temporal distribution

There was a significant difference in the sighting rate of minke whales (number of whales observed per trip) from year to year ($\chi^2_{13} = 2188.7$, $P<0.001$); the maximum sighting rate was recorded in 1989 and the minimum in 1982 and 1986 (Fig. 2). Minke whales were observed in all months except January and February and showed significant differences in abundance by month (pooled over years) (Fig. 3). Pairwise comparisons of mean monthly values for the period of greatest effort (March through October) were conducted by using a one-way analysis of variance and are revealed in Table 2. There were no significant differences in the number of sightings between the months of March, April, May, and June (hereafter collectively termed "spring"), nor between July, August, September, and October (hereafter referred to as "summer-autumn") (Table 2). However, three of the four months of spring differed significantly from those of summer-autumn in all pairwise comparisons. The exception was March, for which sighting rates were not significantly different from those of any other month.

Calves

Only three calves were observed during the entire study period. Each sighting occurred at a different time of year: 8 May 1981, 3 October 1989, and 28 August 1991. Two of the calves were part of a pair, and the third was part of a group of three.

Table 1

The number of cruises conducted each year and each month for all years combined (1979-92) for minke whales, *Balaenoptera acutorostrata*, in Massachusetts Bay and Cape Cod Bay. Cruises in fog or where the sea state exceeded Beaufort 4 were excluded.

	Year													
	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
No. of cruises	127	207	414	517	630	723	789	878	875	972	989	979	1110	1039

	Month (all years combined)											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
No. of cruises	26	57	114	532	1409	1625	2091	2118	1415	793	44	25

Group-size frequency

A total of 5,806 minke whale sightings were recorded for which the group size could be reliably determined. Observed group-size frequency ($\bar{x}$=1.06, SD=0.315) for singletons (n=5,536) was 95.3%, for pairs (n=223) 3.8%, and for trios (n=46) 0.8%. With the exception of a single group of five whales, no groups larger than three were observed during this study.

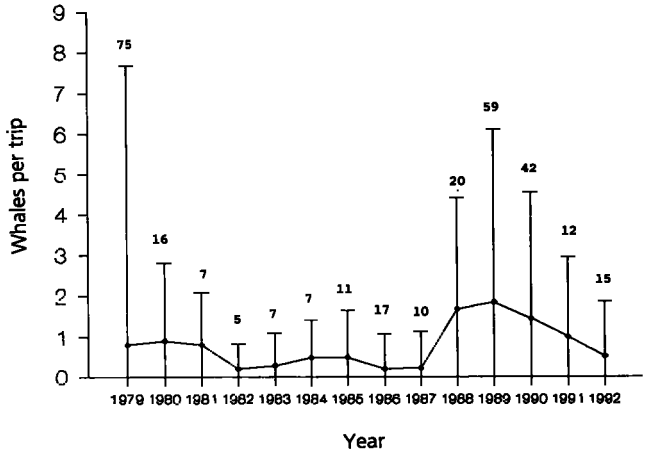

Figure 2

Observed variations in occurrence (mean and standard deviation) of minke whales, *Balaenoptera acutorostrata*, by year (1979–92) in Massachusetts Bay and Cape Cod Bay. Numbers above the bars represent maximum value for any one trip in that year.

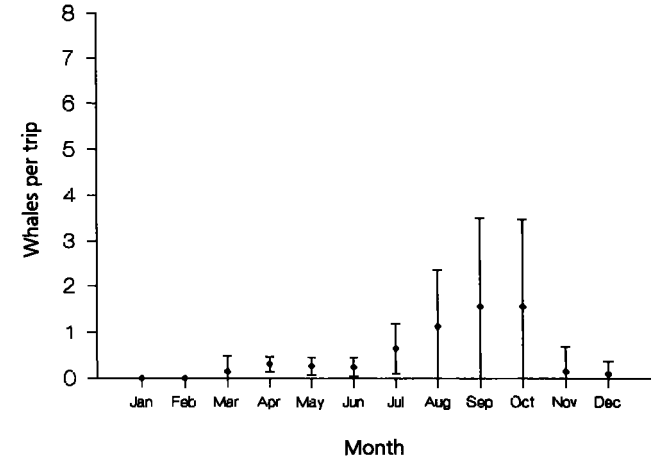

Figure 3

Observed variations in occurrence (mean and standard error) of minke whales, *Balaenoptera acutorostrata*, in Massachusetts Bay and Cape Cod Bay by month for all years (1979–92) of the study.

Feeding behavior

A total of only 27 (0.4%) of 6,266 sightings involved confirmed feeding at the surface. These sightings occurred in all months between May and October inclusively. In 24 of the 27 sightings of feeding, group size was recorded: single animals accounted for 21 (87.5%) of these, two sightings involved pairs, and one sighting a group of three whales.

Discussion

Temporal occurrence

Minke whales appear to arrive in the waters of Cape Cod Bay and Massachusetts Bay in the early spring and in some years occurred as late as December. The considerable interannual variability in the abundance of minke whales probably reflects variation in effort (see Table 1) or fluctuations, or both, in the abundance and distribution of prey. That it may be linked to the latter is suggested by the very low sighting rates recorded in 1986 and 1987, two years in which the local abundance of sand lance (*Ammodytes* spp.) is known to have been at a minimum and when other piscivorous mysticetes were largely absent from the study area (Payne et al., 1990). However, the concentration of effort on other mysticetes (and consequently on areas preferred by them) may have introduced a bias against minke whale sightings if these whales exhibit significant differences in habitat preference (this is currently unknown). Interannual variability in abundance has also been reported in other areas and has been similarly linked to prey availability, as well as to effort and, in Arctic areas, distribution of sea ice (Sigurjónsson, 1982; Larsen and Øien, 1988).

There was also considerable variation in abundance from month to month. The data reported here indicate a distinct peak in abundance beginning in July and continuing through September. No minke whales were observed in January or February: although this may have been due to the markedly decreased sampling effort during these two months, this appears unlikely given the dedicated (i.e. non-whale-watching) nature of the surveys conducted at this time and the frequently calm conditions which were a prerequisite for such cruises.

This general pattern of occurrence (abundant in summer, scarce or absent in winter) is similar to that reported for other high-latitude

Table 2

Results (from a one-way analysis of variance) of pairwise comparison of monthly mean sighting rates for minke whales, *Balaenoptera acutorostrata*, in Massachusetts Bay and Cape Cod Bay (1979–92). Figures shown are *P* values; significant differences are shown in bold type.

Month	Apr	May	Jun	Jul	Aug	Sep	Oct
Mar	0.69	0.88	0.98	0.06	0.05	0.06	0.08
Apr		0.64	0.44	**0.01**	**0.01**	**0.01**	**0.02**
May			0.76	**0.01**	**0.01**	**0.01**	**0.02**
Jun				**0.01**	**0.01**	**0.01**	**0.02**
Jul					0.19	0.10	0.13
Aug						0.47	0.58
Sep							0.87

minke whale populations, including those elsewhere in the North Atlantic. Data from Newfoundland, Iceland, and West Greenland show a similar seasonal distribution in which minke whales arrive in spring, are most abundant during mid- to late summer and begin to leave in the autumn (Sergeant, 1963; Mitchell and Kozicki, 1975; Kapel, 1980; Sigurjónsson, 1982). However, a few minke whales have been reported off western Newfoundland and Iceland in both November and December (Sergeant, 1963; Sigurjónsson, 1982), and minke whales have occasionally been caught off West Greenland between November and February (Kapel, 1980). The same seasonal occurrence is seen in the waters off Norway and in the Arctic where a few whales have been observed through the winter (Jonsgård, 1951). High-latitude areas of the North Pacific and the Antarctic are also characterized by a seasonal distribution similar to that observed in the North Atlantic (Shimadzu, 1980; Dorsey, 1983; Gong, 1987; Stern, 1990). Since most of these studies were not based on identified individuals, it is not clear whether minke whales in these areas are resident for long periods or whether the reported sightings represent short-term occupancy or transient passage by numerous animals.

If the apparent decrease in abundance of minke whales in Massachusetts Bay in autumn and winter is, as suggested above, unrelated to effort, it may reflect a migration of most minke whales to lower latitudes at that time of year. Data on the winter distribution of minke whales are scarce. In the southwestern North Atlantic, minke whales have been reported in the waters between Bermuda and the Antilles between the months of January and March (Mitchell, 1991; Mattila and Clapham, 1989; Mattila et al., in press). Stranding data show evidence of the presence of minke whales in the waters off Florida from December to February.[1] Winter sightings, while infrequent, have also been reported in the western Gulf of Maine and in waters southeast of Cape Cod (CeTAP[2]).

In the Southern Hemisphere, minke whales are also reported in lower latitudes during the winter. Off Brazil, as well as in the waters of the southwestern Indian Ocean, minke whales are mainly present in winter and spring (Williamson, 1975; Best, 1982). However, some have been reported trapped in sea ice in the Antarctic between May and October (Taylor, 1957); this finding, together with year-round sightings of minke whales in areas such as California (Stern, 1990), Greenland, Norway, and the Arctic suggests that a few animals may overwinter at higher latitudes.

Calves

During the fourteen years of this study only three minke whale calves were observed. Sightings of minke whale calves in high-latitude areas of the North Atlantic are rare; this is not the case for certain other mysticetes (e.g. humpback whales [Clapham and Mayo, 1987]; fin whales, *Balaenoptera physalus* [Clapham and Seipt, 1991]; North Atlantic right whales [Hamilton and Mayo, 1990]). Only two minke whale calf sightings were reported in the 1982 Cetacean and Turtle Assessment Program (CeTAP) study, both occurring just south of Cape Cod (one in

[1] Mead, J. Curator of marine mammals at the Smithsonian Institution. Natl. Mus. Nat. History, Smithsonian Institution, Washington, D.C. 20560. Unpubl. data, 1992.

[2] CeTAP (Cetacean and Turtle Assessment Program). 1982. Characterization of marine mammals and turtles in the mid- and North Atlantic areas of the U.S. Outer Continental Shelf. Final Rep. of the Cetacean and Turtle Assessment Program, Univ. Rhode Island, to the Bureau of Land Management, Washington, D.C.

April and the other in June). In the waters off Quebec, one pair (adult and calf) was observed in late July (Perkins and Whitehead, 1977). Similarly, calves have not been reported in the waters off the west coast of the United States (Dorsey, 1983) and are also not commonly observed on the high-latitude feeding grounds in the Southern Hemisphere (Kasamatsu et al., 1988).

In the North Atlantic, the majority of minke whale calf sightings have occurred in lower latitudes. In the southwestern North Atlantic, calves have been sighted in the waters between Bermuda and the Antilles (Mitchell, 1991) as well as in the northern Leeward Islands (Mattila and Clapham, 1989).

One possible explanation for the absence of calves in higher latitudes is that minke whales wean their calves before entering these waters. According to Jonsgård (1951), North Atlantic minkes are thought to calve between November and March, and nursing is believed to last for only four to five months. This information would concur with reports of no or few lactating females found during the summer off both Norway (Jonsgård, 1951) and Newfoundland (Sergeant, 1963; Mitchell and Kozicki, 1975).

In the Southern Hemisphere, it also appears that females wean their calves before reaching higher latitudes (Best, 1982; Kato and Miyashita, 1991). However, there is evidence (at least in the Southern Hemisphere) that pairs (mother and calf) may remain in low or middle latitudes until weaning occurs (Kato and Miyashita, 1991), which suggests that some minke whale populations segregate by reproductive class.

Segregation by both sex and age class has been described in many minke whale populations. Whaling data from the North Atlantic, the North Pacific, and the Southern Hemisphere suggest that minke whales segregate by sex during their summer migration (Jonsgård, 1980; Kasamatsu and Ohsumi, 1981; Sigurjónsson, 1982; Larsen and Øien, 1988; Wada, 1989) as well as on their feeding grounds (Jonsgård, 1980; Ohsumi, 1983; Larsen and Øien, 1988; Wada, 1989; Kato et al., 1990a). Segregation by maturational class has also been recorded in minke whales (Best, 1982; Ohsumi, 1983; Wada, 1989; Kato et al., 1990a). Jonsgård (1951) suggested that newly weaned calves and juveniles off Norway probably do not migrate north together with larger animals, which is in agreement with data reported by Wada (1989) for areas off the Pacific coast of Japan.

Neither the sex nor age class of the minke whales in the waters of Cape Cod and Massachusetts Bay areas is known because it is not currently possible to determine either in the field. Stranding data from this area give a mean length for minke whales of 505 cm (n=35, SD=140.3 cm); comparison of this figure with data on lengths of individuals caught in North Atlantic whaling operations (Jonsgård, 1951; Sergeant, 1963; Mitchell and Kozicki, 1975; Christensen, 1981) would suggest that the majority of animals that have stranded here were immature. The sex ratio of stranded animals was approximately even. Whether this sample is representative of the general population or only of those more likely to strand is unknown.

Group size

In this study approximately 95% of all minke whale sightings were singletons. Single animals appear to predominate in other studied areas, although there is evidence of group size changing by season, latitude, sex and age class, and when prey is present. In some cases, however, it is unclear whether animals reported in large groups (particularly when feeding) are actually associated with or are simply attracted to a common location by the presence of prey.

Data from the Mingan Islands in the Gulf of Saint Lawrence show that minke whales are usually solitary, although they are seen in large coordinated groups of five to fifteen animals when actively feeding.[3] Aerial surveys conducted off Iceland in June and July reported a mean school size of 1.1 (Gunnlaugsson et al., 1988). Jonsgård (1951) found that minke whales tend to travel alone off the western coast of Norway, noting only a few sightings consisting of pairs; in the Arctic, single animals were predominant in catches, although groups of three to ten animals were more common than pairs. In the western North Pacific off the Chukotka coast, sightings were usually of single animals. However, when polar cod arrive in late June and in July, minke whales are often observed in groups of five or six animals (Ivashin and Votrogov, 1981); again, it is not clear whether such groups are truly associated according to the definition of 'group' used here. Information on minke whales in the Southern Hemisphere also indicates variabilty in group size with changes in latitude and season as well as with differences in maturational class (Williamson, 1975; Best, 1982; Kato et al., 1989; Kato et al., 1990b).

The group size frequency of minke whales observed in the Massachusetts Bay and Cape Cod Bay areas did not appear to change with time of year or with the presence of prey (on the basis of sightings where confirmed feeding occurred). Because the majority

[3] Sears, R., F. W. Wenzel, and J. M. Williamson. 1981. Behavior and distribution observations of Cetacea along the Quebec north shore (Mingan Islands), summer–fall 1981. Mingan Islands Cetacean Study, Montreal, Unpubl. Rep., 72 p.

of sightings were singletons it is possible that sex or age class has little or no effect on group size in this area, unless one sex or class is disproportionately represented here. The apparent predominance of immature whales among stranded specimens may reflect a similar overrepresentation of juveniles in the general population; if this is the case, the abundance of singletons would agree with the finding of Kato et al. (1990b) that immature animals along with mature males tend to be solitary, whereas mature females usually form schools, especially near the pack ice.

Feeding behavior

In this study less than one percent of all minke whale sightings involved confirmed feeding behavior. The CeTAP study (1982) also reported relatively few sightings of surface feeding. The lack of surface feeding in the study area is odd given that sympatric confamilials are commonly observed feeding (e.g. humpback whales [Payne et al., 1986]; fin whales [Overholtz and Nicolas, 1979]). In other areas of the North Atlantic, minke whales are observed feeding, displaying surface lunges and rolling (Sears et al.[3]; Haycock and Mercer[4]). Near the San Juan Islands, off the west coast of North America, minke whales also exhibit lunging and rolling behavior during feeding (Hoelzel et al., 1989; Dorsey et al., 1990).

Off the San Juan Islands minke whales appear to prey mainly on small schooling fish (juvenile herring, *Clupea harengus*; sand lance, *Ammodytes* spp.) (Dorsey, 1983; Dorsey et al., 1990), which are also the principal food source for minke whales off the Mingan Islands (Sears et al.[3]). Both humpback and fin whales feed primarily on herring or sand lance in the southern Gulf of Maine (Overholtz and Nicolas, 1979; Payne et al., 1990); many observers assume that these fish also represent a principal prey of minke whales, a belief which is strengthened by the scarcity of minke whales in Massachusetts Bay during 1986 and 1987 when the local sand lance population crashed (Payne et al., 1990). However, it is not understood why these minke whales rarely exhibit feeding behavior at the surface, unless whales in this area either exploit fish schools at greater depths than do whales recorded for other feeding grounds or employ a foraging technique that does not utilize the surface for catching prey.

Nearly all minke whales observed feeding during this study were singletons, a finding which is similar to that reported from other areas such as the western coast of North America where minke whales appear to act independently of each other even though several individuals may be present in the same area while feeding (Hoelzel et al., 1989; Dorsey et al., 1990). According to many studies (Ivashin and Votrogov, 1981; Bushuev, 1991, Sears et al.[3]), minke whales tend to group together when food is abundant, but it was unclear whether these animals were feeding cooperatively or were drawn to the same area by the availability of food and were feeding independently.

Conclusion

In general, both the yearly and seasonal distribution of minke whales in Massachusetts Bay and Cape Cod Bay is similar to that found for other populations of this species. The data in this study also generally agree with other published information pertaining to group size, feeding behavior, and the occurrence of mother-and-calf pairs. Unfortunately, because the social structure and group composition of the minke whales observed in this study are unknown, it is impossible to determine whether or not the minke whales of Massachusetts and Cape Cod bays exhibit the same segregational patterns that have been suggested for other populations of this species in both the northern and southern hemispheres. It would also be valuable to explore whether individual minke whales return to the same area from year to year as documented off the west coast of North America, or whether the minke whales seen here represent transient individuals from one or more populations. Continued study with an emphasis on photographic identification of individuals is greatly needed as well as continued work in the biopsy of individuals throughout the year in order to gain some insight on the sex ratio, genetic structure, and group composition of this and other populations.

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[4] Haycock, C. R., and S. N. Mercer. 1984. Observations and notes on the abundance and distribution of cetaceans in the Eastern Bay of Fundy near Brier Island, Nova Scotia, in August and September 1984. Unpubl. Rep.

minkes really are whales and for allowing me extra time to see whether they really do anything besides breathe. This study was made possible in part by funding for data management provided by the U.S. National Marine Fisheries Service (Northeast Fisheries Center) under contract 50-EANF-9-00033.

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Activities of juvenile green turtles, *Chelonia mydas*, at a jettied pass in South Texas

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Green turtles, *Chelonia mydas*, have a worldwide distribution in tropical and subtropical regions. Primary nesting areas in the Atlantic region are located at Ascension Island, Aves Island, Costa Rica, and Surinam. The east coast of Florida has the largest breeding assemblage in the United States. The species is listed as endangered by the International Union for the Conservation of Nature (IUCN) (Groombridge, 1982) and is listed as threatened in all areas, except for breeding populations in Florida and the Pacific coast of Mexico, which are listed as endangered (National Marine Fisheries Service, 1991).

During most of the nineteenth century, green turtles were abundant throughout Texas, including the lower Laguna Madre (Hildebrand, 1982; Doughty, 1984). Commercial harvest of these turtles peaked in 1890; Texas landings increased to about 2,160 turtles (265,000 kg) from an estimated 89 turtles (10,909 kg) in 1880. By the early twentieth century the fishery had collapsed (Doughty, 1984).

Understanding habitat needs has been recognized as an essential element for successful recovery of sea turtle stocks in the Gulf of Mexico (Thompson et al., 1990). Distribution, movements, and feeding habits of pelagic hatchlings are unknown. Little research has been conducted on sea turtle populations in Texas. Published stranding data suggest that Texas nearshore and inshore waters are important habitats for juvenile and subadult sea turtles (Rabalais and Rabalais, 1980; Manzella and Williams, 1992). Recent tracking and mark-recapture studies on green turtles indicate that jetties and channel entrances along the south Texas coast serve as summer developmental habitats for this species[1,2] (Manzella et al., 1990; Shaver, 1990, 1994). This is supported by higher numbers of sightings in south Texas versus the upper Texas and west Louisiana coasts (Williams and Manzella, 1991).

Turtles using jetties and channel entrances could interact with human activities, such as channel dredging, shrimping, and recreational fishing and boating. The level of such interaction is dependent on the nature and degree of jetty and channel utilization. Studies conducted during 1991[1,2] indicated that green turtles may utilize jetty habitat to a greater degree than other habitats within Brazos-Santiago Pass, on the basis of sightings and the behavior of a single radio-tracked turtle. The objectives of our study were to describe juvenile green turtle movements within Brazos-Santiago Pass, Texas. We hypothesized that juvenile green turtles select jetty habitat over other habitats within Brazos-Santiago Pass.

Materials and methods

Study area

The study was conducted in the Brazos Santiago Pass area, South Padre Island, Texas (Fig. 1). The pass, extending from the tip of the jetties to the western edge of Barracuda and Dolphin Coves, links the Laguna Madre to the Gulf of Mexico. Landry et al.[1] characterized habitat types within the pass. Using their data, we designated four habitats in the pass area.

The jetty habitat extended 10 m from the visible jetty, with water depths up to 3 m. It contained partially exposed and submerged granite boulders and rubble, which decreased in density as distance from the jetty increased. The highest density and concentration of sessile organisms were found in this habitat. Barnacles (*Balanus* sp.), sea urchins (*Arbacia punctulata*), and

[1] Landry, A., Jr., D. Costa, B. Williams, and M. Coyne. 1992. Turtle capture and habitat characterization study. Final Rep. submitted to the U.S. Army Corps of Engineers, Galveston District, 2000 Fort Point Blvd., Galveston, TX 77553, 112 p.

[2] Renaud, M., G. Gitschlag, E. Klima, S. Manzella, and J. Williams. 1992. Tracking of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles using radio and sonic telemetry at South Padre Island, Texas. June–September 1991. Final Rep. to the U.S. Army Corps of Engineers, Galveston District, 2000 Fort Point Blvd., Galveston, TX 77553, 52 p.

Manuscript accepted 5 December 1994.
Fishery Bulletin 93:586–593 (1995).

three algal species (*Ulva fasciata*, *Podina vickersiae*, and *Bryocladia thysigera*), were the most abundant organisms associated with jetty structure.[1] The near-jetty habitat encompassed areas of barren bottom and scattered boulders on both the Gulf and pass side of the jetty. Channel habitat, the dredged portion of the Brownsville Ship Channel between the jetties, extended seaward from Barracuda and Dolphin Coves to the tip of the jetties. It was characterized by a scoured bottom, nearly void of vegetation. Water depths ranged from 10 to 15.2 m and averaged 12.5 m. Channel width was about 90 m for most of its length. East of the coves, the distance from the jetty to the channel edge ranged from 115 to 152 m. Barren rippled sand, water depths up to 7.5 m, and few organisms were noted within the cove habitat.

Capture of sea turtles

Turtles were obtained from Texas A&M University (TAMU) Institute of Marine Life Science personnel, who were conducting a netting and habitat characterization study at Brazos-Santiago Pass.[3] Turtles were captured either through use of entanglement nets (45.7–91.5 m long, 3.7–7.3 m deep, 12.7 cm bar mesh) set at the Gulf side of the South Jetty, or by encircling a targeted turtle in the shallow coves with the entanglement net. For turtles exhibiting strong site fidelity, 1-m diameter cast nets were used for some captures along the jetties.

Tagging activities

Following capture, turtles were transported 1–2 km to a holding facility where they were kept for 24–48 hours. We recorded turtle weights, straight-and curved carapace lengths and widths, and applied radio and sonic transmitters. Telonics radio transmitters (180 g) with 40-cm antennas were fitted with fiberglass to the second neural scute of nine turtles, and Sonotronics sonic transmitters (36 g) were bolted to the posterior marginal scutes. Turtles were designated T1 through T9. The weight of the backpack-type transmitters never exceeded

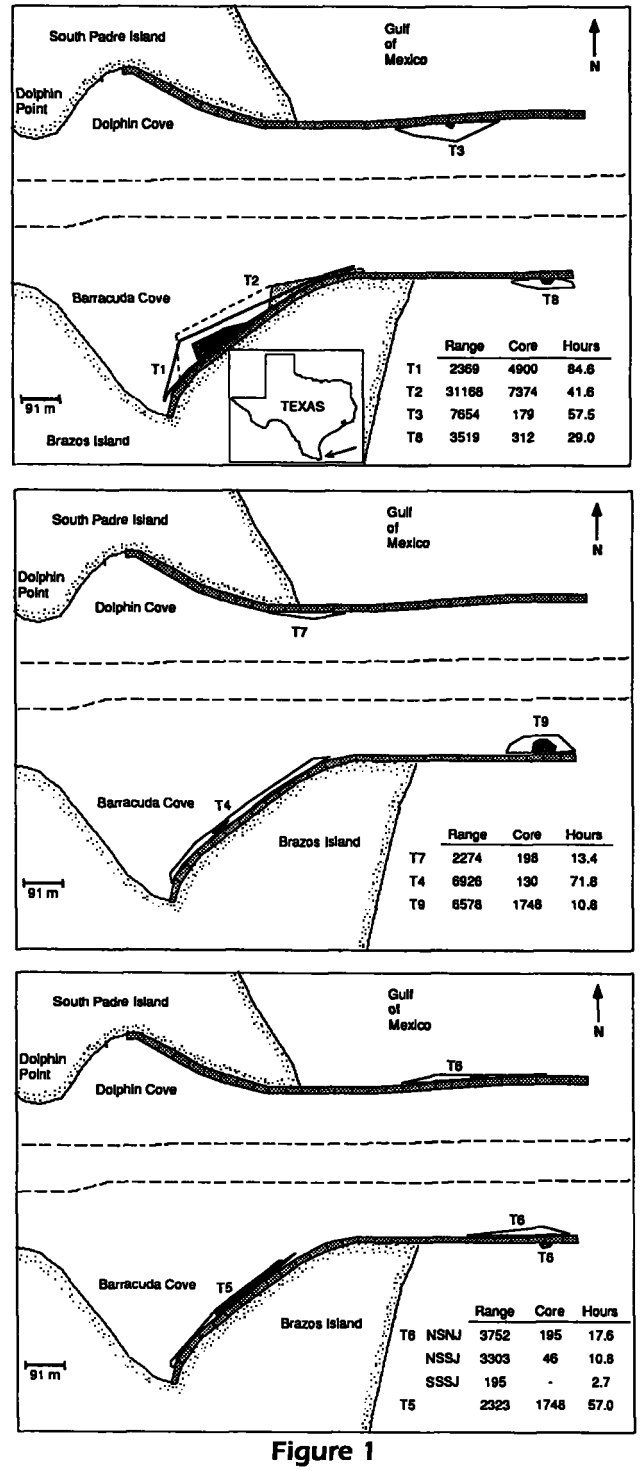

Figure 1

Range (m^2), core area (m^2), and total hours tracked for individual green turtles, *Chelonia mydas*, T1-T9, during August–September 1992. Core area is displayed in solid black and range is enclosed by a solid line for all turtles except T2. T2 has a shaded area representing its core area and a dashed line surrounding its range. For T6, NSNJ = north side of north jetty, NSSJ = north side of south jetty, and SSSJ = south side of south jetty. An inset of the state of Texas with an arrow showing our area of study is located in the upper third of the figure.

[3] Landry, A., Jr., D. Costa, M. Coyne, K. St. John, and B. Williams. 1993. Sea turtle capture and habitat characterization: South Padre Island and Sabine Pass, TX environs. Final Rep. submitted to the U.S. Army Corps of Engineers, Galveston District, 2000 Fort Point Blvd., Galveston, TX 77553, 109 p.

10% of the weight of the turtle, in accordance with the safety recommendations of Brander and Cochran (1969), Bradbury et al. (1979), Aldridge and Bringham (1988), and Byles and Keinath (1990).

Tracking

Turtles were released at their capture sites between 0900 and 1600 hours. We used a Telonics TR2/TS1 receiver-scanner connected to a directional 5-element Yagi antenna to monitor radio transmitters until they became detached from turtles. Maximum radius of signal reception with this equipment is approximately 16 km. When weather prohibited tracking by vessel, turtles were monitored from land. Sonic transmitters were monitored by using a Dukane directional hydrophone with a receiving range between 0.6 and 1.1 km. Sonic tracking alone was used when a turtle had lost its radio transmitter but retained its sonic transmitter or when a second turtle was present in the area of a turtle being monitored by radio.

Data were collected for 12 hours each day. All hours of the day and night were included by offsetting each day's start time by two hours from that of the previous day. We attempted daily to locate every turtle with a functioning transmitter. Up to five turtles were tracked during each day. Geographic location was recorded when a turtle was sighted or its position obtained with sonic telemetry. Reference marks were painted at 50-m intervals on jetty boulders, westward from the seaward tip of each jetty. Locations of turtles were determined with respect to reference marks and to visual estimates of perpendicular distance from the jetties. When possible, turtle locations >40 m from the jetty were recorded by means of a portable global positioning system. The total time spent between jetty reference marks was calculated for each turtle. Each turtle position was given a weight equal to time spent at that position. These weighted positions were then used to calculate a mean position for each turtle. Minimum observation time used for this analysis was 5 minutes. Range (area containing 95% of locations) and core area (area containing 50% of locations) were developed by using the minimum convex polygon method (Mohr, 1947), modified to exclude nonwater areas. To discern differences in movement patterns, the ranges and core areas for each turtle were determined for dawn (0500–0900 h), day (0900–1700 h), dusk (1700–2100 h), and night (2100–0500 h) if at least three days were sampled and >5 h of tracking information were available for a turtle within a time period. To obtain an index of turtle movements, the distance and time between surfacing events were calculated for each turtle and used to estimate mean speed of movements for dawn, day, dusk, night, and all times combined.

Surface and submergence behavior

Surface and submergence times were calculated for each turtle affixed with a radio transmitter. Data collected on the day of release were omitted from analyses of ranges and of surface or submergence behaviors. Surface time was considered to be the interval between the beginning and ending of radio signals (i.e. when the turtle was within 40 cm of the ocean surface). Submergence time was defined as the interval between the end of a radio signal and the beginning of the next signal (i.e. when the turtle was deeper than 40 cm). Overall mean surface and submergence times, and day, night, dawn, and dusk means were calculated for each turtle. A surface or submergence interval overlapping two time periods was included in the period containing the majority of the interval.

Statistical methods

Distribution of variables (surface and submergence times, movement speed) were tested with the Shapiro-Wilk test for normality (α=0.05). The Kruskall-Wallis analysis was used to test for differences in means between dawn, day, dusk, and night (α=0.05) (Sokal and Rohlf, 1981) when the null hypothesis (normal distribution) was rejected. If a significant difference was indicated, a means test described by Conover (1980) was used to determine which means differed, again by using α=0.05.

Results

Sea turtle movement patterns

Nine green turtles (29.1–47.9 cm straight carapace length [SCL], 2.6–14.8 kg) were tracked from 14 to 58 days from 31 July to 26 September 1992 (Table 1). Differences in tracking periods were due to different capture dates and variable tag retention. In addition, on some days certain turtles could not be located owing to inclement weather. All turtles moved away from the jetties immediately following release. Those released between the jetties entered the deeper waters of the channel, but T8, released on the Gulf side of the south jetty, moved south, roughly parallel to the beach. Seven turtles returned to the jetties within an hour. T6 and T7 went offshore after entering the channel and returned to the jetties the next

Table 1

Percent total submergence time (PTST), maximum submergence time (MST, minutes), weight (kg), straight carapace length (SCL, cm), and dates tracked for nine green turtles, *Chelonia mydas*, at South Padre Island, Texas.

Turtle	PTST	MST	Weight	SCL	Date
T1	88.8	24.3	14.8	47.9	31 Jul –26 Sep
T2	92.4	21.4	11.5	44.7	01 Aug–25 Sep
T3	96.3	32.9	3.1	30.1	01 Aug–26 Sep
T4	80.8	31.2	2.7	29.1	01 Aug–26 Sep
T5	90.1	25.4	2.6	29.2	01 Aug–26 Sep
T6	96.3	39.8	3.6	31.5	02 Aug–26 Sep
T7	93.1	25.8	3.9	33.3	06 Aug–26 Sep
T8	96.5	37.8	3.4	31.5	09 Aug–26 Sep
T9	97.8	38.1	4.1	33.0	10 Aug–23 Sep

day. Seven turtles remained in the general area of their capture throughout the study period. Of the others, T6 used three areas along both jetties and T7 moved extensively along both jetties before moving up the channel and into South Bay. Only data from the pass were used in analyses for T7.

Daily movements of turtles along the jetties ranged from less than 50 m to more than 1,000 m. Mean rate of movement ranged from 8 m/h to 568 m/h (Table 2). The least movement occurred at night, ranging from 8–127 m/h. Seventy percent of all locations were within 5 m of the jetties. Only 0.3% were within channel boundaries, including five channel crossings. Overall areal ranges of turtles remaining in the jetty area were from 2,274 to 31,168 m^2. Overall core areas ranged from 130 to 7,374 m^2.

Five of the nine turtles tracked had ranges restricted to the north side of the south jetty (Fig. 1). Northerly winds, in excess of 20 knots, coincided with the movement of T6 from the windward side of the north jetty into protected waters near the south jetty by day 14. Mean locations for three turtles (T1, T4, and T5) were within 400 m of the Barracuda Cove beach. The mean location of T2 was about 650 m from the beach, about halfway up the jetty. The only turtle that had significantly different mean locations for different time periods was T1 ($P<0.05$). The mean dusk location of T1 was about 250 m closer to the jetty tip than its mean dawn and day locations and over 400 m closer than its mean night location. T3, on the south side of the north jetty, also showed greater westward movement at night than at any other time ($P<0.05$).

Table 2

Mean distance (m) moved by hour by time period for nine green turtles, *Chelonia mydas*, tracked near South Padre Island, Texas. A line above mean movements indicates no significant difference ($\alpha=0.05$).

Turtle	Time of day			
T1 Period	Night	Dawn	Dusk	Day
Mean distance	127	161	401	251
T2 Period	Night	Dawn	Day	Dusk
Mean distance	8	148	440	568
T3 Period	Dusk	Day	Dawn	
Mean distance	20	102	323	
T4 Period	Night	Dusk	Dawn	Day
Mean distance	25	223	243	330
T5 Period	Night	Day	Dawn	Dusk
Mean distance	45	144	108	191
T6 Period	Dusk	Day		
Mean distance	59	225		
T7 Period	Night	Dawn	Day	
Mean distance	9	496	517	
T8 Period	Dawn	Dusk	Day	
Mean distance	171	195	201	
T9 Period	Day	Dawn		
Mean distance	114	149		

Submergence and surface behavior

Tracking was conducted for a total of 108 hours at dawn, 247 h during the day, 60 h at dusk, and 151 h at night. Time spent submerged ranged from 80.8 to 97.8% and averaged 91% for all turtles (Table 1). Submergence time ranged from 0.02 to 39.8 minutes. Overall mean submergence time varied from 1.9 to 6.1 min between turtles. Surface time ranged from 1 to 1,146 seconds. Overall mean surface time varied from 8.5 to 26.5 seconds.

A breakdown of submergence time by turtle revealed that 99% of all turtle submergences were <20 min, 74–96% were <10 min, and 38–64% were <1 min (Fig. 2). Submergence patterns were significantly different when data were analyzed by dawn, day, dusk, and night (Table 3). The number of submergences >10 min was higher at night than at other time periods for every turtle tracked at night.

A breakdown of surface time by turtle revealed that 99% of all turtle surfacings were <120 sec, 67–92% were <15 sec, and 41–77% were <5 sec (Fig. 2). Surface patterns also were significantly different when

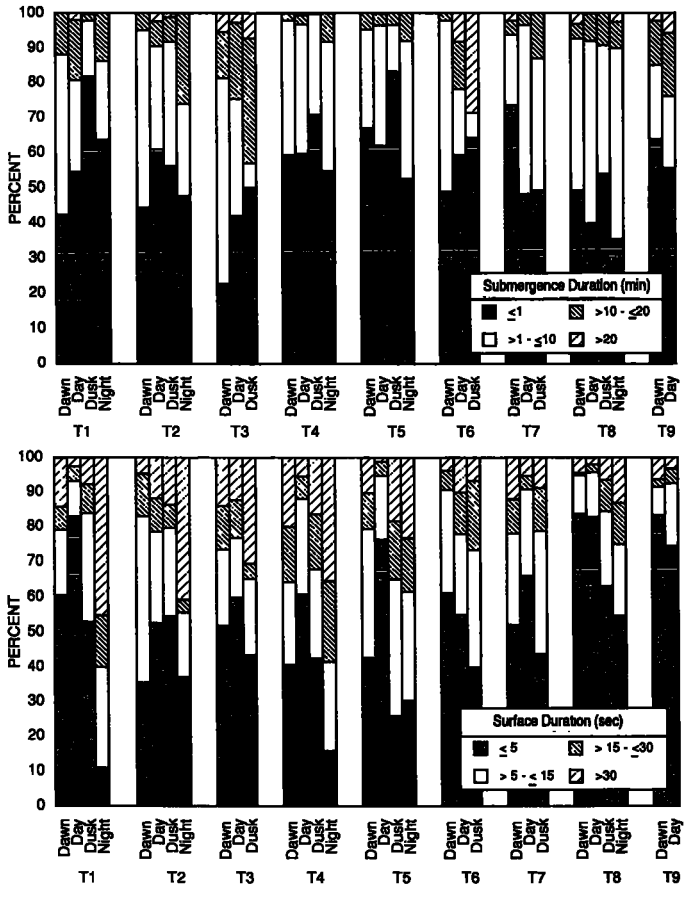

Figure 2

Green turtle, *Chelonia mydas*, submergence and surface durations by specified time intervals in hours, dawn (0500–0900), day (0900–1700), dusk (1700–2100), and night (2100–0500).

data were analyzed by dawn, day, dusk, and night (Table 3). The number of surfacings >15 sec was higher at night than at other periods for every turtle tracked at night. The mean surface time was significantly higher at night than at all other time periods for four of six turtles tracked at night.

Discussion

Movements and habitat use

Habitat use by juvenile green turtles in the Brazos-Santiago Pass was not proportional to available habitat.[1,2] The jetty habitat, which contained extensive algal mats, received a disproportionately high amount of use, suggesting that turtles possibly congregated there for food. Analysis of stomach contents of juvenile green turtles by Landry et al.[3] support the utilization of algal food sources. Turtles in this study were seen feeding on algal growth along the jetties, especially at dusk. The abundance of food may account for the high site fidelity and small core areas. Other studies of similar-size green turtles described their food source as algae (Wershoven and Wershoven, 1989; Wershoven and Wershoven, 1991), both algae and sea grasses (Burke et al., 1991), and primarily sea grasses (Ogden et al., 1983). Mendonca (1983), working with larger turtles (7.8–54.5 kg) postulated that green turtles prefer sea grass. Sea grasses were present within 1 km of the jetty habitat of our study area.[4] One turtle from our study entered and remained in a sea grass habitat for over a month; however, no fecal or stomach samples were taken while it was in this habitat. Bjorndal et al. (1991) suggested that green turtles possess gut microflora for digestion of both algae and seagrass and that the relative abundance of microbial species would vary in response to longterm changes in diet. Therefore, turtles could take advantage of a local abundance in either food source.

All of the turtles in this study had small ranges of movement. A juvenile green turtle tracked at the jetties in 1991 also showed limited movements.[2] The most limited movements were at night, suggesting that resting was most common at night. This hypothesis is supported in studies by Bjorndal (1980), Mendonca (1983), and Ogden et al. (1983) who documented resting areas for turtles at night coupled with a shorter range of movements compared with activity during the day. Mendonca (1983) noted that during summer months the resting sites of green turtles on consecutive nights were within meters of the previous night's rest site. The reason for the westward movements of T1 at night is unknown. The more sheltered jetty habitat adjacent to the cove may have been preferred for resting at night, whereas a broader stretch of the jetty was utilized for daytime foraging activities. Turtles at the jetties apparently have an abundant food source in proximity to resting sites. In contrast, Mendonca (1983) recorded areal ranges of 0.48 to

[4] Quammen, M., and C. Onuf. 1991. Laguna Madre: seagrass changes continue decades after salinity reduction. Rep. to the National Wetlands Center, U.S. Fish Wildl. Serv., Campus Box 39, 6300 Ocean Dr., Corpus Christi, TX 78412, 27 p.

5.06 km^2 for juvenile green turtles. Ogden et al. (1983) found turtles moved up to 0.5 km between feeding and resting sites, but they did not report ranges of movement.

Turtles appeared to select for the south jetty. Landry et al.[3] also recorded many more turtle sightings at the south jetty than at the north jetty. Of two turtles caught at the north jetty, only one remained there longer than two weeks. The other moved to the south jetty during northerly winds in excess of 20 knots. Because of its accessibility, the north jetty received much more use by the public than the south jetty. The effect of this disproportionate use on turtle presence or behavior, or both, during the study is unknown.

Submergence behavior

Green turtle behavior was characterized by numerous short submergences and surfacings. Submergences ≤5 min occurred mostly during dusk and dawn when active periods of foraging were observed. We felt this was a direct effect of the shallow habitat occupied by the turtles. The transmitter antenna could be exposed at times when the turtle was still submerged. Submergence ≥10 min was observed at night and minimally during the afternoon.

Submergence durations by green turtles in our study was similar to that for green turtles studied by Renaud et al.[2] Eighty-nine to ninety-nine percent of the submergences were <10 min in duration and 17–56% were <1 minute. Mean submergence times for turtles in our study were considerably shorter than the mean submergence times of Kemp's ridleys found by Byles (1989) (18.1 min), and Mendonca and Pritchard (1986) (16.7 min). This may be a result of the different habitats and feeding behaviors of Kemp's ridleys and the green turtles in our study. Our turtles also were smaller than turtles in the other two studies.

The percentage of submerged time for each 24-h day ranged from 80.8–97.8%. The turtles with the three lowest percent submerged times were observed for long periods with their antenna only partially exposed. This behavior undoubtedly lowered their submerged to surface ratio. Balazs (1994), through satellite telemetry, found that two migrating adult green turtles in the Pacific Ocean spent 95–96% of their time submerged. Renaud and Carpenter (1994) found percent submerged time to be 90.0–95.7% for three satellite-tracked juvenile loggerhead turtles, *Caretta caretta*, in the Gulf of Mexico. Two satellite-tracked juvenile Kemp's ridley sea turtles, in the Atlantic and Gulf of Mexico, had percent submerged times of 94.0–98.6% (Renaud, in press). Byles (1989), studying adult Kemp's ridleys in the Gulf of Mexico with satellite telemetry, found that they spent an average 96% of the time submerged. A study of radio-tracked loggerheads with 64.0–91.9 cm carapace length (straight or curved not specified) in the Canaveral Channel, Florida, revealed that they averaged 96.2% of the time submerged (Kemmerer et al., 1983).

Table 3

Mean surface and submergence times (nearest sec) by time period, for nine green turtles, *Chelonia mydas*, tracked near South Padre Island, Texas. A line above mean values indicates no significant difference (α=0.05). D = day; K = dusk; N = night; W = dawn.

Turtle		Time of day			
T1	Surface	D5	K11	W13	N47
	Submerge	K60	N172	W214	D236
T2	Surface	D15	K21	W10	N26
	Submerge	D142	K143	W153	N320
T3	Surface	D12	W13	K16	N56
	Submerge	D327	W366	K446	N1371
T4	Surface	D19	K24	W29	N35
	Submerge	K58	D102	W108	N169
T5	Surface	D5	W13	K19	N20
	Submerge	K70	D102	W109	N187
T6	Surface	W7	D11	K15	N80
	Submerge	W125	D321	K501	
T7	Surface	D9	K12	W14	
	Submerge	W123	D145	K184	
T8	Surface	D5	W6	K9	N13
	Submerge	K171	D174	W175	N258
T9	Surface	W6	D6		
	Submerge	W212	D313		

Channel use

During our study, turtles remained primarily near the jetties, probably because food was abundant there and virtually absent in the channel and barren bottom areas. Turtles were found in the channel <0.3% of the time. They appeared to use the channel for transit to other areas or as presumed escape cover.

Conclusions

Our data, combined with numerous sightings of turtles at the jetty[3] and with the fact that there was no appreciable movement away from the jetties by tracked turtles, support the hypothesis that juvenile green turtles in Brazos-Santiago Pass, south Texas, selected for jetty habitat over other habitats available. If this pattern is consistent for all times that green turtles inhabit the pass, then it would indicate that potential harm from hopper dredging or channel boat traffic would be minimal. Our study included only nine turtles and was limited to August–September 1992. Therefore, caution should be used in extrapolating our results to other years or times of the year. The study was timed to coincide with the period of highest turtle abundance in the pass. Data gathered by TAMU indicate that use of the pass by green turtles increases during June–September.[1,3] Turtles appear to be rare from December to March and gradually begin to increase in numbers starting in April. We were unable to monitor turtle behavior during dredging, because no dredging was done during the study; therefore, we do not know how dredging of the channel may affect behavior of turtles occupying the jetty habitat.

Because green turtles are herbivorous, there is very little danger of hook and line captures from jetty fishing. The greatest impact on turtle behavior may be simply that of human activity on the jetties. The level of that impact is currently unknown. We encourage further study, particularly during other times of the year.

Acknowledgments

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Determination of age and growth of swordfish, *Xiphias gladius* L., 1758, in the eastern Mediterranean using anal-fin spines

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Estimates of growth rates of billfish are important because they are necessary elements of population dynamics models used in the assessment of stocks for this family of fish. Otoliths have been used for ageing most billfish species (Radtke, 1983; Radtke and Hurley, 1983; Wilson and Dean, 1983; Prince et al., 1984; Hill et al., 1989) but several authors have pointed out that the use of dorsal- and anal-fin spines are more practical in terms of ease of collection and processing (Berkeley and Houde, 1983; Hedgepeth and Jolley, 1983; Hill et al., 1989; Tsimenides and Tserpes, 1989). Other skeletal structures such as vertebrae have rarely been used and results have been poor (Prince et al., 1984; Hill et al., 1989).

The swordfish, *Xiphias gladius*, is a cosmopolitan billfish species that is highly exploited in the Atlantic Ocean and the Mediterranean Sea. In the Mediterranean the average size of harvested swordfish has declined over the last decade such that juveniles compose as much as 50–80% of the catch (Di Natale, 1990; Tserpes et al., 1993). However, the existence of contradictory estimates of growth parameters makes assessment of swordfish stocks difficult (Anonymous, 1990; 1993).

Age of swordfish has been estimated from otoliths (Radtke and Hurley, 1983; Wilson and Dean, 1983), and sections of anal-fin spines (Berkeley and Houde, 1983). Of these ageing methods only Ehrhardt (1992) achieved partial validation of the anal-fin method through marginal increment analysis. This analysis assumes that time of annulus formation corresponds to the time when marginal increments are minimal, and it has been widely used to determine the timing of annual increment formation in otoliths and scales of various fish species (Wenner et al., 1986; Maceina et al., 1987). Although the assumption of the analysis is valid for any ageing structure, the method has rarely been applied to structures other than otoliths and scales.

Tsimenides and Tserpes (1989) conducted growth studies on swordfish from the Aegean sea using anal-fin spines but did not attempt validation. They concluded that there was "a degree of uncertainty" in age estimates due to the loss of the first annulus in older animals.

The primary goal of this paper is to determine whether growth bands in anal-fin spines used for age determination of swordfish are deposited annually. Because Ehrhardt (1992) reported that the von Bertalanffy growth function did not adequately represent swordfish growth, we propose a second objective, namely to compare the growth function proposed by Ehrhardt (1992) with the standard von Bertalanffy model for representing growth of Mediterranean swordfish.

Materials and methods

Fish sampling and spine preparation

A total of 1,325 swordfish samples were obtained from commercial longline catches landed at the ports of Kalimnos (n=782), Kithnos (n=185), and Chania (n=358) in the Aegean sea. These ports, located on the islands of Kalimnos, Kithnos, and Crete are part of a national project addressing the fishery and biology of swordfish in the Greek seas (De Metrio et al., 1989). Samples were collected from 1987 to 1992 during alternate months from February to October. However, most were collected from May to September when the majority of catches occur.

Measurements of lower-jaw fork length (LJFL to nearest cm) were taken for all fish, sex was determined, and the anal fin removed and frozen for storage. In the laboratory, fins were thawed and sections of the second spine of the anal fin were prepared for reading according to the method described by Tsimenides and Tserpes (1989). Specifically, each anal fin was immersed in boiling water for a few minutes before the second spine was removed, freed from skin and tissue, cleaned with water, and left

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to dry completely. A section about 2 cm thick was cut with an electric saw from each dried spine at the point where the spine flares (condyle). Each section was placed in a plastic cylinder (3 cm diameter and 2 cm height) which was then filled with liquid resin. These were left to dry for at least 12 hours, the plastic case was removed, and two or three sections about 1 mm thick were cut distally with a "Stuers" accutom.

Age determination

Spine sections were read under a binocular microscope at 12× magnification by using reflected light and a dark background. The distances from the focus to the edge of the section on the dorsal rim (spine radius) and from the focus to each annulus were measured with an optical micrometer. Sections were read by two readers and identical counts were obtained in >80% of the cases; samples were considered unreadable and were excluded from the analysis if discrepancies in counts could not be resolved.

Typically, broad opaque bands and narrow translucent ones could be seen alternating outwards from the central core. Translucent bands that form around the entire circumference of the spine were considered to be annuli and the total number of these bands was recorded (Fig. 1).

Age classes were assigned on the basis of the number of annuli and the following characteristics of the bands: 1) the disappearance of the first annulus from older fish and 2) the existence of multiple bands mainly in larger fish. Preliminary analysis of LJFL measurements taken in nursery areas of the Aegean sea have shown that swordfish reach a length of about 80–90 cm at one year of age. The first annulus could be seen in fish of this size at an average distance of 1.5 mm (SD=0.08) from the focus, but it was usually not visible at lengths greater than 100 cm (Fig. 1). In such cases, and if the total spine radius was greater than 1.5 mm, one year was added to the assigned age. As described by Berkeley and Houde (1983), multiple bands are those which form around the entire circumference of the spine such that the distance between them is substantially less than that of the preceding and following annual bands. In these cases, the clearest band was considered an annulus and the others were ignored. However, if it was not possible to identify such a band, the specimen was considered unreadable. When the opaque-translucent zonation was such that annuli could not be defined, such specimens were also considered unreadable.

Data analysis

The marginal increment ratio (MIR) was estimated for each specimen according to the formula:

$$MIR = (S - r_n) / S,$$

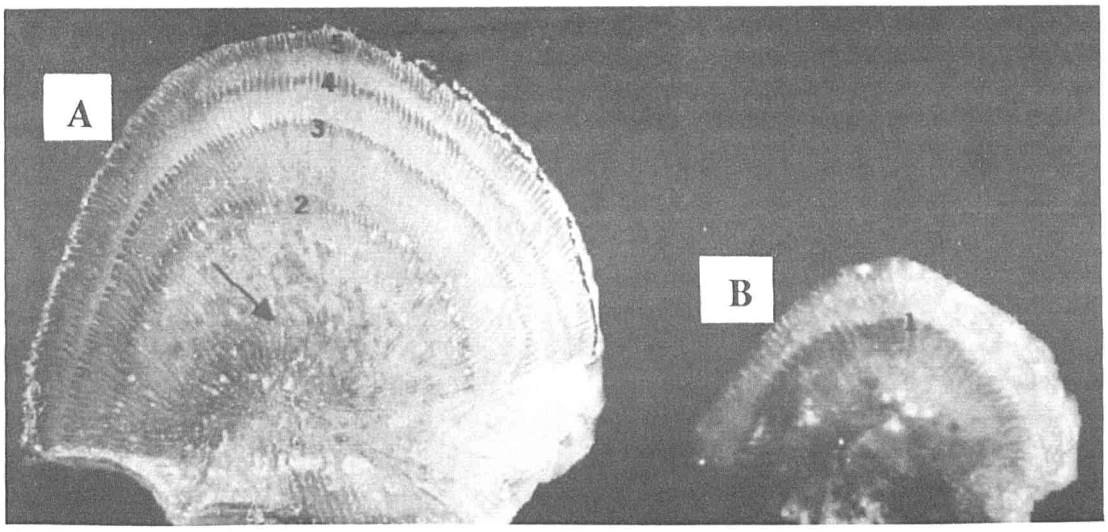

Figure 1

Sections of second anal-fin spine with five growth zones (**A**) and one growth zone (**B**) used for age determination of swordfish, *Xiphias gladius*, from the eastern Mediterranean. First annulus is missing in section (A) whereas it can be clearly seen in section (B). Estimated location of first annulus in section (A), based on its location in section (B), is indicated by an arrow. Lower-jaw fork lengths (LJFL) of animals (A) and (B) were 162 and 95 cm, respectively.

where S = spine radius; and
r_n = radius of the most recent annulus.

The mean *MIR* and the standard deviation were computed for each month and age separately. Marginal increment analysis was not performed for age 1 because the first annulus was usually missing, nor for ages greater than 5 because of a lack of sufficient number of samples.

Estimates of theoretical growth in length were obtained by fitting mean monthly length-at-age data to two forms of the von Bertalanffy growth equation: 1) the standard form and 2) the generalized form as proposed by Chapman (1961).

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

$$L_t = \left[L_\infty^{(1-\delta)} - \left(L_\infty^{(1-\delta)} - l_0^{(1-\delta)}\right)e^{-k(1-\delta)t}\right]^{1/(1-\delta)} \quad (2)$$

where L_t = LJFL at age t, L = asymptotic length, k = growth coefficient, t_0 = theoretical age at zero length, l_0 = length at zero age, and δ = fitted fourth function parameter.

Mean data were used in order to assign equal weight to all observations. Only mean values from samples of greater than five fish were used. Growth parameters of both models were estimated iteratively by using the Simplex minimization algorithm (Wilkinson, 1988). The measure of goodness of fit was the coefficient of determination (r^2). Date of birth was set at 1 June because swordfish spawn in the Mediterranean sea in early summer (Palco et al., 1981).

Growth parameters were estimated for males, females, and sexes combined, and sex differences were tested by analysis of the residual sum of squares (ARSS) as suggested by Chen et al. (1992). This method is a modification of the ARSS originally developed for the comparison of linear models (Zar, 1984).

Back calculations of length at age were estimated in two ways.

1 From a modified version of the direct proportion formula (Fraser, 1916; Lee, 1920):

$$L_n - c = (S_n / S)(L - c),$$

where L_n = LJFL when the annulus n was formed;
L = LJFL at time of capture;
c = intercept on length axis from linear regression of length on spine radius;
S_n = distance from spine focus to annulus n; and
S = spine radius.

2 From the formula of Monastyrsky (Bagenal and Tesch, 1978):

$$L_n = (S_n / S)^b L$$

where L_n = LJFL when the annulus n was formed;
L = LJFL at time of capture;
b = the exponent of the regression of length (L) on spine radius (S) which is assumed to be a power function of the form $L=aS^b$;
S_n = distance from spine focus to annulus n; and
S = spine radius.

The constant b was calculated from the logarithmic form of the power function.

In both cases the relation between spine radius and LJFL was determined for males and females and for sexes combined. Moreover, the regression lines for males and females were tested for equality of slopes and if significant differences were found, intercepts were tested by means of analysis of covariance (Dixon and Massey, 1985). No back calculations were attempted for age one because the first annulus was missing in the vast majority of the specimens. All statistical inferences were based on the 0.05 significance level.

Results

Of the 1,325 swordfish sampled, 1,100 were aged successfully (521 males and 579 females). The lengths of individuals ranged from 62 to 210 cm (Fig. 2). In 64 of the 225 unreadable spines, no annuli could be identified because the opaque-translucent zonation was unclear. The remaining 161 spines were considered unreadable owing to the existence of multiple bands which made the identification of annuli difficult or which resulted in ageing discrepancies between the readers, or both.

Up to 9 rings, assumed to be annuli, were visible in the anal-fin spines sampled. Sample sizes for all age classes were greater than 20, except for class 9 (15). Two-year-old fish were the dominant age class and over 80% of the fish were less than 5 years old. Differences in mean size between the successive age classes were calculated to reveal any peculiarities in growth patterns. In theory, absolute growth was expected to be rapid at first and to decrease progressively in later life. The pattern observed for swordfish generally agreed with these expectations (Table 1). Monthly means of MIR indicated that an annu-

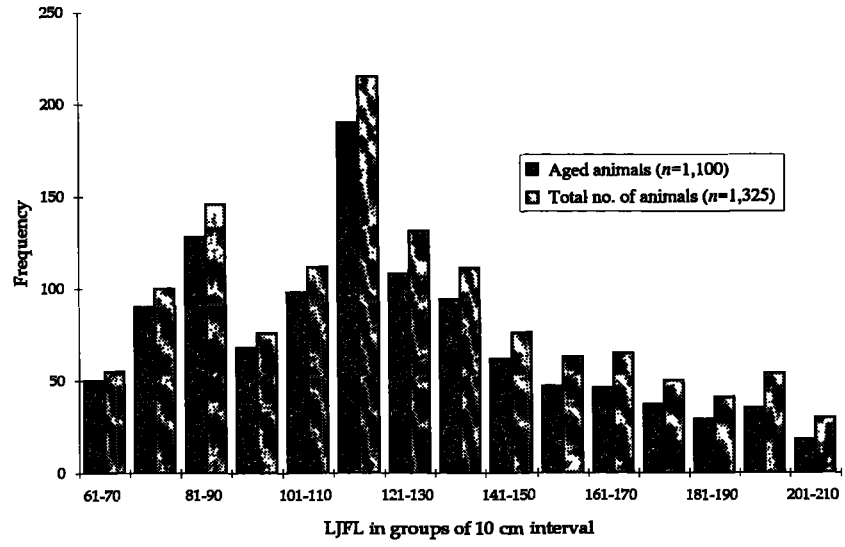

Figure 2

Length-frequency distribution of swordfish, *Xiphias gladius*, from the eastern Mediterranean indicating the total number of fish and the number of those with readable spines (aged animals). LJFL = lower-jaw fork length, n = sample size.

lus is formed from middle spring to early summer for all ages examined (Fig. 3).

Parameters of the standard von Bertalanffy growth function and the generalized model were computed for males, females, and sexes combined (Tables 2). Both models provided a good fit to the data (Fig. 4). Results of the ARSS revealed that growth differences between sexes were always highly significant (F=8.22, P<0.001 for the standard growth function; F=7.41, P<0.001 for the generalized model).

The intercept values used in the proportional formula of back calculation were obtained from the linear regression of LJFL on spine radius:

$LJFL = 59.09 + 18.32(S)$ [r^2=0.98 for males];
$LJFL = 62.43 + 17.02(S)$ [r^2=0.98 for females]; and
$LJFL = 61.45 + 17.39(S)$ [r^2=0.98 for both sexes combined],

where $LJFL$ = lower-jaw fork length (cm);
S = anal-fin spine radius (mm); and
r^2 = coefficient of determination.

Males and females had significantly different slopes (F=44.85, P<0.001).

The constant b used for the nonlinear method of back calculation was obtained from the slope values of the relation between $LJFL$ and spine radius:

Table 1

Summary statistics on sizes of aged swordfish, *Xiphias gladius*, from the eastern Mediterranean. LJFL = lower-jaw fork length.

Age	Sample size	Mean LJFL (cm)	Standard error	LJFL range (cm)	Mean size increment
0	128	72.59	0.51	62–88	—
1	232	89.71	0.52	75–115	—
2	326	114.90	0.33	102–130	25.19
3	153	134.20	0.59	119–153	19.30
4	84	150.46	0.97	126–169	16.26
5	48	162.35	1.04	148–176	11.89
6	54	174.37	0.93	159–185	12.02
7	27	186.81	1.11	179–199	12.44
8	33	198.27	1.13	190–210	11.46
9	15	199.40	1.09	193–205	1.13

$\ln(LJFL) = 4.30 + 0.43(\ln S)$ [r^2=0.94 for males];
$\ln(LJFL) = 4.30 + 0.44(\ln S)$ [r^2=0.96 for females]; and
$\ln(LJFL) = 4.30 + 0.44(\ln S)$ [r^2=0.96 for both sexes combined].

The slope of the relationship differed significantly between males and females (F=6.33, P=0.01).

The statistically significant differences between the sexes for the LJFL spine-radius relation are likely

Table 2

Parameter estimates for the standard von Bertalanffy and the generalized von Bertalanffy growth model for swordfish, *Xiphias gladius*, from the eastern Mediterranean. Corresponding r^2 values are shown in parenthesis. See text for parameter definitions.

	Standard von Bertalanffy			Generalized von Bertalanffy		
Parameter	Male (r^2=0.99)	Female (r^2=0.99)	Sexes combined (r^2=0.99)	Male (r^2=0.99)	Female (r^2=0.99)	Sexes combined (r^2=0.99)
L_∞	203.076	226.525	238.582	292.967	274.914	385.503
k	0.241	0.210	0.185	0.020	0.037	0.011
t_0	−1.205	−1.165	−1.404			
l_0				0.000	0.000	0.002
δ				−1.434	−1.140	−1.393

due to the small variance of the recorded values rather than to a morphometric discrimination between sexes. This can be seen by solving the equations for different spine-radius values. For example, the computed LJFL values for a spine radius of 2 mm are: 1) 95.73 for males and 96.47 cm for females from the linear method; and 2) 99.29 for males and 99.98 for females from the nonlinear method.

The LJFL at the end of each year of life was backcalculated for each individual and these lengths were averaged for males and females separately to obtain mean back-calculated lengths at age. These generally agreed with lengths at age predicted by the growth models and show that females grow faster than males after an estimated age of 3 years (Table 3).

Discussion

Swordfish anal-fin spines have been used previously for ageing Atlantic swordfish (Berkeley and Houde, 1983). Ehrhardt (1992) attempted to validate the method by means of marginal increment analysis and reported that growth bands 1 to 4 were deposited annually during the winter months. Results of marginal increment analysis of the present study demonstrated that growth bands for fish 2 to 5 years of age are deposited annually. In both the previous cases, marginal increment analysis was successful in showing the seasonality of band deposition; however, although these results partially validate the method, it cannot be considered successful until all reported ages of each population are validated (Beamish and McFarlane, 1983). Marginal increment analysis has also been successful in elucidating the time of annulus formation in dorsal spines of *Tandanus tandanus* (Davis, 1977). It is unlikely, however, that application of marginal increment analysis to older ages, in which spine growth is considerably reduced, would show any seasonality in band deposition. In general, validation of ages of older fish requires either a mark-recapture study or the iden-

Table 3

Back-calculated and predicted lower jaw fork lengths (LJFL-cm) at age for swordfish, *Xiphias gladius*, from the eastern Mediterranean.

	Back-calculated (proportional formula)		Back-calculated (nonlinear method)		Predicted (standard von Bertalanffy)		Predicted (generalised von Bertalanffy)	
Age	Male	Female	Male	Female	Male	Female	Male	Female
1	—	—	—	—	83.71	82.76	83.79	82.52
2	106.85	108.84	110.82	112.98	109.28	109.99	110.30	112.03
3	126.14	128.44	131.03	136.06	129.36	132.06	129.03	133.00
4	141.34	145.48	146.28	153.79	145.15	149.96	143.81	149.48
5	153.80	159.88	158.22	167.15	157.55	164.46	156.10	163.04
6	165.06	172.64	168.19	178.00	167.30	176.21	166.65	174.52
7	173.32	182.24	177.11	186.76	174.96	185.74	175.87	184.41
8		190.17		193.10	180.98	193.47	184.05	193.04
9		195.16		196.67	185.72	199.73	191.38	200.63

tification of known-age fish in the population (Beamish and McFarlane, 1983).

The present work showed that annuli are formed from late spring to early summer which is the spawning period for swordfish in the Mediterranean (Palco et al., 1981). Since it has been suggested that swordfish use particular spawning grounds in the Mediterranean (Rey, 1988; Cavallaro et. al., 1991), annulus formation may be related to migration of fish to these grounds. A relation between annulus formation and migration has been suggested for the Atlantic swordfish as well (Berkeley and Houde, 1983).

Our findings indicate that anal-fin spines are useful for ageing swordfish. These are important because

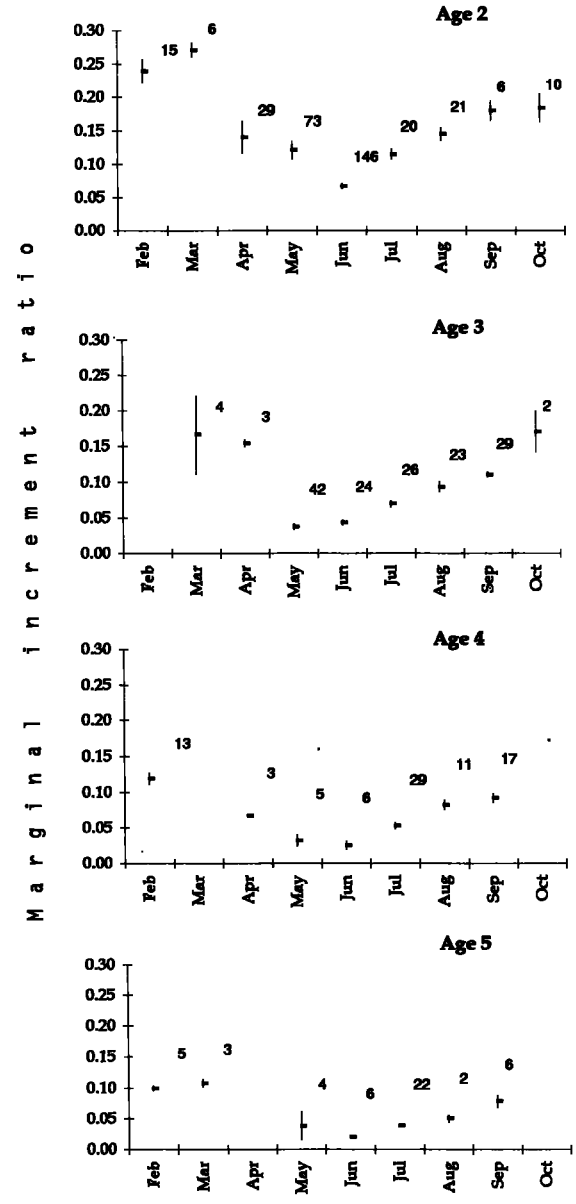

Figure 3

Mean monthly marginal increment ratio for swordfish, *Xiphias gladius*, ages 2–5 from the eastern Mediterranean. Vertical bars represent ±1 SE. Numbers are sample sizes.

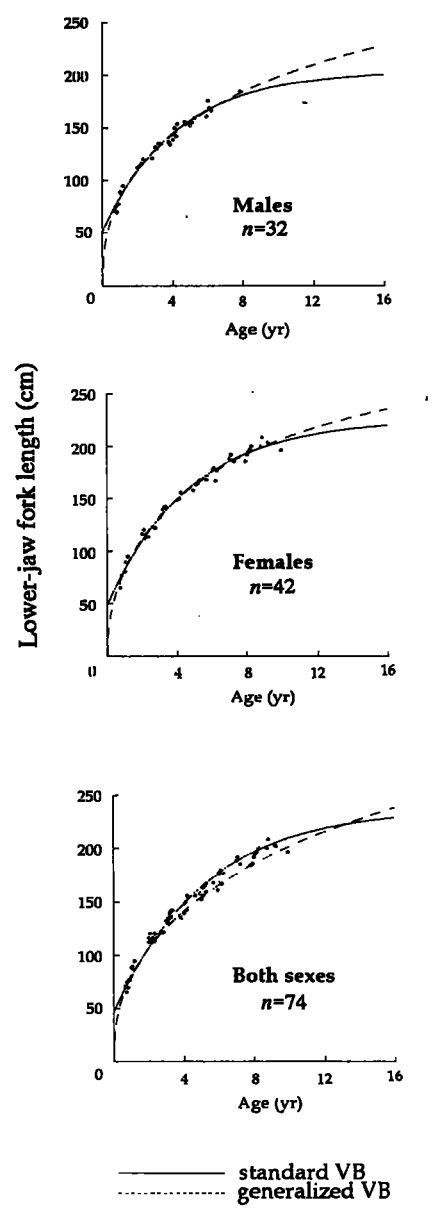

Figure 4

Standard and generalized von Bertalanffy (VB) growth curves for swordfish, *Xiphias gladius*, from the eastern Mediterranean; *n* = sample size.

Table 4

Estimated lower-jaw fork lengths (LJFL to nearest cm) at age for swordfish, *Xiphias gladius*, from studies in the Atlantic (A) and the Mediterranean (M).

	Berkeley and Houde (1983) (A)		Radtke and Hurley (1983) (A)		Wilson and Dean (1983) (A)		Ehrhardt (1992) (A)		Tsimenides and Tserpes (1989) (M)	
Age	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1	97.2	98.0	84	73	116.9	122.9	89.7	89.8	103.2	103.1
2	118.5	119.9	98	85	123.3	130.6	117.0	118.9	129.5	129.1
3	136.0	139.7	110	114	130.2	138.8	137.3	142.9	148.1	149.3
4	150.4	157.8	122	131	137.4	147.5	153.4	161.3	161.4	165.0
5	162.3	174.3	133	147	145.0	156.8	168.9	177.2	170.8	177.3
6	172.0	189.3	143	160	153.0	166.6	181.8	189.6	177.5	186.8
7	180.0	202.9	153	172	161.5	177.1	195.3	204.4	185.2	194.2
8	186.6	215.3	161	183	170.4	188.2	206.1	214.7		

swordfish have no scales and otoliths are not amenable to traditional ageing techniques owing to their small size (Ovchinnikov, 1970; Becket, 1974). Successful otolith readings have been performed only through the application of scanning electron microscopy (Radtke and Hurley, 1983; Wilson and Dean, 1983). Moreover, the use of spines has the advantage that the material can be obtained relatively easily without reducing the economic value of the fish. The main problems associated with the spine method are the existence of multiple bands and the missing first annulus. An experienced reader can overcome the problem of multiple bands by determining whether they continue around the entire circumference of the spine and by recording their distance from the preceding and following annuli. The problem of the missing first annulus in larger fish can be resolved by identifying its position on sections from younger specimens where the annulus is visible. Difficulties in defining the location of the first annulus in older animals have also been reported for Atlantic swordfish (Berkeley and Houde, 1983) and Pacific blue marlin, *Makaira nigricans* (Hill et al., 1989).

Ehrhardt (1992) suggested that the standard von Bertalanffy growth function does not adequately represent the growth of swordfish and proposed the use of the generalized growth function of Chapman (1961). The present estimates of r^2 indicate that both models describe swordfish growth equally well over the age ranges considered and give almost identical results for the first eight years of growth (Fig. 4). Although the extrapolation of regression curves beyond the data is not advisable, it is interesting to note that the generalized model gives much more realistic results for ages less than one because it forces the growth curve to pass close to the origin of both axes. On the other hand, estimates of asymptotic length from this model are questionable because it is unlikely that females have lower asymptotic lengths than males, given that all the large animals in the sample were female. Therefore, the generalized model appears to overestimate asymptotic length (especially that of males).

Although results of both back-calculation methods generally agreed with the values predicted by the growth equations, the estimates of the nonlinear method are in slightly closer agreement (Table 3). The use of a nonlinear function for the LJFL spine-radius relation is preferable because it is more realistic for small animals, which have near zero spine-radius values and very small LJFL values. Ehrhardt (1992) also suggested the use of a nonlinear function to describe the LJFL spine-radius relation.

Growth studies carried out in the Atlantic together with previous work (Tsimenides and Tserpes, 1989) have shown that females grow faster than males (Table 4). Therefore, the calculation of a common growth equation is not valid and may be useful for management purposes only under certain circumstances. However, it should be noted that in previous work (Tsimenides and Tserpes, 1989), lengths at age were overestimated because the position of the first annulus was misidentified.

In the case of swordfish it seems that the use of a relatively wide range of size data and mean values for fitting the growth curves has resulted in relatively unbiased estimates of swordfish growth parameters in the eastern Mediterranean. Since all Mediterranean swordfish are proposed to belong to the same stock (Magoulas et al., 1993), our findings

are appropriate for assessment studies of this stock. The use of the standard von Bertalanffy growth model is recommended for such studies because the generalized model overestimates the asymptotic length, an essential parameter for population dynamics models.

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Abstract.—A midwater trawl survey was conducted during July 1991, to examine the large-scale distribution patterns of late larval and early juvenile walleye pollock, *Theragra chalcogramma*, and associated fish taxa in the western Gulf of Alaska. Gear comparisons between the anchovy and Methot trawls were conducted to evaluate which was the more efficient sampler for the size range of *T. chalcogramma* present during this time of the year. Both gears showed similar densities through the dominant size class of fish caught, but the Methot trawl caught significantly more *T. chalcogramma* in the smallest (mostly larval) size ranges available. Accordingly, a grid of stations was occupied in which only the Methot trawl was used.

Although 53 fish taxa were collected overall in the 61 Methot trawls, the majority (84%) of the larval catch consisted of only five taxa: flathead sole, *Hippoglossoides elassodon*; walleye pollock, *T. chalcogramma;* arrowtooth flounder, *Atheresthes stomias;* Pacific cod, *Gadus macrocephalus;* and unidentified sculpins, *Icelinus* spp. *Theragra chalcogramma* and *G. macrocephalus* were the dominant (>99%) juveniles collected in the survey. The highest catches of larval (13–25 mm SL) and juvenile (26–52 mm SL) *T. chalcogramma* were found inshore along the Alaska Peninsula and near offshore island groups. Recurrent Group Analysis and Two-way Indicator Species Analysis both showed that *T. chalcogramma* tended to be frequently associated with a large heterogeneous grouping of taxa, including *G. macrocephalus*, several pleuronectids, and other winter-spring spawning species. The rankings of the dominant taxa in the Methot trawl survey exhibited a greater coherence to the rankings of adult fishes from bottom trawl surveys in the previous year than did those of an ichthyoplankton survey that used bongo nets a few months earlier than the Methot trawl survey.

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Summer distribution of early life stages of walleye pollock, *Theragra chalcogramma*, and associated species in the western Gulf of Alaska*

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The spatiotemporal distribution of the pelagic early life stages of marine fishes is influenced by a number of biotic and oceanographic processes. Thus, with sufficient elapsed time since spawning, the distribution of late larvae and early juveniles of many species shows only a limited relationship to the distribution of spawning adults. The taxa that make up an assemblage of larval fishes show a high diversity of sizes, stage durations, morphologies, and behaviors (Moser, 1981; Matarese et al., 1989; Moser and Smith, 1993) that can affect their distribution patterns in a dynamic and fluid environment, as is the situation in most coastal areas. The early larval stages have received the most attention from fisheries oceanographers because of their presumed importance in regulating recruitment variability but also because of the ease of sampling such weakly swimming organisms (Heath, 1992). Recent observations, however, have given rise to the suggestion that later larval and early juvenile stages may be as important as early larval stages in regulating year-class strength (Peterman et al., 1988; Campana et al., 1989; Bailey and Spring, 1992), which has stimulated development of new sampling gear to quantitatively assess the abundance of larger ichthyoplankton and micronekton (Methot, 1986; Munk, 1988; Potter et al., 1990; Dunn et al., 1993).

The Fisheries Oceanography Coordinated Investigations (FOCI) program is a joint effort by scientists at the Alaska Fisheries Science Center (AFSC) and the Pacific Marine Environmental Laboratory (PMEL) to understand the biological and physical processes which cause variability of recruitment in commercially valuable fish and shellfish stocks in Alaskan waters. The primary goal of the FOCI program is to understand the effects of the biotic and abiotic environment on the early life stages of walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska (Schumacher and Kendall, 1991). A secondary objective is to provide quantitative estimates of population size to predict recruitment strength for fisheries management (Schumacher and Kendall, 1991; Bailey and Spring, 1992). Other than the study of Hinckley et al. (1991) in late

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June, no data are available on the distribution and abundance patterns of late larval or early juvenile *T. chalcogramma* during mid-summer, when they are at a size that makes them vulnerable to plankton gear. Moreover, little is known about the relationship of *T. chalcogramma* distribution to that of the other common ichthyoplankton taxa that are caught with the same type of gear. Our aim in this study was to examine the large-scale distribution patterns of age-0 *T. chalcogramma* and their associations with other larval and juvenile fishes. We also estimate for the first time the relative abundance of age-0 *T. chalcogramma* compared with other co-occurring early life history stages of marine fish taxa present during mid-summer on the continental shelf in the western Gulf of Alaska.

Methods

A FOCI survey of late larval and early juvenile *T. chalcogramma* was conducted aboard the NOAA ship *Miller Freeman* from 23 to 31 July 1991 (Dewitt and Clark[1]). The Methot trawl was selected as the most appropriate sampling gear for this stage of *T. chalcogramma* life history on the basis of previous gear comparisons (Shima and Bailey, 1994). The 5-m^2 rigid frame trawl (2 × 3 mm oval mesh) is designed to sample micronekton that evade smaller plankton nets and that pass through the mesh of larger trawls (Methot, 1986). A grid of stations perpendicular to the coast along the Alaska Peninsula was occupied (Fig. 1) and 61 successful Methot trawls were completed (39 day and 22 night), with repeat tows at several stations. All tows were made at an average ship speed of 6 km·h^{-1} and in a double oblique pattern to within 10–20 m of the bottom. Temperature profiles were taken at each station by using expendable bathythermographs.

[1] Dewitt, C., and J. Clark. 1993. Fisheries Oceanography Coordinated Investigations: 1991 field operations report. NOAA Data Rep. ERL PMEL-41, 112 p.

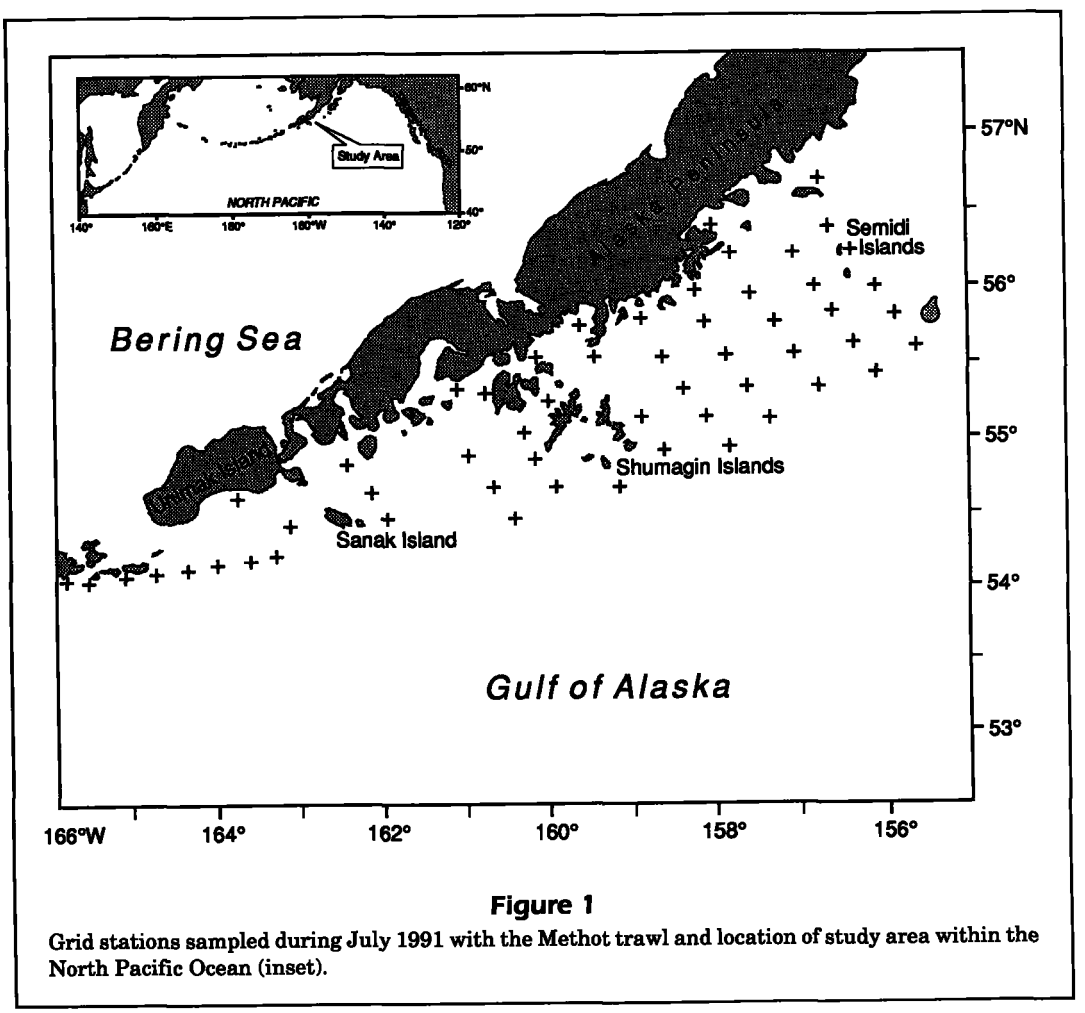

Figure 1

Grid stations sampled during July 1991 with the Methot trawl and location of study area within the North Pacific Ocean (inset).

Because we were uncertain whether any larger *T. chalcogramma* were present at the time of sampling, we conducted a set of gear comparisons at four different stations to examine whether the Methot trawl was adequately sampling the largest age-0 individuals available. Paired tows (2 pairs during the day and 2 at night) were made with the Methot trawl and an anchovy trawl. The anchovy trawl has a variable mouth opening depending on depth and was estimated to range from 110 to 135 m^2 for the four tows on the basis of the relationships given by Wilson et al. (in press). The trawl body contained variable-size mesh grading from 15.2 cm (stretched) in the forward section to 3.8 cm in the codend, which contained a 3-mm liner. At each gear comparison station, oblique tows with each gear type were done in random order down to the same depth. Standardized catches of *T. chalcogramma* in each gear were compared by length categories by using a nested ANOVA, with haul as the nesting factor.

The trawl samples were preserved in 5% formalin buffered with marble chips. The samples were later sorted in the laboratory and all the fish were removed. Fish were identified by using Hart (1973), Eschmeyer et al. (1983), and Matarese et al. (1989). Standard length (SL) of all fish was measured to the nearest millimeter with a stage micrometer or measuring board. Larval and juvenile stages were separated by using a combination of information on length of transformation and osteology provided by Matarese et al. (1989) and Busby (unpubl. data). Larval and juvenile *T. chalcogramma* and Pacific cod, *Gadus macrocephalus,* were separated at 25.0 mm SL by using the criteria of Dunn and Matarese (1987).

Raw numbers of larvae and juveniles from each taxon collected were converted to number per unit area or density per volume filtered. Consistent with the results of previous studies on larval and juvenile *T. chalcogramma* (Hinckley et al., 1991; Shima and Bailey, 1994), we did not find significant density differences overall between day and night sampling (Mann-Whitney Test, $P=0.09$); thus, we did not make corrections in our abundance estimates for time of day of sampling. Total abundance of each taxon in the study area was calculated by multiplying the weighted mean catch per 10 m^2 for each station by the polygonal area represented by that station (see Richardson [1981] and Kendall and Picquelle [1990] for details). Abundances were calculated separately for both larval and juvenile *G. macrocephalus* and *T. chalcogramma* and then summed for the total abundance for each taxon.

Classification of the catches was done with analyses by using both occurrence and abundance data. Species associations were identified on the basis of co-occurrence of taxa in catches by using Recurrent Group Analysis (Fager, 1957). This analysis places taxa that co-occur into groups based on an affinity level set at 0.4, as previously used for other assemblage analyses in this region (Kendall and Dunn, 1985; Doyle et al., 1995). Only taxa that occurred in more than 15% of the collections were included in this analysis. A second type of hierarchical classification was performed on the abundance data to see whether a different technique produced different results in identifying assemblages. Two-way Indicator Species Analysis, a polythetic, divisive technique (Gauch, 1982), was used in conjunction with the program TWINSPAN (Hill, 1979). This analysis starts with all the entities (taxa or stations) belonging to one group and then ordinates them by reciprocal averaging. Each group is progressively divided until it contains no more than the predetermined minimum number of members, as opposed to an agglomerative technique, such as cluster analysis, which starts with individual entities and progressively combines them. Station groupings were also formed by using TWINSPAN, and these were described in relation to the species matrix on the basis of whether a particular taxon had a high or low affinity with that station grouping.

To interpret the ecological significance of these station groupings, we examined environmental and station variables such as water depth and temperatures from different depth intervals available from expendable bathythermograph data taken at each station. We also calculated station position variables, such as distance from nearest land (including islands) and alongshore distance from a line perpendicular to the coast just northeast of our first transect of stations (Fig. 1). Differences among the median values for all variables by the different TWINSPAN groupings were tested by using a Kruskal-Wallis test.

We compared the abundance estimates from the 1990 AFSC Gulf of Alaska groundfish trawl survey with those determined from the Methot trawl survey and another ichthyoplankton survey conducted a few months earlier than our study. The trawl survey took place from 1 June to 9 September 1990, covered a broader area of the Gulf of Alaska (132–170°W), and sampled depths ranging from 20 to 530 m (see Stark and Clausen [1995] for additional sampling details). For the purposes of this analysis, only abundances from the western Gulf of Alaska strata (506 stations) were summarized. Abundances for each stratum were estimated by dividing the biomass of each species caught by its mean weight (given in Stark and Clausen [1995]), and then these were summed across all depths and strata.

Ichthyoplankton collections were made at 92 stations off Kodiak Island and the Alaska Peninsula (151–159°W) from 17 to 25 May 1991 by using a 60-cm bongo with either 333- or 505-μm mesh. Processing of these samples and abundance estimates were done as described for the Methot trawl collections. More complete sampling details are provided by Dewitt and Clark.[1]

Results

Gear comparisons

The two gear types did not show significant differences in overall mean standardized catches of age-0 *T. chalcogramma* for the four paired gear-comparison hauls, but when the densities were partitioned by size of fish, the Methot trawl caught significantly more fish in the smallest size groups, although there were no density differences between the two gears for the size groups >35 mm (Fig. 2). Although it was not possible to examine diel differences in overall age-0 densities for both gear types from only four stations taken in different locations, it appears that the catchability of small *T. chalcogramma* by the anchovy trawl is relatively poor during the daytime. In all four comparisons, the Methot trawl caught smaller individuals and a broader overall range of age-0 sizes than did the anchovy trawl, but the distributions of lengths were significantly different in only two of the four tows (Fig. 3). The overall average (±SD) length of individuals caught by the Methot net was 34.5 (±7.0) mm, whereas the average length of fish caught by the anchovy trawl was 36.3 (±4.5) mm.

Taxonomic composition and abundance

Altogether, 53 larval and 4 juvenile taxa were identified in the Methot trawl survey (Tables 1 and 2). Several taxa, notably *Sebastes* spp. and Cyclopteridae, were probably represented by several as yet unidentifiable species; therefore, the overall taxonomic diversity was probably underestimated. The family Cottidae exhibited the greatest diversity, with at least 15 taxa represented (Table 1).

Hippoglossoides elassodon, *T. chalcogramma*, and, to a lesser extent, *Atheresthes stomias*, *G. macrocephalus*, and *Icelinus* spp., were the dominant taxa collected on the basis of mean density (Table 1). *Hippoglossoides elassodon* larvae were the most abundant overall and occurred at all but one station. Most of the fish caught were late-stage larvae, but *T. chalcogramma* and *G. macrocephalus* were also represented by a large number of juveniles (Table 2). On the basis of total abundance in the study area, *H. elassodon*, *T. chalcogramma*, and *A. stomias* are clearly the most abundant taxa; there is less distinction among the rest of the dominant taxa (Fig. 4). The abundance of *H. elassodon* (3.24×10^{10} fish) was almost three times that of the next most abundant species *T. chalcogramma* (larvae and juveniles combined: 1.12×10^{10} fish) and represented 53.6% of the estimated total abundance of ichthyoplankton in the survey area (6.04×10^{10} fish).

Spatial and length-distribution patterns

The geographic and length distributions of the six most abundant larvae and *T. chalcogramma* and *G. macrocephalus* juveniles are shown in Figures 5–8. The distribution of *T. chalcogramma* larvae and that of juveniles were very similar, with centers of abundance near the Semidi and Shumagin Islands (Fig. 5). *Gadus macrocephalus* juveniles tended to be distributed slightly more offshore and farther west (downcurrent) than were larvae (Fig. 6). *Hippoglossoides elassodon* larvae were found in greatest numbers near the Alaska Peninsula and Shumagin Islands, whereas *A. stomias* larvae were collected over a broad size range and displayed no distinct patterns of distribution (Fig. 7). In contrast, *Icelinus* spp. larvae showed a narrow size distribution and were found in high concentrations northeast of Sanak Island

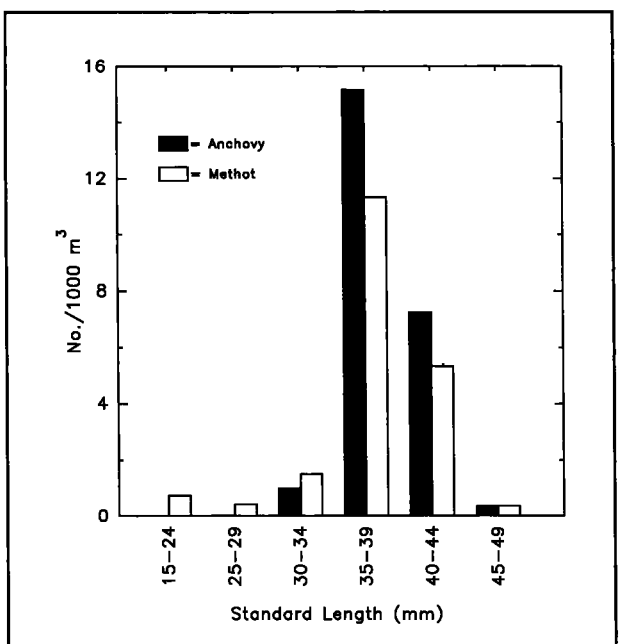

Figure 2

Comparison of the standardized catches for the Methot and anchovy trawl by length category in the gear comparison tows.

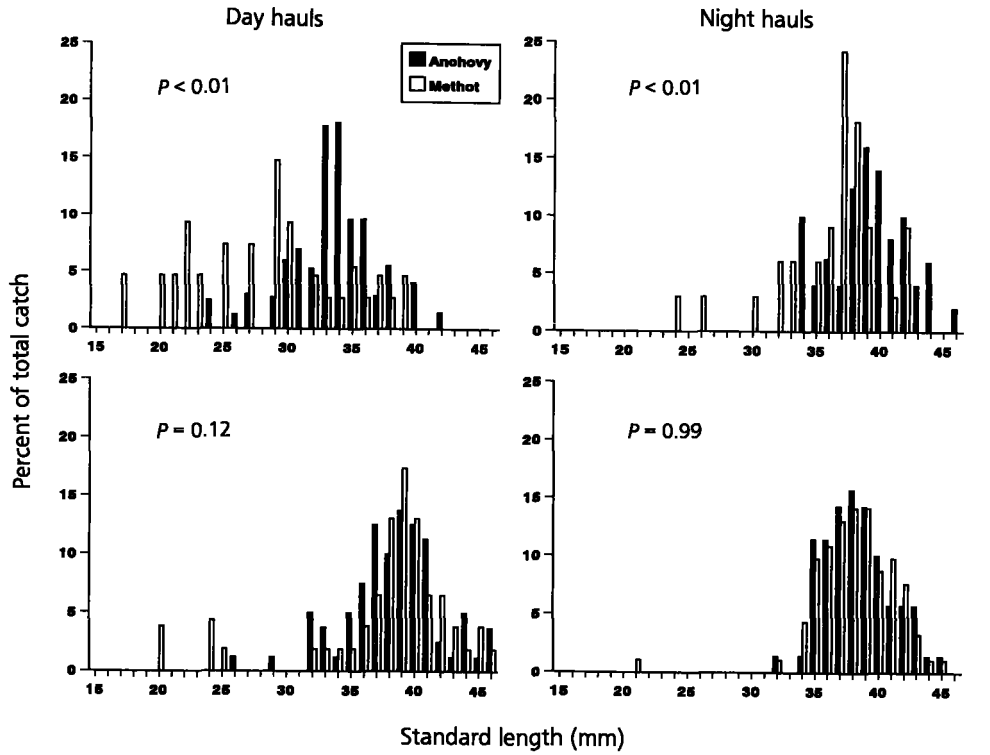

Figure 3

Comparison of the length distributions by haul for the Methot and anchovy trawls for the four paired comparisons done at different stations. Also shown are the results of a Kolmogorov-Smirnov test in which the distributions of each gear type were compared.

(Fig. 8). *Sebastes* spp. catches also comprised relatively small larvae and were found almost exclusively at offshore stations but were evenly distributed among these stations (Fig. 8).

Species associations

The Recurrent Group Analysis identified one main grouping of taxa that showed a common affinity level of at least 0.40 (Fig. 9). Curiously, the nine taxa with the highest densities were members of this grouping, even though the groupings are formed on the basis of common occurrences. *Zaprora silenus* larvae were associated with eight of the nine taxa but showed a low association with *Sebastes* spp. larvae. The larval and juvenile stages of *T. chalcogramma* and *G. macrocephalus* occurred within the same species grouping and thus were not differentiated in this analysis.

The TWINSPAN results were similar to the Recurrent Group Analysis in that a large grouping was formed. However, in this instance, *Sebastes* spp. larvae were not closely related to this grouping, but *Ammodytes hexapterus* larvae were related (Fig. 10).

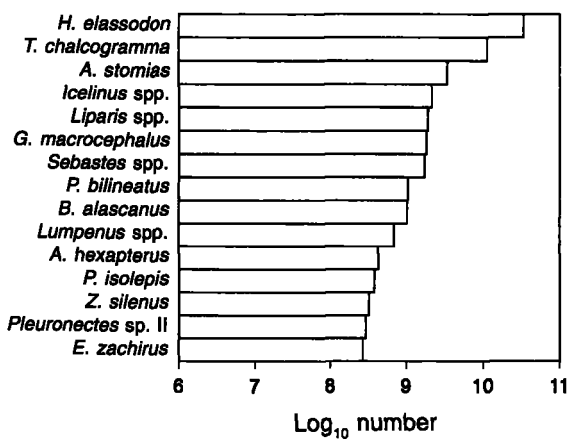

Figure 4

The estimated total abundance in the survey area for the 15 most abundant taxa collected in the Methot trawl survey. Abundances for *Theragra chalcogramma*, *Gadus macrocephalus*, and *Zaprora silenus* include combined totals for larval and juvenile stages.

Table 1

Summary of fish larvae collected in Methot trawls during 1991. Scientific names follow Robins et al. (1991) with the exception of the family Agonidae which follows Kanayama (1991).

Scientific name	Common name	Percent occurrence	Mean abundance (no./1000m^3)	Length range SL (mm)
Clupea pallasi	Pacific herring	1.64	<0.01	21.8
Mallotus villosus	capelin	3.28	0.01	52.0–60.0
Thaleichthys pacificus	eulachon	3.28	<0.01	63.0–75.0
Bathylagus pacificus	Pacific blacksmelt	1.64	<0.01	19.0
Leuroglossus schmidti	northern smoothtongue	8.19	0.01	22.0–34.0
Stenobrachius leucopsarus	northern lampfish	1.64	<0.01	10.8
Gadus macrocephalus	Pacific cod	34.43	0.15	15.1–22.0
Microgadus proximus	Pacific tomcod	1.64	<0.01	17.5–18.5
Theragra chalcogramma	walleye pollock	78.69	1.03	13.0–25.0
Gadidae	unidentified gadids	18.03	0.04	15.1–22.0
Macrouridae	unidentified grenadiers	1.64	<0.01	28.0
Sebastes spp.	unidentified rockfishes	49.18	0.30	6.0–18.0
Artedius fenestralis	padded sculpin	1.64	<0.01	12.0
Artedius harringtoni	scalyhead sculpin	3.28	<0.01	11.1–11.7
Artedius lateralis	smoothhead sculpin	1.64	<0.01	10.9
Ruscarius meanyi	Puget Sound sculpin	3.28	0.01	12.0–15.1
Clinocottus acuticeps	sharpnose sculpin	3.28	0.01	13.0–15.0
Clinocottus embryum	calico sculpin	1.64	<0.01	13.0
Dasycottus setiger	spinyhead sculpin	6.56	0.01	15.0–21.8
Icelinus borealis	northern sculpin	1.64	<0.01	13.5
Icelinus spp.	unidentified sculpins	72.13	0.57	10.0–18.0
Malacocottus zonurus	darkfin sculpin	1.64	<0.01	10.0
Nautichthys oculofasciatus	sailfin sculpin	1.64	<0.01	23.2
Psychrolutes paradoxus	tadpole sculpin	3.28	<0.01	15.9–16.3
Psychrolutes sigalutes	soft sculpin	4.92	0.01	12.0–17.0
Radulinus asprellus	slim sculpin	6.56	0.01	13.0–16.0
Rhamphocottus richardsoni	grunt sculpin	6.56	0.02	11.7–14.4
Cottidae	unidentified sculpins	3.28	0.01	15.0–18.0
Anoplagonus inermis	smooth alligatorfish	1.64	<0.01	19.0
Bathyagonus alascanus	gray starsnout	68.85	0.21	10.5–19.0
Bathyagonus infraspinatus	spinycheek starsnout	27.87	0.04	12.0–18.0
Bathyagonus spp.	unidentified poachers	1.64	<0.01	12.0
Leptagonus frenatus	sawback poacher	1.64	<0.01	26.2
Aptocyclus ventricosus	smooth lumpsucker	13.11	0.02	8.5–14.0
Liparis spp.	unidentified snailfishes	63.93	0.29	9.5–27.0
Careproctus spp.	unidentified snailfishes	1.64	0.01	10.7–17.8
Cyclopteridae	unidentified snailfishes	1.64	0.01	15.0
Ronquilus jordani	northern ronquil	1.64	<0.01	12.5
Lumpenus maculatus	daubed shanny	4.92	0.01	44.0–53.0
Lumpenus spp.	unidentified pricklebacks	16.39	0.14	37.0–59.0
Cryptocanthodes aleutensis	dwarf wrymouth	6.56	0.01	26.2–32.2
Ptilichthys goodei	quillfish	4.92	<0.01	91.0–105.0
Zaprora silenus	prowfish	26.23	0.05	9.6–30.0
Ammodytes hexapterus	Pacific sand lance	22.95	0.10	38.5–57.0
Atheresthes stomias	arrowtooth flounder	72.13	0.60	15.0–40.0
Embassichthys bathybius	deepsea sole	4.92	0.01	10.2–15.3
Errex zachirus	rex sole	26.23	0.06	19.0–39.5
Hippoglossoides elassodon	flathead sole	98.36	7.52	12.0–36.0
Hippoglossus stenolepis	Pacific halibut	6.56	0.01	20.4–24.0
Platichthys stellatus	starry flounder	6.56	0.01	8.1–9.5
Pleuronectes bilineatus	rock sole	65.58	0.26	10.0–27.0
Pleuronectes sp. II[1]	unidentified sole	19.67	0.05	7.0–18.0
Pleuronectes isolepis	butter sole	13.11	0.06	13.5–19.5

[1] See Matarese et al. (1989).

Table 2

Summary of juvenile fish collected in Methot trawls during 1991.

Scientific name	Common name	Percent occurence	Mean abundance (no./1000m^3)	Length range SL (mm)
Gadus macrocephalus	Pacific cod	65.57	0.44	26.0–43.5
Theragra chalcogramma	walleye pollock	88.52	1.42	26.0–52.0
Leptagonus frenatus	sawback poacher	3.28	<0.01	30.0–31.0
Zaprora silenus	prowfish	11.48	0.02	31.0–71.0

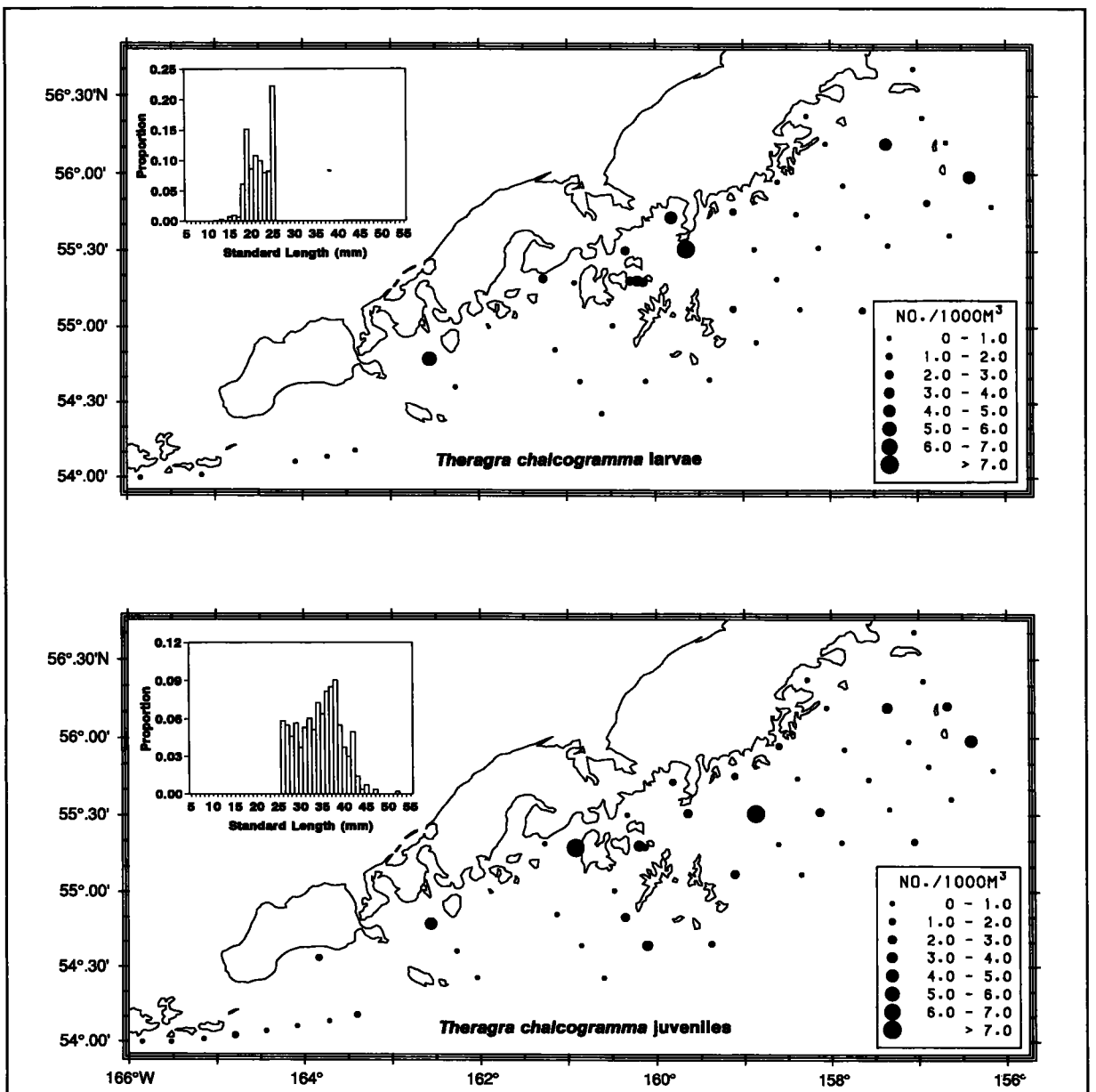

Figure 5

Distribution of larval and juvenile stages of *Theragra chalcogramma* in the study area. Also shown are the standardized length distributions for each life stage (inset).

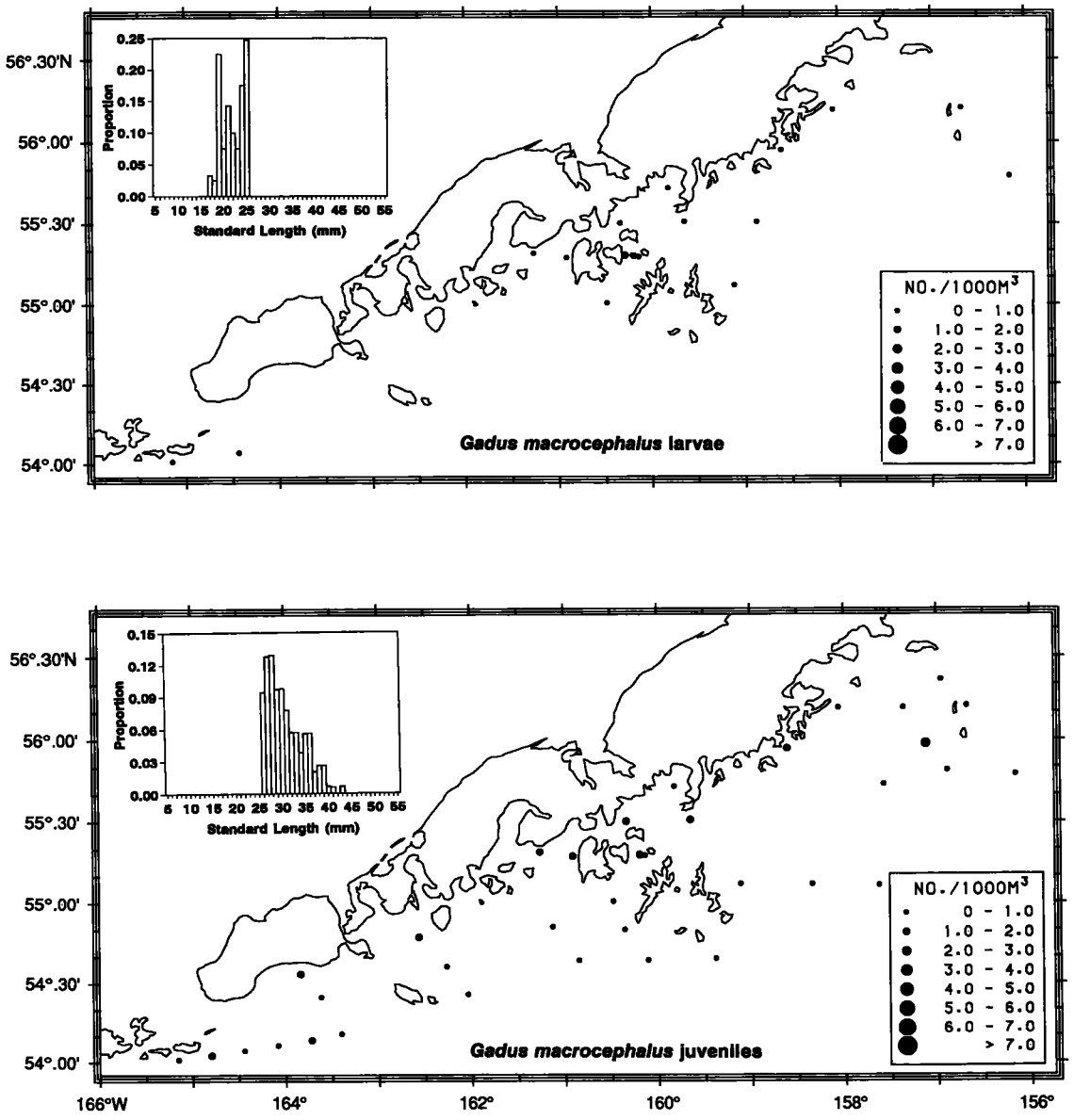

Figure 6

Distribution of larval and juvenile stages of *Gadus macrocephalus* in the study area. Also shown are the standardized length distributions for each life stage (inset).

Gadus macrocephalus larvae were differentiated from juveniles on the basis of this analysis.

Four station groupings were recognized by TWINSPAN (Fig. 11). An inshore group (group 4) showed a high positive association for *G. macrocephalus*, *T. chalcogramma*, and *H. elassodon* larvae and a negative association for *Sebastes* spp. larvae (Table 3). An offshore group (group 3) showed a high affinity for *Sebastes* spp. and *Bathyagonus alascanus* larvae and a low affinity for *A. hexapterus*, *H. elassodon*, and *Icelinus* spp. larvae. Many taxa, including larval and juvenile *T. chalcogramma*, *H. elassodon*, *A. hexapterus*, *Lumpenus* spp., and *A. stomias* showed high affinities, whereas *Bathyagonus infraspinatus* and *Sebastes* spp. larvae showed low affinities with a widely scattered midshelf grouping (group 2). Finally, a poorly defined grouping (group 1) was positively associated with *Sebastes* spp. larvae and negatively with *G. macrocephalus* and *Z. silenus* larvae. Ichthyoplankton densities were rela-

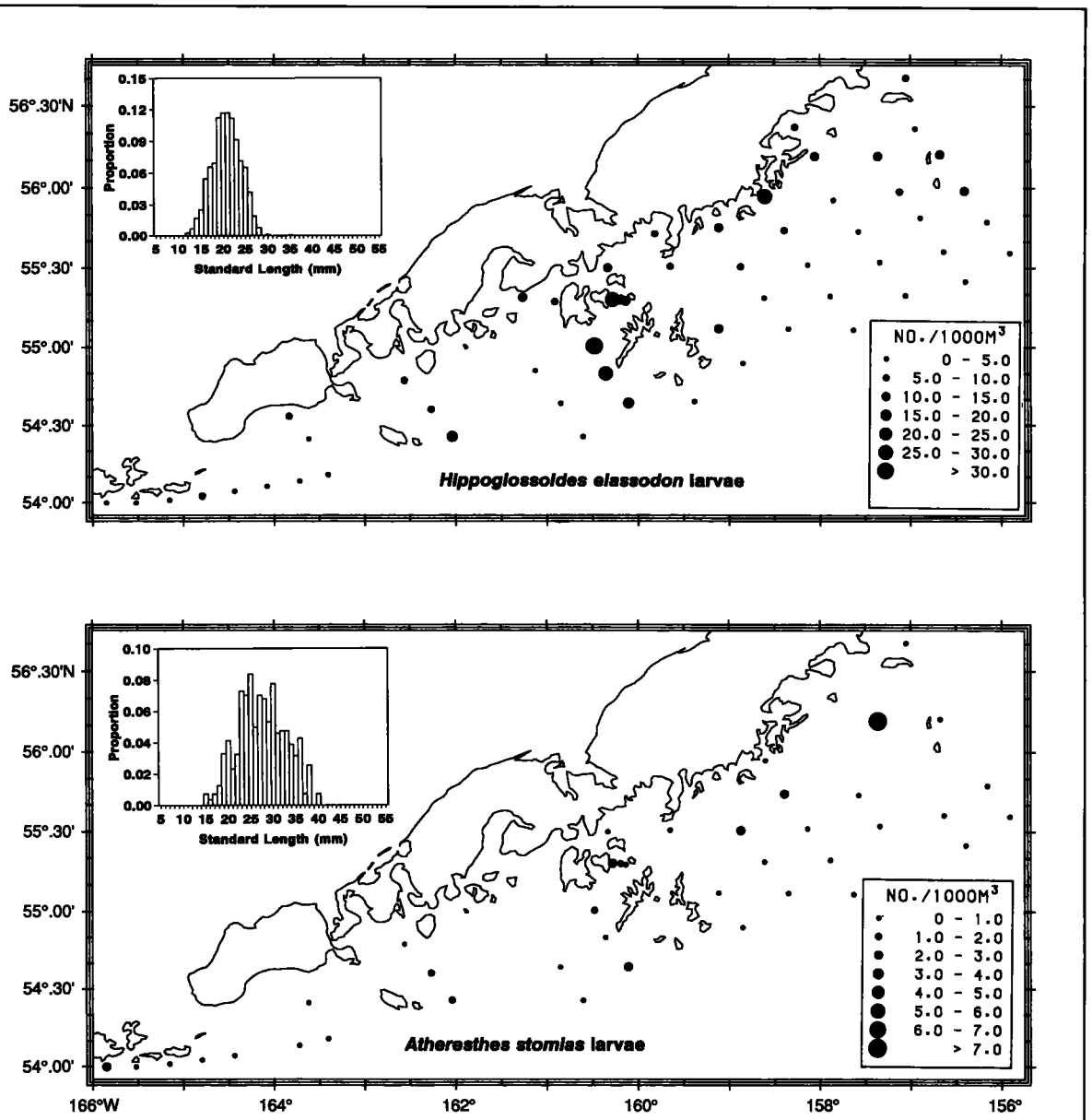

Figure 7

Distribution of larvae of *Hippoglossoides elassodon* and *Atheresthes stomias* in the study area. Also shown are the standardized length distributions for each species (inset).

tively high in group-2 and group-4 stations and low in group-1 and group-3 stations (Table 3).

Station groups showed little correspondence with the environmental variables examined. Distance from shore was the only variable that showed a clear relationship to the station groups (Table 4). Group 3 (offshore) and group 4 (inshore) were clearly differentiated from the remaining two midshelf groups. Although group 4 was the closest to shore, it also showed the greatest average bottom depth. Group 2 exhibited the shallowest mean depth and warmest mean surface temperature of the four station groupings (Table 4). Among the six variables examined, only distance from shore ($P<0.001$) and water temperature at 50 m depth ($P=0.048$) showed significant differences among the four groupings. In addition. the group closest to shore (group 4) had the warmest temperatures at 50 m ($\bar{x}=7.1°C$) and the one farthest from shore (Group 3) was colder ($\bar{x}=6.4°C$) at 50 m than the intermediate groupings (Fig. 11).

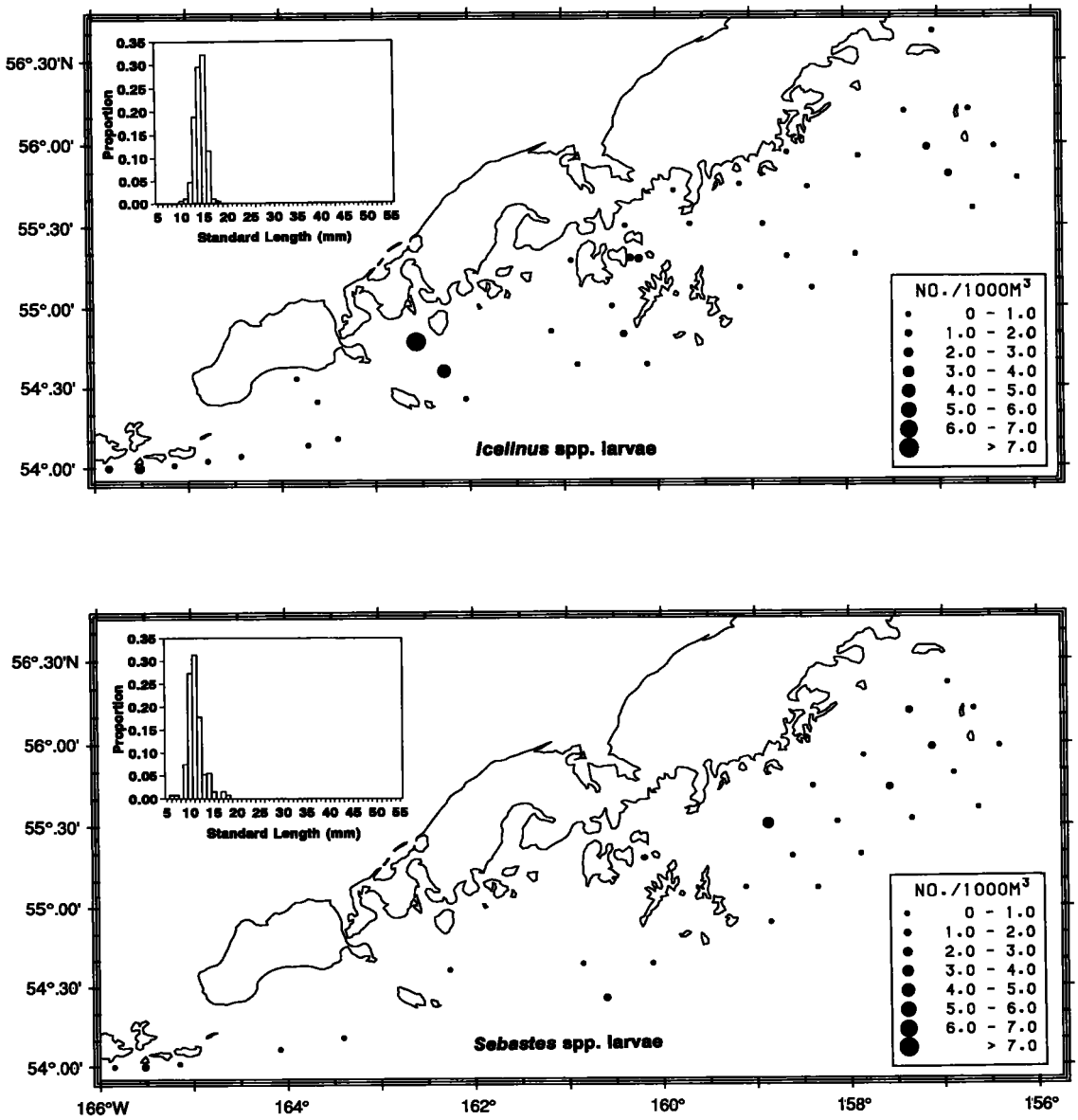

Figure 8

Distribution of larvae of *Icelinus* spp. and *Sebastes* spp. in the study area. Also shown are the standardized length distributions for each species (inset).

Comparison of abundance rankings with other surveys

The abundance rankings of the dominant taxa estimated showed some similarities among the three surveys (Table 5). The six most abundant taxa in the bottom trawl surveys were represented in the 10 most abundant taxa in both ichthyoplankton surveys, but the coherence was stronger (top three species the same) for the July Methot trawl survey than for the May bongo-net survey. The seventh most abundant species in the trawl survey, *Errex zachirus*, was ranked 14th in the Methot trawl collections but did not appear in the bongo-net sampling. A comparison of the ranks of only the taxa that were mutually present in samples from each gear type showed that the trawl survey was more similar in ranking to the Methot trawl survey data (Spearman Rank Correlation, $r_s = 0.50$) than to the bongo-net survey data ($r_s = 0.23$).

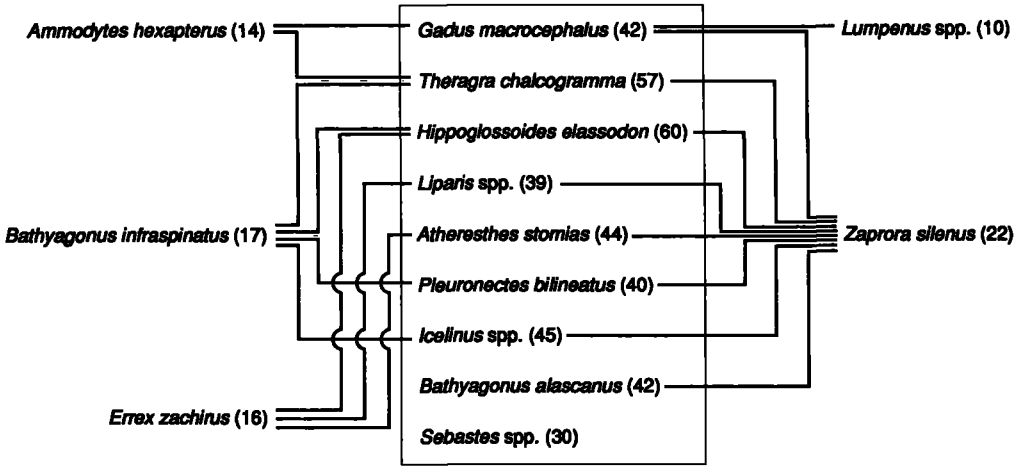

Figure 9

Results of the Recurrent Group Analysis showing the main grouping (within box) and associated taxa (outside box) at an affinity level of 0.40. The numbers in parentheses are the occurrences of each taxon.

Discussion

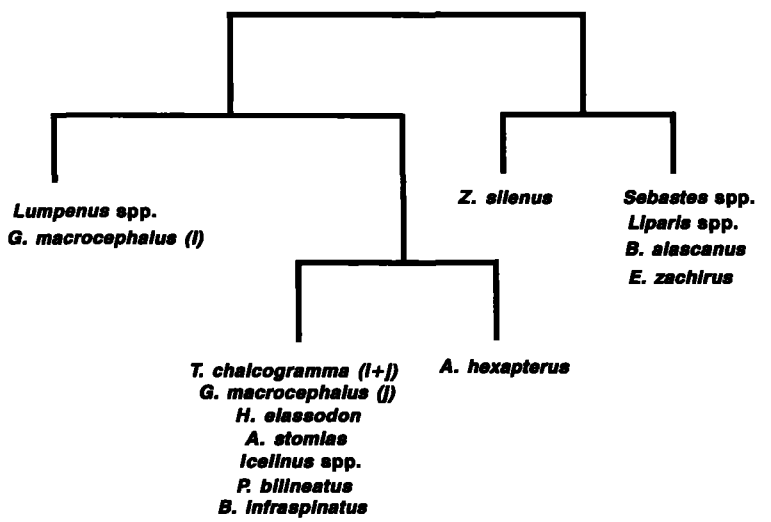

Figure 10

Taxa groupings resulting from the Two-way Indicator Species Analysis. The larval (*l*) and juvenile (*j*) stages of *Theragra chalcogramma* and *Gadus macrocephalus* are indicated separately.

Despite the relatively large biomass of adult fishes that inhabit this region, the mid-summer abundance and distribution patterns of ichthyoplankton have received little attention. The one previous study (Hinckley et al., 1991), which used a Methot trawl to sample the western Gulf of Alaska in June and July 1987, examined only the distribution of late larval and early juvenile *T. chalcogramma*. The highest densities of this species were found east of the Shumagin Islands, a finding that was similar to what we found. The only other surveys conducted during the summer employed net gear with small mouth openings (see Kendall and Dunn [1985] and references therein) and caught mainly eggs and early larvae. Some of the differences in species composition between the most commonly used ichthyoplankton gear (e.g. bongo nets) and that used in this study are likely due to extrusion of smaller larvae through the meshes of the Methot net. For example, one of the numerically dominant taxa collected during June and July in small-mesh bongo-net gear is *Bathymaster* spp. (Kendall and Dunn, 1985; Rugen[2]) which did not, however, occur in our Methot trawl collections. Since *Bathymaster* spp. larvae average only around 10 mm in length in early June (Rugen[2]), they are probably too small to be caught by the Methot trawl in July. Conversely, some taxa (e.g. *T. chalcogramma*) that

[2] Rugen, W. C. 1990. Spatial and temporal distribution of larval fish in the Western Gulf of Alaska, with emphasis on the period of peak abundance of walleye pollock (*Theragra chalcogramma*) larvae. NWAFC Proc. Rep. 90-01, 162 p. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

Table 3

Two-way table of dominant taxa showing the station and species groups as determined by TWINSPAN. Numbers in parentheses represent the number of stations in each station group. The numbers within the matrix correspond to the mean density (no./1000 m^3) of that taxon for each station grouping (— = taxon not present). Life stages of *T. chalcogramma* and *G. macrocephalus* are designated after species name (l=larvae, j=juvenile). The total ichthyoplankton for each station group represents all species including the rare taxa not included in the TWINSPAN analysis.

	Station group			
Taxon	1 (13)	2 (6)	3 (22)	4 (19)
Lumpenus spp.	0.02	1.05	—	0.09
G. macrocephalus (l)	—	0.02	0.02	0.38
A. hexapterus	0.08	0.66	—	0.05
H. elassodon	5.02	13.10	2.11	14.15
T. chalcogramma (l)	0.36	1.96	0.28	2.53
G. macrocephalus (j)	0.44	0.53	0.36	0.71
Icelinus spp.	0.70	1.88	0.28	0.44
P. bilineatus	0.34	0.24	0.10	0.40
A. stomias	0.44	2.18	0.44	0.45
T. chalcogramma (j)	0.63	6.33	0.70	1.35
B. infraspinatus	0.06	—	0.03	0.05
Z. silenus	—	0.10	0.30	0.08
B. alascanus	0.19	0.15	0.31	0.15
Liparis spp.	0.30	0.42	0.36	0.16
E. zachirus	0.10	0.12	0.02	0.04
Sebastes spp.	0.47	0.21	1.04	0.08
Total ichthyoplankton				
Mean	9.16	29.74	5.52	21.11
Standard deviation	3.63	5.19	2.84	8.12

spawn during spring are poorly sampled as late larvae and early juveniles by bongo-net gear in summer (Shima and Bailey, 1994).

Another study that examined the distribution of late larvae and early juveniles in our study area used neuston sampling gear, which tends to capture significantly larger specimens than do bongo nets (Doyle et al., 1995). These collections, however, were made mostly before June, and the taxonomic composition of the catch was markedly different from that of the present study in that only 3 of the 15 most abundant larvae (*A. hexapterus, T. chalcogramma*, and *Mallotus villosus*) caught in the neuston nets occurred in our samples.

One motivation for conducting ichthyoplankton surveys is to provide an alternative estimate to trawl surveys for the abundance of commercially exploitable fishes (Heath, 1992). Although there are biases involved with both ichthyoplankton and trawl surveys that may result in an incomplete picture of true fish population sizes, it is of interest to compare the results of these two assessment methodologies for the stocks in the western Gulf of Alaska (Kendall and Dunn, 1985). Trawl surveys tend to exclude small and cryptic taxa, particularly those that inhabit untrawlable bottom types. Diel differences in vertical distribution and aggregation patterns may also influence trawl survey abundance estimates. Ichthyoplankton surveys are restricted to sampling only the life stages that are pelagic at the time of the survey, therefore they are strongly dependent on the timing of spawning and the mode of development. Moreover, extrapolation of catches to population abundance requires additional information on basic life history strategies (e.g. hatch size, pelagic/demersal eggs, number of spawning events, oviparity/viviparity), spawning locations, population egg production, and mortality rates.

Differences in life history patterns may explain some of the disparities observed between the trawl and ichthyoplankton rankings. Two abundant trawl species, *Pleuronectes asper* and *Microstomous pacificus*, spawn in late spring and early summer off Alaska (Hirschberger and Smith, 1983; Matarese et

Table 4

Mean values of station and environmental variables for the four TWINSPAN station groups. Numbers in parentheses below each station group represent the number of stations in each group. Standard deviations are given in parentheses below each mean.

	Station group			
Mean variables	1 (13)	2 (6)	3 (22)	4 (19)
Surface temperature (°C)	12.80 (0.68)	13.06 (1.10)	12.83 (1.41)	12.73 (0.83)
50-m temperature (°C)	6.89 (1.01)	6.99 (0.95)	6.44 (1.19)	7.06 (0.54)
100-m or bottom temperature (°C)	6.22 (0.83)	6.42 (0.75)	6.05 (1.07)	6.38 (0.55)
Bottom depth (m)	103.5 (24.8)	87.0 (39.9)	116.4 (54.9)	137.9 (48.3)
Distance from shore (km)	28.8 (17.8)	25.9 (19.7)	54.4 (33.6)	13.9 (9.7)
Distance alongshore (km)	233.4 (205.2)	263.6 (127.2)	282.8 (223.4)	224.3 (103.1)

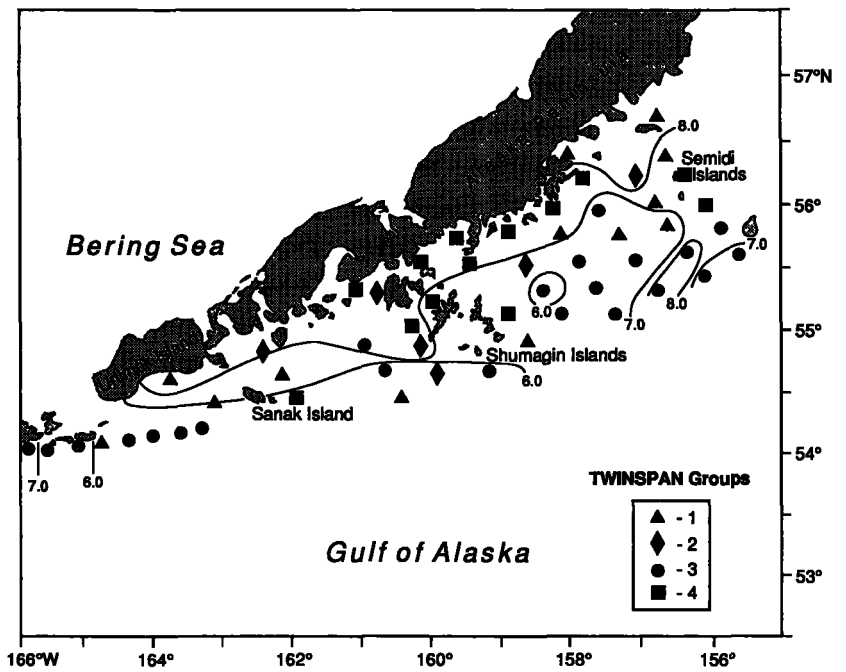

Figure 11

Station groupings from Two-way Indicator Species Analysis displayed on a map of the study area. See Table 3 for the dominant species comprising each station grouping. Also shown are the isotherms at 50 m measured at the time of sampling.

al., 1989) and are not usually represented as larvae in Gulf of Alaska ichthyoplankton sampling (Kendall and Dunn, 1985; Rugen[2]). Rex sole, *Errex zachirus*, spawn in the southern part of their range and are also rarely found in ichthyoplankton collections in the area. The other dominant trawl species, *Clupea pallasi*, spawns demersally in shallow water, and the early life stages are generally restricted to nearshore environments. Conversely, several taxa that are abundant in the ichthyoplankton samples are not well represented in the trawl sampling. These include fish of small maximum size (e.g. *A. hexapterus, Icelinus* spp., *Liparis* spp.), nearshore distribution (e.g. *B. alascanus, Z. silenus, Lumpenus* spp.) (Hart, 1973), or mesopelagic species that are found primarily offshore, but whose larvae are advected onshore (e.g. *Stenobrachius leucopsarus*).

Table 5

The top 10 most abundant taxa in the western Gulf of Alaska based on research trawl surveys during the summer of 1990 and on ichthyoplankton surveys during May and July of 1991.

Rank	Trawl survey	Bongo-net survey	Methot survey
1	*A. stomias*	*T. chalcogramma*	*H. elassodon*
2	*T. chalcogramma*	*A. hexapterus*	*T. chalcogramma*
3	*H. elassodon*	*Bathymaster* spp.	*A. stomias*
4	*Sebastes* spp.[1]	*A. stomias*	*G. macrocephalus*
5	*P. bilineatus*	*H. elassodon*	*Icelinus* spp.
6	*G. macrocephalus*	*Sebastes* spp.	*Sebastes* spp.
7	*E. zachirus*	*S. leucopsarus*	*P. bilineatus*[2]
8	*P. asper*	*G. macrocephalus*	*Liparis* spp.
9	*C. pallasi*	*P. bilineatus*[2]	*B. alascanus*
10	*M. pacificus*	*Icelinus* spp.	*Lumpenus* spp.

[1] Because larvae of *Sebastes* are presently not identifiable to species, all adult rockfishes from the trawl survey were combined into this category.
[2] Includes larvae of *Pleuronectes* sp. II which are morphologically similar to *P. bilineatus*. Adults were not distinguished in the trawl survey.

Despite the limitations involved with conducting ichthyoplankton abundance surveys with only one gear type (Suthers and Frank, 1989), our sampling with a relatively small number of Methot trawls during mid-summer of 1991 provided abundance

rankings that were quite similar to the groundfish abundance rankings estimated during 1990 and were much more similar than those estimated from larval collections only two months earlier in 1991. Additional collections taken earlier in 1991 (late April and early May) showed even less coherence with the adult groundfish community (Brodeur, unpubl. data). Apparently, many of the smaller species not vulnerable to the survey trawls leave the plankton and settle to rocky habitats or in nearshore areas during the summer, leaving many of the numerically dominant gadids and pleuronectids to be sampled. We chose to correlate the rankings rather than the actual abundance of species among the surveys because small differences in timing of spawning relative to the timing of the survey can have drastic effects on abundance owing to mortality and changes in catchability. For example, on the basis of the Methot trawl catches, *H. elassodon* appear to be much more abundant than *T. chalcogramma* in our survey area. This may be due to the fact that they hatch out about one month later than pollock (Rugen[2]) and thus have undergone substantially less larval mortality. Subsequent studies have also indicated that the 1991 year class of *T. chalcogramma* had very high larval mortality owing to either poor feeding conditions or to advection off the shelf (Bailey et al., 1995), resulting in very low recruitment that year (Bailey et al.[3]).

The similarity in the species groupings found with the two methods (Recurrent Group Analysis and TWINSPAN), each of which uses different resolutions of the same data (presence/absence vs. abundance), substantiates the conclusion that certain taxa tend to be associated in our study area. Whether these groupings result from behavioral aggregation by certain species that have been adapted to a particular habitat (Frank and Leggett, 1983) or whether hydrographic conditions passively transport larvae spawned in the same area to the same nursery area (Richardson et al., 1980; Olivar, 1987; Sabatés and Masó, 1990), or some combination of both (Cowen et al., 1993), cannot be determined from our data. However, many of the specimens collected in the Methot net may no longer be considered passive organisms because they can actively swim against currents while seeking out or remaining within favorable habitats. Because juvenile fishes respond not only to environmental conditions but also readily respond to the presence of conspecifics and potential predators (Olla et al., in press), several factors can influence their distribution patterns in natural conditions.

The lack of clearly defined boundaries between the station groups that we observed may be characteristic of this dynamic environment. In our study area, vigorous mixing and strong currents (Reed and Schumacher, 1986) do not allow formation of well-defined mesoscale physical boundaries (see also Doyle et al., 1995). However, the mid-summer ichthyoplankton community appears to reflect a large-scale onshore to offshore gradient of environmental characteristics that include midwater temperatures.

The ultimate usefulness of age-0 surveys for predicting year-class strength depends upon the relative mortality pressure occurring after the survey period. Although managers seek information on the relative strength of a year class as early as possible, the accuracy and precision of the index may be low for this life history stage for species that suffer variable late juvenile predation losses. For *T. chalcogramma*, substantial predation upon juveniles may occur in late summer (Livingston[4]), which may affect the magnitude of subsequent recruitment during some, if not all, years. A distinct advantage for early or mid-summer surveys of juveniles is that fish at this stage have not developed complicated diel vertical and inshore migrations or complex aggregation and schooling patterns that generally make later stage assessment so difficult (Koeller et al., 1986; Godø et al., 1991; Lough and Potter, 1993; Wilson et al., in press). Determining whether year-class strength for this population is set by mid-summer will require more years of abundance estimates, as well as sampling for several other life history stages in months both before and after the period surveyed in this study (Bailey and Spring, 1992; Bailey et al.[3]).

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Age and growth of tarpon, *Megalops atlanticus*, from South Florida waters*

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Abstract.—We examined 1,469 tarpon, *Megalops atlanticus*, ranging from 102 to 2,045 mm fork length (FL) collected in South Florida waters from 1988 to 1993. Females had a mean length of 1,677 mm FL (n=322) and were significantly larger than males, which had a mean length of 1,447 mm FL (n=125). Ages of 977 tarpon were estimated from thin-sectioned otoliths (sagittae). Eighteen tarpon were marked with oxytetracycline (OTC) to form a reference point on the otolith and were held in captivity for periods ranging from 13 to 50 months. Examination of OTC-marked otoliths suggested that a single annulus was formed each year. Marginal increments of young of the year and 1-year-old tarpon showed a single annual minimum during April–June. Tarpon are long-lived and reach a maximum age of at least 55 years. Growth of the tarpon in our study was rapid until an age of about 12 years and then slowed considerably. Male tarpon (n=141) ranged from 0 to 43 years in age, and female tarpon (n=298) ranged from 0 to 55 years in age. The von Bertalanffy growth equation for females was $FL = 1{,}818(1 - e^{(-0.103(Age+1.410))})$ and for males was $FL = 1{,}567(1 - e^{(-0.123(Age+1.575))})$. Estimates of the von Bertalanffy growth parameters L_∞ and K for males and females were significantly different. Predicted lengths of females were greater than those of males for all ages greater than 4 years.

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Tarpon, *Megalops atlanticus*, are large, migratory, elopomorphic fish that frequent coastal and inshore waters of the tropical and subtropical Atlantic Ocean. In the western Atlantic, tarpon regularly occur from Virginia's eastern shore to Central Brazil and throughout the Caribbean Sea and the Gulf of Mexico (Wade, 1962; Hildebrand, 1963; de Menezes and Paiva, 1966; Zale and Merrifield, 1989). In South Florida and parts of Central America, tarpon are the basis of economically important recreational fisheries. In Florida, the fishery is intensely regulated, and anglers are required to purchase a permit before harvesting a fish. Since the establishment of the permit system in 1989, the harvest of tarpon in Florida has declined to less than 100 fish per year, and the fishery is now mostly catch-and-release. Tarpon occur in a variety of habitats ranging from freshwater lakes and rivers to offshore marine waters, but large tarpon targeted by Florida's fishery are most abundant in estuarine and coastal waters. In Florida, the fishery is seasonal; most tarpon are caught during May–July, although some fish are caught in all months.

Tarpon life history has not been adequately described. Breder (1944) examined gonads of tarpon from Florida waters but did not fully describe either temporal spawning patterns or age and size at sexual maturity. De Menezes and Paiva (1966) macroscopically examined gonads of tarpon from Brazilian waters and reported on temporal spawning patterns and size at sexual maturity. Most information on tarpon reproduction in Florida waters has been inferred from early life history studies (Smith, 1980; Crabtree et al., 1992; Crabtree, 1995). Larval distribution patterns suggest that tarpon in Florida waters spawn offshore from May through August (Smith, 1980; Crab-

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tree et al., 1992; Crabtree, 1995). Smith (1980) estimated the length of the larval phase to be 2–3 months, but little is known about the processes that transport larvae from offshore spawning grounds to inshore juvenile habitat. Metamorphic larvae are typically found inshore in mangrove-lined estuaries but also occur in temperate *Spartina* marshes (Harrington, 1958 and 1966; Erdman, 1960; Wade, 1962; Mercado and Ciardelli, 1972; Tucker and Hodson, 1976; Chacón et al., 1992). Young-of-the-year (YOY) tarpon occur in small stagnant pools and sloughs of various salinities and have been reported from North Carolina (Hildebrand, 1934), Georgia (Rickards, 1968), Florida (Wade, 1962 and 1969), Texas (Simpson, 1954; Marwitz, 1986), Caribbean islands (Beebe, 1927; Breder, 1933), and Central America (Chacón et al., 1992).

Age and growth of tarpon are poorly documented. Previous age estimates based on the examination of scales suggest a maximum life span of about 15 years (Breder, 1944; de Menezes and Paiva, 1966). Studies on a variety of species show that scales are not reliable for ageing long-lived fishes and that scale-derived age estimates are typically lower than estimates derived from sectioned otoliths (Beamish and McFarlane, 1983; Casselman, 1983). Ageing of tarpon based on sectioned otoliths is needed to evaluate the accuracy of the ages estimated by Breder (1944) and de Menezes and Paiva (1966). In this article, we describe age and growth of tarpon from South Florida waters on the basis of an examination of sectioned otoliths.

Methods

We obtained tarpon from a variety of sources throughout South Florida from April 1988 to November 1993. Most large fish (>1,100 mm FL) were obtained from taxidermists in Fort Myers and Fort Lauderdale; the fish had been caught in either the Florida Keys or Boca Grande Pass on Florida's Gulf coast (26°43'N, 82°16'W). A second source of large fish was tournaments held in the Keys, Boca Grande Pass, and the Tampa Bay area (27°40'N, 82°35'W). All large tarpon were caught with hook-and-line gear. Small tarpon (<1,100 mm FL) were taken with cast nets, hook-and-line gear, electroshockers, trammel nets, and gill nets at various locations in South Florida. Young-of-the-year tarpon were caught most effectively with cast nets of various mesh sizes and ranging in radius from 2.1 to 3.1 m. We sampled YOY tarpon monthly from November 1988 to April 1991 at two sites in South Florida. On the Atlantic coast, we sampled Jack Island State Park (27°30'N, 80°18'W), a 159.5-ha, impounded saltmarsh immediately adjacent to the Indian River Lagoon. The site consisted of a series of ditches that surrounded brackish wetlands and that were connected by flood gates to the Indian River Lagoon. The second site was located on the Gulf coast approximately 1.6 km south of U.S. Highway 41 and 3.2 km east of Collier-Seminole State Park near Naples (25°58'N, 81°33'W). This site consisted of a series of mangrove-lined ponds and borrow ditches resulting from road construction in the salt marsh.

Standard length (SL), fork length (FL), and total length (TL) were measured to the nearest millimeter (mm). All lengths reported are fork lengths. Large tarpon (>1,100 mm) were weighed to the nearest 0.5 kg, and smaller tarpon were weighed to the nearest gram. Otoliths (sagittae) were removed, cleaned with bleach (5.25% sodium hypochlorite), and rinsed first in water and then in 95% ethanol. Otoliths were stored dry or in 95% ethanol until sectioned. Sex was recorded and confirmed histologically.

Undamaged otoliths were weighed to the nearest 0.01 mg. Weights of left and right otoliths were not significantly different (paired t-test, n=270, t=0.039, P=0.97); therefore, otolith weights were pooled for analysis. If both left and right otolith weights were available for an individual fish, the mean of the two weights was calculated. Linear regressions were fit to $\log_{10}$-transformed otolith weight and age data and were compared with a t-test (Zar, 1984).

Generally, the left sagitta was used for age estimation; however, if the left otolith was broken, lost, or destroyed during processing, the right otolith was substituted. We prepared otoliths for age estimation by embedding them in Spurr (Secor et al., 1992), a high-density plastic medium. A 1–2 mm thick transverse section containing the otolith core was cut with a Beuhler Isomet low-speed saw with a diamond blade. The section was mounted on a microscope slide with thermoplastic glue (CrystalBond 509 adhesive) and polished with wet and dry sandpaper (grit sizes ranging from 220 to 2,000) until the annuli were visible. Sections were then polished on a Beuhler polishing cloth with 0.05-μ gamma alumina powder to remove scratches. Annuli were counted three times by each of two independent readers using compound microscopes. Mean counts of each reader were not significantly different (paired t-test, n=1,099, t=1.30, P=0.193); therefore, all six counts were used to calculate a mean age. All counts and measurements were made along the ventral sulcal ridge (Fig. 1A); the dorsal ridge was used only as an aid to interpretation. Measurements were made with an ocular micrometer.

Tarpon otoliths were often difficult to interpret; therefore, we established the following criteria to

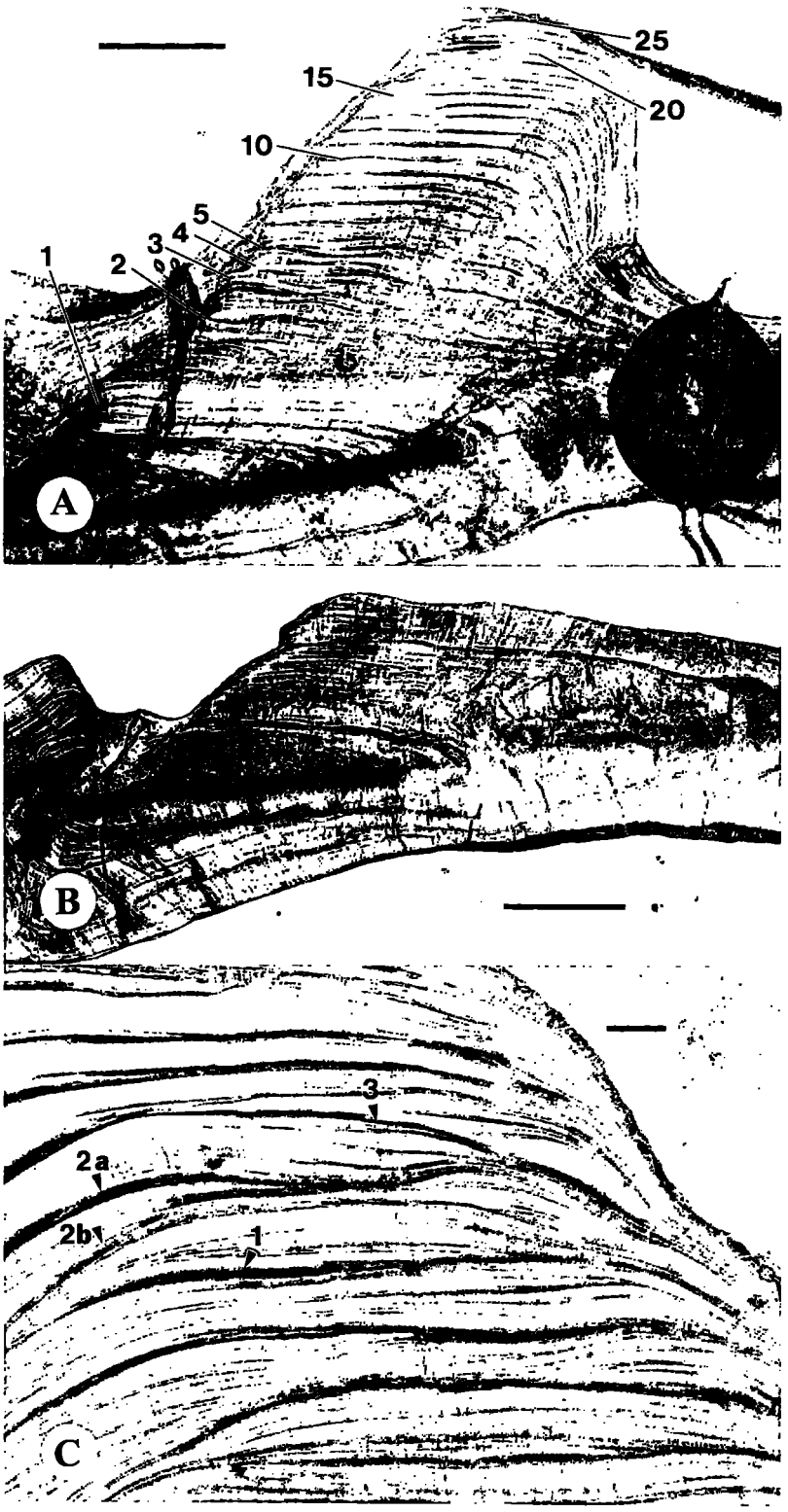

Figure 1

Transverse sections of tarpon, *Megalops atlanticus*, otoliths. (**A**) Section from a 25-year-old tarpon (1,727 mm FL) showing the annuli counted for age estimation. Scale bar = 500 μ. (**B**) Section from a 2-year-old tarpon (506 mm FL) showing the notch formed on the edge of the sulcal ridge. Scale bar = 500 μ. (**C**) Section from a 33-year-old tarpon (1,615 mm FL) showing confluent annuli that were interpreted as a single annual mark. Marks 2a and 2b were counted as a single annulus. Scale bar = 50 μ.

provide a consistent basis for determining whether an annulus should be counted as an annual mark. For the 4–5 annual marks closest to the core, a notch was usually present on the ventral edge of the sulcal ridge (Fig. 1B). The notch was typically accompanied by an annulus extending outward to the otolith's ventral margin. If a distinct notch was present, the annulus was counted even if the mark extending outward was indistinct. Confluent annuli were counted as a single annual mark unless the two annuli were confluent for only a short distance (Fig. 1C). If many confluent marks were present, the otolith was rejected as unreadable.

Annulus counts for individual otoliths often showed some level of variation among readings. We established criteria for accepting or rejecting individual otoliths by calculating a coefficient of variation $(CV) = (S/\bar{y} \times 100\%)$, where S = the standard error of counts for a given otolith, and $\bar{y}$ = the mean annulus count for a given otolith. CV precision criteria were calculated as $CV = \sqrt{(n \times d^2)/t^2}$, where n=the number of readings for a given otolith (6), d=the deviation allowed between the estimated mean increment count and the true count for a given otolith, and t=a one-tailed Student's t-statistic with $\alpha = 0.05$ and $n-1$ degrees of freedom. We allowed a maximum deviation (d) of 10%, which corresponds to a CV of 12.16%. After six readings were completed, otoliths for which there were significant disagreements among readings (CV≥12.16%) were again examined by both readers in an attempt to reconcile differences. After discussing possible explanations for the variability among readings, a decision was made regarding the readability of the otolith. If both readers judged the otolith to be readable, it was again read independently by each reader without knowledge of the previous readings. The reading showing the largest difference from the mean of all readings was then discarded and replaced by a new reading. This protocol was repeated twice, and if the CV remained ≥12.16%, the otolith was rejected.

Tarpon typically spawn during May–August (Crabtree et al., 1992; Crabtree, 1995), and annulus formation took place during January–May. Consequently, annulus counts were not always equivalent to age in years. To resolve this discrepancy, fish collected before 1 July (the approximate middle of the spawning season) that had recently formed an annulus during the winter or spring (determined on the basis of the proximity of the annulus to the otolith's margin) were assigned an age *one less* than the annulus count. Fish collected after 1 July were assigned an age *equal to* the annulus count.

The von Bertalanffy (1957) growth equation $FL_t = L_\infty(1 - e^{(-K(t-t_0))})$ was fit to observed age-length data with the nonlinear regression procedure of Statgraphics. Likelihood-ratio tests were used to compare parameter estimates (Kimura, 1980; Cerrato, 1990). Length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data and were compared with a t-test (Zar, 1984).

Tarpon were captured from the Sebastian River, located on Florida's Atlantic coast, by electroshocking or with trammel nets for age-validation experiments (Table 1). After capture, fish were sedated with MS–222, measured for fork length, and tagged with dart-type tags. After tagging, tarpon were injected with Liquamycin LA-200 (200-mg oxytetracycline [OTC]/mL) in the dorsal musculature at a dosage of 100-mg OTC per kg fish weight. Fish weight was estimated with a length-weight equation. Tarpon were then transported to one of three holding facilities located in Florida, where they were held for 13 to 50 months (Table 1). Two fish were held in a 25-m by 13-m by 2.7-m deep public aquarium at Mote Marine Laboratory in Sarasota, six were held in a 33.5-m by 5.5-m by 0.75-m deep pond at the Keys Marine Laboratory in Long Key, and 10 were held in a 9.1-m diameter by 2.0-m deep tank at the Florida Marine Research Institute's Stock Enhancement Research Facility (SERF) at Port Manatee. Fish were held at ambient temperatures in all facilities except in SERF, where heaters were used during the winter to prevent temperatures from dropping below 14°C. Tarpon were fed as much frozen fish as they would consume at least three times a week. Otolith sections were examined with a compound microscope (40–100×) equipped with ultraviolet light so that the fluorescent OTC marks could be detected.

Results

The 1,469 tarpon we examined ranged from 102 to 2,045 mm in length; 740 (50.4%) of these were YOY or 1-year-old fish (<400 mm). Of these 740 small fish, we examined 179 histologically but could sex only 11 (6.1%); consequently, the sex of most YOY and 1-year-old tarpon was unknown and they were excluded from sex-specific regressions. Neither slopes (t-test, df=602, t=0.039, P=0.484) nor elevations (t-test, df=603, t=0.205, P=0.419) of the length-weight equations for male and female tarpon were significantly different. The pooled length-weight equation for sexed and unsexed fish and the relationships between SL, FL, and TL are presented in Table 2.

Female tarpon attained larger sizes than did males. Among the fish that we sexed, females ranged from 331 to 2,045 mm in length (median=1,635 mm, upper quartile=1,752 mm, n=412) and were signifi-

Table 1

Data for oxytetracycline (OTC)-injected tarpon, *Megalops atlanticus*. Otolith measurements were made along the ventral sulcal ridge from the otolith core to the OTC mark, annuli, and the otolith's edge. Measurements were made to the annulus at or just before the OTC mark and all subsequent annuli. Holding facilities are MOTE = Mote Marine Laboratory, KML = Keys Marine Laboratory, and SERF = Florida Marine Research Institute's Stock Enhancement and Research Facility.

		Injected		Sacrificed				Distance from core (mm)						
Specimen number	Holding facility	Date	Fork length (mm)	Date	Fork length (mm)	Months held	Age (years)	OTC mark	Annulus	Annulus	Annulus	Annulus	Annulus	Otolith edge
1137	MOTE	March 89	580	Oct 90	675	20	?	1.61	1.60					1.84
1138	MOTE	March 89	518	Oct 90	686	20	4	1.59	1.60	1.69				1.78
1486	KML	March 90	640	Sep 92	791	32	5	1.51	1.50	1.57	1.65			1.71
1487	KML	March 90	663	Sep 92	762	32	7	2.06	2.06	2.16	2.29			2.35
1488	KML	March 90		Sep 92	749	32	6	2.06	2.07	2.16	2.39			2.45
1489	KML	March 90	617	Sep 92	785	32	6	1.53	1.53	1.67	1.75			1.82
1490	KML	March 90	548	Sep 92	727	32	4	1.33	1.32	1.41	1.49			1.61
1568	KML	March 90		May 94	802	50	9	1.84	1.84	1.88	1.94	2.00	2.04	2.04
1548	SERF	Sep 92	570	Oct 93	762	13	?	1.67						1.80
1549	SERF	Sep 92		Oct 93	859	13	?	1.94						1.96
1559	SERF	Sep 92	890	May 94	1,005	21	?	2.25	2.25	2.35				2.37
1560	SERF	Sep 92	670	May 94	805	21	7	1.84	1.81	1.86	1.98			1.98
1561	SERF	Sep 92		May 94	790	21	5	1.65	1.63	1.67	1.80			1.86
1562	SERF	Sep 92	750	May 94	900	21	8	2.04	2.04	2.16	2.24			2.25
1563	SERF	Sep 92	670	May 94	900	21	6	1.84	1.81	1.88	1.99			2.00
1564	SERF	Sep 92		May 94	805	21	4	1.53	1.44	1.55	1.76			1.78
1565	SERF	Sep 92	615	May 94	850	21	?	1.51						1.76
1566	SERF	Sep 92	760	May 94	950	21	?	1.80	1.82					1.86

cantly larger than males, which ranged from 203 to 1,884 mm in length (median=1,346 mm, upper quartile = 1,467 mm, n=203; Mann-Whitney U-test, $P<0.001$). The recreational harvest of tarpon in Florida consisted principally of large fish. Among the fish sampled from the recreational fishery, females ranged from 1,193 to 2,040 mm in length (mean = 1,677 mm, SD=141.5, n=322) and were significantly larger than males, which ranged from 901 to 1,884 mm in length (mean=1,447 mm, SD=130.2, n=125; t-test, t=15.77, $P<0.001$).

We examined OTC-marked otoliths from 18 tarpon (Table 1). Individuals showed increases in length ranging from 95 mm in 20 months to 235 mm in 21 months. Otoliths from 12 fish ranging in age from 4 to 9 years showed the expected pattern of otolith growth; one annulus had been formed per year. One tarpon (specimen number 1549) showed little otolith growth and formed no visible annuli while in captivity. Two tarpon (specimen numbers 1559 and 1566) that were sacrificed in May, 21 months after OTC injection, had lower annulus counts than expected. Otoliths from these two fish showed little growth distally to the annulus during their first winter or spring in captivity. Otoliths from three other tarpon (specimen numbers 1137, 1548, and 1565) were problematic, and we were unable to estimate their ages. Annuli on these otoliths were indistinct, and we would have judged these otoliths to be unreadable had they come from wild fish. Five of the six fish whose otoliths were problematic were held in the heated facility at SERF and the other one was held at Mote Marine Laboratory. Otoliths from all six tarpon held in the flow-through facility at Keys Marine Laboratory had the expected pattern of one annulus per year.

Marginal-increment analysis of otoliths from YOY and 1-year-old tarpon suggested that one annulus formed each year. Young-of-the-year tarpon formed an annual mark sometime between December and May, and all YOY and 1-year-old tarpon otoliths had formed a first annulus by June (Fig. 2A). Mean marginal increments showed a seasonal minimum during April–June and a maximum in November (Fig. 2B). Marginal-increment analysis of older tarpon was not possible because of the incomplete seasonal coverage and limited sample sizes.

Table 2

Length-length, length-weight, and otolith weight-age regressions for tarpon, *Megalops atlanticus*, from South Florida waters. TL = total length (mm), FL = fork length (mm), SL = standard length (mm), WT = weight (kg), OWT = otolith weight (g), and AGE= age in years. Sample fork-length range for all length-length regressions was 106–2,045 mm and for length-weight regressions was 102–2,045 mm; age range for the otolith weight-age regressions was 1–55 years for females and 1–43 years for males. Values in parentheses are standard errors.

			$Y = a+bX$		
Y	X	n	a	b	r^2
FL	SL	1,342	10.8404 (0.6339)	1.0423 (0.0007)	0.999
FL	TL	1,061	−10.8096 (0.8084)	0.8967 (0.0007)	0.999
SL	FL	1,342	−9.9770 (0.6131)	0.9588 (0.0007)	0.999
SL	TL	1,051	−21.1779 (1.0181)	0.8606 (0.0009)	0.999
TL	FL	1,061	12.6345 (0.8937)	1.114 (0.0009)	0.999
TL	SL	1,051	25.5839 (1.1622)	1.1607 (0.0012)	0.999
$\log_{10}$WT	$\log_{10}$FL	1,262	−7.9156 (0.0124)	2.9838 (0.0045)	0.997
$\log_{10}$OWT (females)	$\log_{10}$AGE	193	−1.2083 (0.0199)	0.5476 (0.0152)	0.872
$\log_{10}$OWT (males)	$\log_{10}$AGE	106	−1.1734 (0.0183)	0.4614 (0.0162)	0.886

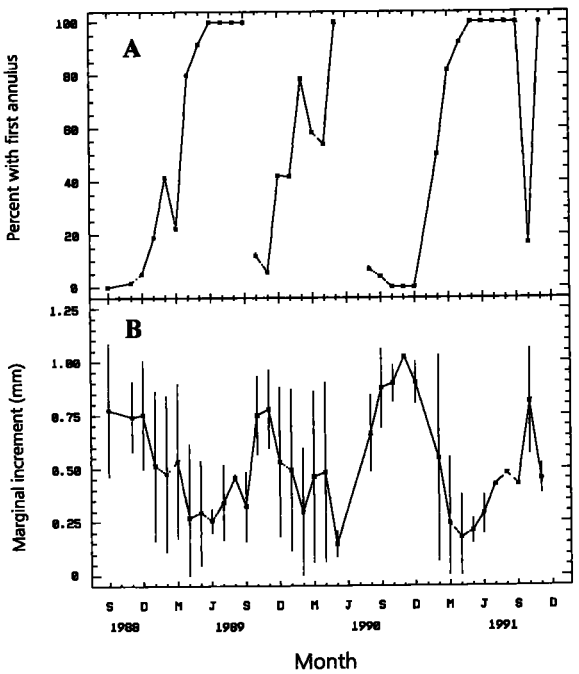

Figure 2

(**A**) Percentage (by month) of otoliths from young-of-the-year and 1-year-old tarpon, *Megalops atlanticus*, that had formed a first annulus. (**B**) Monthly mean marginal increment width and standard deviation for otoliths from young-of-the-year and 1-year-old tarpon.

Table 3

Parameter estimates for the von Bertalanffy growth model for tarpon, *Megalops atlanticus*, collected in Florida. Values in parentheses are standard errors.

Sex	n	L_∞(mm)	K	t_0	r^2
Males	141	1,566.6 (23.65)	0.123 (0.0090)	−1.575 (0.2519)	0.933
Females	298	1,817.7 (16.14)	0.103 (0.0049)	−1.410 (0.2158)	0.930

Of 1,231 otoliths processed for age estimation, 138 (11.2%) were judged unreadable by one or both readers and were not assigned ages, and an additional 116 (9.4%) otoliths were rejected for having high variation among readings (CV≥12.16%); thus 977 (79.4%) otoliths were accepted for age estimates. Of these 977 otoliths, 470 (48.1%) were from YOY tarpon. The length-frequency distribution of fish whose otoliths were rejected because they were unsuitable for age estimation was not significantly different from that of all fish whose otoliths were examined (χ^2=12.4, df=19, P=0.86).

Tarpon are long-lived; the oldest fish examined was a 2,045-mm female estimated to be 55 years old. The oldest male was 43 years old and had a length of 1,710 mm. Tarpon growth was rapid until an age of about 12 years, after which growth slowed considerably (Fig. 3). Likelihood-ratio tests showed a significant difference in the overall von Bertalanffy growth models for males and females (χ^2=122.70, df=3, P<0.001, Table 3). Estimates of L_∞ (χ^2=51.31, df=1, P<0.001) and K (χ^2=4.48, df=1, P=0.036) also differed between the sexes, while t_0 was not significantly different (χ^2=0.28, df=1, P=0.58). Lengths at age predicted by the von Bertalanffy equation agreed with the average observed lengths of both female and male tarpon (Fig. 3). Predicted lengths at age of females were greater than those of males for all ages greater than 4 years (Table 4).

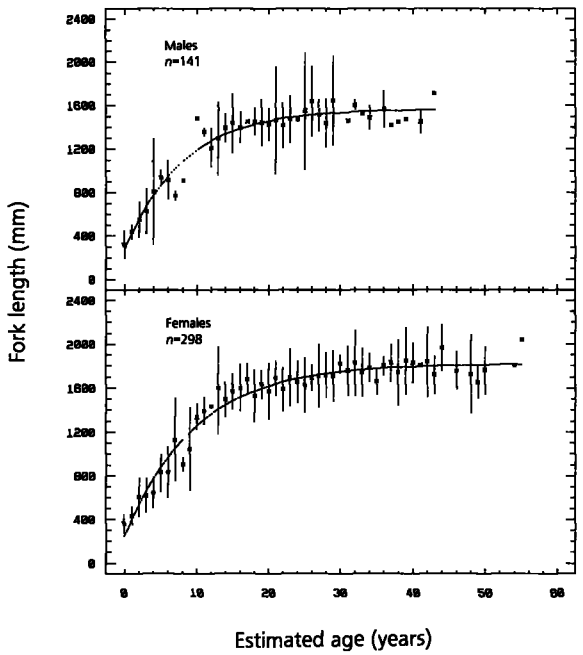

Figure 3

Average observed lengths (± two standard deviations) and predicted lengths from the von Bertalanffy growth model for male and female tarpon, *Megalops atlanticus*.

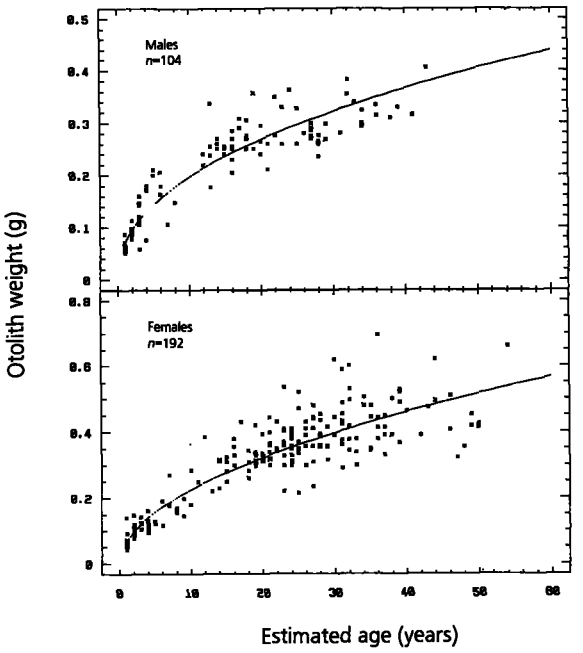

Figure 4

Growth of otoliths (g) of male and female tarpon, *Megalops atlanticus*. The equation for the regression of $\log_{10}$-transformed data is presented in Table 2.

Otolith weight was significantly related to age (Fig. 4). The slopes of the otolith weight-age equations (Table 2) were significantly different for males and females (t-test, t=3.69, df=295, P<0.001).

Discussion

We obtained tarpon from a variety of fishery-independent and fishery-dependent sources; consequently, our sample was biased towards certain size classes, and the size-frequency distribution of our sample may not reflect that of the population. Most small fish (<1,100 mm) came from fishery-independent sources, and larger fish were sampled from the recreational fishery. Our size distributions were bimodal and contained many small and large fish, but only a few fish 900–1,200 mm in length because these intermediate-size fish were too large to be sampled effectively by our gear and were rarely harvested in the recreational fishery. The size frequency of tarpon sampled from the recreational fishery was probably biased towards larger individuals. Most fish were caught during tournaments or were kept as trophies to be mounted by a taxidermist; presumably in both situations anglers selectively kept larger fish. Sometimes tournaments imposed minimum size requirements of as much as 50 kg on the fish harvested. Because males were typically smaller than females and rarely exceeded 45 kg, our samples from the recreational fishery contained roughly twice as many females as males, but this probably does not reflect the population's sex ratio. Among the smaller tarpon (<1,100 mm) obtained from fishery-independent sources, there were 79 males and 85 females and the sex ratio was not significantly different from 1:1 (χ^2=0.230, df=1, P=0.064).

Age-validation experiments with OTC-marked otoliths supported the hypothesis that tarpon otoliths formed annual marks. Otoliths from 3 of the 18 OTC-injected tarpon showed fewer than the expected number of increments. These fish showed relatively little otolith growth following capture, and we were unable to resolve annuli that might have been present on the otolith's margin. We could not read the otoliths from three other tarpon and were unable to validate the periodicity of annulus formation for these fish. It is not surprising that several otoliths from OTC experiments were rejected as unreadable because almost 21% of otoliths from wild fish were unreadable;

Table 4

Average observed and predicted fork lengths (mm) for male, female, and unsexed tarpon, *Megalops atlanticus*. Values in parentheses are standard error and sample size.

	Males		Females		Unsexed
Age (yr)	Average observed	Predicted	Average observed	Predicted	Average observed
0	321 (26.5;6)	276	362 (24.9;3)	246	239 (2.3;461)
1	440 (10.0;11)	425	434 (13.5;10)	400	396 (21.0;21)
2	552 (26.7;9)	557	607 (26.0;12)	538	547 (11.9;20)
3	626 (31.0;12)	674	621 (23.6;12)	664	626 (32.1;9)
4	806 (140.9;3)	777	645 (23.9;9)	777	
5	940 (20.8;3)	869	830 (36.6;6)	878	786 (154.0;2)
6	918 (45.4;4)	950	831 (58.7;4)	970	
7	774 (16.5;2)	1,021	1,130 (94.8;4)	1,053	
8	909 (1)	1,084	903 (22.5;2)	1,128	1,143 (1)
9		1,140	1,044 (95.3;4)	1,196	1,100 (1)
10	1,480 (1)	1,189	1,337 (41.5;2)	1,256	
11	1,359 (13.0;2)	1,233	1,391 (36.9;3)	1,311	921 (1)
12	1,205 (52.3;3)	1,272	1,435 (1)	1,361	1,310 (68.0;2)
13	1,295 (69.6;6)	1,306	1,601 (152.5;2)	1,406	
14	1,392 (29.7;5)	1,336	1,495 (39.6;4)	1,446	
15	1,435 (60.7;5)	1,363	1,568 (30.4;7)	1,482	1,385 (114.5;2)
16	1,400 (26.9;7)	1,386	1,602 (38.2;8)	1,515	1,538 (1)
17	1,451 (2.3;3)	1,407	1,684 (31.4;5)	1,545	1,317 (39.7;5)
18	1,450 (23.0;8)	1,426	1,527 (39.2;9)	1,572	
19	1,443 (47.9;5)	1,442	1,633 (20.9;10)	1,596	
20	1,428 (42.8;3)	1,456	1,571 (49.1;7)	1,617	
21	1,465 (143.0;3)	1,469	1,691 (19.9;16)	1,637	
22	1,417 (61.3;3)	1,480	1,589 (41.8;6)	1,655	1,397 (1)
23	1,473 (76.0;2)	1,490	1,695 (37.7;12)	1,671	1,397 (1)
24	1,470 (5.0;2)	1,499	1,656 (23.1;17)	1,685	1,750 (1)
25	1,550 (190.0;2)	1,507	1,625 (47.0;7)	1,698	1,498 (152.0;2)
26	1,639 (114.5;2)	1,514	1,691 (24.1;6)	1,710	
27	1,513 (30.2;6)	1,520	1,710 (50.8;8)	1,720	
28	1,438 (55.7;4)	1,525	1,715 (34.6;9)	1,730	1,675 (1)
29	1,648 (119.2;3)	1,530	1,706 (38.5;9)	1,738	1,848 (120.5;2)
30		1,534	1,818 (18.2;5)	1,746	
31	1,460 (1)	1,538	1,760 (29.7;15)	1,753	
32	1,604 (16.0;2)	1,541	1,824 (61.8;6)	1,759	
33	1,525 (1)	1,544	1,741 (38.6;8)	1,765	1,473 (1)
34	1,489 (32.8;3)	1,547	1,782 (37.6;3)	1,770	
35		1,549	1,658 (25.3;6)	1,775	
36	1,570 (60.0;2)	1,551	1,802 (19.2;5)	1,779	
37	1,422 (1)	1,553	1,830 (38.1;5)	1,783	
38	1,450 (1)	1,555	1,741 (85.0;3)	1,786	
39	1,473 (1)	1,556	1,846 (77.0;4)	1,789	
40		1,557	1,827 (52.4;3)	1,792	
41	1,448 (38.0;2)	1,558	1,800 (1)	1,795	
42		1,559	1,835 (115.0;2)	1,797	1,580 (1)
43	1,710 (1)	1,560	1,718 (49.5;3)	1,799	
44			1,965 (75.0;2)	1,801	
45				1,802	
46			1,755 (50.3;3)	1,804	
47				1,805	
48			1,727 (127.0;2)	1,806	1,679 (73.0;2)
49			1,656 (44.1;3)	1,808	
50			1,762 (63.2;3)	1,809	
51				1,809	
52				1,810	
53				1,811	
54			1,800 (1)	1,812	
55			2,045 (1)	1,812	

thus, we expected at least this percentage of otoliths from captive fish to be unreadable. Indeed, it is likely that captive conditions and nonseasonal food availability diminished the seasonal nature of otolith growth in captive fish and thereby increased the difficulties in otolith interpretation. Our use of heaters at SERF during the winter reduced the seasonal change in water temperature; five of the six fish with problematic otoliths were held at this facility. We used the heaters at SERF during winter cold fronts when water temperatures might have reached low levels lethal to tarpon. Otoliths from all six of the tarpon held in the flow-through facility at Keys Marine Laboratory, where water at ambient temperature was continuously pumped from Florida Bay, showed the expected pattern of one annulus formed per year.

Marginal-increment analyses also supported our hypothesis that the marks we counted formed once per year. The consistent marginal-increment minima observed for YOY and 1-year-old tarpon suggest that the marks present on otoliths of these fish were annual marks formed during winter or spring.

Additional support for the validity of our age estimates comes from the life span of a captive tarpon placed in the John G. Shedd Aquarium in Chicago, Illinois, in November 1935. This tarpon was still alive in April 1994 and was at least 59 years old[1] confirming that tarpon can reach ages of more than 50 years as our data suggest.

Tarpon otoliths had annuli on both the dorsal and ventral sulcal ridges that were similar in appearance to validated annuli in other species. Typically, annuli on the ventral ridge were more easily distinguished, and annulus counts from this ridge were usually higher than annulus counts from the dorsal ridge. Some otoliths had regions where bands were distorted, unclear, or confluent, making counts difficult or impossible. In other otoliths, portions of the sulcal ridge were dark in color and annuli were obscured. Our rejection of many otoliths as unreadable could have biased our growth-parameter estimates, but the size distribution of tarpon with otoliths judged to be unreadable was not significantly different from that of all tarpon examined for age and growth. Thus, we did not systematically reject a higher proportion of larger and presumably older fish than smaller and presumably younger tarpon. We do not know if rejected otoliths tended to come from faster- or slower-growing tarpon; this is a potential source of bias in our growth-parameter estimates.

We could not sex most of the 0-, 1-, and 2-year-old tarpon examined and this is another potential source of bias in our growth models. Observed lengths at age for the males and females we could sex at ages 0–2 were larger than the observed lengths of unsexed fish (Table 4). It is likely that the 0-, 1-, and 2-year-old fish we could sex were precocious and thus larger than comparably aged fish that we could not sex. Consequently, our sex-specific growth models were biased towards larger fish at these young ages; however, the predicted lengths at age from both sex-specific growth models at ages 0, 1, and 2 were between the observed lengths of sexed and unsexed fish, thus this bias was probably small. In addition, because both growth models included over 40 year classes, this bias probably had little effect on our growth-parameter estimates.

Tarpon scales do not appear to be suitable for age estimation. Scale-derived estimates of tarpon longevity by Breder (1944) and de Menezes and Paiva (1966) suggested a maximum age of only 15 years, much lower than our otolith-derived estimate of 55 years and the known age of captive tarpon. De Menezes and Paiva (1966) presented scale-derived estimates of von Bertalanffy growth parameters for tarpon and estimated that for males, L_∞= 2,062 mm, K=0.084, and t_0=0.20 and for females, L_∞=2,633, K=0.065, and t_0=0.17. These estimates are probably biased by a consistent underestimation of ages and are considerably different from our otolith-derived estimates. Scale-derived estimates of L_∞ are unrealistically high and are much larger than the maximum size documented for any tarpon.

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[1] Anderson, James A. 1994. Assistant Curator of Fishes, John G. Shedd Aquarium, Chicago, IL. Personal commun.

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Abstract.—Samples of *Plectropomus leopardus* collected at two reefs (Glow and Yankee) that have been closed to fishing since 1987 were compared with samples collected at two reefs (Grub and Hopkinson) that were open to fishing to investigate the effects of a 3–4 year closure on the size, age, and sex structure of leopard coralgrouper (also known as "coral trout") populations. There were no significant differences in mean size and age between protected reefs and unprotected reefs. However, mean size and age varied significantly between the two protected and the two unprotected reefs. In the two reefs closed to fishing, the population structure was dominated by the presence of a strong year class which settled in early 1984, indicating the occurrence of strong interannual fluctuations in recruitment. A similar pattern was not observed on the reefs open to fishing, suggesting that fishing mortality may have caused the decrease in abundance of this strong year class on the open reefs. Sex change occurred over a wide range of sizes and ages on the four reefs. A comparison of the frequency of developmental stages between reefs indicated significant variation. The two unprotected reefs had a smaller proportion of males, but that seemed to be compensated for by a larger proportion of transitional-stage fish and young males. Although the distribution of developmental stages in the populations was different, the same final female: male balance was achieved. This suggests that for the leopard coralgrouper, sex change results from a combination of developmental and behavioral processes. Differences in age structure were more obvious than differences in the size structure between closed and open reefs, suggesting that age structure may be far more useful than size structure for comparisons of fishing effects on long-lived fishes such as Epinephelinae serranids. Comparisons of open and closed reefs based solely on mean sizes may fail to detect important differences.

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Population structure of the leopard coralgrouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, Central Great Barrier Reef, Australia

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Fishing is one of the most important human exploitative activities on coral reefs (Munro, 1983; Munro and Williams, 1985; Russ, 1991). It has been suggested that fishing may have a greater impact upon fish populations and communities of coral reefs than upon those of temperate seas because of the more territorial nature of most coral reef fish (Russ, 1991). Therefore, the impact of fishing on populations and communities of coral reef fishes has been of considerable interest. Large predatory species are especially affected by overfishing owing to life history characteristics such as slow growth, high longevity, low rates of natural mortality, and limited adult mobility (Plan Development Team [PTD], 1990; Russ, 1991).

Fishing is known to cause selective removal of larger (and presumably older) individuals, thus reducing their proportion in the population (Ricker 1969; Miranda et al., 1987). Although evidence for effects of fishing on the size structure of populations of coral reef fishes is strong (Munro, 1983; PDT, 1990), there is little evidence for effects of fishing on age structure, probably because of the perceived difficulties in age determination of tropical fishes (Manooch, 1987). On the Great Barrier Reef, for example, information on age structure from a number of reefs exists for only one species, the damselfish *Pomacentrus moluccensis* (Doherty and Fowler, 1994). In the presence of high variability in size at age, information on age structure can provide information on harvesting effects not obtainable by size-structured data alone. Different growth processes can also be associated with selective fishing mortality (Parma and Deriso, 1990), enhancing the importance of analyzing age in assessments of the the effects of fishing on such populations.

Sequential hermaphroditism is common among coral reef fishes (Thresher, 1984). Bannerot et al. (1987) modelled the resilience of protogynous populations to exploitation and concluded that a definite risk existed in managing these stocks by traditional yield-per-recruit models under high fishing pressure. The effects of selective removal of larger individuals (presumably mostly males) on the sex

ratio of a population, however, will depend on the mechanisms controlling sex reversal. For example, for protogynous populations, if female to male sex change is determined by size or age, a decline in the proportion of males will be expected. Such effects have been reported by Thompson and Munro (1983) in comparing populations of serranids subjected to different levels of fishing pressure in the Caribbean. In contrast, no fishing-related effects were detected by Reeson (1983) on populations of scarids. Social induction of sex change is known or claimed for many species of fish (Shapiro, 1987). If this is the case, selective removal of larger individuals would induce female to male sex change, compensating for the effects of fishing on the sex ratio. Consequently, a reduction in the average size and age of sex change would be expected.

A widely recognized management strategy in the conservation of reefs is the implementation of marine fisheries reserves, areas designed to protect stocks of reef fish and habitats from all forms of exploitation (PDT, 1990; Williams and Russ, 1994). The first marine protected area was established in Florida in 1930. Since then, protected marine areas have been implemented all over the world (PDT, 1990). In Australia, the first protected marine areas were established in the Capricornia Section of the Great Barrier Reef Marine Park in 1981, under the first zoning plan to come into operation (Craik, 1989).

Evidence suggests that long-term spatial closure to fishing increases the density, biomass, average size, and fecundity of reef fishes (see PDT, 1990; Russ, 1991; Russ et al., in press, for reviews, but see DeMartini, 1993). Furthermore, by enabling populations of reef fishes to attain or maintain natural levels, marine reserves have been suggested as a means to help maintain or even enhance yields of fishes from areas adjacent to the reserves (Russ, 1985; Alcala and Russ, 1990).

The spatial structure of coral reefs provides an excellent opportunity to test for the effects of different management alternatives (Hilborn and Walters, 1992). The importance of experimental investigations on the effects of fishing on coral reefs that are used as replicate experimental units has been pointed out by various authors (Russ, 1991; Hilborn and Walters, 1992; Walters and Sainsbury[1]). Yet, in spite of the high expectations placed on marine reserves, few direct tests exist on the effects of such protection on yields of marine resources (Alcala and Russ, 1990).

The leopard coralgrouper (also known as "coral trout"), *Plectropomus leopardus*, is a long-lived, protogynous hermaphroditic fish that represents a very important fishery resource over the Great Barrier Reef, Australia. With approximately 1,200 tonnes caught annually, the leopard coralgrouper is the largest single component in the annual commercial catch of Queensland line-fishing (Trainor, 1991). Because of its importance, the leopard coralgrouper has been the subject of many studies on the effects of fishing. These studies have compared the abundance and size structure of populations from open and closed reefs on the Great Barrier Reef (see Williams and Russ, 1994, for review). Most of these studies were conducted by using underwater visual census (UVC) techniques. Increased average size of the leopard coralgrouper on reefs closed to fishing was detected in most cases (Craik, 1981; Ayling and Ayling[2,3]; Ayling and Mapstone[4]). Beinssen[5] used UVC, line fishing, and mark-release-recapture techniques to investigate the effects of a 3.5 year closure on Boult Reef and detected a significant increase in average size of leopard coralgrouper. The same reef was subsequently opened to fishing and after 18 months a significant decrease in the average size of leopard coralgrouper was detected (Beinssen[5]). No study, however, has investigated the effects of fishing on the age and sex structure of leopard coralgrouper populations. The age and growth of *Plectropomus leopardus* has been recently validated (Ferreira and Russ, 1994), making it possible to use age as an indicator of changes in population structure under different levels of fishing pressure and through time.

In 1987 a zoning plan was established in the central section of the Great Barrier Reef Marine Park, Australia, dividing the area into zones that allowed different activities. Under this plan, fishing was excluded from some areas. In this study, samples taken from reefs in the central section of the Great Barrier Reef located in areas closed to fishing (National Park Zones) since 1987, are compared with samples taken from reefs located in areas open to fishing (General Use Zones). The effects of this 3–4 year closure on

[1] Walters, C., and K. Sainsbury. 1990. Design of a large scale experiment for measuring effects of fishing on the Great Barrier Reef. Unpubl. Rep. to the Great Barrier Reef Marine Park Authority (GBRMPA), Australia, 47 p.

[2] Ayling, A. M., and A. L. Ayling. 1984. A biological survey of selected reefs in the Capricorn section of the Great Barrier Reef Marine Park. Unpubl. Rep. to GBRMPA, Australia, 25 p.

[3] Alying, A. M., and A. L. Ayling. 1986. A biological survey of selected reefs in the Capricorn section of the Great Barrier Reef Marine Park. Unpubl. Rep. to GBRMPA, Australia, 25 p.

[4] Ayling, A. M., and B. P. Mapstone. 1991. Unpubl. data collected for GBRMPA from a biological survey of reefs in the Cairns section of the Great Barrier Reef Marine Park. Unpubl. Rep. to GBRMPA, Australia, 30 p.

[5] Beinssen, K. 1989. Results of the Boult Reef replenishment area study. Rep. to GBRMPA, Australia, 28 p.

the size, age, and sex structure of leopard coral-grouper populations are investigated.

Materials and methods

Four mid-shelf reefs off Townsville, Central Great Barrier Reef (Fig. 1), were chosen as the sample reefs for this experiment. Two reefs, Grub and Hopkinson, were located in the General Use Zones and were open to spear-fishing, whereas the other two, Glow and Yankee, were located in National Park Zones, and had been closed to line fishing since September 1987. The four reefs were sampled twice a year, during June–July and September–October, in 1990 and 1991 (Table 1). During each sampling trip, a crew of four line fishermen fished one reef per day (during the daylight hours) for a period of approximately four hours. The same vessel was used for each trip. The fishing crew was relatively consistent in composition, and overall fishing ability was presumably consistent between trips.

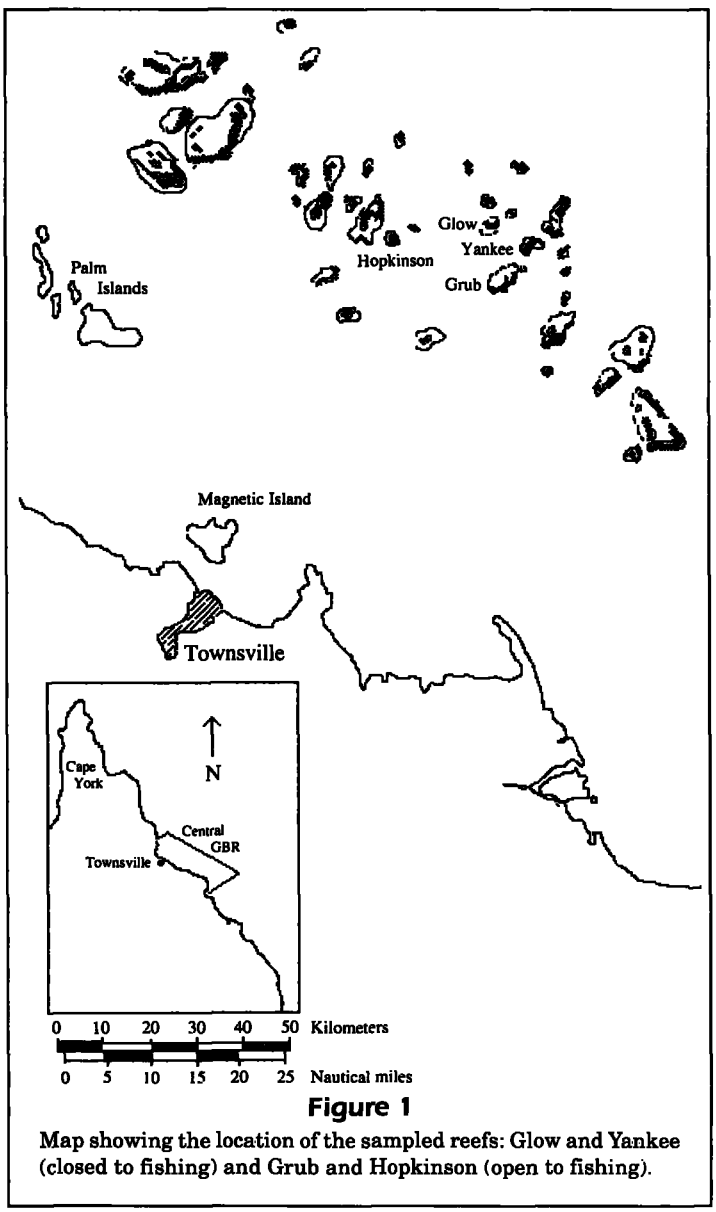

Figure 1

Map showing the location of the sampled reefs: Glow and Yankee (closed to fishing) and Grub and Hopkinson (open to fishing).

Laboratory analysis

All fish were measured and weighed, and their otoliths and gonads were removed. The gonads were preserved in FAAC (formaldehyde 4%, acetic acid 5%, calcium chloride 1.3%) on board, sectioned, and stained by using the standard techniques described in Ferreira (1993). Each gonad was classified into one of the following gonadal developmental stages, following Ferreira (1993, 1995):

Immature female: no evidence of prior spawning.

Mature female: evidence of prior spawning or active vitellogenesis.

Transitional-stage: gonads with proliferating testicular tissue in the presence of degenerating ovarian tissue. Dorsal sperm sinuses absent.

Young male: post-transitional, newly transformed testis. Dorsal sperm sinuses formed. Ovarian tissue dominating the lamellae.

Mature male: developed testes, presenting typical lobular form and presence of intralobular or "central" sperm sinuses.

To determine the age of each fish, the otoliths were read whole and sectioned by following the method described by Ferreira and Russ (1992). The number of opaque zones or rings were counted from the center to the margin of each otolith. Because leopard coralgrouper recruitment occurs in the first months of the year (Doherty et al., 1994), the birth date was assigned as 1 January. Opaque zones are formed once a year, from July to November (Ferreira and Russ, 1994); therefore, they were counted only when there was further deposition of a translucent zone, i.e. from December onwards. In this way, the number of rings corresponded to the real age of the fishes.

Statistical analysis

Nested analyses of variance (reefs nested within fishing status) were used to compare mean age and size of leopard coralgrouper between closed and open reefs (=fishing status). Factorial analyses of variance and Kruskal-Wallis tests

Table 1

Dates and number of leopard coralgrouper, *Plectropomus leopardus*, collected with standardized fishing effort in each one-day sampling trip.

	Closed		Open	
	Glow	Yankee	Grub	Hopkinson
Jun–Jul 1990	51	18	9	14
Sep–Oct 1990	49	42	11	17
Jun–Jul 1991	74	54	14	30
Sep–Oct 1991	23	11	15	15
Total	197	125	49	76

were used to compare mean size and age of leopard coralgrouper on the four reefs, independent of the reef fishing status. Multiple comparisons were performed by using post hoc tests (Tukey-Kramer, level of significance P=<0.05), and pair-wise comparisons by using Kolmogorov-Smirnov tests. Schnute's growth function (1981) was used to fit length-at-age data of leopard coralgrouper for each reef by using standard nonlinear optimization methods (Wilkinson, 1989). Schnute's model includes the von Bertalanffy, Richards, Gompertz, logistic, and linear growth models, which correspond simply to limiting parameter values. To test for differences in size at age between reefs, the linear regressions were compared by using analysis of covariance. Chi-square contingency tables were used to compare the frequency of sexes between reefs. The assumptions of normality and homoscedasticity were examined and data were transformed if needed (transformed data are indicated in tables). Level of significance used was P<0.05.

Results

There were no significant differences in mean size and age between protected reefs and unprotected reefs (fishing status). However, the mean sizes and ages varied significantly between reefs within fishing status level (Table 2).

Post hoc tests showed that mean size and mean age were larger for Glow (closed) than for all other reefs, whereas mean ages for Grub (open) were smaller than for all other reefs. The mean sizes were not significantly different for Yankee, Hopkinson, and Grub, and the mean ages were not significantly different for Yankee and Hopkinson (Fig. 2).

Growth

Schnute's growth function was fitted to size-at-age data for each reef. The submodel corresponding to the von Bertalanffy formula (b=1) provided a good fit to the data from all reefs (Fig. 3). The estimated "a" (corresponding to the von Bertalanffy K) for Grub, however, approached zero, indicating that the data could be described also by a linear regression model.

Ferreira and Russ (1994) found that for the leopard coralgrouper, estimates of growth parameters are affected greatly by different age ranges of size-at-age data. Therefore, for comparison of growth between reefs, the age range was limited to age classes occurring at all four reefs (2 to 10 years), and Schnute's growth function was fitted to these truncated data. For Hopkinson, Grub, and Glow, estimates of "a" approached zero (Table 3), indicating close to linear growth over the age range 2 to 10 years. As the estimate of "a" for Yankee was also low, simple linear models were fitted to the data from all four reefs for comparative purposes (Table 3). Analysis of the sum of squares indicated that linear models were

Table 2

Nested analysis of variance comparing mean size and age of leopard coralgrouper, *Plectropomus leopardus*, from reefs open and closed to fishing. The difference between residual degrees of freedom in the two tables is due to the fact that for some individuals age was not determined. df = degrees of freedom; SS = sum of squares; MS = mean square.

Source	df	SS	MS	F-value	P-value
Dependent variable: FL (cm)					
Fishing status	1	393.6	393.6	1.48	0.35
Reef (fishing status)	2	531.1	265.5	6.23	0.002
Residual	443	18870.6	42.6		
Dependent variable: Log age (years)					
Fishing status	1	0.931	0.931	4.41	0.17
Reef (fishing status)	2	0.422	0.211	9.07	0.0001
Residual	413	9.61	0.023		

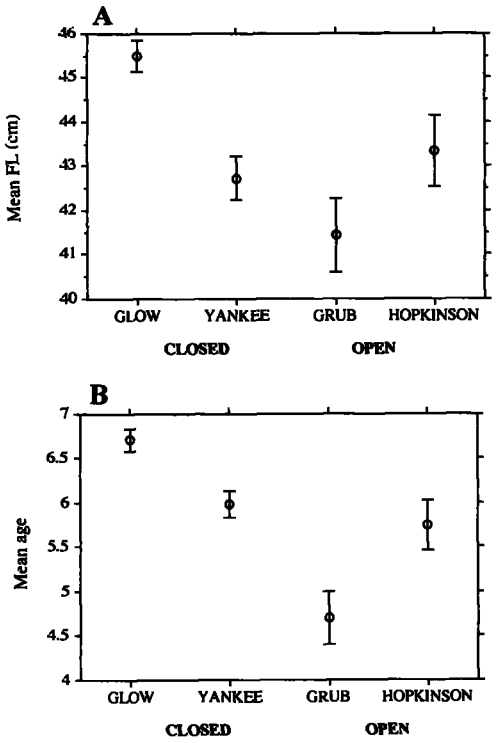

Figure 2

(**A**) Mean fork length of leopard coralgrouper, *Plectropomus leopardus*, for each reef, and standard error bars (years pooled). (**B**) Mean age of leopard coralgrouper for each reef, and standard error bars (years pooled). Sample sizes are presented in Table 1.

more appropriate to describe the growth data over the age range 2 to 10 years for all reefs with the exception of Yankee, for which an asymptotic model was more appropriate. No significant differences were observed between the linear regressions obtained for each reef (P=0.276), indicating that the mean size at age (and therefore growth) did not vary significantly between the four reefs.

Analysis of the age and size distributions at each reef

Glow and Yankee, the two closed reefs, had very strong modes in the year classes 6 and 7 (Fig. 4). In separating age distribution by year (Fig. 5), it is clear that these modes represented a strong year class that comprised 6-year-olds in 1990 and 7-year-olds in 1991. This result rules out the possibility of selection towards one year class by fishing gear or bias in age determination. This strong year class was not as obvious on the unprotected reefs (Fig. 5). At Hopkinson, year class 6 formed a small mode in 1990, but the pattern was not consistent, because year class 7 was not strong in 1991. At Grub, younger ages were proportionally more abundant; the mode was in the 3-year-old class for two consecutive years.

The 6+ year-old age class of 1990 and the 7+ year-old age class of 1991 settled onto the reefs at the beginning of 1984. Because Glow and Yankee have been closed to fishing since 1987 and age of recruitment to the fishery is approximately 3 years of age (Ferreira and Russ, 1994), the individuals settling onto Glow and Yankee in 1984 were protected from fishing for most of their lives. Modal progression was not particularly evident in the size distributions (Fig. 6).

Table 3

Schnute's (1981) parameter "a" and r^2 values for nonlinear and linear growth models for leopard coralgrouper, *Plectropomus leopardus*, ages 2 to 10 years.

	Closed		Open	
	Glow	Yankee	Grub	Hopkinson
a	0.080	0.102	0.004	−0.040
Nonlinear r^2	0.450	0.546	0.754	0.669
Linear r^2	0.445	0.448	0.754	0.666

Sex structure

The distribution of developmental stages by size and age (Fig. 7) indicated that sex change occurs over a wide range of sizes and ages on the four reefs. The frequencies of developmental stages observed for each reef (Table 4) were compared by using chi-square analysis. The frequencies were significantly different between all reefs (P<0.05), with the exception of the frequencies observed for Yankee and Hopkinson (P=0.246). For the calculation of sex ratio, frequencies of young males were pooled with frequencies of mature males, because individuals in both categories were sexually potential males. The resulting sex ratios (Table 4) were not significantly different among reefs (P=0.09).

There were no significant differences between protected and unprotected reefs, but some differences between reefs were detected. The mean size of mature females was not significantly different between reefs (one-way ANOVA, P=0.10). The mean age of mature females, however, was significantly different between reefs (log (age), P=0.008); mature females from Glow were significantly older than mature females from Grub (post hoc, P<0.05). Age and size of

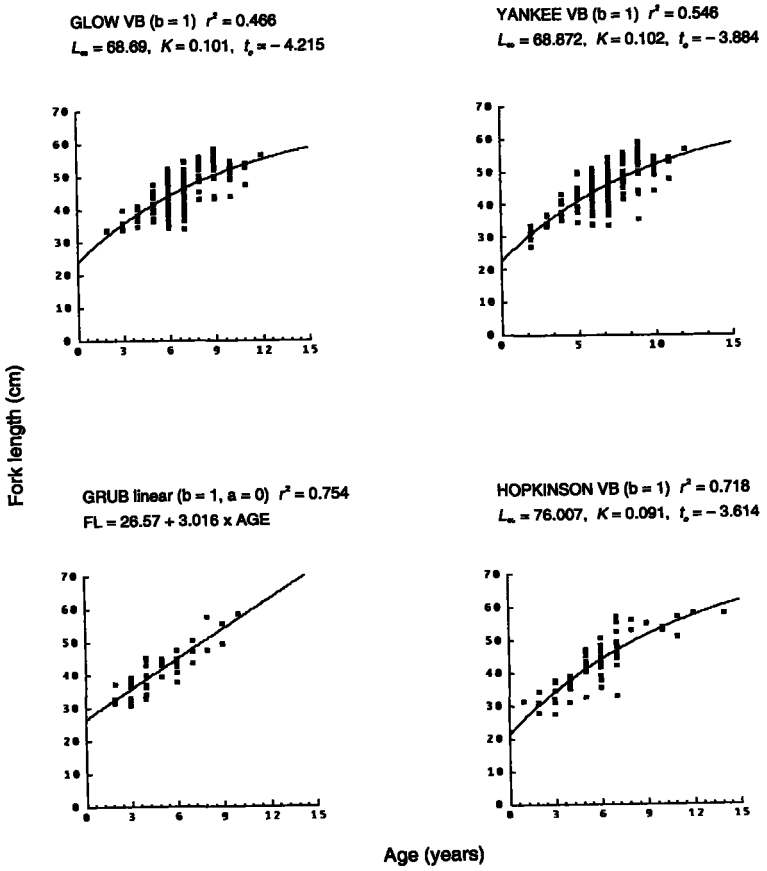

Figure 3

Size-at-age data and estimated growth curve for leopard coralgrouper, *Plectropomus leopardus*, from each sampled reef.

Table 4

Frequency (%) of each developmental stage and sex ratio (mature females:young and mature males) of leopard coralgrouper, *Plectropomus leopardus*, at the four reefs.

	Immature female	Mature female	Transitional	Young male	Mature male	Sex ratio
Closed						
Glow	1	0	8	8	38	1.7:1
	(1%)	59%)	(6%)	(6%)	(28%)	
Yankee	4	40	16	11	3	0.91:1
	(4%)	(38%)	(15%)	(11%)	(32%)	
Open						
Grub	7	15	10	7	5	1.25:1
	(16%)	(34%)	(23%)	(16%)	(11%)	
Hopkinson	5	36	9	4	15	1.9:1
	(7%)	(52%)	(13%)	(6%)	(22%)	

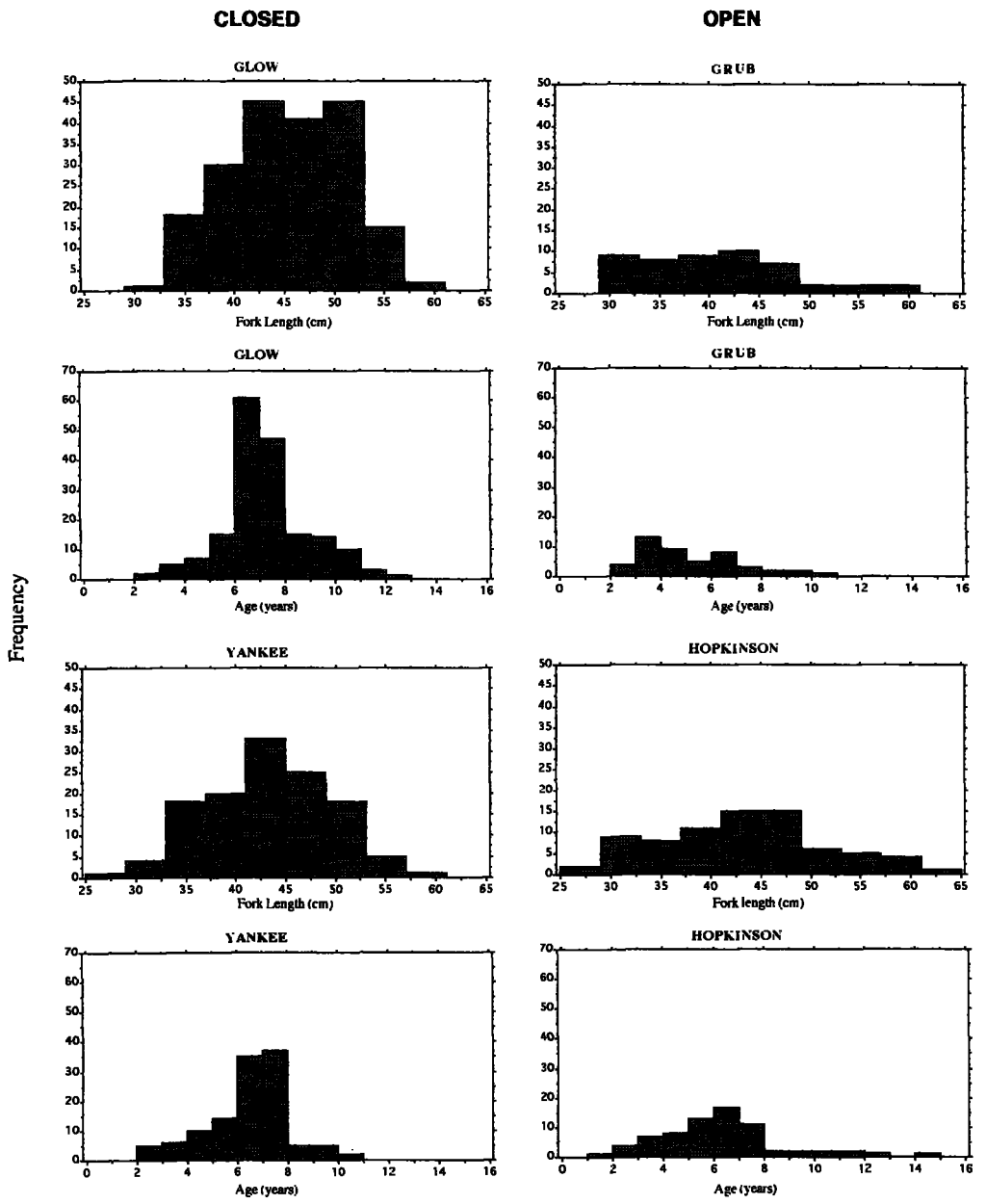

Figure 4

Size- and age-frequency distribution of leopard coralgrouper, *Plectropomus leopardus*, for each reef, 1990 and 1991 data combined.

transitional-stage fish were not significantly different between reefs (FL: P=0.24, log (age), P=0.11). Size of young males was not significantly different between reefs (P=0.2) but ages of young males were significantly different (P=0.03); young males from Glow were significantly older than young males from Grub (post hoc, P<0.05). Age of mature males was not significantly different between reefs (P=0.22). However size of mature males varied significantly between reefs (P=0.001); mature males at Yankee were significantly smaller than mature males at Hopkinson (post hoc P<0.05).

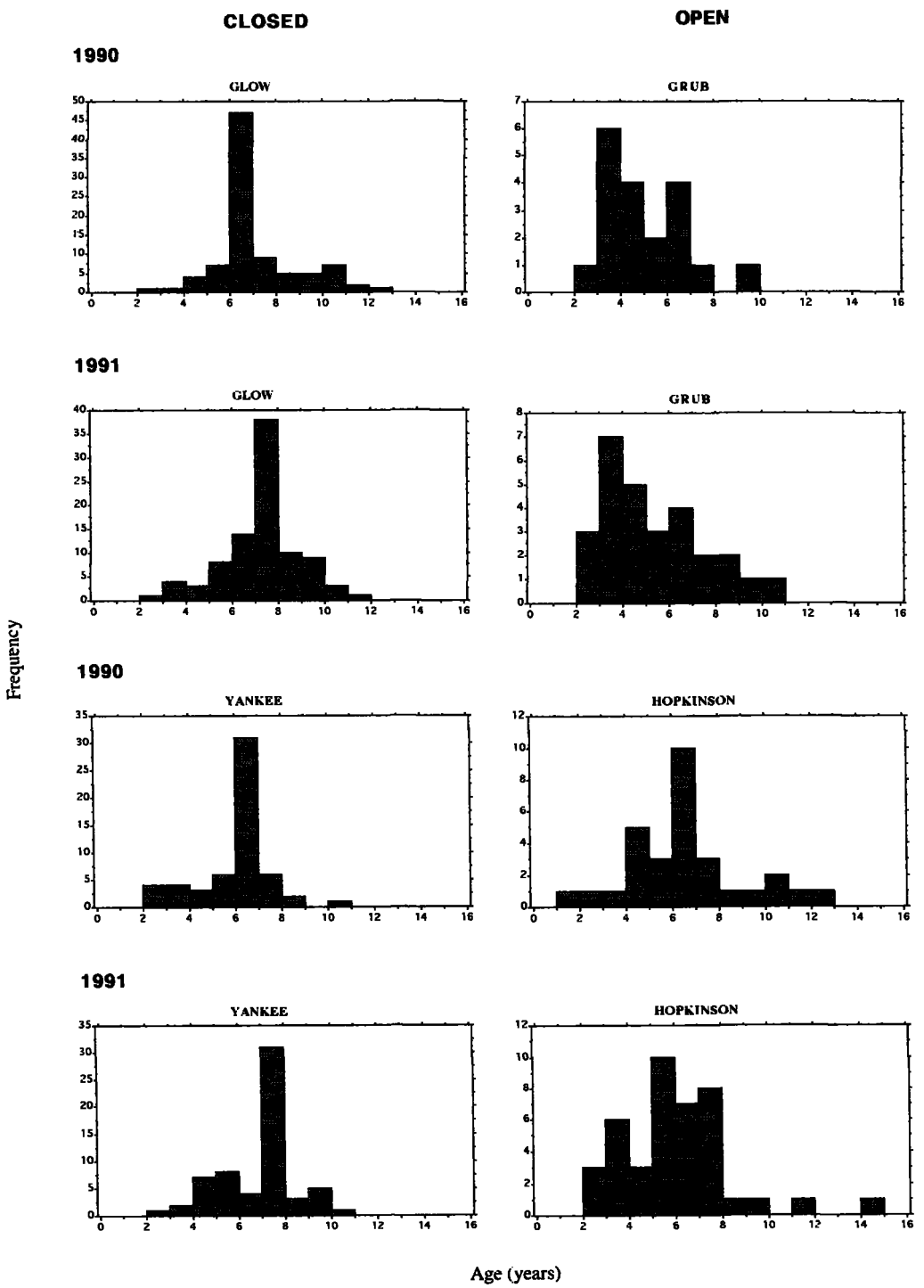

Figure 5

Age distribution of leopard coralgrouper, *Plectropomus leopardus*, for each reef in each sampling year.

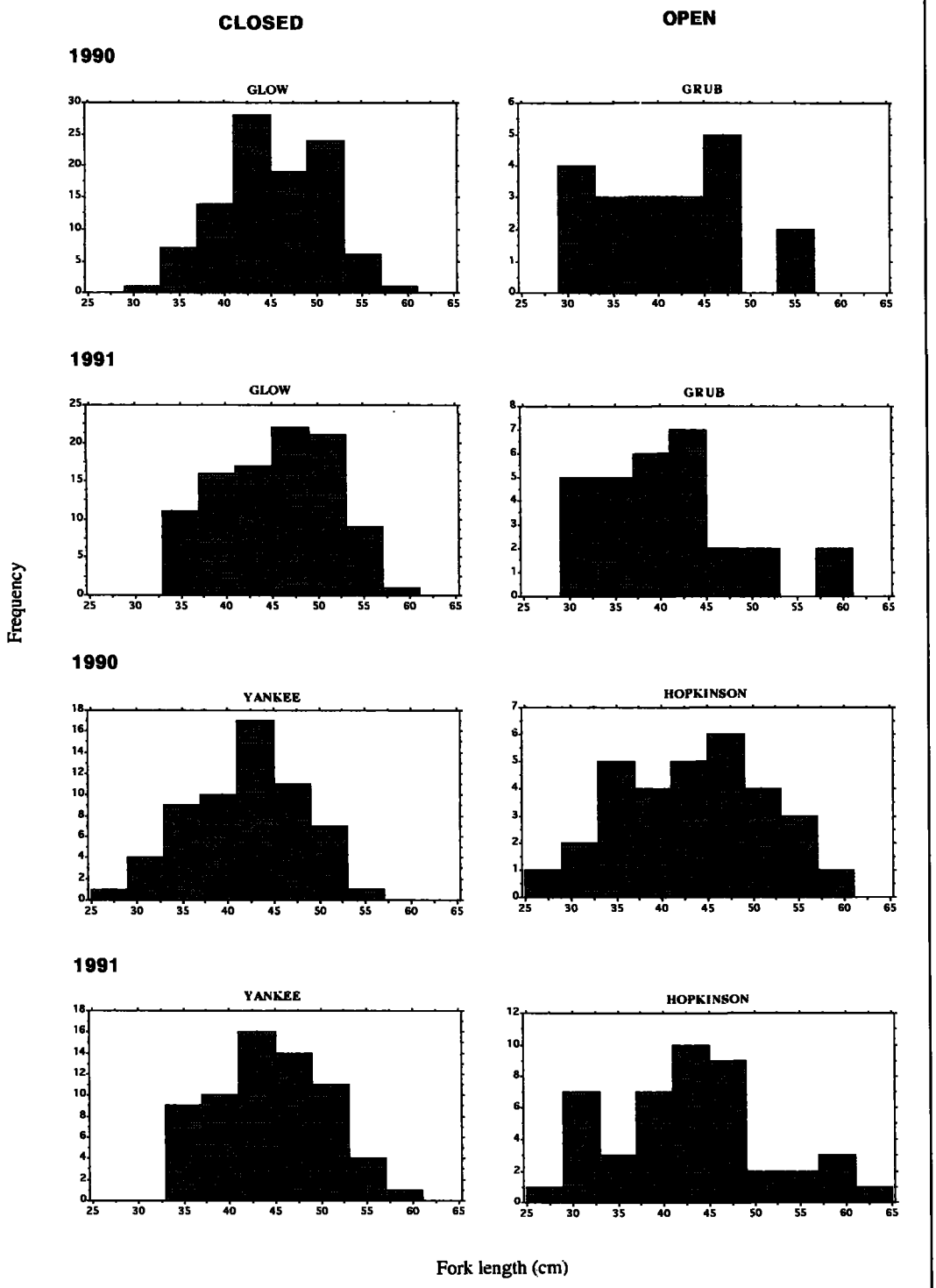

Figure 6

Size distribution of leopard coralgrouper, *Plectropomus leopardus*, for each reef in each sampling year.

Discussion

There are several important assumptions in a comparison of the effects of fishing on populations from areas that are open with those that are closed to fishing. The first assumption is that protection is enforced so as to guarantee effective fishing closure. In the Great Barrier Reef Marine Park, aerial surveillance is conducted on a regular basis and fines are levied on those who fish illegally. Although violations still occur, the fishing pressure is likely to be considerably lower on the closed reefs. The second assumption is that the effects of fish movements across closed and open boundaries do not mask the effects of protection from fishing on the population structure. The minimum distance between two study reefs was of 1.6 km, and depth between reefs of the order of 40–60 m. Tagging studies have shown that reef fishes are highly site-attached, and most studies on movements of serranids have not shown significant movements across distances and depths such as those existing on the present study (PDT, 1990). Davies[6] conducted extensive tagging studies on leopard coralgrouper and showed that fish exhibited extremely limited inter-reef movement in a study of six reefs in the Central Great Barrier Reef.

Expected effects of fishing are a reduction in the size and age range and average size and age of the population (Russ, 1991). In addition, line fishing might select for the larger and older individuals in a population (Ricker, 1969; Miranda et al., 1987), which would exacerbate this effect. Significant differences between size and age structures on closed and open reefs, however, will depend largely on the duration of closure in relation to species longevity and fishing mortality. Therefore, a third assumption is that the duration of effective closure is great enough (in relation to the longevity of the target species concerned) for an effect of closure to be detected. In this study, given the short period of time for which the reefs had been closed (3–4 years) in relation to the longevity of the leopard coralgrouper (14+ years),

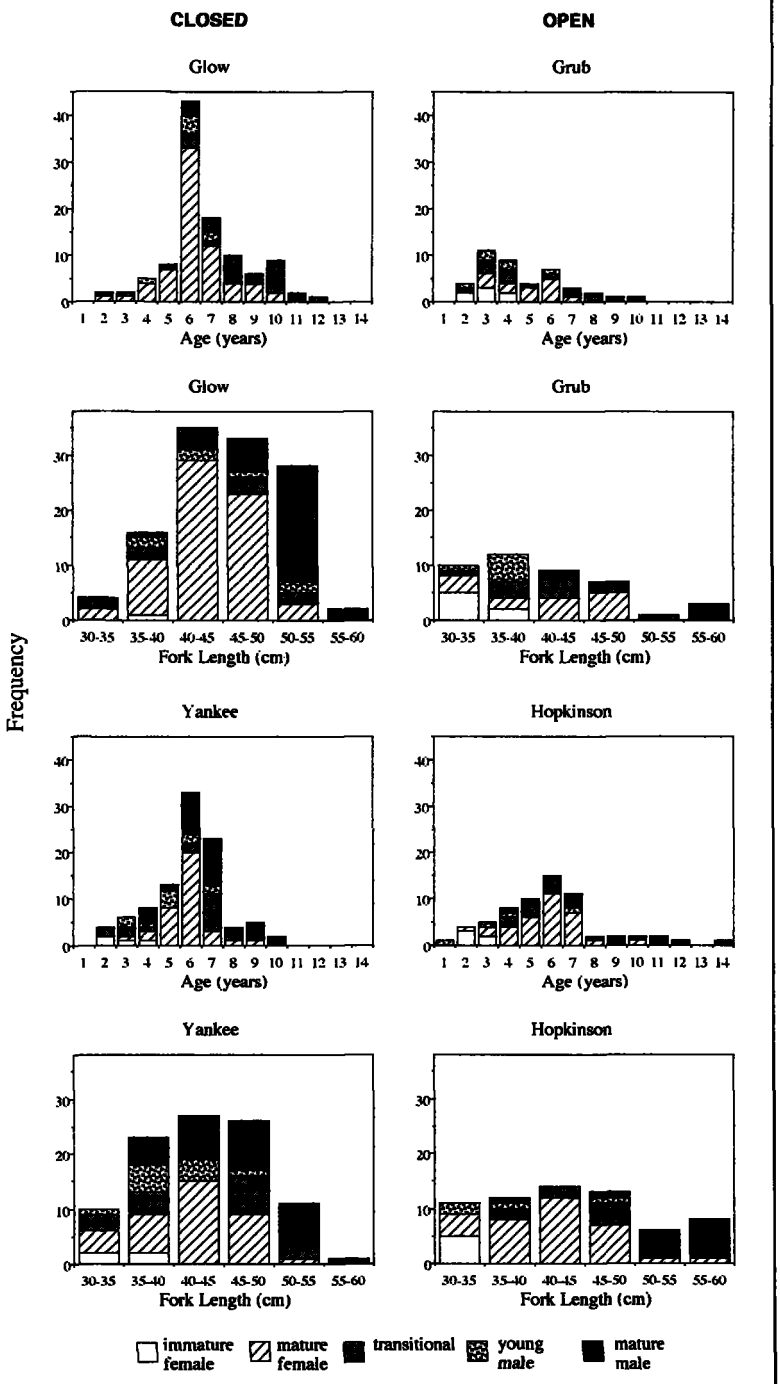

Figure 7

Distribution of developmental stages of leopard coralgrouper, *Plectropomus leopardus*, at each reef by age (years) and size (fork length).

[6] Davies, C. R. 1995. Patterns of movement of three species of coral reef fish on the Great Barrier Reef. Ph.D. diss., Department of Marine Biology, James Cook University of North Queensland, Australia, 170 p. Unpubl. data.

great differences in the size and age structure were not likely to be detected. A fourth assumption is that effects are attributable to fishing and not some other factor. The failure to detect a significant difference between either mean size or age of leopard coral-grouper on open and closed reefs, however, was due largely to variability between replicate reefs. If, in the present study, only Glow (closed) and Grub (open) had been compared, the result would reveal a classic effect-of-fishing scenario, with a larger range of sizes and ages and significantly larger mean sizes and ages observed on the reef closed to fishing. In contrast, if only Yankee (closed) and Hopkinson (open) had been compared, no effect of fishing would have been detected on the population structure. These results emphasize the importance of replicate reefs in analyses of the effects of fishing on coral reef fish populations. More replicates (i.e. more reefs per treatment group) would increase the degrees of freedom and thus the power (i.e. likelihood of detecting a given effect size) of the nested ANOVA.

One possible reason for the differences between the two open reefs is the fact that they are apparently not subject to the same fishing pressure. Grub is renowned for its excellent anchorage, and therefore is a preferred site for recreational and commercial fishing vessels. Aerial surveys conducted by the Great Barrier Reef Marine Park Authority between 1989 and 1992 (GBRMPA[7]), indicated that Grub is frequented by boats 2.2 times more frequently than Hopkinson and that fishing vessels are sighted 3 times more often at Grub than at Hopkinson. Such factors should be taken into account in designing future sampling and experimental programs on the effects of fishing on the Great Barrier Reef.

Nevertheless, there was a major and consistent difference between the open and closed reefs that were analyzed. For the two closed reefs, the population structure was dominated by the presence of a strong year class which settled in early 1984. A similar pattern was not obvious on the open reefs, and a corresponding strong mode was not evident at Grub or at Hopkinson. Occurrence of strong year classes is a well-documented phenomenon in commercial catches of temperate species (Hjort, 1914; Sissenwine, 1984; Rothschild, 1986). For temperate species, year-class strength has been linked to early life history processes since the beginning of this century (Hjort, 1914). However, for populations of coral reef fish, the importance of recruitment as a major driving force in the temporal variability of abundance has been recognized only recently (Williams, 1980; Doherty and Williams, 1988, a and b; Doherty, 1991; Doherty and Fowler, 1994).

There is evidence for the possibility of strong recruitment pulses of reef fishes occurring concurrently on midshelf reefs off Townsville which are separated by distances of up to 10–30 km (Doherty and Williams, 1988, a and b; Williams, 1991). The age-structure data for the two closed reefs provides circumstantial evidence in support of pulses of recruitment being synchronous on reefs at least 10 km apart (Fig. 1). With the assumption that the four reefs received a similar pulse of recruitment in 1984, it is apparent that fishing mortality has operated to largely decrease the abundance of this year class. On the closed reefs, this strong year class was protected from fishing for almost its entire life and as a result its dominance was maintained. In contrast, on the open reefs, the same year class probably supported the fisheries disproportionately in relation to the other age classes, and consequently abundance was reduced. An alternative hypothesis is that the settlement pulse occurred only on the two closed reefs owing to some process independent of fishing.

A common question regarding the effects of fishing on protogynous hermaphroditic fishes is how the sex structure of the population would respond to fishing mortality. If sex change is determined by age and size and selective removal of larger and older individuals occurs, the result would be a decrease in the proportion of males in the population. However, if sex change is behaviorally induced, the population would be expected to compensate to some extent for the selective removal of males by female-to-male sex change, i.e. by changing sex at smaller ages and sizes.

The mean size and age observed for each stage seemed to follow the size and age structure of each population. Mature females and young males were larger and older at Glow than those at Grub. Age and size of transitional-stage fish did not differ significantly between reefs, but this is not surprising given the high variability in the age and size of sex transition characteristic of leopard coralgrouper and the small numbers of transitional individuals. Mature males from Yankee were smaller than those at Hopkinson. This is possibly a consequence of the age distribution and consequent size distribution. Yankee had proportionally more 6- and 7-year-old fish and not many in the older age classes; therefore most males would be 6- or 7-year-olds, resulting in a small overall mean size. At Hopkinson, the age frequency was more evenly distributed, without strong modal classes for years 6 and 7 and having a wider range of age classes.

The comparison of frequency of developmental stages between reefs showed significant variation.

[7] GBRMPA data base. 1992. Great Barrier Reef Marine Park Authority. P.O. Box 1379, Townsville, Q4810, Australia.

When immature males were pooled with mature males for sex ratio calculations, the resulting sex ratio was not significantly different among reefs. Therefore, it appears that despite the differential distribution of developmental stages in the populations, the same final female:male balance was achieved. This result suggests that behavioral mechanisms are probably contributing to the determination of the distribution of sexes in the populations of leopard coralgrouper. It is possible that for the leopard coralgrouper, sex change results from a combination of a developmental process, in which individuals are more susceptible to sex change as they grow larger and older, and from a social process through behaviorally induced stimuli. Genetic variability would widen the range over which sex change can occur and phenotypic plasticity would allow individuals to respond to different social structures. Manipulative experiments are probably necessary to detect the exact mechanisms determining the distribution of sexes in leopard coralgrouper populations.

Estimations of mortality rates are essential to fishery management, and yet few studies have made estimates of the rate of total mortality of coral reef fishes (Russ, 1991). However, an important assumption of catch curve analysis, one of the most commonly employed methods to estimate mortality (Beverton and Holt, 1957), is that all age groups have been recruited with the same abundance (Pauly, 1984). The present data represent a clear example of the problems that can result from the presence of strong recruitment pulses in calculating the total mortality rate Z from age- or length-structured catch curves. Because of a strong year class, estimates of Z calculated from the right-hand slopes of the catch curves would suggest very high mortality rates for the two closed reefs, in contrast with much lower mortality rates on the open reefs. Mortality estimates drawn from the present data or from similar cases where significant recruitment fluctuation is retained in the age structure would be very imprecise.

For the leopard coralgrouper, our results suggest that the occurrence of strong interannual fluctuations in recruitment were retained in the age structure. With recruitment as a major factor driving the patterns of abundance, recovery of leopard coral grouper populations after closure to fishing may be largely dependent on a good pulse of recruitment. Thus recoveries of populations after closure to fishing are likely to be "events" rather than gradual "processes," and recovery may be rapid or slow, depending on the timing of closure with respect to the occurrence of a very large year class.

Differences in the age structure were more obvious than differences in the size structure between open and closed reefs. As the leopard coralgrouper is a relatively slow-growing fish, differences in the size structure of a population will take longer to become evident than will differences in the age structure. Additionally, owing to considerable variability in size at age (Ferreira and Russ, 1994), recruitment fluctuations may also pass unnoticed if size-structure data alone are examined. The results presented here indicate that age structure may be far more useful than size structure for comparisons of fishing effects on long-lived fishes such as Epinephelinae serranids. Comparisons based solely on mean sizes of reefs open to fishing with those closed to fishing may fail to detect important differences.

Marine fishery reserves are a management strategy with excellent potential for maintaining high abundances of reef fishes (Alcala and Russ, 1990). However, to understand better the processes determining differences in abundance, it is important that studies on the effects of closures to fishing on long-lived species include examination of age structure. Furthermore, such studies must replicate reefs, take into account strong recruitment pulses that may mask fishing effects, and consider the effects of strong recruitment pulses when estimating mortality from catch curves.

Conclusion

In this study we found 1) no significant differences between the mean size and age of leopard coralgrouper on open and closed reefs were detected (such a result could have been a consequence of the design constraints of this study, such as not accounting for variability among replicate reefs, or the duration of closure (3–4 years); 2) that there were no differences in the overall sex ratio, despite observed differences in the sex structure, suggesting social induction of sex change; 3) that a strong recruitment pulse occurred, an event that may be extremely important in determining variation in abundance of leopard coralgrouper, and therefore very relevant to the fisheries; and 4) that age structure is more useful than size structure in detecting effects of fishing on leopard coralgrouper, and, therefore, age determination should be a routine component in the management of leopard coralgrouper populations.

Acknowledgments

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Abstract.—Weakfish, *Cynoscion regalis*, were collected in 1989–93 from commercial catches in the Chesapeake Bay region, and special collections of large fish were made in Delaware Bay. Ages were based on sectioned otoliths. Most weakfish were 200–600 mm TL and ages 1–4 years. Maximum age was 17 years from a 1985 Delaware Bay fish. Maximum current observed ages were 12 years in Chesapeake Bay and 11 years in Delaware Bay. However, fish older than age 6 were rare in both areas. There was no evidence that Delaware Bay fish reached a larger maximum size or maximum age than Chesapeake Bay fish. Although weakfish size was a poor predictor of age, weakfish growth was well described by the von Bertalanffy growth model (r^2=0.98, n=854). Maximum size and age has fluctuated in both Chesapeake and Delaware Bays over the past thirty years. In both areas the maximum size of fish, based on citation records, greatly increased from the late 1960's until the mid-1980's, as did the numbers of these large fish. These fluctuations appear to be due to a series of strong year classes, beginning in the late 1960's.

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Age and growth of weakfish, *Cynoscion regalis*, in the Chesapeake Bay region with a discussion of historical changes in maximum size*

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The weakfish, *Cynoscion regalis*, is a recreationally and commercially important sciaenid which ranges from eastern Florida to Massachusetts but is most abundant from North Carolina to New York (Mercer, 1985). Although believed to be resident year-round in the Carolinas, weakfish occur farther north only seasonally (Bigelow and Schroeder, 1953). In the spring, weakfish migrate northward and inshore to estuarine feeding and spawning grounds; this pattern is reversed in the fall (Wilk, 1979), and most fish are believed to overwinter off North Carolina (Pearson, 1932). Weakfish occur in Chesapeake Bay, roughly from April through November (Pearson, 1941; Massmann et al., 1958), where they support one of the region's most important fisheries (Rothschild et al., 1981).

Although weakfish have been important in Atlantic coast fisheries since the 1800's (Mercer, 1985), weakfish landings have fluctuated widely. Changes in maximum size and age have occurred concurrently with fluctuations in presumed abundance (Massmann, 1963; Joseph, 1972; Feldheim, 1975; Villoso, 1989). For example, in Chesapeake Bay, the largest reported weakfish was 16 lb (7.3 kg) in 1921 (Hildebrand and Schroeder, 1928). However, by the mid-1950's, when landings were low, mean size decreased and few fish weighed more than 2 lb (0.91 kg) (Massmann, 1963). Large fish again became common in Chesapeake Bay as the fishery recovered in the 1970's and early 1980's; a 19-lb (8.6 kg) weakfish was caught in Chesapeake Bay in 1983 (Mercer, 1985).

It is necessary to understand age structure and growth, and how they vary regionally and temporally, in order to gain insight into the causes of historical fluctuations in weakfish landings and abundance. Although there have been many studies on weakfish age and growth (e.g. Taylor, 1916; Nesbit, 1954; Perlmutter et al., 1956; Massmann, 1963; Merriner, 1973; Feldheim, 1975; Seagraves, 1981; Shepherd and Grimes, 1983; Hawkins, 1988), all have been based on scales which underage older fish of many species (Beamish and McFarlane, 1987),

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including weakfish (Lowerre-Barbieri et al., 1994). Thus, ages based on scales may lead to inappropriate growth and mortality estimates, which can affect yield modeling results and management decisions.

Weakfish age and growth have been reported to vary geographically, increasing with latitude (Pearson, 1932; Nesbit, 1954; Shepherd and Grimes, 1983). However, it is unclear whether these differences are due to different population segments (Nesbit, 1954; Perlmutter et al., 1956; Seguin, 1960) or to differential migration (Vaughan et al., 1991). Regardless of the cause, if these differences exist, estimates of growth and longevity throughout the weakfish range will be necessary for proper management. Weakfish age and growth in the Chesapeake Bay region have not been examined since Massmann (1963). A current study is necessary because changes in landings and maximum size and age suggest that weakfish age structure may have changed.

This study was undertaken to determine the current age structure and growth of weakfish in the Chesapeake Bay region, by using a validated ageing method (Lowerre-Barbieri et al., 1994). The hypothesis that weakfish in the Chesapeake Bay region reach a lower maximum size and age than weakfish in Delaware Bay (Shepherd and Grimes, 1983) is evaluated, as are historic trends in maximum size and abundance of large fish (≥3.6 kg, or ≈8 lb) in Chesapeake and Delaware Bays.

Methods

A total of 4,137 weakfish were collected in 1989–92 from pound-net, haul-seine, and gillnet fisheries in the Chesapeake Bay region. On each sampling date either a 22.7 kg (50 lb) box of each available market grade (fish large enough to be sold for human consumption, graded as small, medium, or large) or the total catch was purchased and processed for biological data. Because boxes could not be randomly selected, our size and age compositions were not expandable to the overall fishery. However, Chittenden (1989a) found little or no variation in fish size (total length) among boxes, within grades. To obtain year-round samples, 344 fish were collected in winter (when weakfish do not occur in Chesapeake Bay: Pearson, 1941; Massmann et al., 1958) from the trawl fishery operating in Virginia and North Carolina shelf waters north of Cape Hatteras. Since age-1 fish are not fully recruited to market grades (see Size and Age Composition heading in Results section), an additional 200 age-1 and young-of-the-year fish were collected by the Virginia Institute of Marine Science (VIMS) juvenile trawl survey from May to August 1990–92 in Chesapeake Bay. Details on sampling design and gear of the VIMS survey can be found in Chittenden (1989b) and Geer et al. (1990).

To increase the number of large fish in this study for comparison of maximum size and age in Chesapeake and Delaware Bays: 1) 35 fish were collected from the 1992 World Championship Weakfish Tournament in Dover, Delaware; 2) 10 fish (≥3.6 kg total weight) from Delaware Bay and 5 fish (≥3.6 kg total weight) from Chesapeake Bay were collected from commercial catches in 1992 and 1993; and 3) 41 fish (≥500 mm total length) taken in Delaware Bay in 1985 and 1986 by Villoso (1989) were included in the analysis. Fish ≥3.6 kg (≈8 lb) or ≥500 mm total length (TL) were targeted because these fish were beyond the range common in our regular Chesapeake Bay samples (see Size and Age Composition heading in Results section). To evaluate historic trends in maximum size and abundance of large fish, the annual number of citation-size fish and the total weight (TW) of the largest fish reported were obtained from the Virginia Saltwater Fishing Tournament (1958–92) and from the Delaware State Fishing Tournament (1968–92). Citation-size fish are large and rare enough to be considered trophy fish. Citation size may change if larger fish become more numerable (e.g. weakfish citation size has fluctuated from 1.8 to 5.5 kg in the Chesapeake Bay over the past 25 years).

In general, collections were processed for biological data as follows: fish were sexed, measured for TL (nearest mm), total gutted weight (TGW, nearest gram), and gonad weight (GW, nearest gram). Gutted weights included GW and were used (rather than total weights) because weakfish are piscivorous and can swallow fish a third of their own weight, a characteristic that could greatly bias somatic weights (Lowerre-Barbieri, 1994). Somatic weight (SW) was calculated as TGW minus GW.

Otoliths from 3,290 fish were sectioned and aged by using the validated method described in Lowerre-Barbieri et al. (1994). Of 1,191 otoliths read by two separate readers, 99.8% of the assigned ages agreed. In addition, otolith annuli did not show severe crowding at older ages and were easily distinguished (even in a 17-year-old, the oldest fish aged [Fig. 1]). More than 95% of the fish sampled were aged each year except 1990. In 1990, when many small fish were sampled, those to be aged (794 out of 2,098) were selected by systematic subsampling. Ages were assigned assuming 1 January as an arbitrary birthdate (Jearld, 1983; Shepherd, 1988). This birthdate was selected so that fish of the same year class collected in April and May—before annuli form (Lowerre-Barbieri et al., 1994)—would be assigned the same age as those collected after annuli had formed.

To determine whether the population growth rate was representative of the true growth rate (i.e. whether there was not size-selective mortality within year classes), size at first annulus formation was evaluated for sectioned otoliths from fish ages 1–12 (Ricker, 1975). Otolith radius to the first annulus (distance from the nucleus to the proximal edge of the first annulus) was measured by using a Via-100 camera and monitor system with a dissecting microscope at 24× (Lowerre-Barbieri et al., 1994). Measurements were taken on 403 Chesapeake Bay fish collected in 1989 and 1992–93 and on 47 Delaware Bay fish from 1992 to 1993. Given the strong relationship between otolith radius and fish total length (Lowerre-Barbieri et al., 1994), size of the otolith at the first annulus was considered an indicator of fish size at age 1. A one-way analysis of variance (ANOVA) was used to determine whether otolith size at first annulus was significantly different by age.

Growth was evaluated by using nonlinear regression (Marquardt method) to fit the von Bertalanffy model (Ricker, 1975) to observed, individual lengths of Chesapeake Bay fish ages 1–12. To remove seasonal effects, only fish collected in April and May were used for calculations. These months are the period when 1) somatic growth rate increases; 2) otolith annuli form; and 3) the largest range of sizes and ages occur in Chesapeake Bay. Finally, to examine differences in growth by sex, observed mean size at age in Chesapeake Bay was calculated for each sex and compared by using a *t*-test.

Linear regression was used to determine a SW-TL relationship on log-transformed data from fish collected in Chesapeake Bay. To include the greatest possible range of sizes (188–875 mm TL and 71–6,137 g SW), data were pooled over gears (pound nets, haul seines, and gill nets). A *t*-test was used to determine if the slope of the SW-TL regression was significantly different from 3—a slope of 3 indicating isometric growth. When only TL was given in the historic literature, conversions were made by using a TGW-TL relationship based on fish collected in April and May in Chesapeake Bay 1989–93, ranging from 20 to 6,276 g TGW and from 140 to 875 mm TL. This same relationship was used to estimate TL for citation-size fish.

All data were analyzed by using statistical methods available in SAS (1988). Model assumptions were evaluated by examination of residuals (Draper and Smith, 1981). Rejection of the null hypothesis was based on an α level of 0.05, unless otherwise noted, and *F*-tests in ANCOVA were based on type III sums of squares (Freund and Littell, 1986).

Results

Size and age composition

Most weakfish collected from Chesapeake Bay commercial fisheries during 1989–92, excluding those targeted for their large size, were 200–600 mm TL (98%) and ages 1–4 years (97%). However, observed sizes ranged from approximately 200 mm TL to 850 mm TL, and observed ages ranged from 1 to 8 years (Fig. 2). The smallest fish (≈200 mm TL) collected from market grades were similar each year. However, the largest observed fish varied from approximately 650 mm TL in 1990 to 850 mm TL in 1989 and 1992. In 1990, a larger percentage (78%) of small (<300 mm TL), young weakfish were collected and no fish were older than age 5 (Fig. 2). Most of these small fish (<300 mm TL) were collected by haul seine and pound net (Fig. 3), whereas gill nets caught fish primarily in the 300–400 mm TL range.

Weakfish were not fully recruited to market grades until age 2. Young-of-the-year and yearling

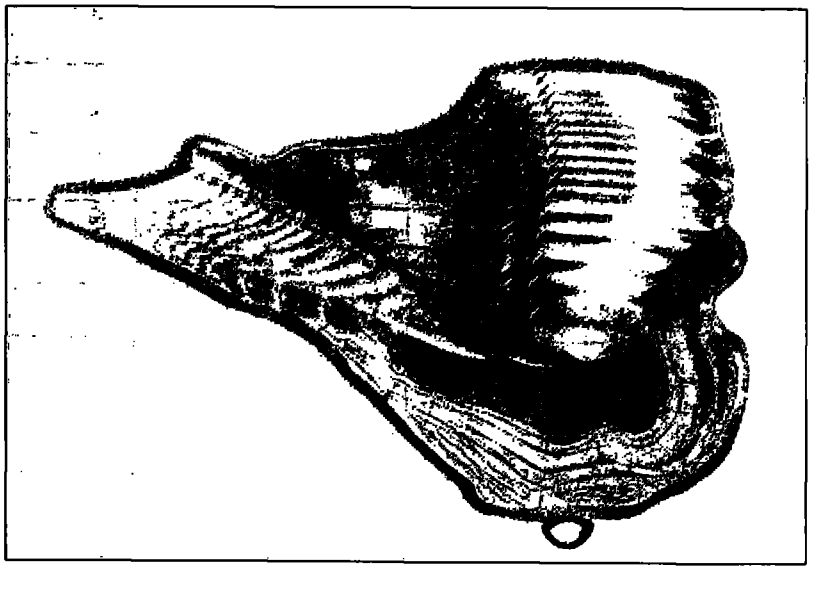

Figure 1

Transverse otolith section of an age-17 weakfish, *Cynoscion regalis*, caught in May 1985 in Delaware Bay. Arrows indicate annuli.

fish occurred in Chesapeake Bay, making up 99% (n=200) of the fish analyzed from the VIMS juvenile trawl survey. However, young-of-the-year fish were not present in market grades, and yearlings were not fully recruited, as evident by their low frequency in annual age compositions (Fig. 2).

Older, larger weakfish occurred in Chesapeake Bay primarily in the spring, when they appeared to arrive before younger fish. Fish age 4 and older occurred in the spring in relatively large numbers, making up 51% and 27% of April and May samples (1989–92), respectively (Fig. 4). However, few fish older than age 4 were sampled after May, and they never made up more than 8% of the fish observed in later months. In contrast, few age-1 fish were observed in either market grade samples or in the VIMS trawl survey until June, after which they made up roughly 30% of the market grade fish sampled.

Mean monthly size at age also differed seasonally. Mean size at ages 3–6 of Chesapeake Bay fish collected in April and May, 1989–92, were larger than those collected in August and September (Table 1). In 1992, mean monthly TL of age-2 and age-3 fish (the most abundant ages in the samples) decreased steadily from April through July (Fig. 5). Although the pattern was less clearly defined in other years, a decrease in mean TL for the observed age-3 fish from April to June was evident. The mean TL of age-2 fish also declined from April to May in 1991 and 1992.

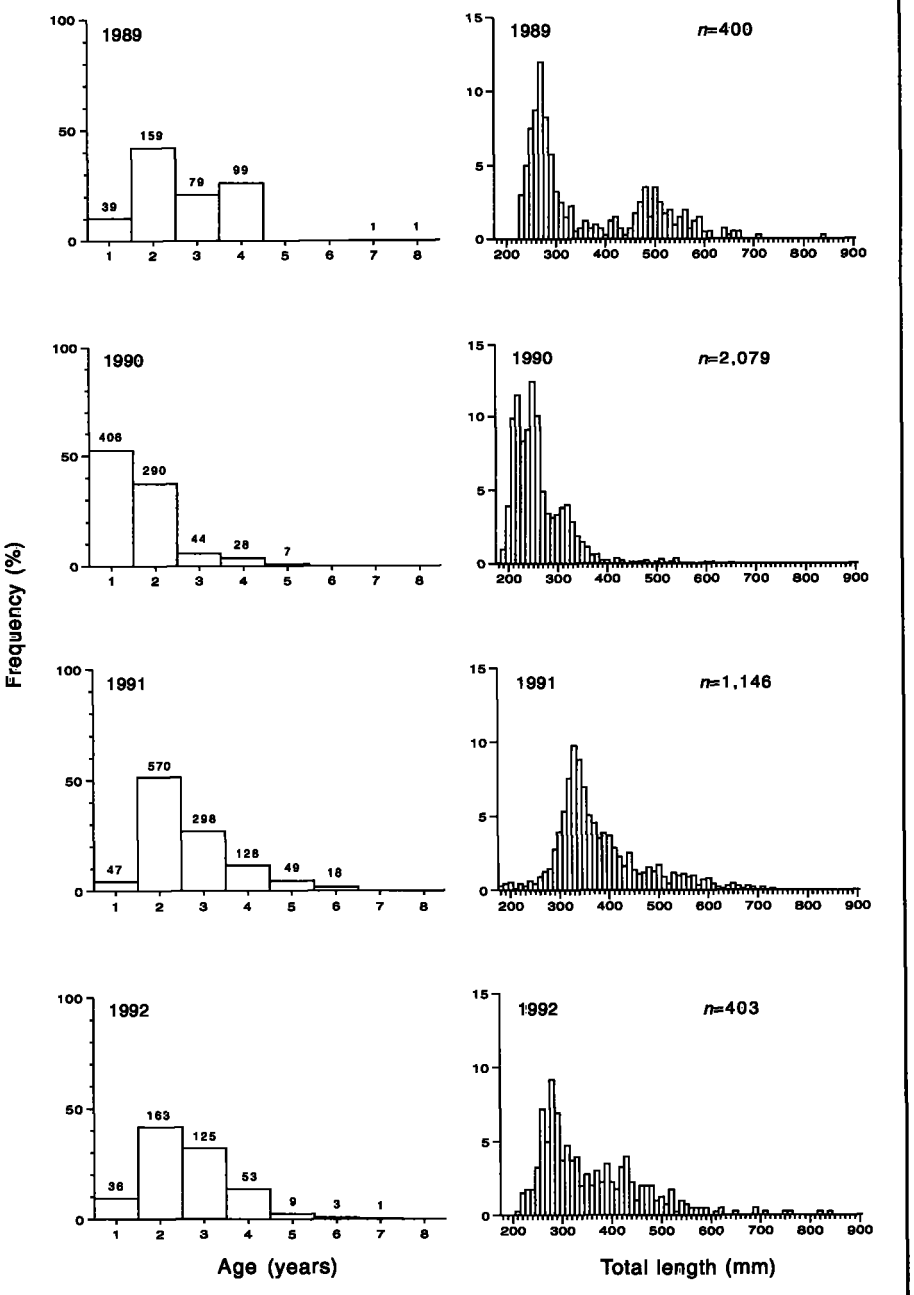

Figure 2

Age and length frequencies of Chesapeake Bay weakfish, *Cynoscion regalis*, by year (1989–92) pooled over gears. Sample sizes are indicated above each age. Total annual sample size is noted for lengths.

There was no evidence that weakfish from Delaware Bay reached a larger maximum size or age than those in Chesapeake Bay. Maximum observed age of Chesapeake Bay fish was 12. However, annual observed maximum age of fish not selected for their large size varied: 8 in 1989 (n=378), 5 in 1990 (n=775), 6 in 1991 (n=1,110), and 7 in 1992 (n=391). Maximum observed age in Delaware Bay was 11. Fish older than age 6 were rare in both regions. Only four fish ≥3.6 kg were collected in 1992 in Chesapeake

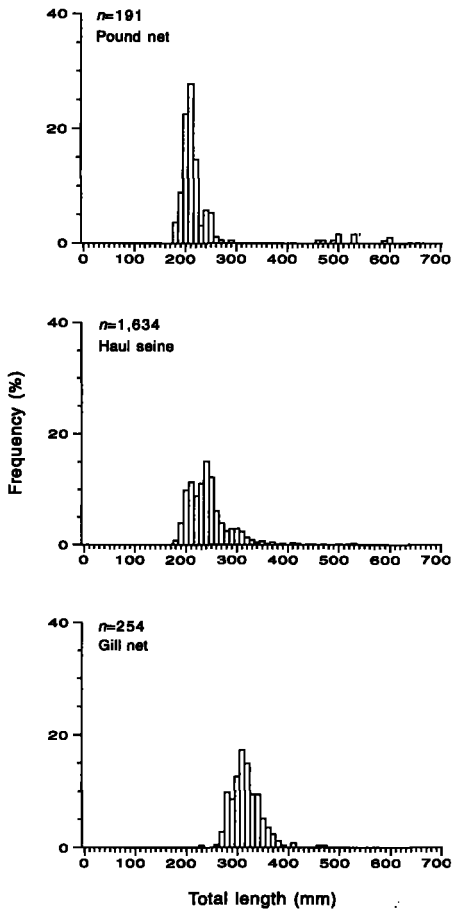

Figure 3
Length frequencies of Chesapeake Bay weakfish, *Cynoscion regalis*, by gear in 1990.

Bay—three age 6 and one age 10. In Delaware Bay in 1992, seven fish were collected—one age 4, one age 5, four age 6, and one age 8. An additional six fish ≥3.6 kg were collected at the 1992 World Championship Weakfish Tournament in Delaware, all age 6. In 1993, only four fish ≥3.6 kg were collected—one age-12 fish from Chesapeake Bay, and three fish from Delaware Bay, ages 6, 8, and 11. Maximum TL observed in both regions was 875 mm. Maximum TGW was 6.3 kg in Chesapeake Bay and 6.6 kg in Delaware Bay. Ten fish collected from Delaware Bay >age 8 were similar in size to the two fish collected in Chesapeake Bay (See Fig. 7 below).

Growth

Weakfish size (TL) was a poor predictor of fish age. Ages 1 and 2 were the only groups which did not have overlapping size distributions (Fig. 6). In contrast, TL's of fish (ages 2–5) collected in April and May, showed broad ranges, much overlap, and multiple modes (Fig. 6). A fish 350 mm TL or 350 g TGW (Table 2) could potentially be any of these ages (2–5).

Table 1
Mean total length (TL) at age for Chesapeake Bay weakfish, *Cynoscion regalis*, collected in April–May and August–September, 1989–92.

Age	*n* April–May	Mean April–May	*n* Aug–Sep	Mean Aug–Sep
1	89	176	311	251
2	246	311	516	312
3	246	411	119	402
4	213	511	50	507
5	46	558	8	549
6	13	631	2	626

Observed size at age was used to estimate weakfish growth, because there was no evidence of size-selective mortality. Mean size at first annulus showed no consistent pattern with increasing age (Table 3), and no significant differences were found between sizes at first annulus by age (n=540, F=1.75, P=0.06).

Weakfish growth was well described by the von Bertalanffy model (Fig. 7). The von Bertalanffy curve was calculated for pooled sexes because weakfish show no readily observed sexual dimorphism. Although lengths at age were similar for both sexes, mean TL's at age were usually larger for females than for males, and significantly so for ages 2 and 3 (Table 4). Mean observed TL's of pooled male and female Chesapeake Bay weakfish in April and May were 176, 311, 412, 510, 558, and 631 mm for ages 1–6, respectively. Despite the high variability in size at age, observed lengths at ages 1–12 showed a good fit (r^2=0.98) to the von Bertalanffy model (Fig. 7). The model's estimated parameters, asymptotic standard errors, and 95% confidence intervals fell within a reasonable range, given the observed data (Table 5).

Although the SW-TL relationship of weakfish collected in Chesapeake Bay differed significantly by sex (ANCOVA, P<0.05), the equations (male SW=9.1×10^{-6} $TL^{3.1}$ and female SW=6.9×10^{-6} $TL^{3.05}$) and coefficients of determination (r^2=0.99) were similar for both sexes. Therefore, an equation for pooled sexes was calculated (Fig. 8):

$$SW = 6.0 \times 10^{-6} TL^{3.04} \ (r^2=0.99, n=3{,}742).$$

The slope (b=3.04, SE=0.005) was not significantly different from 3 (t-test, t=0.002, P>0.05) indicating

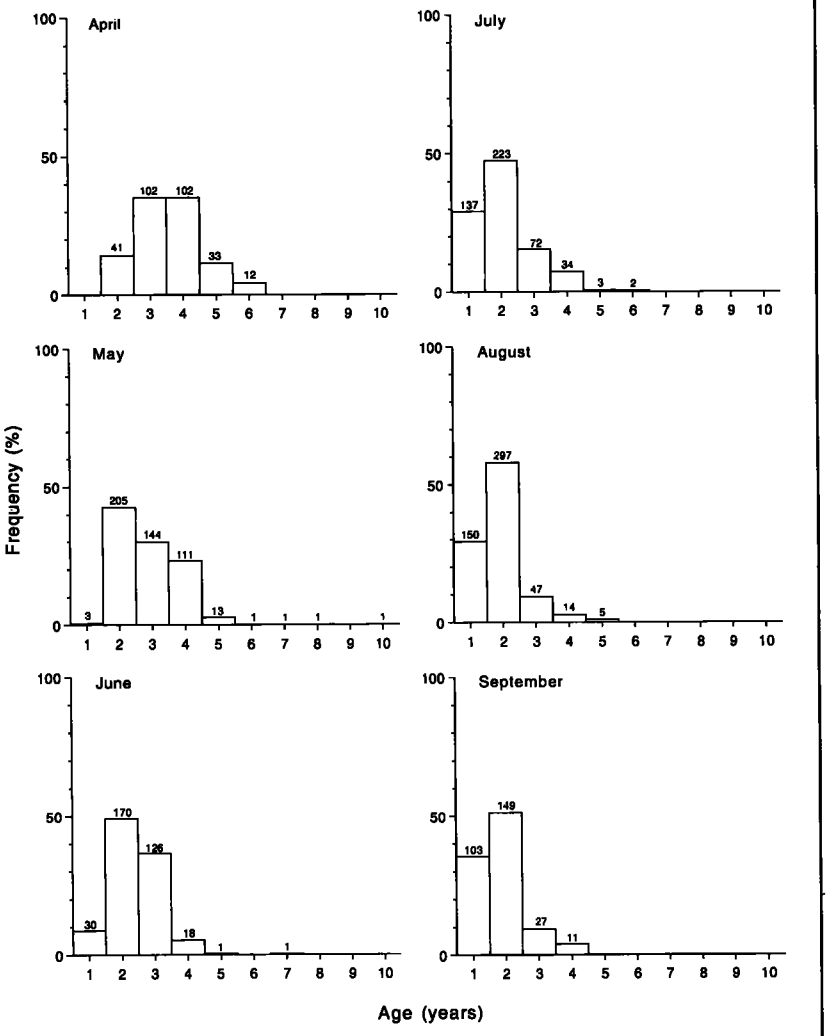

Figure 4

Age-frequency distributions of Chesapeake Bay weakfish, *Cynoscion regalis*, by month, pooled over the years 1989–92. Sample size is indicated above each bar.

isometric growth. The TGW to TL relationship for April and May was

$$TGW = 4.7 \times 10^{-6} TL^{3.13} \ (r^2=0.99, n=950).$$

Historic trends in maximum size and age

Older weakfish were collected in Delaware Bay in 1985–86 than in 1992–93. The mean age of fish ≥3.6 kg in 1985–86 was 9.6 years, significantly higher than that in 1992–93 (6.4 yr; t=3.14, n=26, P<0.05). Of the 10 fish ≥3.6 kg in 1985–86, one was age 4, one age 6, two age 8, two age 9, one age 11, two age 12, and one age 17. In contrast, the maximum age observed in 1992–93 was only 11, and of the 16 fish ≥3.6 kg only three of them were older than age 6.

Maximum sizes of weakfish began to increase in Chesapeake and Delaware Bays in the early 1970's, concurrent with the recovery of the weakfish fishery. From 1958 to 1968, the largest weakfish reported to the Virginia Saltwater Fishing Tournament was 3.1 kg (662 mm TL, Fig. 9). Similarly, the largest fish caught in Delaware Bay in 1968 and 1969 (when citation records began) was 2.6 kg (626 mm TL). However, in 1970 maximum size in Chesapeake Bay was >3.1 kg (662 mm TL) for the first time since 1958, and maximum size in Delaware Bay increased from

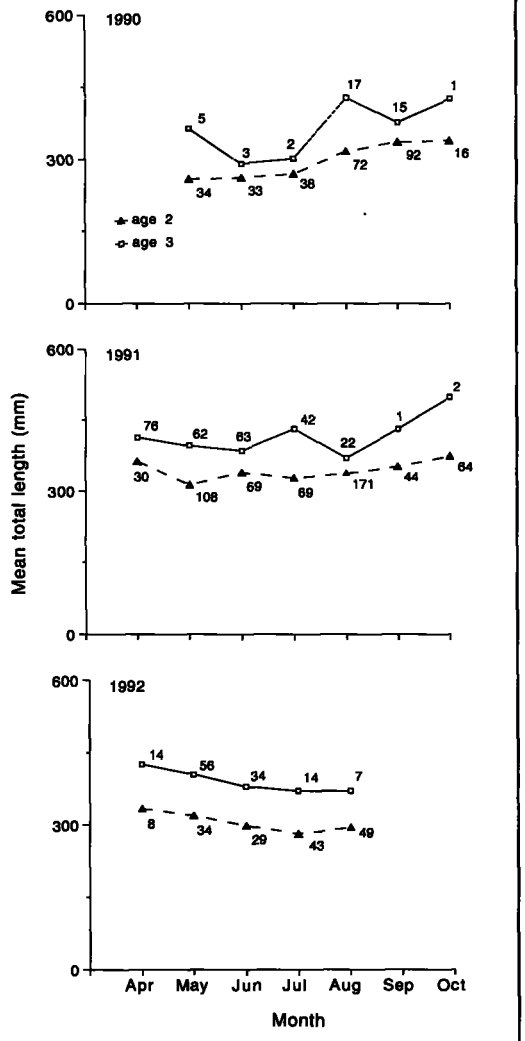

Figure 5

Mean monthly total lengths at age 2 and 3 of Chesapeake Bay weakfish, *Cynoscion regalis*, 1990–92. Sample size is indicated next to each point.

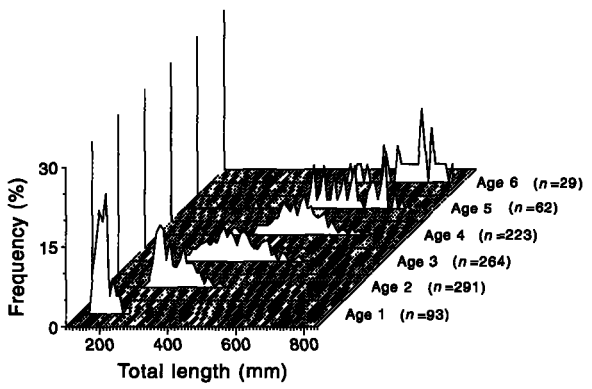

Figure 6

Length frequencies at age for weakfish, *Cynoscion regalis*, collected in April and May 1989–92, pooled over gears and locations.

Table 2

Mean total gutted weights (TGW), range and standard errors at age for Chesapeake Bay and Delaware Bay weakfish, *Cynoscion regalis*, collected in April and May, pooled over gears, 1989–93.

Age	*n*	Mean (g)	Range (g)	Standard error
1	91	49	20–161	2.4
2	285	310	113–1,038	10.3
3	263	778	160–2,099	28.3
4	223	1,494	342–3,866	37.4
5	62	2,126	284–4,031	105.0
6	29	3,268	1,507–5,360	197.3
7	1	3,257	—	—
8	4	5,230	3,370–6,475	591.5
9	1	5,311	—	—
10	1	6,260	—	—
11	1	6,190	—	—
12	1	6,276	—	—

2.6 kg (626 mm TL) in 1969 to 3.9 kg (712 mm TL) in 1970. By 1973 maximum weight had more than doubled, compared with that in the late 1960's, with 6.4 kg (834 mm TL) in Virginia and 5.9 kg (813 mm TL) in Delaware. Maximum sizes continued to increase until 1985 and remained high until 1989 in Virginia and 1990 in Delaware.

The abundance of large fish in Chesapeake and Delaware Bays also increased in the early 1970's, concurrent with the increase in maximum size. From 1958 to 1968, only 64 fish >1.8 kg (556 mm TL) were reported in Virginia (Fig. 10). Similarly in 1968 and 1969, only 13 fish >1.4 kg (513 mm TL) were reported in Delaware Bay. However the number of fish >1.8 kg (556 mm TL) reported in Virginia increased from 2 in 1969 to 83 in 1970. Similarly, in Delaware Bay, the number of fish >1.4 kg (513 mm TL) increased from 12 in 1969 to 121 in 1970. By 1980, 1,399 fish >5 kg (771 mm TL) received citations in Virginia, and 1,229 fish >4.6 kg (751 mm TL) received citations in Delaware.

Both Chesapeake and Delaware Bay have recently shown a marked decrease in maximum size and abundance of large weakfish. The number of large

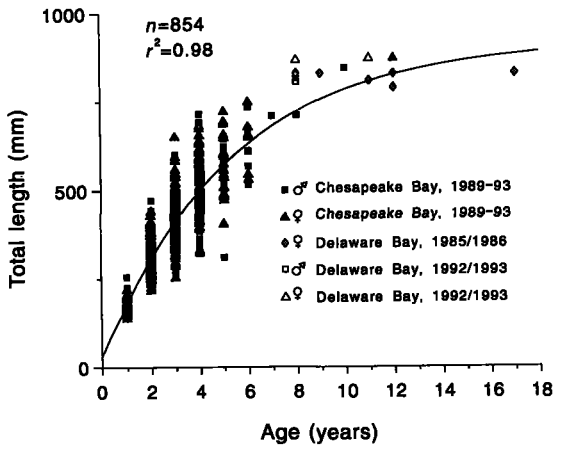

Figure 7

Observed lengths at age and fitted von Bertalanffy regression line for Chesapeake Bay weakfish, *Cynoscion regalis*, in April and May and for three fish from Delaware Bay. Weakfish in the asymptotic size range collected in Delaware Bay are included as reference points but were not used in calculations.

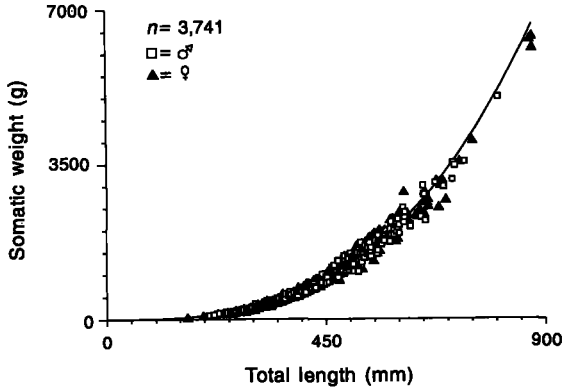

Figure 8

Somatic weight-length relationship of weakfish, *Cynoscion regalis*, in the Chesapeake Bay region, 1989–93.

Table 3

Mean, range, and standard error of otolith sizes at first annulus (mm) for weakfish, *Cynoscion regalis*, ages 1–12 (no age-9 fish were collected) from Chesapeake Bay and Delaware Bay.

Age	*n*	Mean (g)	Range (g)	Standard error
1	111	0.84	0.61–1.09	0.010
2	167	0.86	0.61–1.09	0.007
3	137	0.83	0.61–1.15	0.009
4	76	0.84	0.64–1.06	0.010
5	24	0.85	0.59–1.08	0.022
6	18	0.88	0.73–1.20	0.025
7	1	0.80	—	—
8	3	0.80	0.76–0.88	0.038
10	1	0.67	—	—
11	1	0.84	—	—
12	1	0.90	—	—

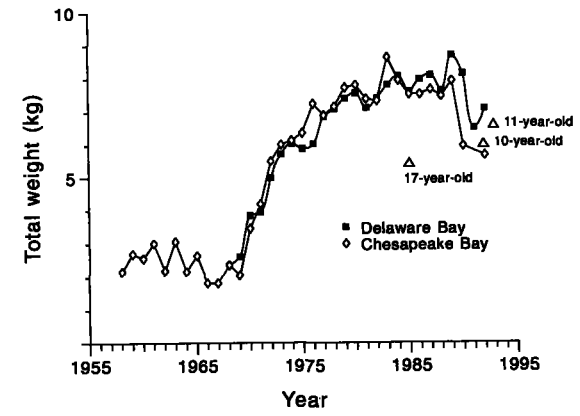

Figure 9

Maximum total weights of weakfish, *Cynoscion regalis*, reported in the Delaware Sport Fishing Tournament and the Virginia Saltwater Fishing Tournament, 1958–1992. The oldest and two heaviest fish from the present study are included as reference points.

fish reported in Virginia dropped sharply in 1981 and has remained low. Only 12 fish >5.45 kg (792 mm TL) were reported in 1989 and 1990, no fish in 1991, and 3 fish >5.0 kg (771 mm TL) in 1992. During 1990–92, maximum size in Virginia was below 6 kg (817 mm TL) for the first time since 1972. Delaware Bay reported large numbers of fish >4.6 kg (751 mm TL) until 1989. However, the number of fish >5.0 kg (771 mm TL) decreased from 981 in 1989 to 11 in 1990. Only 18 fish have been reported since 1990. In 1991, maximum size of Delaware Bay fish dropped below 7.5 kg (878 mm TL) for the first time since 1981, and remained low in 1992.

Discussion

Size and age composition

Most weakfish in Chesapeake Bay in 1989–93 were 200–600 mm TL and ages 1–4, but fish as old as age

Table 4

Mean total length (mm) at age by sex of male and female weakfish, *Cynoscion regalis*, from Chesapeake Bay in April and May 1989–92, and *t*-test results ($\alpha = 0.05$, * = $P < 0.05$).

Age	Mean TL males	*n*	Mean TL females	*n*	*t*-value	Significance
1	176.3	42	175.9	47	0.14	NS
2	295.8	76	318.3	170	3.33	*
3	376.5	70	425.7	174	5.10	*
4	501.8	100	518.0	112	1.67	NS
5	553.9	24	562.5	22	0.37	NS
6	735.0	7	752.0	6	0.40	NS

Table 5

Von Bertalanffy model parameter estimates, standard errors and 95% confidence intervals estimated for weakfish, *Cynoscion regalis*, in the Chesapeake Bay region collected in April and May 1989–93.

Parameter	Estimate	Standard error	95% confidence intervals
L_∞	918.89	58.09	804.87–1032.91
K	0.19	0.02	0.15–0.24
t_0	–0.13	0.09	–0.29–0.04

12 and as large as 875 mm TL were observed. Population size and age compositions could not be estimated from our samples, because they were not randomly selected and came from several gear types. However, our samples should represent the population range. Hildebrand and Schroeder (1928) reported a similar size range (76–838 mm TL, n=280) in the 1920's. However, Massmann (1963) reported most weakfish in the 1950's were <300 mm TL, with a maximum size of 445 mm TL (n=14,516) and a maximum age of 5.

Chesapeake Bay weakfish are fully recruited to market grades by age 2. Joseph (1972) also reported age 2 as the first age fully recruited to the Chesapeake Bay pound net catch. However, yearlings sometimes make up a large portion of the commercial catch, as we observed in 1990, and clearly are vulnerable to the gear—especially pound nets and haul seines. Such small, young fish are often sold as scrap and do not show up in market grades. McHugh (1960) found weakfish to be the second most important food fish in scrap from the Chesapeake Bay pound-net fishery, and Massmann (1963) reported the number of weakfish in pound-net scrap often exceeded that in market grades. Thus, although Chesapeake Bay weakfish are fully recruited to market grades at age 2, age at recruitment to pound nets and haul seines is younger.

Large, older weakfish occur seasonally in Chesapeake Bay. From 1989 to 1992, older fish (ages 4 and older) were relatively abundant only in April and May. Hildebrand and Schroeder (1928) and Massmann (1963) also reported seasonal availability of large weakfish in Chesapeake Bay. Although Massmann (1963) collected few weakfish >2 lb (0.91 kg) or age 4, the largest fish in his study (2- and 3-year-olds) were relatively more abundant in April and May, similar to the present study. However, Hildebrand and Schroeder (1928) reported weakfish >3 lb (1.36 kg) to be more common in both spring and late fall. Thus, although large fish occur regularly in the spring, their appearance in the fall may be variable.

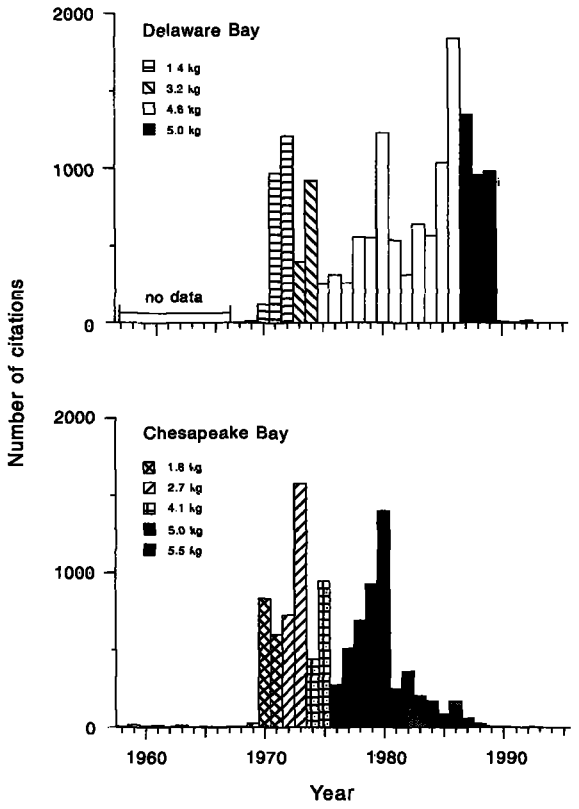

Figure 10

Number of weakfish, *Cynoscion regalis*, citations reported in the Delaware Sport Fishing Tournament and the Virginia Saltwater Fishing Tournament, 1958–92. Minimum citation weights are indicated by year. In 1972, the Delaware citation weight changed mid-year from 1.4 to 2.3 kg.

Age compositions of weakfish in Chesapeake Bay commercial catches are affected by migration. The pattern found in this study—of older fish arriving in Chesapeake Bay in April and May and then apparently leaving approximately when yearlings arrive—was also reported by Nesbit (1954) and Massmann (1963). This pattern indicates that Chesapeake Bay catches at any one time do not accurately represent relative weakfish abundance at age in the Bay. It is not known whether the old fish that occur in Chesapeake Bay originated there, nor is it known where they go after leaving the Bay. It has been reported that some weakfish that spend their younger years in Chesapeake Bay migrate farther north as they grow older, and that large fish are more abundant farther north (Pearson, 1932; Nesbit, 1954; Perlmutter et al., 1956). The location of large fish may also vary from year to year. For example, fish ≥age 4 made up only 4.5% of our 1990 Chesapeake Bay samples but 17.1% and 17.6% of the 1991 and 1992 samples, respectively.

The occurrence of a 17-year-old fish suggests past estimates of weakfish longevity and natural mortality may need to be reevaluated. The maximum age previously reported was age 12 (Shepherd, 1988). However, all former maximum ages were based on scales, which underage weakfish older than age 6 (Lowerre-Barbieri et al., 1994). The 17-year-old was aged as 7 by using scales (Villoso, 1989)—suggesting older fish may have occurred in the late 1970's and early 1980's but were underaged. The occurrence of a 17-year-old seems to indicate weakfish are longer-lived and experience lower natural mortality than previously believed, given the relationship between longevity and natural mortality (Hoenig, 1983; Gulland, 1983; Vetter, 1988).

Growth

Adult weakfish size at age showed a large range and much overlap. Broad size-at-age distributions have been reported for weakfish and attributed to the long spawning season from May through August (Welsh and Breder, 1923; Massmann et al., 1958; Thomas, 1971; Chao and Musick, 1977). An extended spawning season affects size at age in two ways: 1) true age at first annulus deposition varies from 7 to 12 months, depending on birthdate; and 2) fish born in different months encounter different environments, e.g. temperature, salinity, and prey availability, which affect larval growth (Goshorn and Epifanio, 1991) and mortality rates (Thomas, 1971). In addition, spawning pulses may result in several distinct size groups or modes within juvenile size distributions (Massmann et al., 1958; Thomas, 1971).

Delaware Bay fish did not demonstrate a greater longevity or maximum size than Chesapeake Bay fish in 1992–93. Maximum age was 11 in Delaware Bay and 12 in Chesapeake Bay. Maximum size in both regions was 875 mm TL. This is in contrast to Shepherd and Grimes' (1983) hypothesis that weakfish show different regional patterns, longevity and growth being lowest in the South Atlantic region, intermediate in the Chesapeake Bay region, and highest in Delaware Bay and northward. Shepherd and Grimes (1983) observed a maximum age of 11 (810 mm TL) in the northern region and 6 (710 mm TL) in the Chesapeake Bay region. However, they sampled the two regions differently. Samples representing the Chesapeake Bay region came only from a NMFS groundfish trawl survey along the Atlantic coast, whereas sampling in more northern regions included commercial fisheries within Gardiners Bay, New York; Sandy Hook Bay, New Jersey; and Delaware Bay. Because large fish are able to avoid trawls (Gunderson, 1993), estimates of maximum age may have been inaccurate owing to their sampling method (Hawkins, 1988). The Virginia Saltwater Fishing Tournament data show that more than 1,000 fish >5 kg (771 mm TL) were captured in 1980, indicating that large fish did occur in the area.

Recent studies have reported similar asymptotic lengths for weakfish throughout their range. Our estimate of L_∞ (919 mm TL) is comparable to recent estimates from different regions: 893 mm TL from Delaware Bay (Villoso, 1989) and 917 mm fork length from North Carolina (Hawkins, 1988). In contrast, Shepherd and Grimes (1983) reported much lower L_∞ estimates for the Chesapeake Bay region (686 mm TL) and North Carolina (400 mm TL).

Differential migration by size is an alternative explanation for the reported higher abundance of large, presumably older weakfish in the northern end of the range (Pearson, 1932; Nesbit, 1954; Perlmutter et al., 1956). Because swimming speed is a function of body size (Moyle and Cech, 1988), larger weakfish would be expected to travel faster and farther than smaller fish in a given amount of time. If weakfish constitute a single coastwide stock, as genetic research suggests (Crawford et al., 1988; Graves et al., 1992), and most fish overwinter off North Carolina (Pearson, 1932; Hawkins, 1988), then larger fish would arrive in northern estuaries before smaller ones in the spring. This is the pattern observed in Chesapeake Bay (Hildebrand and Schroeder, 1928; Massmann, 1963; the present study) and Delaware Bay (Feldheim, 1975; Villoso, 1989). In addition, because larger fish would travel farther north, they would be more abundant at the northern end of the weakfish range, thus causing a size-dependent distributional pattern similar to that reported for Atlantic menhaden, *Brevoortia tyrannus* (Ahrenholz et al., 1987).

The complex spatial and temporal distribution of weakfish may also affect estimates of seasonal growth. Growth of temperate-water fish usually follows the seasonal cycle; it is faster in summer and slower in winter (Moreau, 1987). Juvenile weakfish have been shown to grow rapidly during June–September (Mercer, 1985). However, mean size at age for Chesapeake Bay weakfish ages 3–6, was smaller in fall-caught than in spring-caught fish (Nesbit, 1954, the present study). Thus, it may be difficult to follow seasonal growth patterns in Chesapeake Bay commercial catches.

Historic trends in maximum size and age

The population structure of Chesapeake Bay weakfish has dramatically fluctuated since the 1920's. Hildebrand and Schroeder (1928) reported that most fish in Chesapeake Bay commercial catches weighed from 0.5 lb to 3 lb (0.23 kg to 1.36 kg) and that 6–10 lb fish (2.72–4.54 kg) were not uncommon. By the 1950's, however, Massmann (1963) reported that most fish were about 0.25 lb (0.11 kg) and few weighed more than 2 lb (0.91 kg). Massmann (1963) concluded that the uniformity in size structure from 1954 to 1958 indicated that there were no large fluctuations in year-class abundance; rather, he suggested that the weakfish population had stabilized at a low level of abundance. In 1970, however, the maximum size and number of large fish began to increase, peaking in 1980. Although the maximum size and number of large fish have declined recently, the current maximum size of 875 mm TL and maximum age of 12 remain well above those for the 1950's and 1960's (445 mm TL and age 5) (Massmann, 1963; Joseph, 1972).

Similar historic changes in maximum size and age have been reported over much of the weakfish range, with higher maximum ages and sizes during periods of higher landings and presumed abundance (Fig. 11). During the high landings of 1925–45, the maximum size was 865 mm TL (Nesbit, 1954), and maximum age was 8 (Perlmutter et al., 1956). However, during the 1950's and 1960's when landings were low, maximum size decreased to 760 mm TL and the maximum reported age was 6 years (Perlmutter et al., 1956). In the 1970's and 1980's, maximum size and age increased to 960 mm TL (Villoso, 1989) and 12 years (Shepherd, 1988), concurrent with increased weakfish landings. Because all previous ages were based on scales, the historic pattern of higher maximum ages during periods of higher landings are probably valid, even though actual ages may have been underestimated.

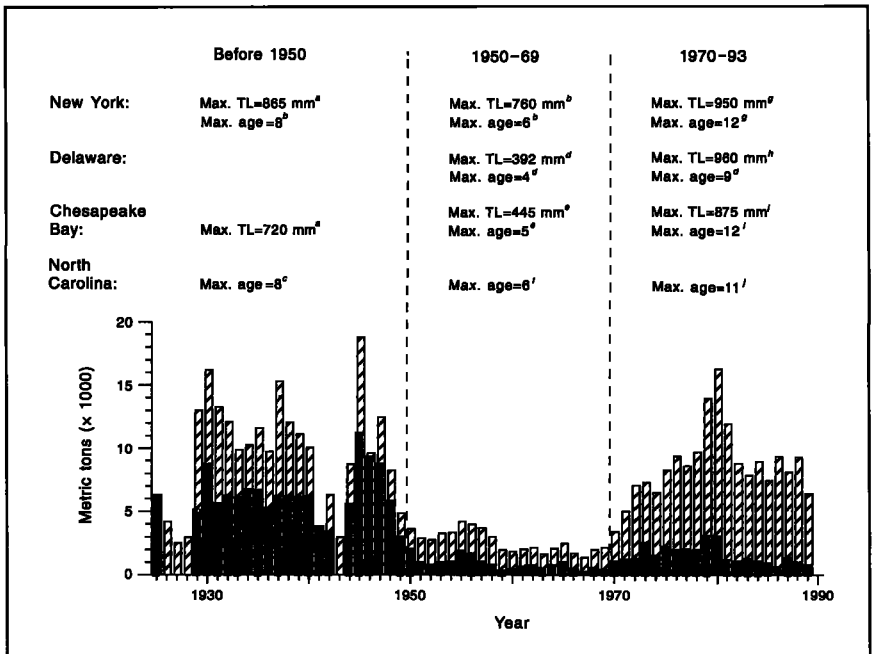

Figure 11

Commercial landings of weakfish, *Cynoscion regalis*, coastwide (hatched bars) and in Chesapeake Bay (black bars), 1925–89, with maximum reported sizes and ages (in years) for periods of high and low landings. Taken from: [a]Nesbit (1954), [b]Perlmutter et al. (1956), [c]Taylor (1916), [d]reported in Seagraves (1981), [e]Massmann (1963), [f]Merriner (1973), [g]Shepherd (1988), [h]Villoso (1989), [i]present study, [j]Hawkins (1988).

Citation data indicate an abrupt increase in maximum size and abundance of large weakfish in Delaware Bay in 1970 and in Chesapeake Bay in 1971. Maximum size rose steadily from 1970 to 1979 and then remained relatively constant until 1989 in both areas. Abundance of increasingly large fish (Fig. 10) also rose until 1980 in Chesapeake Bay and 1989 in Delaware Bay. Although these data have no estimates of effort associated with them, the general pattern appears accurate. Greater effort might increase the number of rare, large individuals being caught even if their abundance remained constant, but it would not be expected to cause such a dramatic change in the numbers and size of large fish being caught (i.e. in Chesapeake Bay no fish >3.5 kg TW from 1958 to 1969 to more than 1,000 fish >5 kg TW in

1980). In addition, citation-size fish have recently declined even though recreational effort has remained high.

The increased abundance of large, presumably older fish apparently reflects increased recruitment or year-class strength in the late 1960's. There is no evidence that fishing mortality decreased. In contrast, effort increased during this same period (Wilk, 1981), and peak regional landings shifted to North Carolina, where exploitation of smaller weakfish is higher than in more northern regions (Hawkins, 1988). The importance of fish born in the late 1960's is indicated by the increase of fish >1.8 kg (556 mm TL) in Chesapeake Bay and >1.4 kg (513 mm TL) in Delaware Bay in 1970 and 1971, respectively. Based on current TGW-at-age data (Table 2), the age of these fish would be 4–5 years, and they would have born between 1965 and 1967. By 1976, these fish would be 9–11 years old and >5 kg TGW. The stepwise increase in abundance of fish >5 kg in Chesapeake Bay and of fish >4.6 kg in Delaware Bay from 1976 to 1980 indicates that more fish were growing into this size range than were being removed, which would be expected if large numbers of several strong year classes were reaching age 8 or older during this time period.

Several lines of evidence suggest more than one year class contributed to the increase in abundance of large weakfish in the 1970's and 1980's. First, in Chesapeake Bay the number of citation-size fish >5 kg in 1980 was larger than the number of citation-size fish >1.8 kg in 1970. Similarly, in Delaware Bay the number of citation size fish >4.6 kg in 1986 was larger than the number of citation-size fish >1.4 kg in 1971 and 1972. If only one year class was involved, the number of fish surviving to older and larger sizes would decrease rather than increase. Second, the pattern in Delaware Bay—of increasing numbers of fish >4.6 kg from 1975 to 1980, with a decrease in 1981 and 1982 and then a second increase until 1986—suggests the contribution of more than one year class. Third, it is unlikely that the more than 1,300 fish >5.0 kg recorded in Delaware Bay in 1987 were solely from the late 1960's year classes, because they would then be 19–21 years old.

The factors which produced the large year classes and allowed large numbers of weakfish to survive to older ages are not clear. Joseph (1972) suggested reproductive failure as the cause of the low landings in the 1950's and 1960's, and thus increased reproductive output and recruitment in the late 1960's could have caused increased year-class strength. That there was a shift in recruitment appears to be corroborated by the fact that weakfish larvae were rare in Chesapeake Bay in the 1960's (Joseph, 1972); yet in 1971–73 Olney (1983) found them to be second in abundance only to the bay anchovy, *Anchoa mitchilli*. Such a large shift in recruitment should be reflected in juvenile indices. However, the index of juvenile weakfish abundance, based on trawl surveys of the York River, Virginia, from 1955 to 1982, showed only a small increase in abundance in 1968—one that did not exceed levels in the 1950's—a larger peak in 1970, and an extreme peak in 1980 (Mercer, 1985).

In addition to variable recruitment, there also may have been changes in adult natural mortality rates. Such fluctuations are not uncommon, although they are difficult to document (Vetter, 1988; Hilborn and Walters, 1992). Factors such as increased food availability, which would increase reproductive output (Houde, 1989), would also be expected to decrease adult natural mortality rates.

Future research is necessary to understand better fluctuations in year-class strength and interactions between weakfish and other species. Stock-wide mortality rates need to be estimated and weakfish migration needs to be understood better. It is especially important that ages be based on sectioned otoliths—a validated ageing technique—so that future estimates of growth parameters, mortality, and longevity can be better compared over time and space.

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Estimating the predictability of recruitment

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Abstract.—A simple analytical technique is developed for estimating the predictability of recruitment, that is, correlations between recruitment and stage-specific mortalities or abundances. The method requires the input of estimates of the variability of stage-specific mortalities, which may be calculated from mean stage-specific mortalities by applying a published regression. It is shown that modification of this regression to compensate for sampling error in field measurements of abundance significantly reduces the estimated standard deviation of log-recruitment, which is an important factor in the predictability calculations. It is concluded that the prospects for predicting recruitment from egg or larval surveys or from environmental variables are quite poor for fish stocks showing the typical distribution of mortality across stages.

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The problem of predicting recruitment remains central to fisheries science (e.g. Bradford, 1992). Approaches to this task may involve finding environmental correlates of recruitment or the field sampling of prerecruit life history stages. In this study we present simple analytical formulae that permit one to estimate the potential explainable variance of recruitment without the use of detailed, specific data.

Certain environmental factors may be correlated with recruitment. Wind speed has been proposed as a determinant of recruitment because storm-driven mixing can disperse larvae and their prey, reducing food availability (Lasker, 1975, 1981; Buckley and Lough, 1987; Peterman and Bradford, 1987). Larval food supply may also be influenced by the lag between appearance of larvae and the peak abundance of their prey (Cushing, 1990). The intensity of turbulence may control the frequency of contact between larvae and their prey (Rothschild and Osborn, 1988). Larvae may be exported to inhospitable waters by the action of wind driven currents (Nelson et al., 1977) or by the incursion of Gulf Stream rings (Flierl and Wroblewski, 1985; Myers and Drinkwater, 1989). (For thorough discussions of environmental influences on recruitment see Fogarty [1993] or Wooster and Bailey [1989].) In each example noted above, some measurable physical quantity may be plausibly postulated to be a proxy for (say) larval mortality, in a qualitative sense; it is our aim to quantify the expected predictive power of an environmental variable. Alternatively, but much more expensively, larval mortality could be estimated from field studies (Butler, 1991). We calculate the likely strengths of the correlations between mortality for an early life history stage and recruitment. A related problem that is addressed is the correlation between recruitment and abundance in an early life history stage, which can be determined from field studies (Peterman et al., 1988; Bradford, 1992). This treatment is an analytical complement to the simulation studies presented in Bradford (1992).

In the analysis to follow we first show how variability of mortality may be estimated from mean mortality while accounting for the effect of sampling error in the field measurements. We then proceed to formulate simple relationships permitting the calculation of the correlation coefficients between log-transformed or raw recruitment and stage-specific mortality or abundance, using only estimates of variability in stage-specific mortality. These two sets of analyses are then combined to provide estimates of the predictability of recruitment for a number of fish species.

Methods and analysis

Variability of mortality

To calculate correlations between stage-specific mortalities (or abundances) and recruitment, we required estimates of variability of mortality for each stage. Bradford (1992) compiled from the literature a large set of data on mortality rates and their interannual variabilities for the prerecruit stages of marine fishes. From this consolidation of data, Bradford regressed the interannual variance of daily mortality on its mean (averaged over years). We adopt the following notation: $\hat{M}$ represents an estimate of M from a single year's survey (often only two abundance estimates are used to calculate $\hat{M}$); $\overline{M}$ represents the average over a number of years of $\hat{M}$ values; $\mathrm{Var}(\hat{M})$ is the estimate of the variance of the mortality calculated from a number of years of $\hat{M}$ data. Note that $\mathrm{Var}(\hat{M})$ is not equal to the true variance, $\mathrm{Var}(M)$, an issue dealt with below. Bradford found the following fit, holding across both stages and species: $\ln[\mathrm{Var}(\hat{M})] = 2.231 \ln \overline{M} - 1.893$ ($r^2 = 0.90$; $P<0.0001$). We can rewrite this relation as

$$\mathrm{Var}(\hat{M}) = 0.15\overline{M}^{2.2}. \quad (1)$$

This very appealing relationship specifies an almost constant CV for mortality; however, it is unclear if it is affected by measurement error.

When mortality is calculated from the difference of two field estimates of log abundance each with error ε, the following relationships hold:

$$\hat{M} = (1/T)[\ln N(t_1) - \ln N(t_2) + \varepsilon(t_2) - \varepsilon(t_1)], \quad (2)$$

$$\mathrm{Var}(\hat{M}) = \mathrm{Var}(M) + (2/T^2)\sigma_\varepsilon^2, \quad (3)$$

where N represents the true abundance, σ_ε is the standard deviation of the estimation error ε, and $T = t_2 - t_1$. Approximately 70% of the mortality estimates in Bradford (1992) were obtained as the difference of two abundance estimates.

When mortality is estimated from a regression equation, by using a slope of log numbers versus time with n observations equally spread over time interval T, then we can use the standard formula in regression for the variance of the estimate of a slope to obtain

$$\frac{\sigma_\varepsilon^2}{\sum_{i=1}^{n}(t_i - \bar{t})^2} = \frac{\sigma_\varepsilon^2}{\frac{T^2 n(n+1)}{(n-1)^2}\left(\frac{2n+1}{6} - \frac{n+1}{4}\right)}, \quad (4)$$

where t_i is the time of the ith observation. This reduces to the right-hand side of Equation 3 when n=2, and decreases asymptotically as $1/n$ for large n. For 10 evenly spaced observations, the estimation error variance will be approximately reduced by one-half, compared with the case of two observations. To a good approximation, Equation 3 will provide a good estimate of the estimation error variance because only a few percent of the data used by Bradford had n larger than 10.

Predictability of recruitment: no density dependence

We can write recruitment as

$$R(t) = E(t)\exp[-(C_1(t) + C_2(t) + \ldots)], \quad (5)$$

where t refers to a specific year, E is the total number of eggs produced, and C_i is the cumulative mortality in stage i. To be specific, we designate $i = 1$ for the egg stage, $i = 2$ for early larvae, $i = 3$ for late larvae, and $i = 4$ for juveniles. In accord with Equation 5, the abundance of prerecruits, N_i, at the end of stage i, is

$$N_i(t) = E(t)\exp\left[-\left(C_1(t) + C_2(t) + \ldots + C_i(t)\right)\right]. \quad (6)$$

These equations form the basis of the forthcoming analysis.

Let $C_i(t) = \overline{C_i} + \Delta C_i(t)$, and

$$\ln E(t) = \overline{\ln E} + \Delta \ln E(t),$$

$$\text{then } \ln R(t) = \overline{\ln R} + \Delta \ln E - \left(\Delta C_1(t) + \ldots + \Delta C_4(t)\right). \quad (7)$$

It follows from Equation 6 that

$$\ln N_i(t) = \overline{\ln N_i} + \Delta \ln E - \left(\Delta C_1(t) + \ldots + \Delta C_4(t)\right). \quad (8)$$

Equations 7 and 8 are general, they hold whether or not correlations are present between stages. We make immediate use of these equations to examine the predictability of recruitment in the absence of interstage correlations, a simple case which serves well to illustrate the technique.

In the following calculations we concentrate on environmentally induced recruitment variations and neglect the contribution of interannual variations in egg production. Accordingly, we remove the stock effect from data-based estimates of recruitment variability before comparison with model-based values. Only trivial modifications are necessary to include the egg production factor should this be desired. In the absence of interstage correlations of mortality, it is easily shown that

$$(\sigma_{\ln(ni)})^2 = (\sigma_{c1})^2 + \ldots + (\sigma_{ci})^2, \quad (9)$$

where $\sigma_{\ln(ni)}$ is the standard deviation of $\ln N_i$, and σ_{ci} is the standard deviation of C_i. Correspondingly,

$$(\sigma_{\ln R})^2 = (\sigma_{c1})^2 + \ldots + (\sigma_{c4})^2. \quad (10)$$

We designate the correlation coefficient relating log recruitment and log abundance in stage i to be r_{ni}, and the corresponding coefficient relating log recruitment and stage-specific mortality to be r_{ci}. With Equations 7, 8, 9, and 10, it is easily demonstrated that

$$r_{ni} = \frac{\sigma_{\ln(ni)}}{\sigma_{\ln R}}; \quad (11)$$

this relation holds for i = 1,2,3; for i = 4, one has a correlation coefficient of 1.0, because we have stipulated that abundances are evaluated at the end of a given stage. Corresponding to Equation 11 we have

$$r_{ci} - \frac{\sigma_{ci}}{\sigma_{\ln R}}. \quad (12)$$

Predictability of recruitment: density dependence

We prescribe density dependence of the form discussed by Myers and Cadigan (1993, a and b), which is the same form as that used in key factor analysis (Varley and Gradwell, 1960; Manly, 1990; Bradford, 1992). In this formulation, mortality during the juvenile stage is increased (decreased) for years in which larval abundance is high (low). Specifically,

$$\Delta C_4 = \alpha \Delta \ln N_3 + \varepsilon, \quad (13)$$

where α gauges the strength of the density-dependence and ε (which should not be identified with the ε introduced in section 2) represents the portion of juvenile mortality uncorrelated with late-larval abundance. It follows that

$$\sigma_{c4}^2 = \alpha^2 \left(\sigma_{\ln(n3)}\right)^2 + \sigma_\varepsilon^2, \quad (14)$$

where σ_ε is the standard deviation of ε. With this formulation the quantities of interest can be readily calculated.

The quantities $\sigma_{\ln(ni)}$ remain as given in Equation 9, for i = 1,2,3; for i = 4, again, $\sigma_{\ln(ni)} = \sigma_{\ln R}$, which is now given by

$$(\sigma_{\ln R})^2 = (1-2\alpha)\left[(\sigma_{c1})^2 + (\sigma_{c2})^2 + (\sigma_{c3})^2\right] + (\sigma_{c4})^2. \quad (15)$$

The correlation coefficients of interest may also be calculated:

$$r_{ci} = -(1-\alpha)\frac{\sigma_{ci}}{\sigma_{\ln R}} \quad (i = 1,2,3) \quad (16)$$

$$r_{c4} = -\frac{-\alpha\left[(\sigma_{c1})^2 + (\sigma_{c2})^2 + (\sigma_{c3})^2\right] + (\sigma_{c4})^2}{\sigma_{\ln R}\sigma_{c4}}.$$

The coefficients r_{ni} are given by

$$r_{ni} = (1-\alpha)\frac{\sigma_{\ln(ni)}}{\sigma_{\ln R}} \quad (i = 1,2,3), \quad (17)$$

and, again, r_{n4} = 1.

This treatment may be generalized to any case in which there exists a linear relation, analogous to Equation 13, among the stage-specific mortalities and log abundances. One could easily examine the case where two or more stage-specific mortalities are positively correlated, an effect that would enhance predictability. However, a relationship of this sort will also increase σ_{lnR}, an outcome which is undesirable, as we show in the results section, when calculated values of σ_{lnR} are compared with those estimated from fisheries data.

Predictability of raw recruitment

Thus far, we have formulated relationships bearing on the predictability, from prerecruit mortalities or abundances, of log-transformed recruitment. It seems intuitively likely that raw recruitment will be considerably less predictable, which is unfortunate, because it is the untransformed recruitment which is sought for fisheries management purposes. In this section we undertake a quantitative investigation of the predictability of recruitment. The results that follow do not depend on the presence or absence of density dependence (or other interstage correlations).

Let r'_{ci} be the coefficient for the correlation between R and C_i. We wish to find a relationship between this quantity and the coefficient for the correlation between $\ln R$ and C_i, r_{ci}. This quantity, r'_{ci}, is calculated from

$$r'_{ci} = (\sigma_{ci}\sigma_R)^{-1}\left[\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} p(R,C_i)\,dR\,dC_i - \overline{C}_i\overline{R}\right]. \quad (18)$$

The joint probability $p(R,C_i)$ is obtained through

$$p(R,C_i) = p(\ln R, C_i)\frac{d(\ln R)}{dR}, \quad (19)$$

and, by assuming that ln R and C are normal, $p(\ln R,C_i)$ may be obtained from standard texts:

$$p(\ln R,C_i)=\frac{1}{2\pi\sigma_{\ln R}\sigma_{ci}(1-r_{ci}^2)^{1/2}}\times \tag{20}$$

$$\exp\left[\frac{-1}{2(1-r_{ci}^2)}\left(\frac{(\Delta C_i)^2}{\sigma_{ci}^2}-\frac{2r_{ci}\Delta C_i\Delta R}{\sigma_{ci}\sigma_{\ln R}}+\frac{(\Delta\ln R)^2}{\sigma_{\ln R}^2}\right)\right].$$

Equations 20 and 19 may be substituted into Equation 18 to obtain an expression for r'_{ci}.

The integrations in Equation 18 can be straightforwardly executed to show that

$$r'_{ci}=r_{ci}\times\frac{\sigma_{\ln R}}{\left[\exp(\sigma_{\ln R}^2)-1\right]^{1/2}}. \tag{21}$$

It is evident from this expression that if $\sigma_{\ln R}$ is small, then $r'_{ci}=r_{ci}$.

An identical result holds for the coefficient of correlation between R and ln N_i, designated r'_{ni}; it is given by

$$r'_{ni}=r_{ni}\times\frac{\sigma_{\ln R}}{\left[\exp(\sigma_{\ln R}^2)-1\right]^{1/2}}. \tag{22}$$

The coefficient of correlation between R and N_i, designated r''_{ni}, can be found through a procedure analogous to that employed in the calculation of r'_{ci}. The result is

$$r''_{ni}=\frac{\exp(r_{ni}\sigma_{\ln R}\sigma_{\ln(ni)})-1}{\left[\exp(\sigma_{\ln R}^2)-1\right]^{1/2}\left[\exp(\sigma_{\ln(ni)}^2)-1\right]^{1/2}}. \tag{23}$$

In the limit that $\sigma_{\ln(ni)}\ll 1$, Equation 23 reduces to $r''_{ni}=r'_{ni}$.

Results

Variability of mortality

To obtain a relationship between the true variance of mortality, Var(M), and mean mortality we can substitute Equation 3 into Equation 1. However, it must be borne in mind that there is likely to be a relationship between $\overline{M}$ and T (Taggart and Frank, 1990). To address this problem, we extracted, from the sources cited in Bradford (1992), the sampling period for the surveys providing mortality estimates and then plotted ln $\overline{M}$ versus ln T in order to test for the existence of a power law relationship between these two variables (Fig. 1). The regression (Fig. 1) yields ln $\overline{M}$ = –0.991 ln T + 0.776, or, equivalently

$$\overline{M}=2.17T^{-1}. \tag{24}$$

This apparent tendency of $\overline{M}$ and T^{-1} to covary may stem from the existence of excluded regions of the $\overline{M}$, T^{-1} plane. If $\overline{M}$ is small, mortality will be detectable only if sampling times are well separated, implying that small $\overline{M}$ corresponds to large T. Similarly, if $\overline{M}$ is large, the interval between samples cannot be great, because the abundance will possibly decline rapidly below the threshold of detectability; thus, large $\overline{M}$ corresponds to small T.

We can now use Equation 24 to obtain a relation for the true variance of M, Var(M), by substituting Equations 1 and 3 and then substituting Equation 24 into the result, with the outcome

$$\mathrm{Var}(M)=(0.15\overline{M}^{0.2}-0.42\sigma_\varepsilon^2)\overline{M}^2. \tag{25}$$

Even for a given life history stage, there can be great differences in the estimation error for abundance. For the Peterman (1981) salmon smolt study, $\sigma_\varepsilon\approx$ 0.08, whereas for the juvenile groundfish surveys examined in Myers and Cadigan (1993, a and b), σ_ε

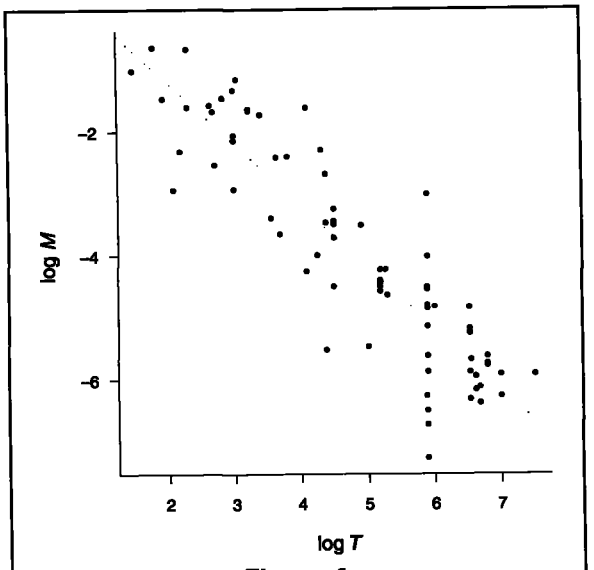

Figure 1

The natural logarithm of the daily mortality rate versus the natural logarithm of the sampling duration for prerecruit stages of marine fish, based on sources listed in Bradford (1992).

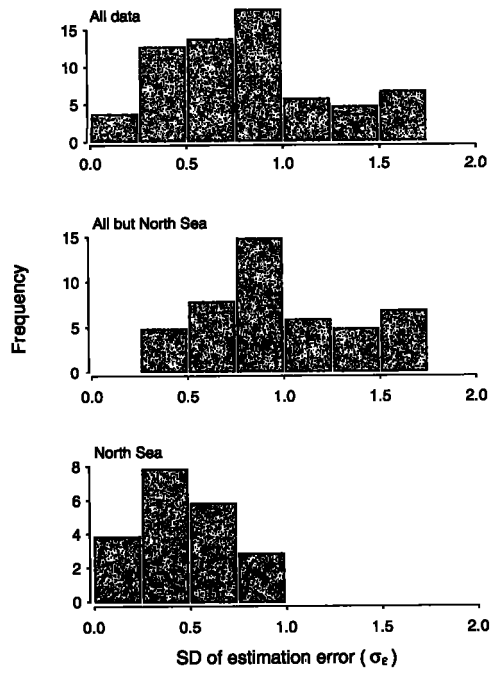

Figure 2

Histograms of the standard deviation of the estimation error of log abundance for the juvenile groundfish survey data treated in Myers and Cadigan (1993, a and b).

has a median value of about 0.75 (Fig. 2). Of necessity, the discussion of the importance of measurement error cannot be precise. We examine the effect of σ_ε in the interval 0.3 to 0.5, a range about midway between 0.08 and 0.75, on the variance of M estimates.

If the error in the log-transformed survey abundances is characterized by $\sigma_\varepsilon = 0.3$ (corresponding to a CV of approximately 30% in the untransformed abundances), then for the range of mortalities in Bradford's regression, $\hat{M} \approx 10^{-4}$ to $0.4 d^{-1}$, Equation 25 shows that estimation error accounts for 30% (upper end of range) to 100% (lower end of range) of the variance in M. In other words, the true variance in M amounts to between 0% (lower end of range) and 70% (upper end of range) of the variance of M. If $\sigma_\varepsilon = 0.5$, then the true variance represents 0% (lower end of range) to 20% of the estimated variance of M. Of more interest is the range of mortalities for major fish species, entered in Table 1 of Bradford (1992), $\hat{M} \approx 10^{-2}$ to 10^{-1} d^{-1}. For this range, with $\sigma_\varepsilon = 0.3$, we find that the true variance constitutes about one-half of the estimated variance of M. If $\sigma_\varepsilon = 0.5$, then the true variance is estimated to make no contribution to the estimated variance. On the basis of these numbers, but somewhat arbitrarily, we assume, for the range $\overline{M} \approx 10^{-2}$ to 10^{-1} d^{-1}, that the true variance represents 25% of the estimated variance of M, so that $\mathrm{Var}(M) \approx 0.04\ \overline{M}^2$ or

$$\sigma_m \approx 0.2\overline{M}, \tag{26}$$

where σ_m is the standard deviation of M.

Finally, we wish to utilize Equation 26 to obtain a relationship between the interannual variability in cumulative mortality in a given stage and the mean cumulative mortality. Since the M values in Bradford's data base are largely stage averages, the cumulative mortality is just $C = M t_s$, where t_s is the stage duration. It also follows that the standard deviation of cumulative mortality σ_c, is given by $\sigma_c = \sigma_m t_s$. Applying these relations to Equation 26, we arrive at $\sigma_c = 0.2\overline{C}$, where we have placed a bar over the C to indicate that we are relating the interannual variability of C (represented by σ_c) to its mean value ($\overline{C}$). We can be more specific, since Bradford's regression applies across stages, and make the standard deviation and mean specific to each stage i:

$$\sigma_{ci} = 0.2\overline{C}_i. \tag{27}$$

The coefficient in Equation 27 is only half as large as that in Bradford's regression (i.e. the square root of the factor 0.15 which appears in Equation 1). This adjustment of slope, arising from correction for estimation error, could be too severe (Bradford and Cabana, in press; Bradford[1]); nevertheless, we take Equation 27 at face value, use it to predict $\sigma_{\ln R}$, and compare the derived values to data. In the discussion we comment on the influence of the slope parameter in Equation 27 on the predictability calculations.

Predictability of recruitment: no density dependence

In Table 1 we present the estimates of the correlation coefficients derived from Equations 11 and 12; in the final column the calculated $\sigma_{\ln R}$, from Equation 10, appears. If we had used relation (Equation 1) in the calculation of $\sigma_{\ln R}$, without adjusting for measurement error, then the calculated values of $\sigma_{\ln R}$ would be one and a half times as large. It is evident that (Fig. 3) $\sigma_{\ln R}$ is overestimated for cod, anchovies, and plaice. Myers and Cadigan (1993, a and b) have shown that density-dependent juvenile mortality can be expected to appreciably attenuate larval variability in cod and plaice.

[1] Bradford, M. Dept. 1994. Fisheries and Oceans, West Vancouver Laboratory, 4160 Marine Dr., West Vancouver, B.C. V7V 1NG, Canada. Personal commun.

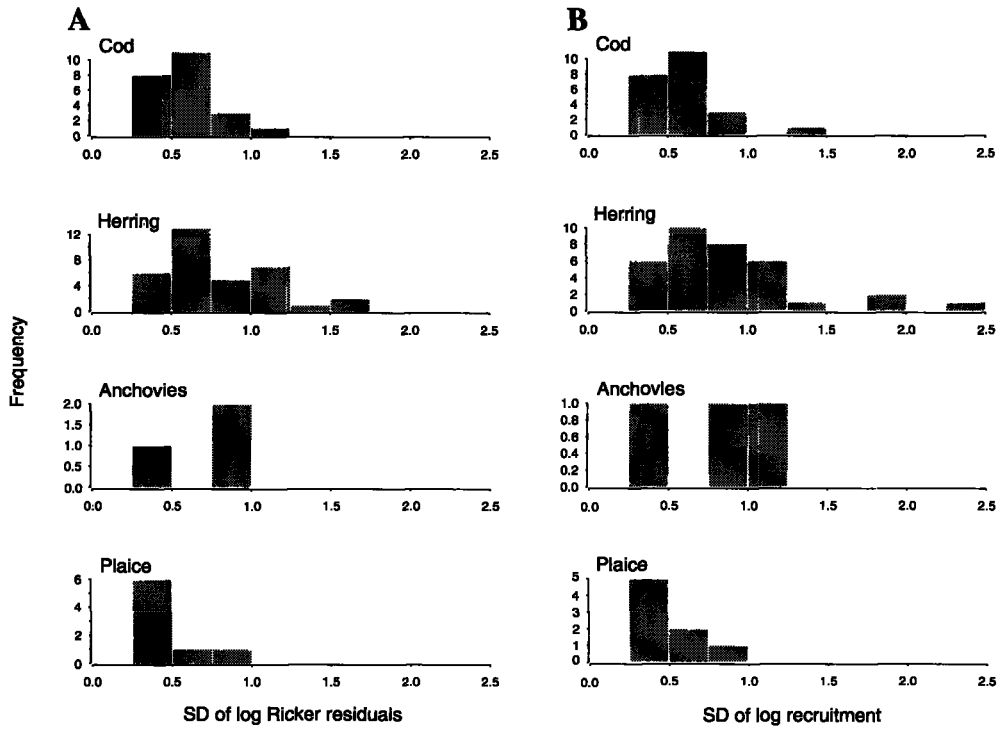

Figure 3

(A) Histograms of the standard deviation of the log-recruitment residuals from a Ricker fit to the stock-recruit relation for four species of marine fish. (B) Histograms of the standard deviation of log recruitment (without adjustment for stock size) for four species of marine fish.

Predictability of recruitment: density dependence

It is evident from Equation 15 that the effect of positive α is to reduce $\sigma_{\ln R}$, which is desirable here, because the formulation with $\alpha = 0$ overestimated $\sigma_{\ln R}$ for cod and plaice (Table 1).

We now select cod for closer examination, since there are reliable estimates for the strength of density dependence in this species (Myers and Cadigan [1993a]). Our parameter α corresponds to $1-\lambda$ in Myers and Cadigan (1993a). They found that λ was typically about 0.5 for a cod stock, suggesting $\alpha = 0.5$. With this specification we find from Equation 15 that $\sigma_{\ln R} = 0.58$, which is in good agreement with Figure 3A. For this case, $\alpha = 0.5$, the correlation between ΔC_4 and $\Delta \ln N_3$ is 0.6, so that about 36% of the variance in juvenile mortality is related to larval abundance (see Eq. 13).

With α fixed we have recalculated, r_{ci} and r_{ni}, for cod using the equations above, and have displayed them in Table 2 along with their counterparts calculated for Table 1 (for which $\alpha = 0$ was assumed). It is apparent that the prescribed density dependence has appreciably lowered the correlation coefficients. There is a particularly large reduction in r_{c4}, stemming from the fact that the juvenile mortality has two components which tend to offset one another (in the limit $\varepsilon = 0$, in Equation 13, juvenile mortality will actually be *positively* correlated with recruitment). Thus, realistic levels of density dependence (Myers and Cadigan, 1993a) have the effect of substantially reducing the predictability of log-recruitment from prerecruit mortalities or abundances.

Predictability of raw recruitment

For $\sigma_{\ln R} = 0.5$ we find from Equation 21, $r'_{ci}/r_{ci} = 0.94$ and for $\sigma_{\ln R} = 1.0$ we have $r'_{ci}/r_{ci} = 0.76$. It is evident that the predictability of raw recruitment (r'_{ci}) declines relative to the predictability of log recruitment (r_{ci}) as $\sigma_{\ln R}$ increases.

In Table 3 we have completed the presentation for the cod case, showing the $r'_{ci}, r'_{ni}, r''_{ni}$ in comparison to

Table 1

Calculated parameters relevant to the predictability of recruitment analysis, for four fish species: σ_{ci} is the standard deviation of total mortality for stage i; $\sigma_{\ln(ni)}$ is the standard deviation of log abundance in stage i; $\sigma_{\ln R}$ is the standard deviation of the log recruitment; r_{ci} is the coefficient of correlation between log recruitment and mortality for stage i; r_{ni} is the coefficient of correlation between log recruitment and log abundance in stage i. The quantities $\sigma_{\ln R}$, r_{ci}, and r_{ni} were calculated by assuming no inter-stage correlations.

	Egg	Early larvae	Late larvae	Juveniles	
Cod					
σ_{ci}	0.22	0.32	0.58	0.58	$\sigma_{\ln R} = 0.91$
$\sigma_{\ln(ni)}$	0.22	0.39	0.70	0.91	
$\lvert r_{ci} \rvert$	0.24	0.35	0.64	0.64	
r_{ni}	0.24	0.43	0.77	1.0	
Herring					
σ_{ci}	0.21	0.16	0.48	0.79	$\sigma_{\ln R} = 0.96$
$\sigma_{\ln(ni)}$	0.21	0.26	0.55	0.96	
$\lvert r_{ci} \rvert$	0.22	0.17	0.49	0.82	
r_{ni}	0.22	0.28	0.57	1.0	
Anchovy					
σ_{ci}	0.35	0.32	0.79	0.65	$\sigma_{\ln R} = 1.13$
$\sigma_{\ln(ni)}$	0.35	0.47	0.92	1.13	
$\lvert r_{ci} \rvert$	0.31	0.28	0.70	0.57	
r_{ni}	0.31	0.42	0.82	1.0	
Plaice					
σ_{ci}	0.52	0.21	0.70	0.39	$\sigma_{\ln R} = 0.97$
$\sigma_{\ln(ni)}$	0.52	0.56	0.90	0.97	
$\lvert r_{ci} \rvert$	0.53	0.22	0.72	0.40	
r_{ni}	0.53	0.57	0.92	1.0	

the r_{ci}, r_{ni}. It is clear in these examples that predictability is lost when one works with the untransformed recruitment or abundance.

Peterman et al. (1988) have investigated the predictability of recruitment from surveys of prerecruit abundances. Equations 22 and 23 shed some light on how predictability is influenced by log transforming the prerecruit abundances. Recall that when $\sigma_{\ln(ni)} \ll 1$, then $r''_{ni} = r'_{ni}$, i.e. the raw recruitment is predicted equally well by abundance or log abundance. However, if $\sigma_{\ln(ni)}$ is considerably larger than $\sigma_{\ln R}$, then $r'_{ni} > r''_{ni}$ (e.g. for $\sigma_{\ln R} = 1.0$, $\sigma_{\ln(ni)} = 2.0$, $r_{ni} = 0.5$, then $r'_{ni} = 0.38$, whereas $r''_{ni} = 0.18$). Conversely, if $\sigma_{\ln R}$ is considerably larger than $\sigma_{\ln(ni)}$, then, $r''_{ni} > r'_{ni}$ (e.g. for $\sigma_{\ln R} = 2.0$, $\sigma_{\ln(ni)} = 1.0$, $r_{ni} = 0.5$, then $r'_{ni} = 0.14$ and $r''_{ni} = 0.18$). This implies that whether or not one will achieve a better correlation between recruitment and log abundance (of prerecruits) than between recruitment and abundance depends on the relative magnitudes of $\sigma_{\ln R}$ and $\sigma_{\ln(ni)}$.

Discussion

CV for mortality

The incorporation of estimates of measurement error into the relationship between variability of mortality and mean mortality indicates that the slope coefficient (see Eq. 27), which is the mortality CV, may be substantially altered by measurement error. However, removal of the error component does not destroy the intuitively appealing approximate proportionality between variability of mortality and its mean.

In the presence or absence of density dependence the slope parameter in Equation 27 does not affect the predictability of log recruitment; see Equations 11, 12, 16, and 17. Increasing this parameter inflates $\sigma_{\ln(ni)}$ and σ_{ci} but it also increases $\sigma_{\ln R}$ by the same proportion, leaving the correlation coefficients r_{ni} and r_{ci} unchanged. This invariance of the correlation coefficients with respect to the mortality CV is a useful result stemming from our treatment of the predictability problem. The predictability of raw recruitment is influenced by the mortality CV, because $\sigma_{\ln R}$ depends on this CV and because $\sigma_{\ln R}$ affects the correlation coefficients for raw recruitment (Eqs. 21 and 22).

The true size of the mortality CV cannot be determined with certainty, because the degree of inflation of the true CV by measurement error cannot be accurately ascertained. However, Equation 27, which specifies a mortality CV of only 0.2, gives reasonable estimates for the magnitude of the recruitment variability ($\sigma_{\ln R}$). Comparison of Table 1 and Figure 3A shows that Equation 27 (with Equation 10) overpredicts the median $\sigma_{\ln R}$ in three cases (cod, anchovies, and plaice). Underestimation of recruitment variability due to ageing errors by 20–30% (Bradford, 1991; Bradford[1]) could rectify this discrepancy. For cod and plaice it is likely that density dependence is in part responsible for the discrepancy between calculated (from Equation 27) and empirical values of $\sigma_{\ln R}$ (see Myers and Cadigan, 1993, a and b). In any case, the approximate agreement between calculated and observed values of $\sigma_{\ln R}$ is powerful verification for the general validity of Bradford's (1992) regressions.

Table 2

The coefficients of correlation for log recruitment of cod (see Table 1) versus stage-specific mortality, r_{ci}, and for log recruitment versus stage-specific log abundance, r_{ni}. The label "no d.d." implies absence of density dependence; the label "d.d." signifies that the parameters were calculated for the density-dependent case.

	Egg	Early larvae	Late larvae	Juveniles
$\lvert r_{ci} \rvert$ (no d.d.)	0.24	0.35	0.64	0.64
$\lvert r_{ci} \rvert$ (d.d.)	0.19	0.28	0.50	0.28
$\lvert r_{ni} \rvert$ (no d.d.)	0.24	0.43	0.77	1.0
$\lvert r_{ni} \rvert$ (d.d)	0.19	0.33	0.60	1.0

Table 3

The coefficients of correlation for log recruitment of cod versus stage-specific mortality, r_{ci}; for recruitment versus stage-specific mortality, r'_{ci}; for log recruitment versus stage-specific log abundance, r_{ni}; for recruitment versus stage-specific log abundance, r'_{ni}; and for recruitment versus stage-specific abundance, r''_{ni}. All examples shown are calculated for the density-dependent mortality case.

	Egg	Early larvae	Late larvae	Juveniles
$\lvert r_{ci} \rvert$	0.19	0.28	0.50	0.28
$\lvert r'_{ci} \rvert$	0.17	0.26	0.46	0.26
$\lvert r_{ni} \rvert$	0.19	0.33	0.60	1.0
$\lvert r'_{ni} \rvert$	0.17	0.30	0.55	0.92
$\lvert r_{ni} \rvert$	0.19	0.33	0.60	1.0
$\lvert r''_{ni} \rvert$	0.17	0.30	0.55	1.0

Research needs

For research purposes one may seek correlations between recruitment and an environmental variable assumed to be a proxy for mortality during some prerecruit stage. It is apparent that there is no meaningful distinction between log recruitment and raw recruitment for the purposes of correlation analysis provided $\sigma_{\ln R} \leq 0.4$. For the optimal case of minimal density dependence, correlations between log recruitment and mortality seldom exceed 0.6 to 0.7 (Table 1). This implies that any environmental variable that is to serve as a proxy for mortality must be very tightly correlated with mortality if there is to be a significant correlation between the proxy variable and recruitment. Similar results were found by Bradford (1992).

Management needs

The criterion for successful recruitment prediction for stock management suggested by Walters (1989) requires that the proxy should explain 80% of the variance in log recruitment, or, equivalently, $r_{ci}, r_{ni} \approx 0.9$. Equations 11 and 12 allow a ready appraisal of the likelihood of meeting this criterion; the application of these equations yields the results in Table 1, indicating that this criterion is never fulfilled unless one samples late in the juvenile phase. The inclusion of density dependence (Eqs. 16 and 17) generally reduces the correlation coefficients r_{ci} and r_{ni}. These findings agree with those of Bradford (1992).

A management strategy requiring predictions of recruitment (rather than log recruitment) is not likely to be viable if the stock under consideration has high recruitment variability. For a stock with $\sigma_{\ln R} = 1.0$, if 80% of the log recruitment variance can be explained by a proxy, only 46% (Eq. 21 or 22) of the variance of recruitment itself will be explained by this proxy. For a $\sigma_{\ln R}$ of 1.5, appropriate to some herring stocks, only 21% of recruitment variance could be explained by a proxy accounting for 80% of log recruitment variance. These calculations bear on the question of whether or not large year classes can be predicted (Bradford and Cabana, in press; Anderson, 1988). Capturing the size of a large year class requires an estimate of raw (rather than log-transformed) recruitment; however, those stocks which produce the most notable year classes (those with large $\sigma_{\ln R}$) are the least predictable.

Summary

The analysis presented here complements that of Bradford (1992). We have shown that correction for measurement error can appreciably reduce the CV for mortality, while not destroying the appealing proportionality between variability of mortality and mean mortality. We have demonstrated that in many cases the predictability of recruitment can be determined analytically. It is evident from our treatment that raw recruitment is considerably less predictable than log recruitment for stocks with high recruitment variability. Our results concur with those of Bradford, suggesting that the prospects of predicting recruitment from egg or larval surveys or from environmental variables are quite poor. However, it must be borne in mind that some fish stocks will deviate from the general pattern, and thus it is quite conceivable that there will be fish stocks for which a critical stage exists, allowing recruitment predictions from (say) larval abundances.

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Recruitment of bonefish, *Albula vulpes*, around Lee Stocking Island, Bahamas

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Abstract.—The onshore movement of settlement-stage bonefish, *Albula vulpes*, leptocephali was monitored over four consecutive winters (1990–91 to 1993–94) and summer 1992 near Lee Stocking Island, Exuma Cays, Bahamas. Total catch over the four winters ranged from 316 to 1,421 fish per 70-day sampling period, whereas 1,112 were taken during the single 72-day summer sampling period. An analysis of otoliths from 87 fish collected during the last winter indicated continuous spawning activity during the fall and early winter and an estimated larval duration of 41 to 71 days. The collection of larvae in summer 1992 suggested that spawning continues until late spring. Virtually all recruiting leptocephali were collected at night and in the upper 1 m of the water column. Time-series analysis of the four winters linked together by lunar date revealed a strong cyclical pattern of recruitment, with a period of 30 days, and a strong association with the number of hours of flood tide occurring under dark, moonless conditions. The one major peak in the summer samples occurred during the first 12 days of sampling when the hours of dark flood tide was at its maximum level for the month; subsequent dark periods had low levels of recruitment. There were no strong associations between recruitment levels and wind and current patterns. These data suggest that the cyclical pattern in hours of dark flood tide creates "windows of opportunity" for the leptocephali to move onshore at times that minimize their vulnerability to visual predators in reefs and seagrass beds.

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The bonefish, *Albula vulpes*, is found in the tropical western Atlantic and supports substantial recreational fisheries in south Florida, the Bahamas, and many Caribbean islands. Despite their importance as a sport fish, there is little quantitative information available about the abundance of adults in different locations, the temporal trends in population sizes, and the recruitment processes that may have a considerable influence on the size and spatial distribution of adult populations.

Adult bonefish typically inhabit shallow sand and seagrass flats, often in water less than half a meter deep, and feed on crabs, bivalves, shrimp, and small benthic fishes (Bruger, 1974; Colton and Alevizon, 1983). Some information on the seasonality of reproduction is available, but the temporal and spatial scales of spawning activity or spawning behavior itself have not been described. In the Florida Keys, spawning occurs from October to May.[1] Examination of gonads of fishes collected in the Bahamas indicated that fish in spawning condition also predominated between October and May, although some ripe fish were found throughout the year.[2]

In the pelagic environment, *Albula* leptocephalous larvae grow to lengths of up to 70 mm prior to settlement. On the basis of the temporal occurrence of ripe females and the subsequent appearance of metamorphosing leptocephali, Pfeiler et al. (1988) proposed a larval duration of six to seven months for *Albula* sp. from the Gulf of California. As the leptocephali move from offshore to the shallow nursery and adult habitats, their length decreases approximately 50% during their metamorphosis into juveniles. Pfeiler (1984) investigated the movement of *Albula* sp. leptocephali as they entered a hypersaline lagoon (estero) in the Gulf of California. Although sampling was limited to 15–20 minute periods of flood tide on 33 nights from February through May, Pfeiler suggested that larvae

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[1] Crabtree, R. E. 1994. Florida Department of Environmental Protection, Marine Research Institute, St. Petersburg, FL. Personal commun.

[2] Colton, D. E. 1994. 27395 Vista Del Toro Road, Salinas, CA. Personal commun.

moved into the lagoon during the first several hours of the flood tide and that there was no movement into or out of the lagoon during the ebb tide.

Although the leptocephali of *Albula vulpes* have been found throughout the Caribbean from Brazil to Bermuda and the southwestern Gulf of Mexico (Smith, 1989), few previous studies have investigated the larval biology of the species or their movement from the pelagic realm to the shallow juvenile habitat (e.g. Eldred, 1967; Thompson and Deegan, 1982). This study presents data on the recruitment of metamorphic *A. vulpes* in the Bahamas as they move from the deep pelagic Exuma Sound onto the shallow Great Bahama Bank near Lee Stocking Island (LSI). Data collected over four consecutive 70-day winter sampling seasons and one summer season were used to evaluate the effects of various environmental parameters that have been shown to influence recruitment of a variety of taxa (Shenker et al., 1993; Thorrold et al., 1994, a and b). The otoliths of 87 individuals that recruited during the 1993–94 winter season were examined to determine the presumed spawning (hatching) dates and to estimate the larval duration of *A. vulpes* in the Bahamas.

Materials and methods

Data collection

Larval bonefish were collected with moored channel nets suspended in two tidal passes on the western edge of Exuma Sound, Bahamas, immediately north of Lee Stocking Island (Fig. 1). Winter sampling was conducted from 17 December 1990 to 28 February 1991, 13 December 1991 to 26 February 1992, 12 December 1992 to 25 February 1993, and 10 December 1993 to 23 February 1994. Summer data were collected from 25 June to 4 September 1992. Station locations, net designs, and sampling protocols are detailed in Shenker et al. (1993) and Thorrold et al. (1994a). To summarize, each of three stations (corresponding to stations 1, 2, and 3 in Shenker et al., 1993) were equipped with both a surface net (mouth area=2 m wide ×1 m deep) and a midwater net (2 m×2 m) which fished the 2–4 m deep layer. Samples were removed from the 3-mm mesh nets after dawn and before dusk each day. In this study, we pooled catches among all six nets. Because less than 10% of the *A. vulpes* larvae were taken in the day samples, our analysis focuses on only the samples collected at night.

Wind speed and direction data during the first, third, and fourth winters, and the one summer were collected hourly at a Campbell Scientific weather station on LSI. During the second winter, the weather station was inoperative and measurements were recorded twice daily with a hand-held anemometer. After statistical analysis of a summer period when hand-held anemometer and weather-station data were recorded, it was determined that the hand-held anemometer data were consistent with those of the weather station (Thorrold et al., 1994b). No weather data were available for the month of December during the third winter or for the period from 1 through 10 January 1994.

Current patterns were monitored with a General Oceanics Mark II current meter moored on the shelf edge at a depth of 10 meters (Fig. 1). Hourly current data were recorded for one month during the first

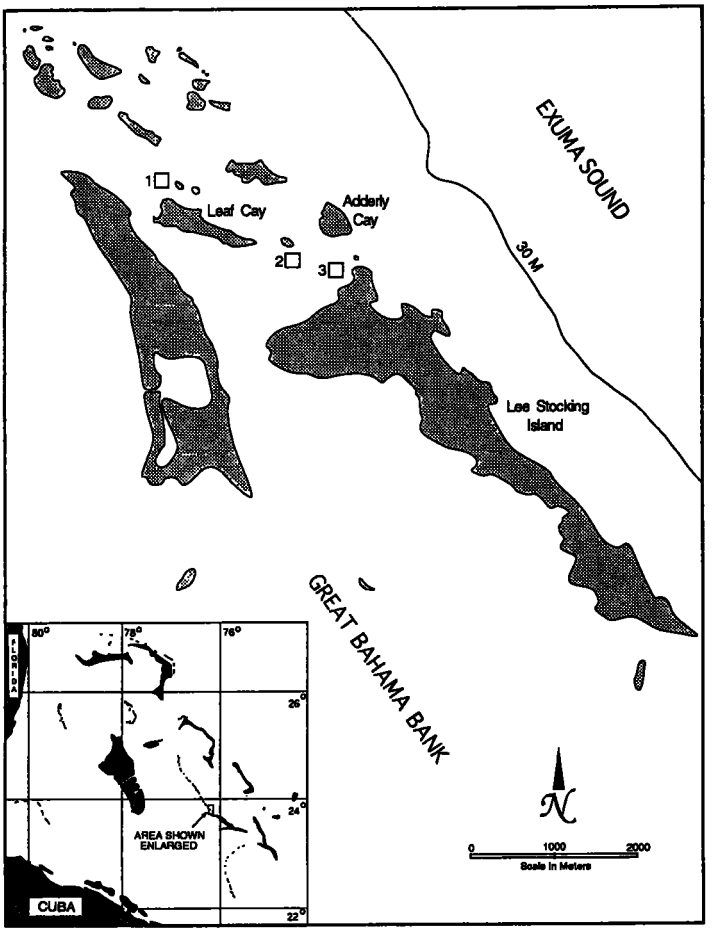

Figure 1
Location of Lee Stocking Island, Bahamas, and channel-net stations.

winter (23 January to 22 February), throughout the entire second and fourth winters, and for the one summer sampling period. Current meter data were not available for the entire third winter. For analysis, hourly wind and current data were averaged over 24 hours to generate estimates of mean flow, which were then decomposed into along-shore and cross-shelf components of motion.

Data analysis

The *A. vulpes* leptocephali from all six nets for each night during the winter sampling periods were summed for time-series analysis. To analyze the relationship between recruitment patterns and lunar phase, time series of fish abundances for the four winters were joined according to lunar month. Nine days were deleted from the beginning and six days from the end of 1991–92 (winter 2), and three days were deleted from the beginning of 1993–94 to ensure continuity with respect to the lunar month. Analyses were carried out on the resultant 277-day period. The time series was log 10 (x+1) transformed to minimize the influence of several large peaks in the data. All time-series analyses were completed by using the statistical package Mesosaur (Kuznetsov and Khalileev, 1991).

A periodogram of the recruitment data was constructed to identify dominant periodicities within the 277-day time series. An autocorrelation function was then plotted to describe more accurately the cyclical patterns of the data. Finally a cross-correlation was run between the abundance time series and the corresponding "hours of dark flood tide" of each night, which previous studies had identified as an important variable affecting recruitment patterns of a number of taxa (Shenker et al., 1993; Thorrold et al., 1994b). The hours of dark flood tide is a measure of the total number of flood tide(s) that occur between sunset and sunrise under moonless conditions. This variable differs from lunar phase in a subtle but significant manner: as the time of moonrise becomes progressively later over consecutive nights, greater portions of the evening flood tide occur during darkness prior to moonrise. Because significant autocorrelations exist in both the larval abundance and the tidal time series, the resultant correlation coefficients could not be assigned statistical significance, and therefore confidence limits are shown only for reference. These plots can be used to center periodicities in recruitment with respect to the hours of dark flood tide.

Cross-correlations were used to examine responses of recruiting larvae to wind and current patterns. Because wind and current data were collected inconsistently over the four winters, each year was analyzed separately. Significant autocorrelations present in both recruitment and environmental data meant that standard correlation coefficients would be artificially high (Chatfield, 1979). To remove the effects of these autocorrelations, ARIMA (Auto Regressive Integrated Moving Average) models were fitted to all data. Residuals generated from the ARIMA models were then used in the cross-correlations. Only those correlations that identified a response of larvae to particular wind and current patterns on a lag of up to three days (i.e. fish moving onshore up to three days after a specific wind or current pattern) are presented. Occasional correlations at lags of greater than three days were observed but are difficult to interpret in a biological sense and may be statistical artifacts.

Although the one set of summer data was not long enough to permit rigorous analysis for cyclical patterns, and the level of recruitment was generally too low for correlation with environmental conditions, the data were examined for resemblance to patterns identified by the time series and correlation analyses of the winter data sets.

Otolith analysis

Otoliths were removed from 150 of the 875 larvae collected throughout the 1993–94 winter season. All fishes collected during this winter were preserved in 70% ethanol. Specimens selected for analysis were chosen from each day when recruits were captured. However, preservation problems in some larger samples prevented a more detailed examination of the hatching patterns of large pulses of recruits.

Sagittae were dissected and mounted in cyanurate glue on a labelled glass slide. After curing for 24 hours, otoliths were polished down to the midplane with a graded series of lapping papers with grits ranging from 9 to 0.3 microns. A circle etched into the slide with an electronic engraver prevented the cyanurate glue from dislodging from the slide during polishing. Prepared slides were projected onto a computer screen at 1000× by using a Sony TR81 camera integrated through a Macintosh 2CI computer equipped with Media-Grabber. This greatly facilitated counting and allowed two readers independently to view the otolith(s) back-to-back under similar lighting conditions. Otoliths were randomized and each otolith was read twice by each reader; if the different readers obtained mean counts within five increments of each other, the mean values were averaged and used for analysis. The otolith was discarded if differences in mean counts were greater than five increments. A total of 87 of the 150 mounted otoliths met this readability criterion.

Results

Winter environmental conditions

Winds in Exuma Sound during the four winters generally blew from the east or southeast; there is a considerable cross-shelf component of motion across the shelf edge that runs northwest-southeast (Fig. 2). The predominant along-shore component of the wind was towards the northwest. Passage of occasional storm fronts or cold fronts with winds from the northeast was characterized by cross-shelf winds at velocities exceeding 5 $m \cdot sec^{-1}$ and by along-shore flow to the southeast.

Currents on the outer edge of the shelf flowed predominantly along the shelf toward the northwest with only a weak cross-shelf component of motion (Fig. 2). Flow onto the shelf, and occasional current reversals along the shelf to the southeast were typically associated with the passage of storm fronts (Shenker et al., 1993).

The hours of dark flood tide cycled throughout the study, ranging from 0 to 7 hours per night (Fig. 3). The nights with 0 hours of dark flood tide occurred when the full moon was visible during the entire night flood tide. During the week after each full moon, moonrise became progressively later each night, and the amount of flood tide occurring between sunset and moonrise increased rapidly.

Temporal patterns of recruitment during winter

A total of 3,079 *A. vulpes* leptocephali were collected during the 277 nights of sampling over four winters (Fig. 3). Recruitment levels varied greatly among years; a low of 316 leptocephali were taken the first winter and 1,421 during the third winter. Several large peaks in recruitment, reaching a maximum of 190 fish/night, were detected during the third and fourth winters. Over all four years, 90.2% of the leptocephali were captured by the nets fishing the upper 1 meter of the water column.

Periodogram analysis of *A. vulpes* recruitment indicated a very strong cycle with a period of 30.7 days, which suggests a lunar or tidally influenced cycle (Fig. 4). Autocorrelation of recruitment data (Fig. 4) also identified cycling centered around 30 days. Cross-correlations between recruitment and hours of dark flood tide (Fig. 4) showed a strong positive association on nights with a high degree of flood tide occurring during moonless portions of the night and a negative relationship centered around the full moon.

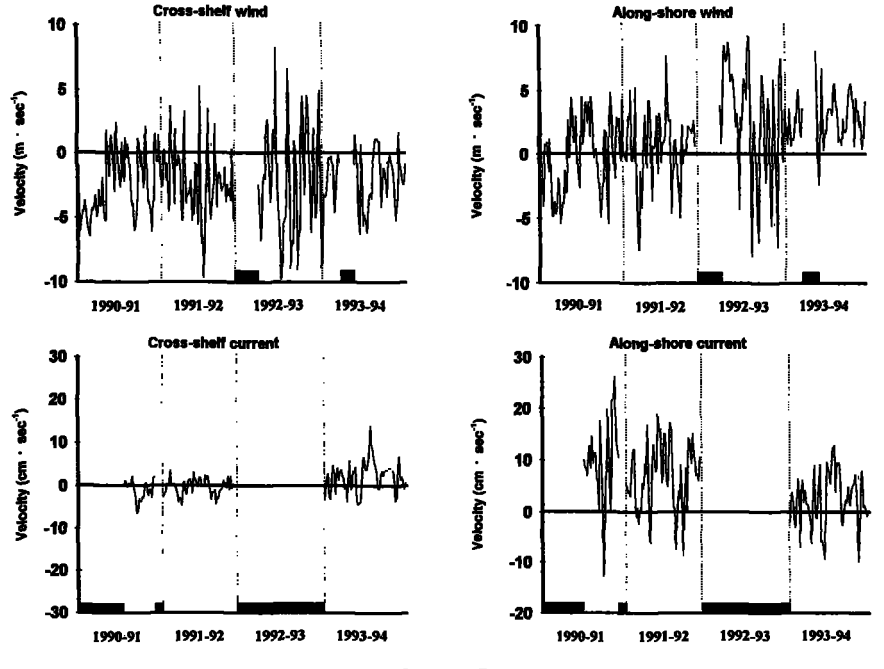

Figure 2

Cross-shelf (above line=movement offshore, below line=movement onshore) and along-shore (above line=to northwest, below line=to southeast) components of motion for wind and currents at Lee Stocking Island. Dotted vertical lines indicate where years are joined by lunar date. Solid bars on abscissae indicate when no data were available.

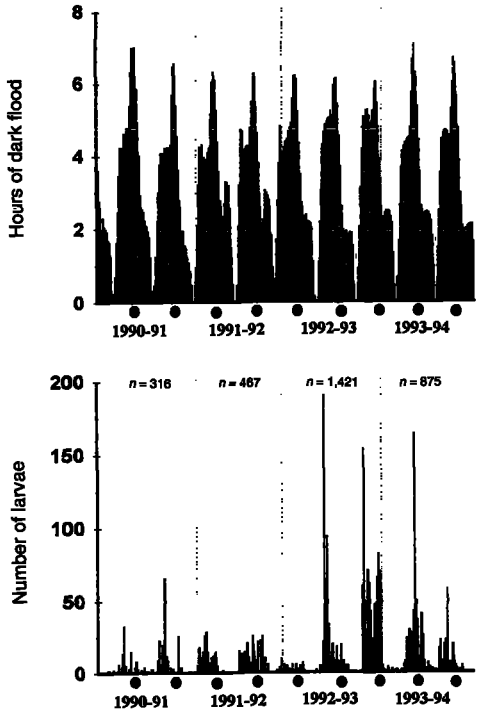

Figure 3

The total hours per night when the moon was below the horizon and the tide was flooding (hours of dark flood) throughout the four winter study periods (top graph). Dotted vertical lines indicate where years are joined by lunar date. Circles on abscissae indicate new moons. Total abundance of bonefish, *Albula vulpes*, larvae collected by channel nets during the four consecutive winters (bottom graph). Values above each year indicate total catch.

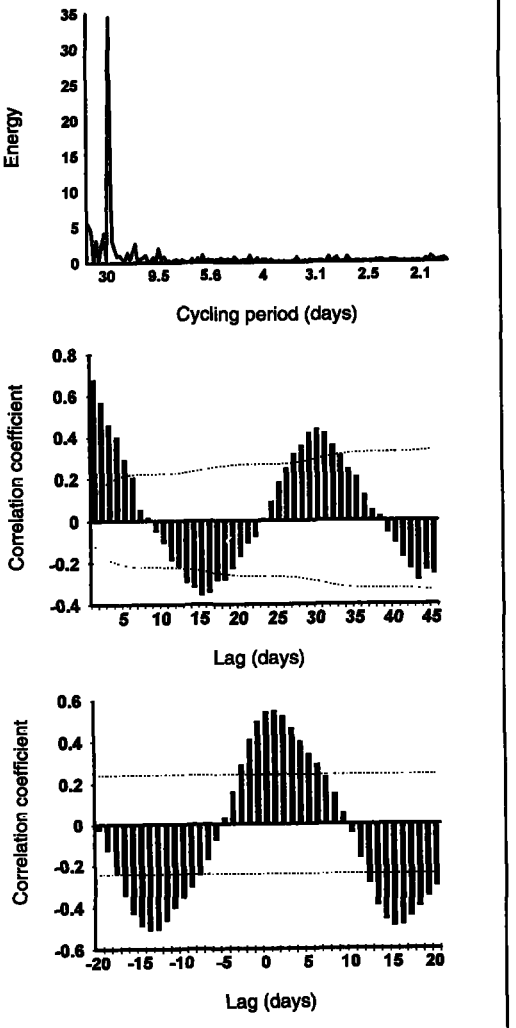

Figure 4

Periodogram plot of logged larval concentrations of bonefish, *Albula vulpes* (top graph), autocorrelation function of log (n+1) larval abundance (middle graph) and cross-correlation function of log (n+1) larval abundance with hours of dark flood tide (bottom graph). All analyses were conducted on the 277-day period which resulted from joining the four years of recruitment (and hours of dark flood) by lunar date. Dashed lines in autocorrelation and cross-correlation plots indicate approximate 95% confidence intervals. The cross-correlation plot coincides with lunar days starting with the new moon (lag of zero).

Few significant correlations between recruitment of bonefish and oceanographic or meteorological conditions were detected (Table 1). Recruitment was positively correlated with along-shore winds to the northwest with a lag of zero days for the 1991–92 season, whereas recruitment peaks the following winter lagged winds to the southeast by three days. No significant relationships between along-shore winds and recruitment were found during the other two winters, nor were relationships detected between recruitment and cross-shelf winds or either cross-shelf or along-shore currents.

Temporal patterns of recruitment during summer

A total of 1,112 *A. vulpes* leptocephali were collected during summer 1992. Over 76% of these fishes were taken during the first 12 days of the 72-day sampling season, and a peak of 160 leptocephali were taken during a single night (Fig. 5). Although this sampling period is too short for time-series analysis, recruitment appears to be limited to periods with relatively high amounts of flood tide occurring un-

der moonless conditions (Fig. 5). The single peak in recruitment was not associated with specific wind or current patterns (data not shown); the very low numbers of fishes collected during following months precluded use of correlation analysis to examine the relationship between recruitment and environmental conditions.

Larval ages and spawning patterns

Though the formation of daily otolith increments for *A. vulpes* has yet to be confirmed, the daily formation of increments in *Anguilla japonica* leptocephali has been verified (Umezawa et al., 1989). We thus assumed that increments are produced daily in bonefish and that deposition of increments begins at hatching. Given these assumptions, the average larval duration was 56 days, a range of 41–71 days (Fig. 6). Regression analysis of back-calculated hatching date and recruitment date revealed a strong relationship. Backcalculation of hatching dates from otolith data indicated continuous spawning from mid-October through early January (Fig. 6). The maximum number of otoliths examined per day was 7 for fish recruiting on 30 January. The back-calculated spawning dates of these fish ranged from 16 November to 27 December.

Table 1

Results of cross-correlation analyses between recruitment of *A. vulpes* and along-shore and cross-shelf wind and current vectors for four winters. The table shows all significant correlation coefficients between larval recruitment and wind and current data, with a lag corresponding to the number of days indicated. Positive correlations indicate signficiant relationships with transport to the northwest (along-shore component) or offshore (cross-shelf component). Numbers below years in parenthesis indicate the number of days used in each analysis. NS = not significant (α=0.05). ID = insufficient current meter data for analysis.

	Wind		Current	
Year	Along-shore	Cross-shelf	Along-shore	Cross-shelf
1990–1991 (72)	NS	NS	ID	ID
1991–1992 (62)	0.28/0 days	NS	NS	NS
1992–1993 (55)	–0.22/3 days	NS	ID	ID
1993–1994 (58)	NS	NS	NS	NS

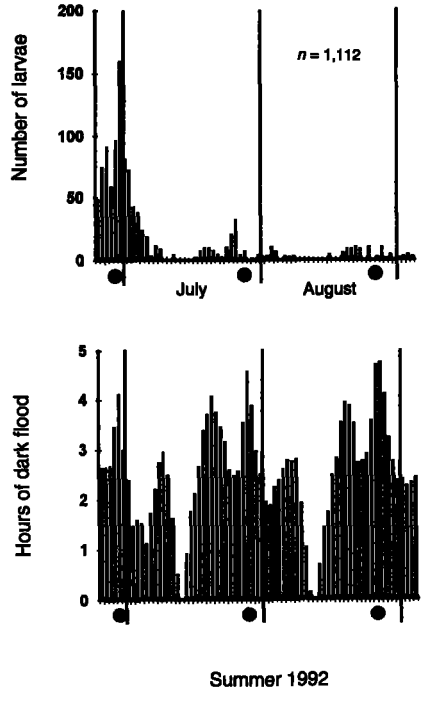

Figure 5

Abundance of bonefish, *Albula vulpes*, larvae collected each night from 24 June to 4 September 1992 (top graph) and hours of dark flood tide during the sampling period (bottom graph).

Discussion

Variation in the recruitment of tropical marine fishes is considered to be a dominant influence on the size and distribution of adult populations. Doherty and Fowler (1994) have shown that variations in the recruitment of a reef-dwelling territorial pomacentrid over a ten-year period could explain 90% of the variation in adult populations. Dramatic variability in larval recruitment has been detected by light trap surveys (e.g. Doherty, 1987; Milicich et al., 1992), visual surveys (e.g. Sale, 1980; Robertson et al., 1988; Robertson, 1992), and calculation of settlement patterns from otoliths (e.g. Thresher et al., 1989; Wellington and Victor, 1989). Recent work in the Bahamas (Shenker et al., 1993; Thorrold et al., 1994, a and b) and French Polynesia (Dufour and Gazlin, 1993) have shown that moored channel nets can be used to monitor onshore larval movement directly

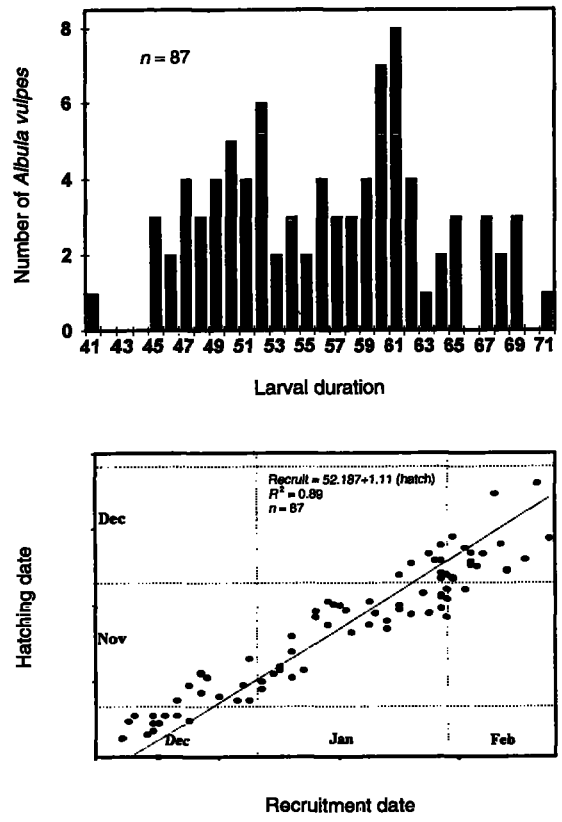

Figure 6

Frequency distribution of estimated larval duration (top graph) and relationship between estimated hatching date and recruitment date (bottom graph) of bonefish, *Albula vulpes*, collected during winter 1993–94.

through tidal passes and can help elucidate the patterns of recruitment and mechanisms driving transport. Although adult population sizes of highly mobile fishes such as *Albula vulpes* have yet to be measured, it is likely that whatever variation does occur in the abundance of adults is at least partially affected by recruitment variability.

A virtually universal pattern observed by studies on daily recruitment of tropical marine fishes is the association of peaks of recruitment with dark phases of the lunar cycle (Pfeiler, 1984; Robertson et al., 1988; Robertson, 1992; Dufour and Gazlin, 1993; Shenker et al., 1993; Thorrold et al., 1994, a and b). This pattern may be a function of a lunar spawning cycle, followed by a fixed larval duration. Alternatively, it may be an active response of fishes, enabling them to remain in the plankton until dark conditions permit them to move onshore, thus enabling them to avoid the "wall of mouths" of visual predators along reef edges (Hamner et al., 1988) and at settlement sites.

Our data suggest that *A. vulpes* follows the latter strategy. Analysis of larval otoliths of winter recruits (assuming that otolith increments are deposited daily, beginning at hatching) indicates that these fish spawn continuously from late October through December (Fig. 6). However, owing to preservation problems with some of the large recruitment pulses (>100 animals/night) in winter 1993–94, when otolith analyses were performed, we cannot exclude the possibility that the level of spawning activity varies over time. Significant spawning activity in the Bahamas probably extends until spring, with the large pulse of recruitment in late June 1992 presumably resulting from spawning in April and May.

After hatching, leptocephali remained in the pelagic environment of Exuma Sound for 41–71 days (with a mean of 56 d) in winter 1993–94. Despite this relatively broad range of larval duration, the metamorphosing larvae exhibited a very strong cyclical recruitment pattern (Fig. 4) that was not consistently related to meteorological conditions or currents measured along the shelf-edge seaward of the sampling stations (Table 1). This response supports the contention of Thorrold et al. (1994, a and b) that various species can actively control their onshore movements in certain environments, perhaps by delaying their metamorphosis until suitable environmental conditions or opportunities develop (Wellington and Victor, 1989). However, variable shrinkage of leptocephali, due to different times between capture, death in the nets, and preservation, prevented backcalculation of growth rates and a test of the ability of *A. vulpes* to delay metamorphosis.

In series of ichthyoplankton surveys from January through February 1991, *A. vulpes* leptocephali were found to be widely dispersed at night over a transect extending from the shelf edge near LSI to 24 km offshore (Drass, 1992), indicating that some larvae were always close enough to the shore so that they might become entrained in the flood tides crossing the narrow shelf. Despite the continuous presence of leptocephali close to the coast, however, their onshore movement was temporally restricted. The occurrence of favorable low nocturnal illumination levels may be the parameter that limits cross-shelf movement of larvae to specific "windows of opportunity." These windows of opportunity were defined by the relationship between lunar and tidal conditions. During bright, moonlit nights, recruitment levels were very low (Figs. 3 and 5); recruitment increased as larger amounts of night-time flood tide occurred prior to the progressively later moonrise. Extremely little recruitment occurred on nights when there were less than two hours of nocturnal flood tide under moonless conditions, whereas the

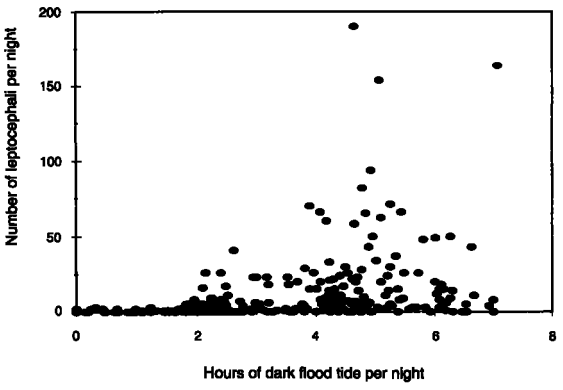

Figure 7

Number of bonefish, *Albula vulpes*, collected versus hours of flood tide occurring under moonless conditions. Most recruitment occurred on nights with >4 hours of flood tide under moonless conditions.

great majority of recruitment was observed on nights with more than four hours of dark flood tide (Fig. 7). The restriction of recruitment to these windows of opportunity may be responsible for the apparent bimodality in the age distribution of leptocephali (Fig. 6), although larger numbers of organisms need to be examined to test this possibility. Additional work is needed to determine whether onshore movement is concentrated in specific portion(s) of a flood tide and how cloud cover can affect lunar illumination and recruitment.

Active vertical migration may be the mechanism by which larvae influence the timing of onshore migration (Shenker et al., 1993). Early larvae were distributed through the pelagic environment of Exuma Sound to depths of 25–50 m (Drass, 1992). Migration of settlement-stage individuals toward the surface only under dark night conditions could enhance the entrainment of larvae into onshore tidal and wind-driven flow. The fact that over 90% of the *A. vulpes* larvae were taken by the channel nets in the upper 1 m of the water column during dark-night recruitment pulses, when only a relatively few larvae were found 2–4 m below the surface, indicates that these leptocephali do indeed selectively utilize the surface layer during their onshore movement.

The recruitment of *A. vulpes* leptocephali varied greatly among days, months, and years. This variability was generally not correlated with specific wind or shelf-edge current patterns (Table 1), unlike the very close association between a major settlement episode of Nassau grouper, *Epinephelus striatus*, and a storm event at LSI in February 1991 (Shenker et al., 1993). Recruitment of *A. vulpes* was thus more similar to that of other taxa recruiting near LSI (e.g. Bothidae and Labridae) that showed a lunar periodicity in recruitment but not a strong association with environmental parameters (Thorrold et al., 1994, a and b). The lack of strong correlation between environmental conditions and recruitment and the high degree of recruitment variability among months and years suggest that the processes controlling the supply of larvae are acting prior to their onshore movement in Exuma Sound. These processes span the range from spawning success to larval survival in the pelagic environment and will require additional sampling for evaluation of their potential roles as bottlenecks in the population of *A. vulpes* in the Bahamas.

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Distribution and life history of windowpane, *Scophthalmus aquosus*, off the northeastern United States

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Abstract.—The windowpane, *Scophthalmus aquosus*, is a shallow water (<110 m), resident species of the Middle Atlantic Bight (and adjacent estuaries) and Georges Bank, although it may undergo short (both inshore-offshore and alongshore) migrations in response to seasonal temperature changes. Spawning occurred throughout the Middle Atlantic Bight during the period from 1977 to 1987 but was most pronounced on Georges Bank. The timing of spawning, determined from the collection of 2–4 mm larvae, varied with location; and a split spawning season (April–May and October–November) was evident in the Middle Atlantic Bight. Spawning on Georges Bank peaked in August. Although spawning occurred over a broad temperature range (5–23°C), the optimal temperature was 16–19°C in the Middle Atlantic Bight and 13–16°C on Georges Bank. Larval development occurred in areas of spawning and was most prolonged on Georges Bank, where the largest larvae (13–20 mm) were consistently found. Few larvae >8 mm were captured in the Middle Atlantic Bight. On the basis of samples from southern New Jersey, settlement probably occurs on the continental shelf and in adjacent estuaries of the Middle Atlantic Bight. The growth patterns of young of the year varied with the timing of spawning and subsequent settlement. In the first six months, fish of the spring-spawned cohort grew to 11–19 cm TL whereas those of the fall-spawned cohort grew to just 4–8 cm TL within that time. These data contribute to our understanding of the distribution and early life history of windowpane on the continental shelf, though the role of estuaries in the Middle Atlantic Bight is incompletely known.

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Fishery Bulletin 93:675–693 (1995).

The windowpane, *Scophthalmus aquosus*, is an endemic bothid of the northwest Atlantic Ocean and is distributed from the Gulf of Saint Lawrence (47°N) to Florida (27°N) (Scott and Scott, 1988) but is most abundant from Georges Bank (42°N) to Chesapeake Bay (38°N) (Bigelow and Schroeder, 1953; Dery and Livingstone, 1982). Windowpane are distributed in shallow waters (<110 m, mostly <56 m) (Wenner and Sedberry, 1989; Thorpe, 1991). Their distribution extends shoreward to depths of 1–2 m (Warfel and Merriman, 1944) and they are often abundant in large estuaries such as Chesapeake Bay (Hildebrand and Schroeder, 1928), Delaware Bay (de Sylva et al., 1962), Sandy Hook Bay (Wilk and Silverman, 1976), Long Island Sound (Moore, 1947), and Narragansett Bay (Oviatt and Nixon, 1973; Jeffries and Johnson, 1973). Distribution patterns of juveniles and adults on the continental shelf between Nova Scotia and Cape Hatteras, North Carolina, are similar and indicate limited seasonal movement (Dery and Livingstone, 1982; Azarovitz and Grosslein, 1987; Thorpe, 1991). However, tagging experiments showed that some adults traveled about 150 km along the coast in three months (Moore, 1947). Juveniles (<24 cm total length [TL]) in the Georges Bank area were concentrated along the southern boundary of the bank and inshore along Long Island during spring (mean depth 26.6 m) and on the central portion of the bank in fall (mean depth 38.3 m) (Wigley and Gabriel, 1991). Recent estimates of length at sexual maturity show that 50% were mature between 21 and 23 cm TL (O'Brien et al., 1993).

Windowpane are currently exploited for human consumption, primarily in the Georges Bank area. Annual commercial landings from 1975 through 1988 averaged 2.03 million kg and peaked in 1985 at 4.21 million kg (ICNAF, 1977–85; NAFO, 1982–91). Relative abundance indices estimated from National Marine Fisheries Service (NMFS) research trawl surveys (Azarovitz, 1981) for 1964–89 show considerable year-to-year fluctuations in both numbers and biomass (Thorpe, 1991). Peaks in biomass appear to have occurred on Georges Bank during the mid-to-late-1970's and again in the mid-1980's.

Gonadal development (Wilk et al., 1990) and egg and larval distribu-

tions (Colton and St. Onge, 1974; Smith et al., 1975; Colton et al., 1979; Morse et al., 1987), show that spawning occurs from April through December. There is contradictory evidence for a split spawning season. Gonadal development (Wilk et al., 1990) indicated that spawning off New Jersey and New York peaks in May and again in September. Split spawning was reported to occur off Virginia and North Carolina (Smith et al., 1975) for Long Island Sound (Wheatland, 1956) and for Great South Bay, New York (Dugay et al., 1989; Monteleone, 1992). However, other studies found no evidence for a split spawning season in either Long Island Sound (Perlmutter, 1939) or in ocean waters north of Virginia (Smith et al., 1975). In addition, Colton and St. Onge (1974) collected larvae on Georges Bank from July to November and found no indication of a split spawning season. Spawning apparently occurs at bottom water temperatures of 6–20°C (Bigelow and Schroeder, 1953; Wheatland, 1956; Smith et al., 1975). Most spawning (70%) off Virginia and North Carolina was found over bottom temperatures between 8.5 and 13.5°C; spawning stopped when temperatures exceeded 15°C (Smith et al., 1975).

This study presents analyses of the reproductive seasonality of windowpane based on seasonal shifts in larval abundance and on their relationships to bottom water temperatures. Bottom trawl catches and published accounts of distribution and abundances are used to follow the fate of the young flatfish after they settle to the bottom. Together these data describe the seasonal distribution, abundance, and life history of windowpane in the Middle Atlantic Bight and on Georges Bank.

Materials and methods

Larvae

Data from a variety of sources have been analyzed (Table 1). Larval windowpane were collected from continental shelf waters from Cape Hatteras, North Carolina, to Nova Scotia during NMFS Marine Resources Monitoring, Assessment, and Prediction (MARMAP) surveys from 1977 to 1987 (Sherman, 1980). Surveys were conducted six to eight times each year and occupied 150–180 stations (Fig. 1). At each station, a 61-cm bongo net array was lowered to within 5 m of the bottom or to a maximum depth of 200 m. Fish larvae from a 0.505-mm mesh net were identified to the lowest taxon possible, enumerated, measured (±0.1 mm) and rounded to the nearest whole millimeter as either notochord or standard length. Catches were standardized to the number of larvae under 100 m^2 of sea surface on the basis of the depth of the tow and the volume of water filtered (Sibunka and Silverman, 1984, 1989). An additional

Table 1

Sources of data on windowpane, *Scophthalmus aquosus*, that were analyzed for this study. See Figures 1 and 2 for location of sampling areas.

Source	Life stage	Location	Collecting gear	Sampling years	Sampling depths (m)	Number of samples	Number of fish collected
NMFS, MARMAP (Sherman, 1980)	Larvae	Nova Scotia–Cape Hatteras	Bongo nets	1977–1987	8–1,500	8,787	14,177
NMFS, Groundfish (Azarovitz, 1981)	Juveniles and adults	Nova Scotia–Cape Hatteras	Bottom trawl	1982–1990	5–366	7,099	26,433
Massachusetts Trawl Survey (Howe et al., 1979)	Juveniles and adults	Coastal Massachusetts	Bottom trawl	1982–1990	4–82	1,688	21,272
Milstein and Thomas, 1977	Eggs, larvae, juveniles, and adults	Great Bay, Mullica River, Beach Haven Ridge, NJ	Beach seines, Plankton nets, Bottom trawls	1972–1975	Seines: < 2 Plankton: 1.5–19.5 Trawls: 1–45	Seines: 1,524 Plankton: 166 Trawls: 717	127 801 5,309
New Jersey Trawl Survey[1]	Juveniles and adults	Coastal New Jersey	Bottom trawl	1988–1992	5–27	603	25,580

See Footnotes 3 and 4 in the text.

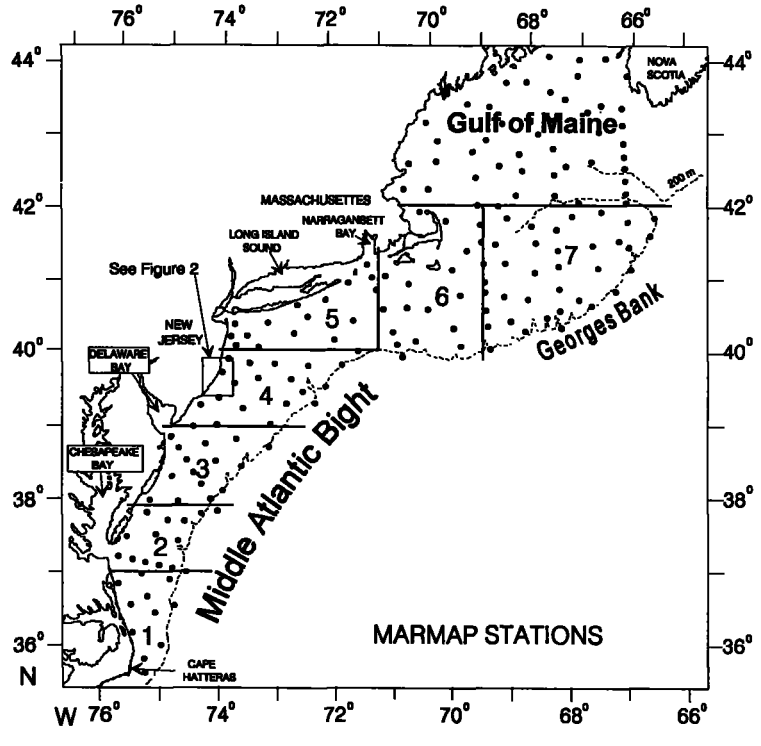

Figure 1

Sampling area for planktonic larvae in the northeastern United States, based on NMFS/MARMAP sampling stations, and important localities that are mentioned in the text. Typical sampling array of stations shown by dots. See Table 1 for further details. Middle Atlantic Bight = subareas 1–6, Georges Bank = subarea 7.

length-dependent correction was made to the catches to account for differences in day, night, and twilight catchability (Morse, 1989). Preliminary analysis of larval occurrence and bottom depth revealed that larvae are restricted to waters ≤100 m deep; therefore, only stations ≤100 m deep were used for calculating larval catch statistics. In addition, larvae were extremely rare north of 42°N (caught at only 24 of 2,470 stations); therefore, this area was not considered in the analysis. Mean catches of windowpane larvae were calculated by using the Delta method of Pennington (1983). Graphical plots of the distribution and abundance of larvae are presented as the average catch per 100 m^2 within 625 km^2 blocks of the survey area. Eggs and larvae were sampled at estuarine and inner continental shelf sites during 1972–75 (Table 1; Fig. 2). These sites included the Mullica River (water depth 1.8–10.6 m), Great Bay (1.5–10.7 m), Little Egg Inlet (4.6–8.8 m), in the vicinity of sand ridges outside Little Egg Inlet (3.0–16.5 m), and farther offshore of the sand ridge sites (16.2–23.5 m). At continental shelf sites, 15-minute tows were made at the surface (1.0-m plankton net, 0.5-mm mesh), at midwater and bottom depths (0.5-m plankton net, 0.5-mm mesh), and as oblique tows (bongo samplers, 0.2-m or 0.36-m diameter, 0.5-mm mesh). In the estuary tow times were reduced to 5–10 minutes but the same three nets were used at the same depths. Estimates of water volume filtered were determined with a flowmeter.

Juveniles and adults

Juvenile and adult windowpane (2–48 cm TL) were collected during the semiannual bottom trawl surveys of NMFS, Northeast Fisheries Science Center, from 1982 to 1991 (Azarovitz, 1981), during inshore surveys of the Commonwealth of Massachusetts Division of Marine Fisheries from 1988 to 1992 (Howe et al.[1]), and during the New Jersey Bureau of Marine Fisheries surveys from 1988 to 1992 (Byrne[2,3]). All three surveys used a stratified random-sampling design, and strata were based on depth and latitude. NMFS spring and fall surveys sampled about 350 stations during a 6–8 week period from Cape Fear, North Carolina, to Nova Scotia in depths from 3 to 366 m. Commonwealth of Massachusetts Division of Marine Fisheries sampled approximately 80–90 stations within 55-m depths in state coastal waters during May and September. New Jersey Bureau of Marine Fisheries sampled 25–39 stations in state coastal waters within 27 m of water every 6–10 weeks.

For the analysis of NMFS bottom trawl and plankton surveys, the sampling area was divided into seven subareas (Fig.1). Data from monthly collections of larval, juvenile, and adult windowpane near Little Egg Inlet, New Jersey, during 1973–74 (Fig. 2) were

[1] Howe, A. B., D. MacIsaac, B. T. Estrella, and F. J. Germano Jr. 1979. Fishery resource assessment, coastal Massachusetts. Completion Rep., Massachusetts Div. Mar. Fish., Commercial Fish. Res. Div. Project No. 3-287-R-1, 34 p.

[2] Byrne, D. M. 1988. Inventory of New Jersey's coastal waters. New Jersey Dep. Environmental Protection, Div. Fish, Game, Wildl. Mar. Fish. Admin., Bur. Mar. Fish. Annual Rep. to U.S. Fish. Wildl. Serv.

[3] Byrne, D. M. 1990. Inventory of New Jersey's coastal waters. NJDEP, Div. Fish., Game, Wildl., Mar. Fish. Admin., Bur. Mar. Fish. Annual Rep. to U.S. Fish. Wildl. Serv.

summarized from Thomas et al.,[4] Thomas et al.,[5] and Milstein and Thomas (1977).

Results

Spawning season and location

We assumed that the temporal and spatial patterns of the distribution and abundance of the smallest larvae (2–4 mm) indicated the timing and the areas of spawning on the continental shelf (Fig. 3). Larvae were distributed from nearshore to mid-shelf in subareas 1–6 and over the shallower portion of subarea 7. The highest average concentrations of small larvae occurred in subarea 7, especially in the central portion. Larvae 2–4 mm long were first captured in April in subareas 1–3 and by May they were in all subareas (Table 2). Catches in subareas 1–4 clearly showed a split spawning season (Fig. 4), and similar, though less pronounced, patterns were evident in subareas 5 and 6. A peak in abundance of small larvae occurred in May and a larger peak occurred in November in subareas 1–4. Subareas 4–5 showed light spawning during spring and a significant peak in October. In subarea 6, split spawning was less discernible; only a slight peak in abundance of small larvae occurred in June, but major spawning was indicated in October. There was unimodal spawning, with the peak abundance in August, in subarea 7. Fall catches of small larvae in subareas 1–6 are often 5–20 times higher than peak catches earlier in the year.

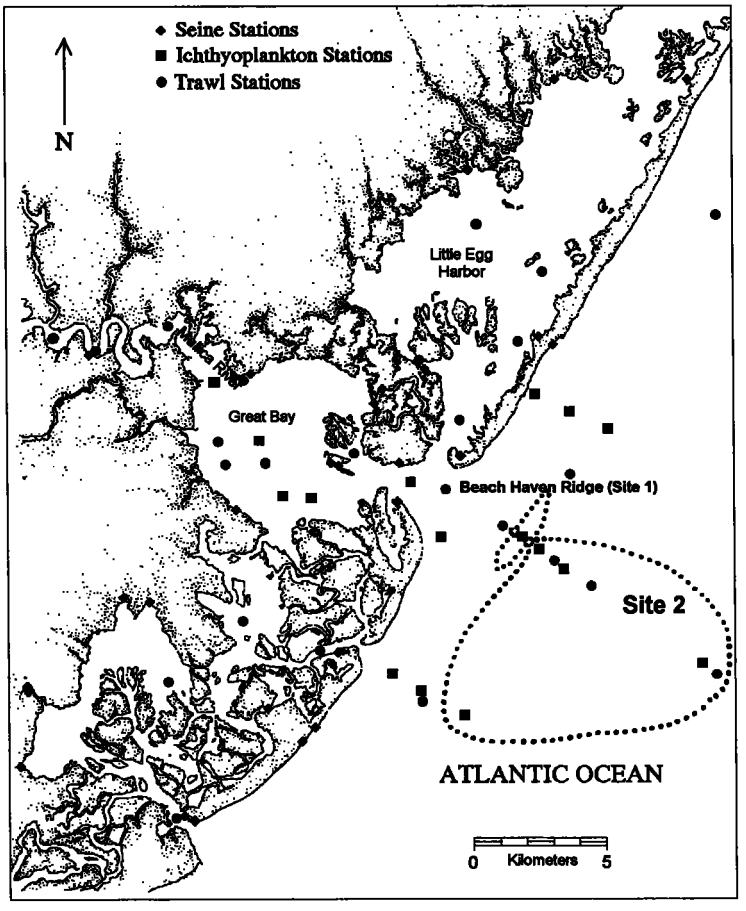

Figure 2

Sampling locations for seine, trawl, and ichthyoplankton samples in southern New Jersey habitats in the vicinity of Great Bay during 1970–74 based on Milstein and Thomas (1977). Site 2 includes all stations offshore of site 1. See Figure 1 for general location of sampling area.

The monthly progression of the peak catches of 2–4 mm larvae from the southern extreme of the study area in May to subarea 7 in July–September and the return of peak catches to subareas 1–3 in November indicate that water temperature may be controlling spawning times and areas (Fig. 4). Windowpane probably spawn on or near the bottom; therefore bottom water temperatures were used to indicate spawning temperatures. Only stations with bottom depths ≤100 m are presented. The maximum abundance of 2–4 mm larvae occurred at temperatures 15–19°C in subareas 1–6 and at 14–15°C in subarea 7 (Fig. 5). The range of bottom temperatures where larvae were caught was 5–23°C. The broadest range of temperatures for 2–4 mm larvae was in subarea 5. Maximum temperature of occurrence was highest in subarea 1 at 23°C and gradually decreased

[4] Thomas, D. L., C. B. Milstein, T. R. Tatham, R. C. Bieder, F. J. Margraf, D. J. Danila, H. K. Hoff, E. A. Illjes, M. M. McCullough, and F. A. Swiecicki. 1974. Ecological studies in the bays and other waterways near Little Egg Inlet and in the ocean in the vicinity of the site for the Atlantic generating station, New Jersey. Progress Rep. for the period January–December 1973. Vol. 1: Fishes. Ichthyological Associates, Inc., 709 p.

[5] Thomas, D. L., C. B. Milstein, T. R. Tatham, R. C. Bieder, D. J. Danila, H. K. Hoff, D. P. Swiecicki, R. P. Smith. G. J. Miller, J. J. Gift, and M. C. Wyllie. 1975. Ecological studies in the bays and other waterways near Little Egg Inlet and in the ocean in the vicinity of the site for the Atlantic generating station, New Jersey. Progress Rep. for the period January–December 1974. Vol. I: Fishes. Ichthyological Associates, Inc., 490 p.

northward to 16°C in subarea 7. Minimum temperatures ranged from 5 to 9°C, but no clear latitudinal trend was evident. Over 80% of all larvae 2–4 mm long throughout the study area were collected over bottom temperatures 16–19°C, which indicate preferred spawning temperatures. Only in subareas 5 and 7 were larvae captured in significant numbers at temperatures below 15°C. Over 85% of larvae in subarea 7 occurred at temperatures 13–16°C, and 16°C was also the maximum bottom temperature recorded in subarea 7.

Although the preferred spawning temperature range (16–19°C) spans just 4°C, the total range of temperatures (5–23°C) indicates that spawning may not be tied exclusively to water temperatures. In subareas 1–3, bottom waters in the preferred range of temperature (16–19°C) are available most months (Fig. 6). However, even though spawning in these subareas is bimodal (see Fig. 4), the peak in spawning clearly occurs at 17°C (see Fig. 5). In subarea 7, spawning occurs at the highest bottom temperatures recorded (13–16°C) in this subarea (Fig. 6). These temperatures are available from July through November (Fig. 6), a range that nearly corresponds to the months of maximum spawning (Table 2; Fig. 4). Thus, in subarea 7 the occurrence of the highest tempera-

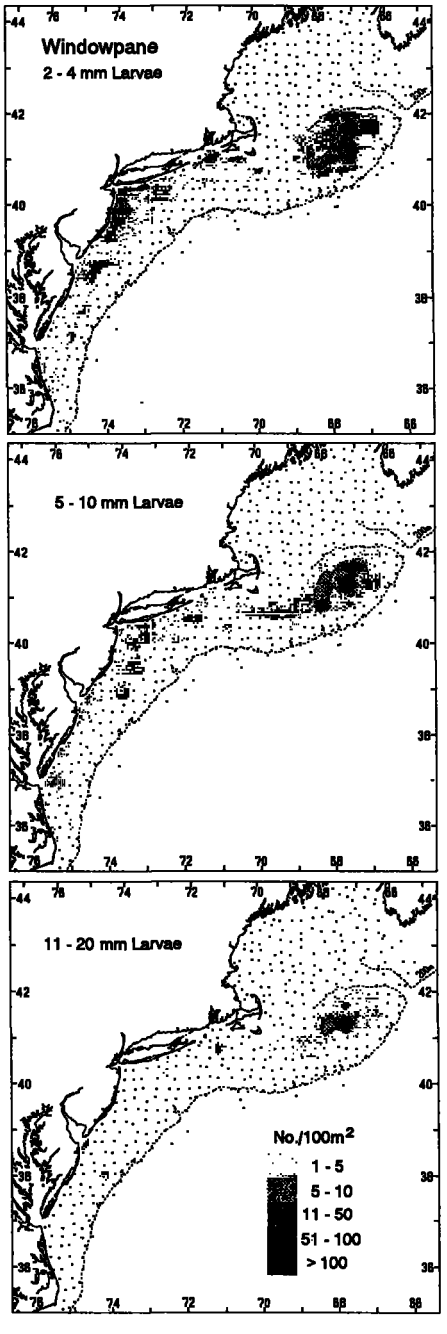

Figure 3

Distribution and abundance of windowpane, *Scophthalmus aquosus*, larvae for three size classes, based on NMFS/MARMAP sample collections. See Table 1 for additional details.

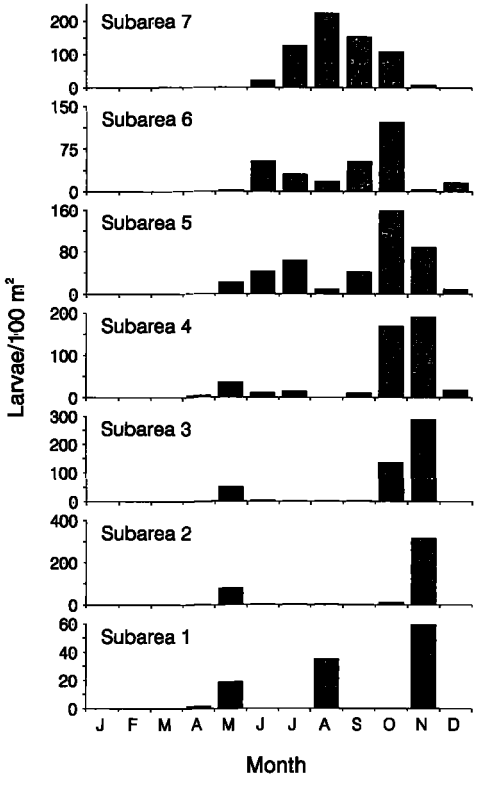

Figure 4

Monthly abundance 2–4 mm windowpane, *Scophthalmus aquosus*, larvae by subarea, based on NMFS/MARMAP sampling.

Table 2

Abundance (mean number/100 m^2) of windowpane, *Scophthalmus aquosus*, larvae by subarea and length (mm) from MARMAP surveys off northeastern United States during 1977–87. N_t = total number of stations sampled; N_0 = number of stations with windowpane; Mn = mean number/100 m^2 for 2–20 mm larvae; and SE = standard error of Mn.

	January							February						
	Subareas							Subareas						
Length (mm)	1	2	3	4	5	6	7	1	2	3	4	5	6	7
2														
3														
4														
5														
6	1.22		1.65		2.42									
7			1.53											
8														
9	0.90	4.82												
10														
11														
12														
13												0.84		
14														
15														
16														
17														
18														
19														
20														
N_t	30	18	24	25	60	52	65	60	41	52	45	39	41	87
N_0	2	1	2	0	1	0	0	0	0	0	0	1	0	0
Mn	1.20	2.68	1.99		1.61							1.03		
SE	0.85	2.68	1.38		1.61							1.03		

	March							April						
	Subareas							Subareas						
Length (mm)	1	2	3	4	5	6	7	1	2	3	4	5	6	7
2										1.05				
3								0.66	0.51	1.56				
4														
5														
6														
7														
8														
9														
10														
11														
12	0.30													
13														
14														
15					0.56									
16														
17														
18														
19														
20														
N_t	121	99	111	102	145	115	89	77	50	80	107	169	112	187
N_0	1	0	0	0	1	0	0	2	1	2	0	0	0	0
Mn	0.28				0.72			0.53	0.59	2.81				
SE	0.28				0.72			0.37	0.59	2.21				

Table 2 (continued)

Length (mm)	May Subareas 1	2	3	4	5	6	7	June Subareas 1	2	3	4	5	6	7
2	1.92	9.08	3.14	7.86	10.98		0.22				4.17	6.11	12.55	5.72
3	11.86	28.37	21.29	14.67	5.28	3.21		0.71		0.46	5.16	19.89	6.81	6.42
4	11.24	11.75	7.14	2.75	1.70			0.74	3.12	1.19	5.75	9.61		4.23
5	4.97	6.03	2.60	1.00	0.63				3.49		3.12	3.14		1.68
6	2.03	1.73	0.78							1.12	1.07	2.36		0.75
7	0.77	1.06	1.07				0.37		1.14	0.86	0.29	0.36		
8		0.92	0.47								0.25			
9										1.63				
10			0.45											
11														
12		0.21												
13														
14														
15							0.21							
16														
17														
18	0.35													
19														
20														
N_t	130	86	112	111	167	121	171	65	48	66	73	93	75	81
N_0	38	28	38	18	22	1	2	1	3	6	16	34	3	8
Mn	48.44	120.31	61.70	22.68	14.44	1.43	0.9	2.54	11.77	7.56	26.32	73.41	25.35	23.87
SE	11.75	35.83	13.19	7.84	4.17	1.43	0.6	2.54	7.65	3.33	9.30	15.62	18.47	12.26

Length (mm)	July Subareas 1	2	3	4	5	6	7	August Subareas 1	2	3	4	5	6	7
2	1.25	0.24	0.57	6.01	0.98	1.99		6.57	0.51			2.29	4.95	10.73
3	1.34		1.77	4.78	12.08	4.23	15.78	5.06	1.57			2.29	3.54	43.10
4		0.47		2.82	8.82	1.95	17.74	1.15	0.66		0.27	0.78	3.44	27.05
5			0.51	2.78	6.44	1.03	21.00	0.18			0.85		0.65	15.49
6				1.83	2.29	3.15	13.79					0.52	3.36	10.08
7				0.95	1.70	0.41	13.58	0.30				0.44	0.45	9.28
8					0.92	1.25	9.62					0.34	1.74	8.05
9					0.64	0.41	4.03						1.50	5.66
10					0.07		9.25							3.49
11							3.89						1.27	2.71
12							2.22						0.31	2.23
13					0.20		0.88							0.43
14				0.21			0.88					0.12		0.48
15							0.67							0.46
16							0.47							0.12
17						0.41								0.33
18														0.21
19														
20														0.24
N_t	70	53	93	112	172	106	130	113	90	104	100	148	114	184
N_0	2	2	5	25	58	14	49	4	4	0	2	19	15	88
Mn	2.67	2.15	4.73	31.08	105.97	25.38	370.70	15.37	4.46		1.96	12.62	33.67	402.90
SE	2.07	1.52	2.23	7.49	18.68	7.61	85. 96	12.42	2.47		1.56	3.25	12.61	69.39

Table 2 (continued)

Length (mm)	September Subareas 1	2	3	4	5	6	7	October Subareas 1	2	3	4	5	6	7
2		0.92	2.62	0.37	5.02	4.79	14.36		2.78	7.42	23.15	16.83	7.26	3.05
3	0.39		3.16	0.86	12.67	34.27	22.09		3.22	27.73	40.14	36.13	21.79	15.46
4			1.89	0.53	12.97	5.50	13.86	1.55	3.50	13.93	17.11	10.47	11.05	13.79
5					4.83	2.69	15.01			8.92	2.60	2.89	5.15	12.85
6		0.48			0.70		11.81			2.74	2.49	2.02	3.57	8.02
7					2.53		9.32			1.17	1.04	0.48	1.48	7.02
8							6.89				1.30	0.26	0.36	3.79
9							5.17					0.86	0.80	2.24
10						1.14	7.94						0.20	1.73
11							3.69							2.78
12							11.18							1.20
13		0.50					0.79							0.41
14	0.56						0.20							0.28
15							0.98							
16							0.23							
17							0.41							
18							0.44							0.08
19							0.84							0.18
20														
N_t	89	70	85	55	78	58	66	38	23	39	86	144	144	207
N_0	3	3	10	3	15	12	39	1	5	9	27	70	43	93
Mn	0.89	2.11	13.14	2.58	64.64	46.80	396.08	1.14	19.13	147.66	211.80	198.13	129.16	258.85
SE	0.56	1.26	4.83	1.79	28.72	18.85	93.03	1.14	10.28	94.39	85.34	39.61	29.41	39.61

Length (mm)	November Subareas 1	2	3	4	5	6	7	December Subareas 1	2	3	4	5	6	7
2	14.79	27.50	35.64	4.83	4.25						3.74	2.68		
3	43.69	68.11	70.02	36.63	24.93		1.20				7.83	9.47	1.95	
4	26.22	29.84	41.32	11.90	13.18	1.32	6.11					4.89	1.83	
5	10.01	9.87	17.29	5.07	6.77	1.57	2.50					4.37		
6	7.11	2.48	12.07	4.65	2.03		4.89			2.20		3.79		
7	1.74	0.20	7.87	0.68	0.62	2.36	6.89			2.52	2.96	1.95		
8	0.63	0.88	0.88	0.77			3.45					3.48		
9			0.48				1.58			4.75			1.60	
10			0.21	0.45								1.24		
11						1.59								
12														
13														
14														
15			0.49											
16														
17										1.61				
18												0.52		
19												0.64		
20														
N_t	87	55	76	68	89	86	118	0	6	12	17	67	66	86
N_0	31	14	24	29	39	5	22		0	2	1	18	3	0
Mn	210.47	364.35	247.31	116.86	80.4	3.63	28.05			27.7	27.35	58.6	3.92	
SE	90.79	196.19	109.43	37.2	18.16	1.64	7.13			20.54	27.35	17.36	2.23	

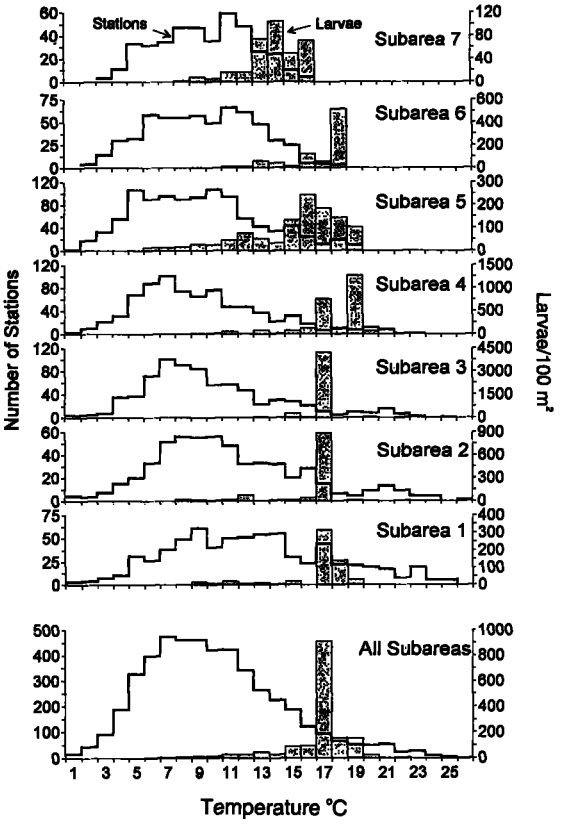

Figure 5

Abundance of 2–4 mm windowpane, *Scophthalmus aquosus*, larvae by subarea relative to bottom water temperature during 1977–87.

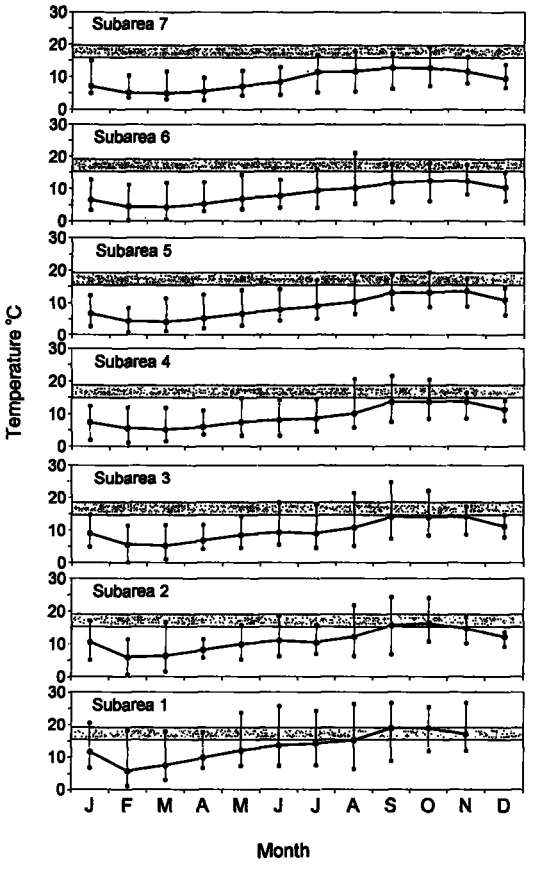

Figure 6

Monthly temperature means and ranges by subarea of the continental shelf of the northeastern U.S. during 1977–87. Shaded bar is the preferred spawning temperatures (16–19°C) for windowpane, *Scophthalmus aquosus*.

tures, which approaches the preferred temperatures, suggests that spawning here may be triggered by the highest temperatures available. Subareas 4 and 5 are intermediate, with preferred temperatures available from July to November (Fig. 6); yet spawning occurs from May to December (Table 2; Fig. 4). Peak spawning occurs in October, a full three months later than the first record of preferred spawning temperatures.

Larval distribution and abundance

Larvae were captured every month on the continental shelf (Table 2). January–April catches were very low in subareas 1–3 and 5 and were totally absent elsewhere. Larvae were caught in all subareas in May and were most abundant in subarea 2. By June, larval abundances were highest in subarea 4, and from July to October subarea 7 had the highest larval catches. Throughout August and September, abundances in subareas 5 and 6 were intermediate, and catches in subareas 1–4 remained very low. By October, catches of larvae decreased somewhat in subarea 7 and increased in all other subareas. November catches showed a continued decline in subarea 7 and began to decrease in subareas 4–6. Catches increased to their highest levels in subareas 1 and 2, whereas subarea 3 catches remained at October levels. In December, no larvae were captured in subarea 7, a few large larvae occurred in subarea 3, and only moderate catches were made in subareas 4–6. The nearly total absence of larvae in subareas 1–4 during December is attributed to the low number of stations sampled and not necessarily to the disappearance of larvae within this area.

The size of larvae captured on the continental shelf varies between subareas (Table 2). Few larvae >8 mm were captured in subareas 1–4; only 18 of 3,282 sta-

tions contained these larvae. In subareas 5 and 6, 27 of 2,461 stations had larvae >8 mm long. Larvae >13 mm were captured in only 10 of 5,743 stations in subareas 1–6. In contrast, in subarea 7, 89 of 1,473 stations had >8 mm larvae and 31 stations had >13 mm larvae. In an attempt to interpret the trend of increasing maximum lengths from south to north, the abundances at length and mortality estimates for larvae ≤20 mm, grouped by subarea, were calculated (Table 3). The maximum larval length of catches >0.1/100m^2 and mortality for each subarea is shown in Figure 7. If avoidance of the sampling gear occurs because of settlement within a narrow size interval (e.g. 1–3 mm), then the catches should show a precipitous decrease in abundance at settlement. No such abrupt decrease can be seen in the data (see Tables 2 and 3); thus the declines in abundance with size are due to other causes. Alternatively, if we assume that decreases in larval abundance are due to mortality, then the percentage of mortality per mm of growth is highest in subarea 1 (63%), intermediate in subareas 2–5 (range 48–56%), declines to 38% in subarea 6, and is lowest in subarea 7 (30%). Estimated mortalities are inversely related to the maximum lengths of captured fish and decrease from south to north along the coast (Fig. 7). The relatively high mortality indicated for larvae in subareas 1–5 could explain the truncated larval length frequencies seen there, particularly during the months of July–October (Table 2).

Larger larvae in the Middle Atlantic Bight subareas may move into or are more abundant in shallow nearshore areas of the continental shelf and estuaries and thus may not be available to the collecting gear. Typically, NMFS/MARMAP sampling is not undertaken in estuaries and is limited to depths >10 m on the continental shelf. During the MARMAP study, approximately 13% of all tows were taken in depths ≤20 m, whereas only 0.3% were taken in water depths <10 m. In the vicinity of Little Egg Inlet, New Jersey, larvae were abundant on the inner continental shelf and in the estuary (Fig. 8). Eggs and larvae were least abundant in the Mullica River, more abundant farther down the estuary in Great Bay and at Little Egg Inlet, and most abundant on the adjacent portion of the inner continental shelf (Fig. 8). Eggs and larvae were abundant in the estuary during spring, but both were most abundant on the continental shelf during the fall.

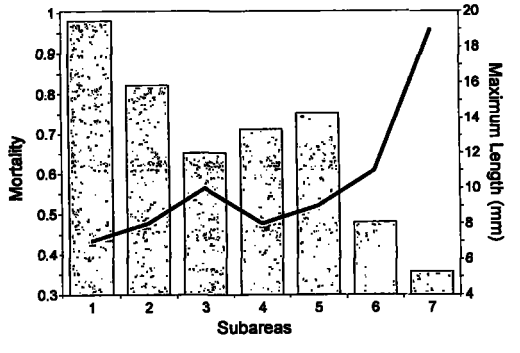

Figure 7

Length-dependent mortality rates and the maximum larval lengths of catches >0.1/100 m^2 by subarea from NMFS MARMAP sampling of windowpane, *Scophthalmus aquosus*, off the northeast United States.

Juvenile and adult distribution and abundance

Windowpane are distributed over much of the continental shelf, as well as in estuaries in the Middle Atlantic Bight. Large juvenile and adult windowpane (>10 cm TL) were collected from the western portion of the Gulf of Maine to Cape Hatteras, North Carolina (Figs. 9, 10), in depths from 5 to 207 m. In the Gulf of Maine, there were few fish of this size collected from coastal Maine, but they were more abundant off the coast of Massachusetts, subarea 6 (Fig.

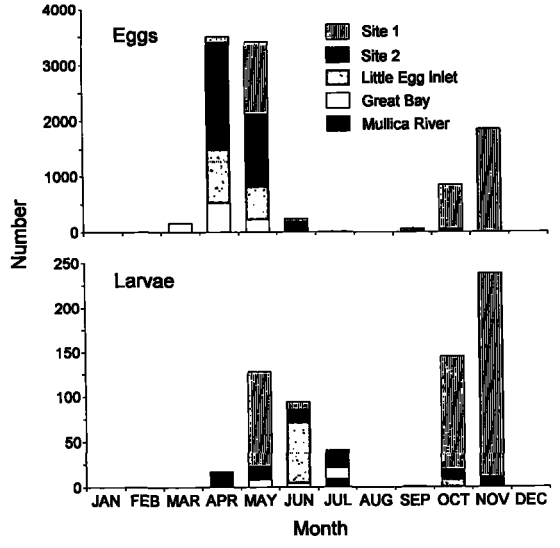

Figure 8

Monthly patterns of distribution and abundance of windowpane, *Scophthalmus aquosus*, eggs and larvae from the vicinity of Little Egg Inlet, New Jersey, during 1972–75, as modified from Milstein and Thomas (1977). See Figure 2 for sampling locations.

Table 3

Mean number (Mn) of windowpane, *Scophthalmus aquosus*, larvae (number/100 m^2) by length (in mm) for seven subareas off northeastern United States, 1977–87. N = Total number of stations sampled in each subarea. An exponential equation, $Mn = a \times \exp(-bL)$, was fit to the data. N_0 = number of stations with windowpane larvae; SE = standard error of the mean; $M(\%)$ = estimated mortality as $\%^{-mm}$ (i.e. $100(1-\exp(-b))$; SEE = standard error of the estimate; and I_L = length interval fit to the equation.

Length (mm)	Subarea 1			Subarea 2			Subarea 3			Subarea 4		
	N_0	Mn	SE	N_0	Mn	SE	N_0	Mn	SE	N_0	Mn	SE
2	23	2.71	0.87	28	4.81	1.44	34	4.49	1.31	40	4.83	1.17
3	48	7.39	1.84	34	12.18	3.67	69	11.94	2.55	77	11.30	2.10
4	37	4.82	1.15	35	5.70	1.33	44	6.15	1.49	46	4.43	0.96
5	26	1.92	0.51	20	2.44	0.73	22	3.03	0.91	36	1.83	0.34
6	14	1.17	0.38	13	0.65	0.20	20	1.75	0.55	17	1.22	0.35
7	7	0.37	0.15	5	0.29	0.16	14	1.24	0.43	8	0.39	0.16
8	1	0.08	0.08	3	0.27	0.16	5	0.23	0.11	7	0.36	0.15
9	1	0.02	0.02	1	0.09	0.09	2	0.17	0.13			
10	—	—	—	—	—	—	4	0.19	0.10	2	0.04	0.03
11	—	—	—	—	—	—	—	—	—	—	—	—
12	1	0.05	0.05	1	0.04	0.04	—	—	—	—	—	—
13	—	—	—	1	0.06	0.06	—	—	—	—	—	—
14	1	0.07	0.07	—	—	—	—	—	—	1	0.03	0.03
15	—	—	—	—	—	—	1	0.06	0.06	—	—	—
16	—	—	—	—	—	—	—	—	—	—	—	—
17	—	—	—	—	—	—	1	0.03	0.03	—	—	—
18	1	0.06	0.06	—	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—	—	—	—
N	716			543			744			768		
a	233.28			133.26			82.22			79.70		
b	0.981			0.822			0.653			0.713		
M (%)	62.5			56.0			48.0			51.0		
r^2	0.96			0.98			0.95			0.97		
SEE	0.457			0.301			0.376			0.263		
I_L	3–9			3–9			3–10			3–8		

Length (mm)	Subarea 5			Subarea 6			Subarea 7		
	N_0	Mn	SE	N_0	Mn	SE	N_0	Mn	SE
2	104	5.77	0.78	37	3.28	0.65	78	4.84	0.74
3	169	12.59	1.33	55	8.18	1.45	174	16.68	1.88
4	110	6.41	0.76	38	3.54	0.65	165	12.98	1.37
5	67	2.93	0.41	19	1.60	0.40	136	10.75	1.28
6	38	1.42	0.25	16	1.59	0.48	122	7.29	0.86
7	22	0.86	0.21	8	0.53	0.20	95	6.55	0.93
8	11	0.35	0.12	4	0.33	0.19	70	4.65	0.77
9	8	0.44	0.22	5	0.56	0.30	33	2.74	0.67
10	1	0.01	0.01	4	0.20	0.10	34	3.18	0.79
11	1	0.06	0.06	2	0.25	0.20	29	2.15	0.55
12	—	—	—	1	0.04	0.041	19	1.86	0.64
13	2	0.05	0.04	1	—	—	14	0.39	0.12
14	1	0.01	0.01	—	—	—	10	0.31	0.11
15	1	0.04	0.04	—	—	—	13	0.31	0.09
16	—	—	—	—	—	—	3	0.12	0.07
17	—	—	—	1	0.05	0.05	4	0.11	0.06
18	1	0.02	0.02	—	—	—	4	0.11	0.06
19	1	0.03	0.03	—	—	—	4	0.12	0.07
20	—	—	—	—	—	—	2	0.05	0.04
N	1286			841			1852		
a	134.70			24.43			67.64		
b	0.754			0.481			0.358		
M (%)	53.0			38.2			30.1		
r^2	0.89			0.92			0.96		
SEE	0.788			0.467			0.387		
I_L	3–11			3–12			3–20		

9). Small juveniles (≤10 cm TL) show a similar distributional pattern, although they tend to be more abundant in shallower depths. Few have been collected in the Gulf of Maine, but they were distributed over most of Georges Bank, especially in the central portion. They were found closer to shore in the Middle Atlantic Bight than on Georges Bank. Small juveniles (≤10 cm TL) were found in 4–82 m in Massachusetts nearshore waters, but their average capture depth was 23 m. In New Jersey nearshore waters (5–27 m), larger juveniles and adults were abundant during all months, but small juveniles (≤10 cm TL) were rare (Fig. 11).

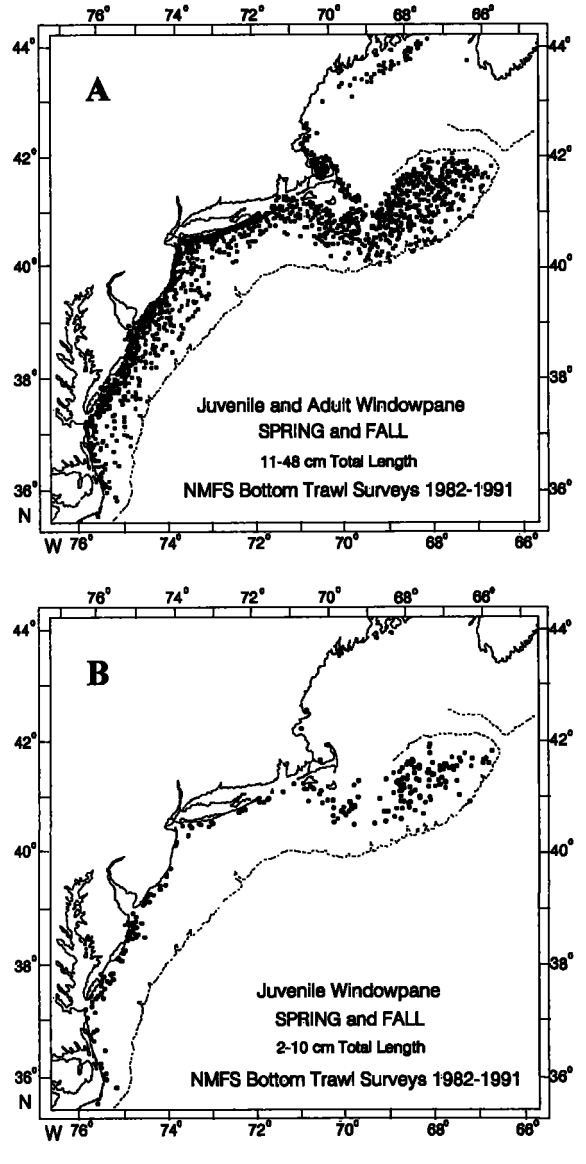

Figure 9

Occurrence of two size classes of windowpane, *Scophthalmus aquosus*, from spring and fall NMFS groundfish surveys during 1982–91.

The seasonal patterns of abundance of windowpane, based on NMFS bottom trawl survey catches, varied markedly on the continental shelf (Table 4). Fall catches of fish ≤10 cm TL in subareas 1–5 averaged ≤0.01 individuals per tow, 0.22 per tow in subarea 6, and 6.24 per tow in subarea 7. Spring catches of these fish ranged from 0.07 to 0.46 fish per tow across all subareas, with the highest catches in subareas 2 and 3, which were 30 to 50 times higher than those in the fall. In contrast to catches of fish ≤10 cm TL, catches of fish 11–20 cm TL showed little variation across subareas in the fall (0.72–1.82 fish/tow), whereas spring catches were low in subareas 1 and 2 (0.09 fish/tow) and high in subareas 5 and 6 (1.15–1.25 fish/tow). In general, adult fish (>20 cm TL) catches were consistently low in subarea 1, increased along the coast in subareas 2–6, and peaked in subarea 7. This pattern of adult catches differed for fish 21–30 cm TL in the spring, when the peak catches occurred in subarea 3.

The NMFS and Massachusetts fall and spring bottom trawl surveys were analyzed to determine whether the abundance of small juvenile windowpane reflects the areal patterns in larval distribution and abundance mentioned above. NMFS stations, for spring and fall combined, at which windowpane (11–48 cm TL) were captured are shown in Figure 9A, and stations that contained juveniles (≤10 cm TL) are shown in Figure 9B. Although adults occur in the northern Gulf of Maine, no juveniles were collected there. The spatial patterns of abundance for juveniles on the continental shelf coincide with the patterns of abundance for larvae (see Figs. 3 and 9B). The inverse relationship of catches of juveniles in the fall with larval mortality (r=–0.99, P<0.05) seems to support the conclusion that mortality is controlling recruitment; however, spring catches show no such relationship (r=0.12, P<0.93). To test the possibility that juveniles migrate to an area nearshore (<10 m depths) or to estuarine habitats in the southern part of the survey area in the fall and were not sampled by the trawl gear, we calculated the weighted mean capture depths in each subarea for five size classes (Table 4). Small juveniles (≤10 cm TL) were captured at only 4 of 779 stations in subareas 1–4 in the fall at depths of 10–24 m. Larger juveniles (11–20 cm TL) were more abundant and were captured at weighted mean depths 17–19 m. Adults (21–30 cm TL) were found in slightly deeper water (means= 22–27 m) and adults >30 cm TL were captured at only 12 stations in mean depths from 14 to 38 m. Weighted mean depths of capture within each subarea differed little between fall (10–38 m) and spring (15–47 m) surveys or between size classes, although a weak trend of increasing depth with size was

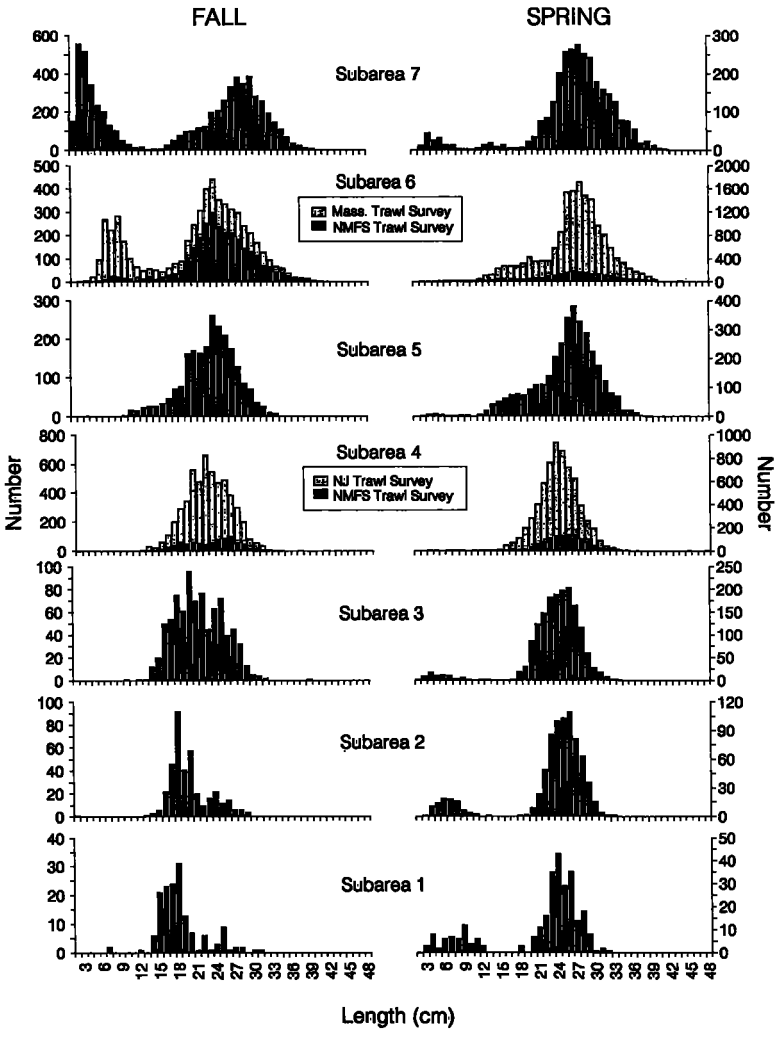

Figure 10

Length-frequency distribution of windowpane, *Scophthalmus aquosus*, from subareas indicated in Figure 1 during NMFS fall and spring groundfish surveys. See Table 1 for additional details.

evident. However, these results do not clearly indicate an inshore movement of juvenile fish during fall on the continental shelf, although eggs, larvae, and juveniles can be found in some estuaries.

Juvenile length frequencies and growth

Understanding patterns of age composition and growth in our study area is confounded by location and timing of spawning. For our purposes we will follow the patterns for Georges Bank (subarea 7) and the Middle Atlantic Bight off New Jersey (subarea 4), because they appear quite different. In subarea 7, where there is a specific peak in spawning, larvae first appear in relatively large numbers in June at sizes ranging from 2 to 6 mm (Table 2). They reach peak abundance in August when they range from 2 to 20 mm (Table 2; Fig. 4). By the fall they are well represented in bottom trawl collections at sizes of 2–14 cm TL (Fig. 10). By spring they are probably represented by the two smaller modes over the range from 3 to 16 cm TL (Fig. 10). The similar size ranges from fall to spring suggest that little or no growth occurs over the winter. By the following fall, this group has probably attained sizes of ≥17 cm TL and cannot be separated from older fish by length alone

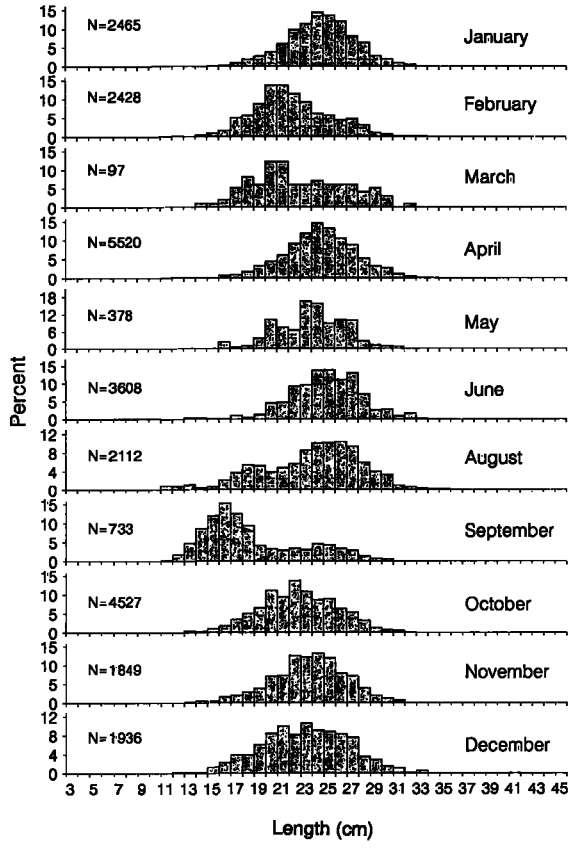

Figure 11

Monthly length-frequency distribution for windowpane, *Scophthalmus aquosus*, collected during an inshore trawl survey off the coast of New Jersey, 1988–92. See Table 1 for additional details.

(Fig. 10). In subarea 4 off New Jersey, where spawning was shown to be bimodal, the earliest peak was in May and the second was in October–November (Fig. 4; Table 2). However, there is no evidence of large numbers of small juveniles in the spring or fall in the NMFS survey (Fig. 10) or in the monthly catches of the New Jersey trawl surveys (Fig. 11). Conversely, in the vicinity of Little Egg Inlet, New Jersey, the appearance of eggs and larvae in both the estuary and in nearshore ocean waters corresponds well with two spawning periods (Fig. 7). Evidence of spring-spawned fish is first indicated by small numbers at 4 cm TL in June (Fig. 12). By July, these fish are 3–8 cm TL and in August they are 4–11 cm TL. In September, catches of small fish decreased, and fish lengths ranged from 8 to 17 cm TL. Catches of these spring-spawned fish further decreased by October, when very few juveniles were captured. This same cohort first appeared in nearshore surveys off New Jersey in August and by September the fish were 11–19 cm TL (Fig. 11). By October they cannot be easily differentiated from older fish on the basis of length, but some of these fish were probably captured in the fall collections by NMFS surveys on the continental shelf (Fig. 10). They do not appear to be abundant in estuary or ocean collections until the following April–May when most are >16 cm TL (Fig. 12).

Fall-spawned larvae were first collected in September in subarea 4 at lengths of 2–4 mm (Fig. 4; Table 2). The peak abundance was in October and November when they were 2–10 mm. These fish first appeared as settled juveniles in the vicinity of Little Egg Inlet in November at 3–4 cm TL, and by December they were 4–7 cm TL (Fig. 12). Fall-spawned juveniles were not evident in the nearshore (Fig. 10) or in deep-water surveys (Fig. 12). During January–March, fish 4–8 cm TL were abundant in the ocean catches and may not have grown much during these cold-water months (Fig. 12). From March to May, small juveniles moved gradually into the bay and began to grow again. A clear separation between the fall-spawned fish (5–12 cm TL) and the spring-spawned fish (>16 cm TL) can be seen in May (Fig. 12). The fall-spawned fish continued to grow and were 18–26 cm TL by October when they were about 1 year old. They may not have grown during the late fall and winter, given the similarities in length frequencies from October to December. These fish left the bay beginning in June, and by October few fall-spawned fish were present in the bay. The evidence for the existence of spring- and fall-spawned cohorts is most evident in July and August in New Jersey where both are represented by the two dominant length-frequency modes in both the bay and the adjacent ocean (Fig. 12).

Discussion

Distribution and abundance

Windowpane is a resident of the Middle Atlantic Bight and Georges Bank, although it does show some small-scale seasonal inshore-offshore movement. Evidence from ocean trawl surveys throughout the study area showed little difference in the preference of juveniles for relatively shallow waters from spring and fall depth distributions (Table 4). Evidence from tagging experiments in Long Island Sound (Moore, 1947) indicates that windowpane do not undertake extensive migrations in response to either seasonal temperature changes or for purposes of spawning. However, research trawl surveys show some evidence of an offshore movement during winter in response to low

Table 4

Summary of fall and spring catches (depths <100 m) of windowpane, *Scophthalmus aquosus*, from NMFS groundfish trawl surveys off the northeast United States, 1982–91. N_t = total stations sampled; D_m = mean depth of N_t; N_0 = number of stations with windowpane; M_t = mean catch per tow for N_t; and D_0 = weighted mean depth of N_0. See Figure 1 for location of subareas.

				Length (cm)													
				≤10			11–20			21–30			31–40			>40	
Subarea	Season	N_t	D_m	N_0	M_t	D_0	N_0	M_t	D_0	N_0	M_t	D_0	N_0	M_t	D_0	N_0	M_t	D_0
1	Fall	178	31	1	0.01	17	34	0.72	18	9	0.15	27	1	0.01	30	0	—	—
2	Fall	185	31	1	<0.01	24	53	1.42	19	40	0.57	27	0	—	—	0	—	—
3	Fall	209	35	1	<0.01	22	66	1.82	19	77	2.27	27	6	0.03	38	0	—	—
4	Fall	211	38	1	<0.01	10	52	1.18	17	91	2.61	22	5	0.04	14	0	—	—
5	Fall	384	36	4	0.01	15	89	1.28	41	176	4.33	43	59	0.22	47	0	—	—
6	Fall	306	49	18	0.22	31	57	1.05	33	105	6.67	35	64	1.35	39	5	0.02	42
7	Fall	435	65	70	6.24	47	76	0.78	48	166	5.61	51	155	2.60	49	2	<0.01	47
1	Spring	199	33	15	0.21	17	10	0.09	22	47	1.04	23	3	0.02	23	0	—	—
2	Spring	179	33	21	0.46	15	11	0.09	19	94	3.34	22	8	0.04	26	0	—	—
3	Spring	209	33	25	0.34	18	28	0.68	17	118	6.95	19	22	0.14	20	0	—	—
4	Spring	226	40	12	0.16	16	31	0.39	17	99	4.36	20	23	0.16	26	2	0.01	47
5	Spring	436	39	18	0.09	24	142	1.15	57	258	5.23	63	146	1.07	47	2	0.01	41
6	Spring	305	49	16	0.07	33	79	1.25	53	147	4.17	53	105	1.94	40	5	0.02	43
7	Spring	368	65	23	0.23	52	43	0.27	73	143	3.40	73	167	2.14	52	4	0.01	57

water temperatures (Wigley and Gabriel, 1991; Lange and Lux[6]).

There appears to be evidence of latitudinal variation in depth preference from south to north (Table 4). The actual depth preference in subareas 1–4 may be shallower than indicated because NMFS seldom samples in depths <10 m. For example, in subarea 4, juveniles migrated or settled into an estuary during spring and tended to move into the ocean during summer (Fig. 12). Few juvenile windowpane were caught inside the estuary by the fall when they had reached lengths between 18 and 26 cm TL. These seasonal movements in and out of estuaries and bays may account for the larger numbers of juveniles taken on the continental shelf in the Middle Atlantic Bight in the spring (Table 4; Fig. 10), although the lack of small juveniles in nearshore waters off New Jersey (Fig. 10) is difficult to explain. In contrast, the Massachusetts trawl survey, which sampled similar depths to those in the New Jersey trawl survey, captured large numbers of juvenile windowpane in the fall. Clearly juvenile windowpane are also a component of fish assemblages in other estuaries on the basis of reports from Narragansett Bay (Herman, 1963), Long Island Sound (Moore, 1947), Sandy Hook Bay (Wilk and Silverman, 1976), Delaware Bay (de Sylva et al., 1962), Chesapeake Bay (Hildebrand and Schroeder, 1928), North Carolina (Weinstein, 1979), South Carolina (Wenner et al., 1982), and Georgia (Dahlberg, 1972). Thus, further sampling in the shallow nearshore ocean waters and in adjacent estuaries will be necessary to understand completely the nature of seasonal movements and the patterns of habitat use of juveniles, at least in subareas 1–5.

Timing and location of spawning

The extensive latitudinal sampling program has helped to discern the seeming inconsistency in the literature regarding the presence of a bimodal spawning season. Split spawning (i.e. peaks in spring and fall) has been previously reported in Long Island Sound, New York (Wheatland, 1956), Great South Bay, New York (Monteleone, 1992), and on the continental shelf off Virginia and North Carolina (Smith et al., 1975). However, Colton et al. (1979), Perlmutter (1939), and Smith et al. (1975) reported no evidence for split spawning north of Virginia. We found evidence for a split spawning season in all areas except Georges Bank (Fig. 4). Taken together, the available information shows that windowpane begin spawn-

[6] Lange, A. M. T., and F. E. Lux. 1978. Review of the other flounder stocks (winter flounder, American plaice, witch flounder and windowpane flounder) off the Northeast United States. U.S. Dep. Commer., NMFS, Northeast Fish. Sci. Center, Woods Hole Lab. Ref. No. 78-44, Woods Hole, MA 02543.

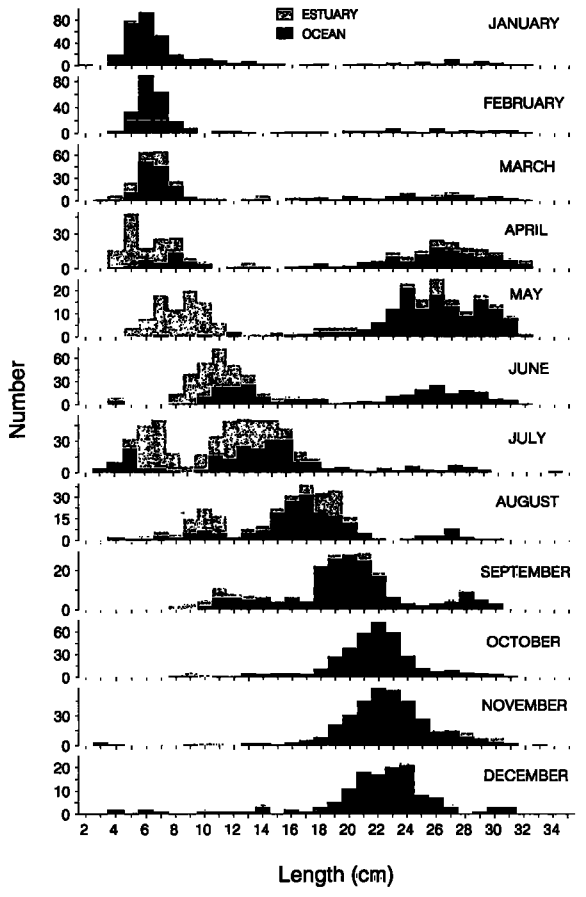

Figure 12

Length-frequency distribution of windowpane, *Scophthalmus aquosus*, by month, based on collections in the estuarine and ocean in the vicinity of Little Egg Inlet, New Jersey, as modified from Milstein and Thomas (1977). Estuarine samples represent all samples not taken in the ocean. Station locations are indicated in Figure 2.

ing at the southern portion of the Middle Atlantic Bight (south of Chesapeake Bay) in April or May. Peak spawning progresses northward as waters warm, and spawning reaches Georges Bank by July and August. As waters cool during fall, spawning moves south to off New York and New Jersey, and by November spawning is again centered in the southern part of the Middle Atlantic Bight. The split spawning season pattern has also been verified for New Jersey in the vicinity of Little Egg Inlet (Fig. 8) and farther south at Hereford's Inlet, New Jersey (Keirans, 1977).

Seasonally varying temperatures clearly influenced the timing of spawning. We found maximum numbers of small larvae at temperatures between 16 and 19°C in subareas 1–5 (Fig. 5), except on Georges Bank where the maximum larval abundance occurred at temperatures (13–16°C), approximately those reported by Smith et al. (1975). They found 70% of small larvae over bottom water temperatures between 8.5 and 13.5°C between Cape Hatteras and Block Island (subareas 1–5). It appears that spawning during the single year (1965–66) of their study occurred at temperatures around 6°C, colder than our findings from a data set that was more extensive both temporally and latitudinally.

Reports of eggs from Great Bay (Fig. 8) and Hereford's Inlet (Keirans, 1977), New Jersey, Chesapeake Bay, Virginia (Olney, 1983; Olney and Boehlert, 1988), Long Island Sound (Wheatland, 1956; Richards, 1959; Perlmutter, 1939), Great South Bay on Long Island (Monteleone, 1992), and Narragansett Bay, Rhode Island (Herman, 1963; Bourne and Govoni, 1988), strongly suggest that spawning occurs in the lower portions of estuaries in the Middle Atlantic Bight. These sources imply that the influence of estuaries on the early life history of windowpane may be important in the Middle Atlantic Bight.

Age and growth

Growth after settlement was markedly different between the spring- and fall-spawned cohorts in New Jersey waters. The spring-spawned cohort grew quickly during the summer and reached sizes of 11–19 cm TL in September, approximately 4 months later (Fig. 12). The fall-spawned cohort, exposed to winter temperatures soon after settlement, apparently did not grow during the winter and grew to only 4–8 cm TL six months later in March (Fig. 12). Thus, the timing of spawning (spring vs. fall) influences growth rates and the age and size composition of young of the year.

Reported estimates of growth from scale annuli, regardless of spawning season, were quite different. In studies for Long Island Sound and North Carolina age-2+ fish averaged only 11.7 cm TL (Moore, 1947) and 10–13 cm TL (Shelton, 1979), respectively. Sizes at age 1 reported for our study area were 18 cm TL (Grosslein and Azarovitz, 1982) and 14.5 cm TL (Thorpe, 1991) and were more consistent with our results, although the season of spawning could easily affect size at age. Clearly, more detailed studies of spawning times and their effects on age composition and growth of juveniles are needed before we can completely understand the population dynamics of this species.

Nursery areas

In general, the distribution of larvae and juveniles on the continental shelf coincided and showed that

at least some juveniles settled in areas of larval concentration, although this pattern was not as strong for the Middle Atlantic Bight as it was for Georges Bank. Larval abundance on Georges Bank was high and recently settled juveniles were clearly abundant there in the fall but less so in the spring (Fig. 10). Slightly larger individuals were also evident off Massachusetts in the fall (Fig. 10), but they were not caught in the deeper waters of the continental shelf further south (subareas 1–5, Fig. 10). Size at settlement appears to differ between Georges Bank and the Middle Atlantic Bight. Larvae >10 mm were collected only rarely in the Middle Atlantic Bight but were relatively abundant on Georges Bank. This pattern of catches could arise from 1) the large larvae avoiding capture by transforming and settling earlier in the south, 2) the differences in mortality between regions, or 3) the unavailability of larger larvae to the sampling gear because they entered the unsampled surf-zone or the numerous estuaries in the southern part of the study area. This last possibility is clearly not an option for Georges Bank larvae that do not make extensive migrations (50–75 km) to the nearshore areas of Massachusetts. We have shown that mortality estimates are higher in the Middle Atlantic Bight than on Georges Bank. Settlement in estuaries in the Middle Atlantic Bight is also possible because larger planktonic larvae (K. W. Able, D. A. Witting, and M. P. Fahay, unpubl. data) and small juveniles were collected from these areas in New Jersey (this study, Figs. 8 and 12; Allen et al., 1978), Delaware (Pacheco and Grant, 1973), and Long Island (Warfel and Merriman, 1944). Yet to be resolved are the reasons for the differences in the size of larvae and the apparent mortalities in the different geographic regions, as well as for the subsequent effect of size on settlement and the location of nursery areas throughout the range of windowpane.

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Trajectory-based approaches to estimating velocity and diffusion from tagging data

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Abstract.—Several new models are developed to estimate the velocity and diffusion of a population from tagging data. The new estimators apply the inverse principle to the individual trajectories of recovered tags rather than to their local abundance. These models require fewer assumptions and less information than do published abundance-based methods. Techniques are presented for a variety of circumstances, and both discrete and continuous parameterizations of the velocity field are included. The sensitivity of the estimators to violations of the assumptions was examined numerically by using stochastic simulations. The results suggest that the estimators are fairly robust but may fail under certain conditions. Extensions to accommodate these situations are discussed.

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Tagging experiments have often been used to delineate animal movements. Historically, many of the analyses were limited to graphical portrayals of apparent migration routes and simple measures of the net swimming speed. Beverton and Holt (1957) introduced more rigorous treatments of tagging data based on the pioneering work of Skellam (1951). They postulated that the Fickian diffusion equation would be an adequate model for the dispersion of fish due to random motions and developed a technique for estimating the diffusion coefficient from tagging data. Subsequently, Jones (1959, 1976) developed a simple estimation procedure that distinguished the diffusion and net drift of returned tags. Saila and Flowers (1969) proposed using a special case of the advection-diffusion equation (Fickian diffusion with constant velocity) to model fish migration and developed a numerical technique to estimate the diffusion coefficient and net drift. More recently, Sibert and Fournier (1994) advocated the use of a more general form of the advection-diffusion equation that allows for mortality and discrete changes in velocity among areas. They also developed a new estimation procedure based on fitting numerical predictions to the observed distribution of recovered tags. Similar methods have been applied to the movements of passive tracers in the ocean by Fiadero and Veronis (1984) and Wunsch (1989).

Beverton and Holt (1957) recognized that the solutions to advection-diffusion equations are greatly complicated by heterogeneous diffusion rates and irregular boundary conditions (e.g. coastlines). They suggested replacing the diffusion equation with a system of area-specific equations linked together by transfer coefficients that measure the movement across the boundary of adjacent areas (box models). This simple abstraction, as well as others like it, has received considerable attention in recent years, and a number of papers have dealt with estimating the transfer coefficients from tagging data (Beverton and Holt, 1957; Sibert, 1984; Hilborn, 1990; Deriso et al., 1991; Hampton, 1991; Schweigert and Schwarz, 1993; Kleiber and Fonteneau, 1994; Salvado, 1994). In principle box models are not very realistic because they assume that movement within and among boxes occurs instantaneously, but in practice they may approximate the dynamics well enough to be useful.

All of the aforementioned procedures (except Jones's) estimate the movement of a population from the local abundance of recovered tags. In contrast, the methods developed in this paper estimate movement from the trajectories of recovered tags. Strictly speaking, the new models address the advection (ex-

pected velocity) and diffusion of a population. As such, they should provide useful alternatives for estimating the movement parameters of the advection-diffusion equation or individual-based simulations. They are applicable to box models only to the extent that such box models are analogous to finite difference approximations to the advection-diffusion equation. (In that case the transfer coefficients can be written as functions of the local velocity and diffusion rates.)

This article is divided into five sections. The first section highlights the conceptual differences between trajectory-based and abundance-based estimators of velocity. The mathematical details of the proposed trajectory models are developed next. Section two focuses on the process of advection and section three on the process of diffusion. The performance of the models and their sensitivity to violations of the assumptions are evaluated by using stochastic simulations in the fourth section. Finally, some practical considerations and extensions to the methodology are discussed.

General concepts

Velocity, advection, and diffusion defined

The term 'velocity' refers to the speed and direction in which an object (tag) moves. Mathematically, the velocity U at position x and time t is defined by the differential equation

$$U(x,t) = \frac{dx}{dt}. \tag{1}$$

The map of U that assigns a velocity to each point in space and time is called the velocity field.

In theory, the position of any given tag at any given time can be predicted from its velocity history by integrating Equation 1. In application, however, it is usually more practical to describe the collective velocity histories of a group of tags in terms of a common expected component $u(x,t)$ and unique random components $u'(x,t)$. The expected component is known as the advection field, and the random component gives rise to the diffusion field. By using this description, the position x_{iT} of the i'th tag after T units of time can be expressed in the general form

$$x_{iT} = x_{i0} + \int_{t_{i0}}^{t_{i0}+T} u(x_t,t)dt + \int_{t_{i0}}^{t_{i0}+T} u'(x_t,t)dt, \tag{2}$$

where x_{i0} and t_{i0} are the initial position and time, respectively.

The first integral in Equation 2 determines the expected position of the tag, and the second integral determines the displacement of the tag relative to its expectation. In terms of a group of tags with common starting points, the first integral describes the advection of the group as a whole, and the second integral determines how the group spreads about its expected center of mass.

Approaches to estimating velocity

The purpose of estimating movement rates and other parameters from tagging data is usually to elucidate the behavior of a larger population—often within the context of managing that population. Any such application implicitly assumes that the tagged and untagged members of the population move the same way. This basic tenet is accepted throughout the remainder of this article. The discussion in this section focuses on the ancillary assumptions that different estimation approaches must make.

The classical formula for estimating the advection of a tag is

$$\hat{u} = \frac{1}{n}\sum_{i=1}^{n} \frac{x_{iT} - x_{i0}}{T_i}, \tag{3}$$

where n is the number of observations. Jones (1959, 1976) developed an alternative formula, which, in the present notation, is

$$\hat{u} = \frac{\sum_{i=1}^{n} x_{iT} - x_{i0}}{\sum_{i=1}^{n} T_i}. \tag{4}$$

The practicality of the estimators (Eqs. 3 and 4) is limited because for these the advection field is assumed to be relatively constant, which is unlikely over the temporal and spatial scales relevant to population management. Therefore, it will often be profitable to enlist a more dynamic model of advection. The parameters of the dynamic model can be estimated by minimizing an appropriate objective function of some measure of the effect of advection on the population. To date, the measure of choice for tagging data has been the local abundance of recovered tags. The measure used in this article is the trajectory of each individual tag.

The accuracy of any estimator depends on the assumptions behind the construction of the objective function. These involve assumptions regarding the probability density of the measure and the structure

of the measure's predictor. To illustrate, consider a least-squares objective function whose measure is the number N of tags recovered in each area a and season s:

$$\sum_s \sum_a (\hat{N}_{as} - N_{as})^2. \quad (5)$$

The predictor, $\hat{N}$, is a function of the parameters of the underlying population dynamics and advection models.

In theory, the parameter estimates that minimize Equation 5 are unbiased if the measure (N) is normally distributed with constant variance and the models behind the predictor are correct. It is generally recognized, however, that the probability density of recoveries is nonnormal and the variance in N may differ widely among areas and seasons, both of which imply that the least-squares solution is inappropriate. For this reason, most of the recent literature has favored maximum-likelihood solutions based on the multinomial distribution instead.

The condition of the predictor ($\hat{N}$) is more difficult to assess because it embodies a suite of assumptions regarding all relevant aspects of the population dynamics. The local abundance of tags may be affected by processes common to both the tagged and untagged populations (e.g. natural and fishing mortality) as well as by processes that are unique to the tagged population (e.g. tag-induced mortality, tag shedding, and failures to report recovered tags).

It would be advantageous to develop a predictor that does not need to account for all the complex processes affecting tag recoveries, but it is clear that a measure other than abundance must be used. The trajectories of individual tags, which can be predicted from their velocity history alone, is one such measure. Tag recovery rates are relevant to trajectories only in the sense that they determine those most likely to be represented in the sample. That is, recovery rates dictate the probability density of observed (recovered) trajectories, but not the predictor. This point, though subtle, has important implications with respect to relaxing the assumptions required to produce unbiased estimates of the advection field.

Consider that the expected position of a tag after liberty time T_i follows from Equation 2:

$$E[x_{iT}] = x_{i0} + \int_{t_{i0}}^{t_{i0}+T_i} u(x_t,t)dt. \quad (6)$$

The expected position of a recovered tag under the same conditions is

$$E_R[x_{iT}] = x_{i0} + \int_{t_{i0}}^{t_{i0}+T_i} u(x_t,t)dt + E_R\left[\int_{t_{i0}}^{t_{i0}+T_i} u'(x_t,t)dt\right],$$

where the subscript R indicates that the expectation includes recovered tags only. The second integral dropped out of the unconditional expectation in Equation 6 because u' is, by definition, a random variable with mean equal to zero. The same would not generally be true of the expectation of recovered tags because some vectors of u' may be more likely to be recovered than others—changing the probability density in some unknown way.

Suppose there exists an objective function $O[x,\hat{x}]$ (maximum likelihood or otherwise) that can produce unbiased estimates of $E[x_{iT}]$ from a random sample of all potential trajectories x_{iT}. (The construction of this function will be discussed later.) The same objective function will also produce unbiased estimates from a random sample of recovered tags provided

$$E_R\left[\int_{t_{i0}}^{t_{i0}+T_i} u'(x_t,t)dt\right] = 0. \quad (7)$$

This constraint is satisfied if either u' is everywhere identically zero or the probability of recovering a tag is independent of its velocity. The latter condition is effectively equivalent to assuming that the processes that influence tag recovery are homogeneous in space and time. It satisfies Equation 7 because it implies that the relative likelihood of observing any given displacement depends solely on the probability density of u'. By definition, the expectation of u' at every point is zero and therefore the expectation of the integral sum of u' is also zero.

It has been shown that, subject to Equation 7, trajectory-based estimators can provide unbiased estimates of the population advection field without recovery rates having to be considered. One can imagine many practical situations where Equation 7 would be approximately satisfied. The spatial and temporal distribution of recovery rates would not normally be a significant factor in experiments involving radio-tracked drifter buoys or ultrasonic tags. Similarly, variations in the velocity of individuals might be expected to be small compared with the average velocity of a population undergoing a seasonal spawning migration. Where Equation 7 is not met, however, tags moving at different velocities may not be equally represented in the recovered sample.

If, for example, faster tags were more likely than slower tags to move into a region where recovery rates are high, then the speed of the advection field would be overestimated.

At this point it seems convenient to examine the proposed trajectory models in closer detail, noting that recovery factors other than advection do not need to be considered when Equation 7 is satisfied. The more complicated matter of accounting for variations in recovery rates when Equation 7 is not met is deferred to the Discussion section at the end of this article.

Trajectory-based predictors for estimating advection

This section focuses on developing the predictor for the directed (advective) component of motion from the trajectories of recovered tags. The remaining portion of the objective function, which quantifies the differences between the observed and predicted values of the measure, depends on the nature of the probability density and is discussed in detail in the subsequent section entitled "Diffusion and the objective function."

The general form of the trajectory predictor may be written

$$\int_{x_{i0}}^{\hat{x}_{iT}} dx = \int_{t_{i0}}^{t_{i0}+T_i} \hat{u}(x_t,t)\,dt, \tag{8}$$

where $\hat{x}_{iT}$ = predicted position of tag i after time at liberty T;
$\hat{u}$ = estimated advection field;
x_{i0} = initial position of tag i; and
t_{i0} = initial date of tag i.

In order to use this prediction equation, one must be able to evaluate the integral on the right. There are two ways to address this problem. One way is to break the temporal and spatial domain into small strata where the advection rates are approximately constant and then to assemble a picture of the large-scale advection field in piece-wise fashion. The other way is to define explicitly a dynamic model of the advection field and to evaluate the integral directly. Each approach is developed in a separate subsection below.

Piece-wise models

This approach seeks to assemble a picture of the overall advection field from estimates of the advection fields in smaller strata. An independent estimate of the average advection in each space and time strata can be obtained from any tag that has remained in that strata the entire time between its release and recovery (or between any two position updates) by using the formula

$$u_i = \frac{x_{iT} - x_{i0}}{T_i}.$$

If observations are available for most of the strata of interest, the entire advection field can be parameterized quite nicely by using a two-way analysis of variance (ANOVA) model:

$$u_i = \bar{u} + A_a + S_s + I_{as} + \varepsilon_i, \tag{9}$$

where u_i = the observed velocity of tag i;
$\bar{u}$ = the overall mean velocity;
A_a = the main effect of area a on u;
S_s = the main effect of season s on u;
I_{as} = the area/season interaction effect; and
ε_i = the error associated with tag i.

In two spatial dimensions a separate ANOVA would apply to each velocity component:

$$u_i = \bar{u} + A_{au} + S_{su} + I_{asu} + \varepsilon_{iu},$$
$$v_i = \bar{v} + A_{av} + S_{sv} + I_{asv} + \varepsilon_{iv},$$

where u_i = the observed velocity in the direction of the first dimension;
v_i = the observed velocity in the direction of the second dimension;
$A_{a\_}$ = the main effect of area a on u or v;
$S_{s\_}$ = the main effect of season s on u or v;
$I_{as\_}$ = area/season interaction effect on u or v; and
$\varepsilon_{i\_}$ = the errors associated with tag i.

Interpolation routines other than ANOVA may also be used to describe the overall advection field, but ANOVA provides a convenient framework for testing whether the advection rates vary among strata. Such tests are valid if the velocity variances are the same in all strata; otherwise one must employ an equivalent nonparametric approach.

ANOVA or other interpolation algorithms are well suited to situations where the positions of tags can be updated frequently. They are especially promising for programs that employ remote tracking devices such as radio or ultrasonic tags (e.g. Quinn, 1988; Hines and Wolcott, 1990; Schulz and Berg, 1992). In some cases the biology of the organism may even permit effective visual tracking (e.g. Stachowitsch, 1979). The ANOVA approach is less suited to

conventional tagging programs because the ability to record the position of the tag is largely beyond the control of the investigator. In this situation a sufficient number of tags would need to be released in each season and area strata to ensure that at least a few would be recovered before straying into other strata. The recovery times must also be short enough to avoid biasing the results toward slower moving tags.

A more flexible estimation procedure, which is capable of incorporating trajectories that reflect the combined effects of several different movement patterns, can be derived by reformulating Equation 8 as

$$\int_{x_{i0}}^{x_{iT}} \frac{1}{u(x,t)}dx = \int_{t_{i0}}^{t_{i0}+T_i} dt. \qquad (10)$$

If $u(x,t)$ is held constant within specific space and time strata but allowed to vary among strata, then Equation 10 may be piece-wise integrated. The solution simplifies to

$$x_{s+1} = \left(t_{s+1} - t_s - \frac{B_{\alpha+1} - x_s}{u_{\alpha s}} - \frac{B_{\alpha+2} - B_{\alpha+1}}{u_{\alpha+1,s}} - \cdots\right)u_{\Omega,s} + B_{\Omega}, \qquad (11)$$

when $u > 0$, and

$$x_{s+1} = \left(t_{s+1} - t_s - \frac{B_{\alpha} - x_s}{u_{\alpha s}} - \frac{B_{\alpha-1} - B_{\alpha}}{u_{\alpha-1,s}} - \cdots\right)u_{\Omega,s} + B_{\Omega+1}, \qquad (12)$$

when $u < 0$.

Here u_{as} = velocity in area a during season s;
B_a = boundaries of the areas (see Fig. 1);
α = first area occupied by the tag during season s;
Ω = last area occupied by the tag during season s;
t_s = date at the onset of the s'th season; and
x_s = position of tag at onset of s'th season.

With these recursions, the position of the tag at the end of each season can be computed from the tag's position at the end of the previous season by using an estimate of the advection field. This procedure can then be applied sequentially to compute the expected position of the tag at the date when it was recovered from its initial position. The "best" estimates of the strata-specific advection rates would minimize some objective function of the differences between the observed recovery positions and those predicted with the recursions. (The appropriate objective function will be discussed in the section on diffusion.)

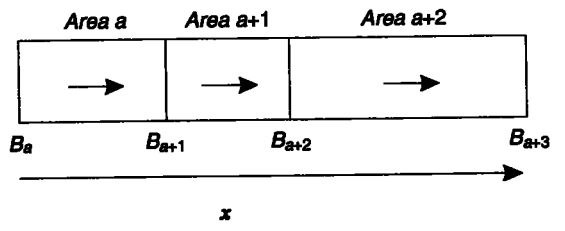

Figure 1
Schematic of a region divided into three areas illustrating the definition of the area boundaries, B.

The sequential procedure itself is accomplished by first determining the starting season s_0 and starting area a for each tag from the date and position where it was released. The position of the tag at the end of the first season (start of season s_0+1) can then be obtained from the recursions, by replacing x_s and t_s with the position and date of release. The recursions are then applied as given until the last season, which is determined by the recovery date. Finally, the formula for estimating the recovery position is obtained by replacing t_{s+1} in the recursions with the recovery date.

Continuous models

The approach proposed in this section involves developing an adequate continuous model of the advection field, $u(x,t)$, and solving Equation 8 for x as a function of t. To illustrate, consider a fish population migrating out of a basin. Suppose each fish swims initially at speed u_0 in the positive x direction and increases its speed as it proceeds. Further, suppose that periodically the fish are either helped or hindered by sinusoidal oscillations in the water currents. A reasonable model for the velocity of the fish might be $u(x,t) = u_0 + ax + b\sin[ct]$. The solution is

$$x = -\frac{u_0}{a} - b\frac{a\sin[ct] + c\cos[ct]}{a^2 + c^2} + \gamma e^{at}, \qquad (13)$$

where

$$\gamma = \left(x_0 + \frac{u_0}{a} + b\frac{a\sin[ct_0] + c\cos[ct_0]}{a^2 + c^2}\right)e^{at_0}.$$

The best estimates of the parameters u_0, a, b, and c would be those that minimize some appropriate func-

tion of the difference between the observed and predicted positions of all the tags.

In practice, models capable of effectively capturing the dynamics of the advection field may not be simple enough to admit an analytical solution. The obvious alternative is to evaluate the right-hand integral in Equation 8 numerically. Press et al. (1986) contributed an excellent review of many of the more powerful numerical integration algorithms.

It may also happen that the system is not understood well enough to construct a detailed model of tag motion. In that case there is no equation to integrate, analytically or otherwise. One option is to resort to the piece-wise methods described earlier. There is, however, a second option available provided the effects of space and time on advection are separable, i.e. provided Equation 1 may be recast as

$$\frac{dx}{g[x]} = h[t]dt, \tag{14}$$

where g and h are functions of space and time, respectively. In this case the right and left sides of Equation 14 may be integrated separately:

$$\int_{x_0}^{x_T} \frac{1}{g[x]} dx = G[x_T] - G[x_0] \tag{15}$$

and

$$\int_{t_0}^{t_0+T} h[t]dt = H[t_0 + T] - H[t_0]. \tag{16}$$

It may not always be possible to derive the functions G and H from g and h, but g and h can always be derived from G and H (provided they are continuous on the interval). To the extent that Equations 15 and 16 are equivalent, the suggestion is to pose flexible functions for G or H and to fit them to the data by minimizing their differences. The least-squares fit, for example, would minimize the quantity

$$\sum_i \left(G[x_{iT}] - G[x_{i0}] - H[t_{i0} + T_i] + H[t_{i0}]\right)^2.$$

The corresponding advection field would be obtained by the formula

$$\hat{u}[x,t] = \frac{d\hat{H}}{dt}\left(\frac{d\hat{G}}{dx}\right)^{-1}$$

(a proof is given in the Appendix).

The efficacy of the separability procedure will depend on the behavior of the functions chosen to represent G and H. Although the functions must be flexible enough to accommodate a wide range of movement possibilities, they must also be compatible with the search routine used to find the best estimates of the parameters. When polynomials are used, for example, the search tends to converge on the trivial solution $G = H = 0$. Depending on the search algorithm, it may be possible to impose constraints that circumvent such problems. In any case, it may help to use a theoretical model for either the spatial or temporal aspect of the problem. For example, if there is evidence to suggest that the pattern of motion is periodic, one might write

$$\int_{x_0}^{x_T} \frac{1}{g[x]} dx = \int_{t_0}^{t_0+T} \sin[c(t-d)]dt,$$

where the frequency (c) and offset parameter (d) are known. The corresponding least-squares function to be minimized is

$$\sum_i \begin{pmatrix} G[x_{iT}] - G[x_{i0}] - \cos[c(t_{i0} + T_i - d)] + \\ \cos[c(t_{i0} - d)] \end{pmatrix}^2.$$

The function G would be some arbitrary, but flexible, function.

Diffusion and the objective function

This section examines the random (diffusive) component of tag motion. There are two perspectives from which to do this: the absolute sense (the displacement of individuals from their expected positions) and the relative sense (the displacement of individuals in a patch relative to one another). The distinction is important because relative diffusion includes only those physical processes acting within the patch and implicitly excludes processes that might cause the patch itself to vary from its expected path. Absolute diffusion, on the other hand, includes random processes operating on all scales. The trajectory approaches espoused in this article model each tag without regard to its proximity to other tags; therefore the statistics they produce are not relevant to the diffusion of a patch. Accordingly, the remainder of this discussion will focus on diffusion in the absolute sense.

Measures of diffusion

Two common measures of absolute diffusion are mean-square dispersion and absolute diffusivity.

Mean-square dispersion is defined as the average of the squared deviations of the tags from their expected positions. It is usually expressed as a function of elapsed time T:

$$\chi^2_{iT} = \frac{1}{n}\sum_{i=1}^{n}(x_{iT} - \hat{x}_{iT})^2, \quad (17)$$

where $\hat{x}_{iT}$ is the predicted position given the estimated advection field, and n is the number of tags in the sample. The absolute diffusivity is defined as one half the time rate of change of the mean-square dispersion:

$$K_T = \frac{1}{2}\frac{d(\chi^2_T)}{dt}.$$

Taylor (1921) showed that the mean-square dispersion of particles in a homogeneous random field increases linearly with time, provided that the particles have been at large long enough for their present motions to become statistically decorrelated from their initial motions:

$$\chi^2 = \beta T.$$

By definition then, the diffusivity associated with homogeneous random motions is constant at $\beta/2$, and the dispersion of particles is governed by the advection-diffusion equation. Under these conditions the diffusivity is synonymous with the "diffusion coefficient" of the Fickian advection-diffusion equation.

Implications for the objective function

The time-dependent nature of the mean-square dispersion has important implications for the nature of the objective function used in estimating the parameters of the advection field. When the diffusivity is constant, the positions of tags with initial conditions i will follow a normal distribution with mean $E[x_{iT}]$ and variance βT (Okubo, 1980). In addition, if the recovery positions are reported with normally distributed errors, the observed positions of the tags will follow a normal distribution with variance $\beta T+\sigma^2$. The maximum-likelihood estimates are therefore those that minimize the weighted least-squares formula

$$\sum_i \frac{(x_{iT} - \hat{x}_{iT})^2}{\beta T_i + \sigma^2}, \quad (18)$$

where $\hat{x}_i$ is the predictor defined by Equation 8. In effect, Equation 18 prevents tags that are expected to have large random displacements from dominating the analysis by down-weighting them according to their time at large.

The variance parameters in Equation 18, β and σ^2, must either be known or estimated as part of the search. However, if there is some evidence that the observation errors are much larger than the displacements attributable to random motions, then Equation 18 reduces to ordinary least squares. Similarly, if the random displacements are much greater than the observation errors, then Equation 18 reduces to

$$\sum_i \frac{(x_{iT} - \hat{x}_{iT})^2}{T_i}. \quad (19)$$

There are many practical circumstances where it may be reasonable to assume a constant diffusivity and to apply Equation 18. Observations in the open ocean suggest that the turbulent motions in many regions are approximately homogeneous (e.g. de Verdiere, 1983; Krauss and Boning, 1987; Figueroa and Olson, 1989; Poulain and Niiler, 1989). Moreover, Porch (1993) points out that random walk models of fish movement also exhibit mean-square dispersions that increase in proportion to time (provided swimming speed does not increase substantially during the time period of interest).

The maximum-likelihood formulation for an inhomogeneous diffusion field is unclear. Equation 18 may be acceptable where the random displacements of the tags increase monotonically with time, but it will not be acceptable in all cases. When animals are aggregating to spawn or feed, for example, the effective diffusivity would be zero or negative. Likewise, the presence of coastal boundaries complicates the matter because the diffusivity in one direction is zero. For this reason, it may be more prudent to consider methods that are robust to inhomogeneous variances, such as least-median-of-squares regression (Rousseeuw, 1984) and least-absolute-value regression (Bloomfield and Steiger, 1983).

Estimating diffusivity

As mentioned previously, the position of a tag at liberty for time T in a homogeneous diffusion field follows the normal distribution with mean $E[x_{iT}]$ and variance βT. This implies that the displacement of the tag relative to its expected position (D) is also normally distributed with mean 0 and variance βT. The squared displacements are therefore gamma-distributed with parameters 1/2 and $1/(2(\beta T+\sigma^2))$. Accordingly, the maximum-likelihood estimates for β and σ^2 are those that satisfy the constraints

$$\sum_i \frac{T_i(D_i^2 - \beta T_i - \hat{\sigma}^2)}{(\beta T_i + \hat{\sigma}^2)^2} = 0$$

and

$$\sum_i \frac{D_i^2 - \hat{\beta} T_i - \hat{\sigma}^2}{(\hat{\beta} T_i + \hat{\sigma}^2)^2} = 0,$$

where $D_i = x_{iT} - \hat{x}_{iT}$. These equations must be solved numerically. When σ^2 is negligible, however, the maximum likelihood estimator for β reduces to

$$\hat{\beta} = \frac{1}{n} \sum_{i=1}^{n} \frac{D_i^2}{T_i}.$$

Less efficient estimates of β and σ^2 can be obtained from a linear regression of the squared displacements on the time at liberty:

$$D_i^2 = mT_i + b + \varepsilon_i,$$

where ε is a random deviation term. The slope of the regression m is an estimate of β and the intercept b is an estimate of σ^2.

Estimator performance

This section presents the results of a series of stochastic simulations designed to test the efficacy of trajectory-based estimators. Although no attempt was made to exhaust the possibilities, a sufficiently broad range of conditions was examined to validate the methodology. The experimental design and results are discussed in the subsections below.

Experimental design

A factorial design was used to study the behavior of the estimator in response to the advection field, level of diffusivity, distribution of recovery rates, and number of tags recovered. Two hundred test data sets were generated for each possible combination of factors. The estimators were then applied to each of the test data sets.

Response variables The accuracy of the estimators was quantified by the percent error of the parameter estimates ($\hat{\theta}$) relative to the actual values (θ_{true}):

$$PE = \frac{1}{200} \sum_{j=1}^{200} \frac{\hat{\theta}_j - \theta_{true}}{\theta_{true}} 100\%.$$

The precision of the estimators was quantified by the coefficient of error (CE),

$$CE = 100\% \sqrt{\frac{1}{200} \sum_{j=1}^{200} \left\{ \frac{\hat{\theta}_j - \theta_{true}}{\theta_{true}} \right\}^2}.$$

The coefficient of error is analogous to the familiar coefficient of variation except that the true values of the parameters are used in place of the average of their estimates. A low CE, therefore, implies that the estimates are both unbiased and precise.

Factor levels Two advection models were considered: the sinusoidal model $dx/dt = u_0 + ax + b\sin[ct]$, discussed earlier in connection with Equation 13, and a discrete model with two areas and semi-annual seasons. The parameters of the first model—u_0, a, b, and c—were valued at 8.6 km·day^{-1}, 0.004 day^{-1}, 17.3 km·day^{-1}, and $2\pi/365$ day^{-1}, respectively. The parameters of the second model are the area and season-specific constant advection rates. The rates in areas 1 and 2 were set equal to 5 and 10 km·day^{-1} during the first season and –7 and –4 km·day^{-1} during the second season. Area 1 extended from negative infinity to 1,000 km and area 2 extended from 1,000 km to positive infinity.

Two diffusivity ($\beta/2$) levels, 0.95 and 822 km^2·day^{-1}, were examined. These levels were derived by assuming that tagged fish move according to the bilateral random walk model (see Porch, 1993) with an average speed of 0.5 or 6 meters per second and change direction an average of once per minute or once every five minutes, respectively.

The effects of variations in tag recovery rates were evaluated by dividing the relevant spatial domain into two zones and by varying the likelihood of recovering a tag between them. Three such scenarios were considered. In the first, the probability of recovery was the same in both zones. In the second, the probability of recovery was ten times higher in zone A than in zone B (1.0 versus 0.1). In the third scenario, no tags were recovered in zone B. The boundary separating recovery zones A and B differed with the advection models. The demarcation point was x = 400 km in the sinusoidal model and x = 0 km in the discrete model.

Test data Each test data set was generated by simulating the individual paths of a prescribed number of tags (n). The release positions were randomly assigned values between 0 and 200 km when the sinusoidal advection model was used and were between –1,000 and 1,000 km when the discrete model was

employed. The release dates were randomly assigned values between day 0 and day 365. These choices mimic an opportunistic tagging program where the number of tags released is relatively constant during the year. The recovery dates were obtained by randomly selecting the liberty times from an exponential distribution with parameter Z (instantaneous mortality rate) equal to 0.4 yr^{-1}.

The displacement of each tag due to advection was computed from its release position and from release and recovery dates by using the solutions to the determinate advection models described above. The solution to the sinusoidal model is given by Equation 13, and the solution to the discrete model is given by Equations 11 and 12. The diffusive effect of random motions was then simulated by adding a random normal deviate with mean 0 and variance βT km^2. Next, an acceptance-rejection criterion was invoked to determine whether or not the tag would be recovered. Candidate tags located in recovery zone A were unconditionally accepted, but candidate tags located in zone B were accepted only with probability P (=1.0, 0.1, or 0). This was done by generating a uniform random number between 0 and 1 and by excluding the tag if that number was greater than the prescribed recovery probability.

The process described above was repeated until a total of n recovery positions were accepted. Normally distributed errors (with variance 25 km^2) were then added to each of the accepted release and recovery positions to simulate imprecise position reporting. In this way an artificial sample of n tag recoveries was created.

Estimation The predictors were fitted to the test data by minimizing the weighted least-squares surface described by Equation 19. The predicted positions were calculated by substituting estimates of the parameters into the same advection equations used to generate the data. This allowed the analyses to focus on the interactions of recovery rates and velocity variance without the confounding effects of model misspecification.

The minimization was accomplished by using the Nelder-Mead simplex algorithm AMOEBA (Press et al., 1986), which, although slower than derivative-based methods such as Marquardt's algorithm, is less sensitive to the discontinuities in the solution surface associated with discrete advection models. Heavy penalties were imposed to prevent the search from extending beyond the bounds of a reasonable domain. For example, the maximum possible sustained speed of a migrating tuna might be the sum of the cruising speed of the fish and the maximum speed of the water currents.

The AMOEBA search was restarted at the point P_0, where a minimum had been found, to avoid local anomalies in the solution surface. Subsequent "restarts" continued until five consecutive sets of parameter estimates differed by less than one percent. New vertices were selected for each restart by using the formula

$$P_{ij} = P_{0j} e^{0.5\lambda\delta_i} \; (i, j = 1, \ldots, \omega),$$

where P_{ij} is the value of the j'th coordinate (parameter) in the i'th vertex of the initial simplex, λ is a standard normal variate, and δ_i is equal to one if i equals j and zero otherwise.

Results

This section is divided into two parts, each focusing on the results pertaining to one of the two types of advection models.

Sinusoidal model

The estimation procedure generally behaved very well when the frequency (c) of the sinusoidal oscillations was known and the diffusivity was low (0.95 $km^2 \cdot day^{-1}$). The CE's, which reflect both accuracy and precision, were very low regardless of the distribution of recovery rates (Fig. 2). For the most part, the estimator continued to perform well at high diffusivities (822 $km^2 \cdot day^{-1}$). When the recovery probabilities were the same in both zones, the estimates were unbiased and the CE's rapidly decreased with increasing sample size to less than 10 percent. The estimates were only slightly biased and similarly precise even with a tenfold difference between the recovery probabilities. It was only when no tags were recovered in zone B (i.e. beyond the 400-km demarcation) that the estimates were significantly biased.

The trends were very similar to those described above when the frequency parameter c was estimated along with the other three parameters. A few of the runs, however, failed to converge to acceptable solutions—the weighted least-squares function being an order of magnitude greater than that expected, given the known diffusivity. This problem is not surprising considering the oscillatory nature of any periodic surface. Even if the true values of the other parameters were known, the surface map of the objective function would be characterized by local peaks and valleys that vary with the estimate of c. This behavior is demonstrated by a simplified model of the residual sum of squares (Fig. 3). Although the amplitudes of the peaks and valleys in the more complicated

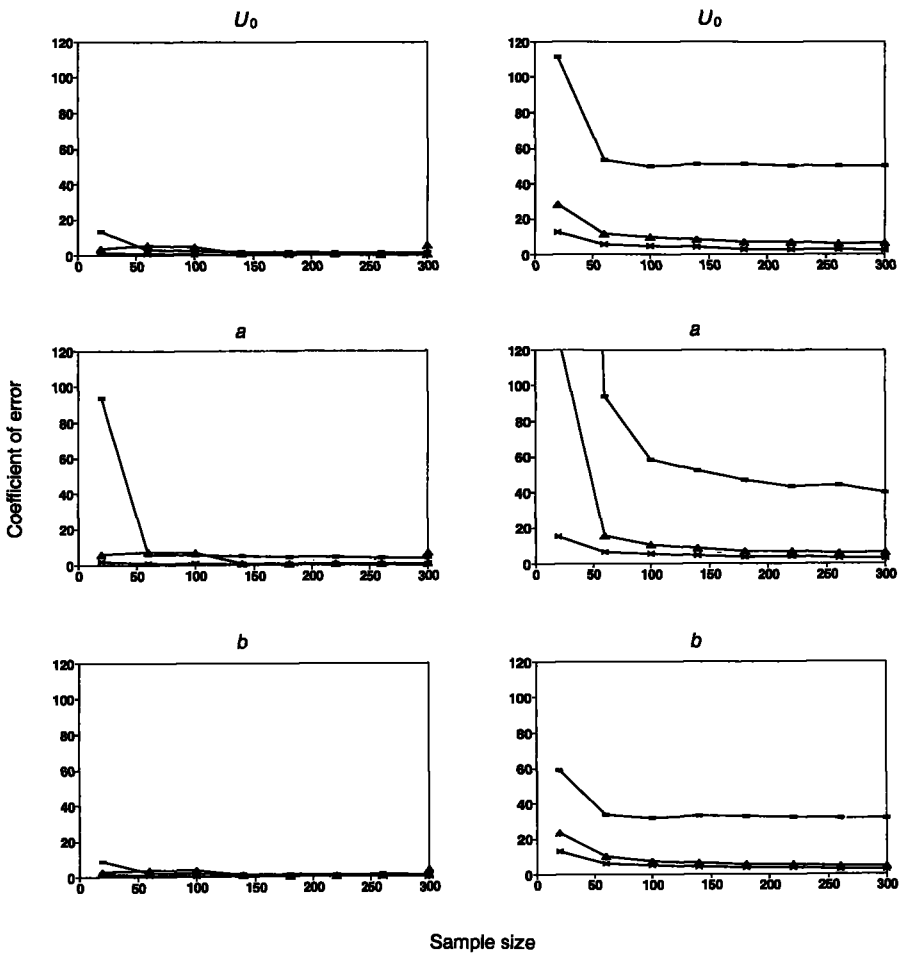

Figure 2

Coefficients of error of the estimates for the parameters of the sinusoidal model. The graphs on the left give the coefficients of error (CE's) under weak diffusivity and the graphs on the right give the CE's under strong diffusivity. The three curves in each graph correspond to zone B recovery probabilities of 0.0 (squares), 0.1 (triangles), and 1.0 (crosses).

model vary (the lowest valley presumably occurring in the vicinity of the true values of the parameters), several of the valleys may be deep enough such that the estimation routine finds a false global minimum.

The convergence problem was eliminated when the search was confined to a relatively restricted range of periodicities and was supplied with good initial guesses. In practice, adequate initial guesses and relatively narrow ranges can usually be deduced even from anecdotal data, therefore this should not prove too serious a limitation to the method. In cases where the periodicity is totally unknown, one should search the entire feasible domain with as fine a resolution as possible.

Piece-wise discrete model

The coefficients of error associated with each parameter were, for the most part, very low when the diffusivity was low (Fig. 4). However, the estimates pertaining to area 2 were highly biased and imprecise when the probability of recovering a tag was 0.0 in zone B. This is not unexpected given that excluding recoveries in zone B (x>0 km) all but eliminates the possibility that any of the recovered tags would ever have encountered area 2 (x>1,000 km). Thus, there is essentially no information on the advection in area 2 and the estimation routine fails. A similar result was not observed when the recovery probabil-

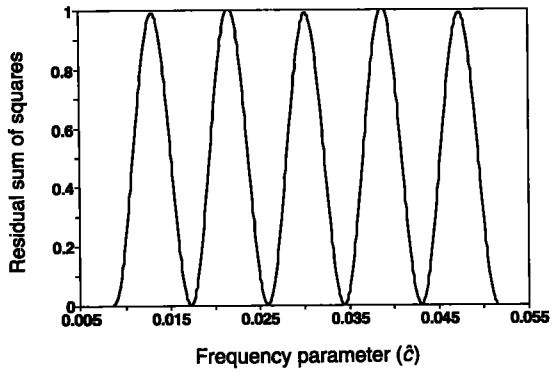

Figure 3

Map of the function $(\sin[ct] - \sin[\hat{c}t])^2$, where c is the true value of 0.0172 day^{-1} and $\hat{c}$ represents an estimate of c.

ity in zone B was 0.1 because a substantial fraction of the tags in each sample were still recovered in advection area 2 (see Fig. 5). Some of the tags recovered in area 1 undoubtedly passed through area 2 at some point as well, further augmenting the amount of information pertinent to estimating the advection in area 2.

The estimation procedure did not perform nearly as well at high diffusivities as it did at low diffusivities except when the recovery rates were the same in both areas (1.0). In that case the estimates remained unbiased and relatively precise—the CE's having dropped rapidly with sample size to less than twenty percent (Fig. 6). The CE's increased dramatically when the recovery rates differed between zones, mostly reflecting the corresponding increase in bias (Fig. 7).

The trends in the CE's also indicate that localized increases in recovery rates may improve the precision of local estimates at the expense of the precision of estimates for the other areas. The CE's in area 2 went down with increased recovery rates in zone B, but the CE's in area 1 went up. This effect, however, is largely an artifact of keeping the sample size fixed; increasing the fraction of recoveries near area 2 directly decreases the effective sample size for area 1 and vice-versa. In reality, local increases in recovery rates should add to the number of local recoveries more than they subtract from the number of recoveries elsewhere, unless the overall recovery rates are very high and there is a great deal of mixing between zones.

Discussion

The methods advanced in this article are fundamentally different from those cited previously because they predict trajectories rather than local abundance. Abundance-based and trajectory-based approaches both assume that tagged and untagged populations move the same way, but they differ in the ancillary assumptions they make. Abundance-based estimators, by their very nature, must enumerate a very large number of assumptions regarding processes that could affect the local abundance of the tags. In contrast, the trajectory-based estimators discussed so far disregard everything but velocity.

It was demonstrated earlier that trajectory-based estimators can produce unbiased estimates of the advection field for the population in general provided that either the tag recovery rates are homogeneous in space and time or the velocity variance is small. If neither of the above conditions are met, the estimates may be biased because faster individuals are more likely to move through regions with different recovery rates and may, therefore, be overrepresented or underrepresented in the sample. This is true even if the data are obtained from archival tags. The simulation experiments, however, indicated that the bias may not be too severe unless the recovery rates differ a great deal between areas. Moreover, recovery rates generally will not be a factor when the tags are tracked by radio, ultrasonic, or visual means.

These conclusions suggest that trajectory-based methods are appropriate for many real data sets. In addition, in many cases they may be much more practical than abundance-based methods. Although all of the derivations so far have been in one dimension, it is relatively simple to extend the methodology to include two or three dimensional movements, as is done in the second subsection. Finally, a third subsection is devoted to discussing the possibilities for adjusting the estimators to account for strongly inhomogeneous recovery rates.

Practical utility of trajectory-based estimators

Trajectory-based estimators have several advantages over their abundance-based counterparts. First, whereas trajectory models operate in continuous space and time, tag abundance models are obliged to operate in discrete space and time (one cannot speak meaningfully of the numbers of tags recovered at infinitesimal points). Thus, abundance models suffer from truncation errors that occur when different positions are lumped in the same category. If the time and space grid is fine enough, the truncation error will be minimal, but there may then arise the practical estimation problem of having very few observations in any given space-time category.

A second practical advantage relates to the choice of models. Both trajectory-based and abundance-

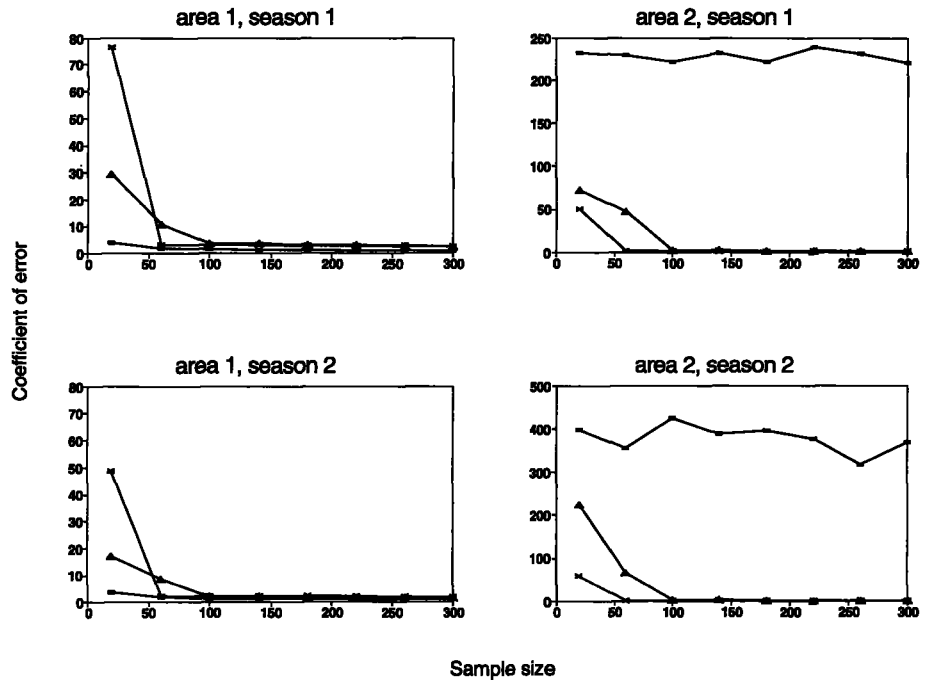

Figure 4

Coefficients of error of the estimates for the parameters of the discrete model under weak diffusivity. The three curves in each graph correspond to zone B recovery probabilities of 0.0 (squares), 0.1 (triangles), and 1.0 (crosses).

based methods must prescribe a velocity model, but the latter must also specify models for a great many other processes. Even if the velocity model is correct, abundance-based estimates may still be biased if any of the models for the other components are misspecified. Furthermore, because abundance-based methods estimate many parameters, they tend to require a large amount of data. In the absence of such a large data base, trajectory-based approaches may be the only reasonable option.

Another attractive feature of trajectory-based approaches is that they naturally accommodate data from archival tags. The chronological sequence of n position updates from each tag can be treated as though it were a sample of n independent tags with short liberty times. Conventional abundance-based methods cannot take advantage of this additional information.

Trajectory-based approaches do have their limitations. One is that they are not useful for assessing aspects of the population dynamics other than velocity. This point is especially important when the behavior of the population is being investigated within a management context. Under these circumstances abundance-based methods would seem to be the more viable option because they can, at least in principle, be formulated to estimate any relevant parameter. The enormous number of parameters required of such models, however, compromises the efficiency of the parameter search. Moreover, abundance-

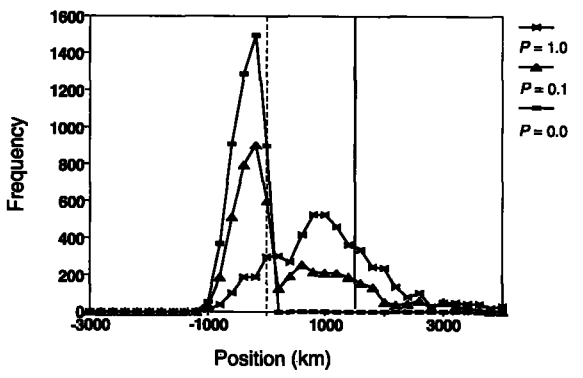

Figure 5

Distribution of 2,000 recovery positions generated by using the discrete advection model and weak diffusivity. The legend refers to the probability (P) of recovering a tag in zone B (right side of dashed vertical line). The solid vertical line marks the boundary between areas 1 and 2.

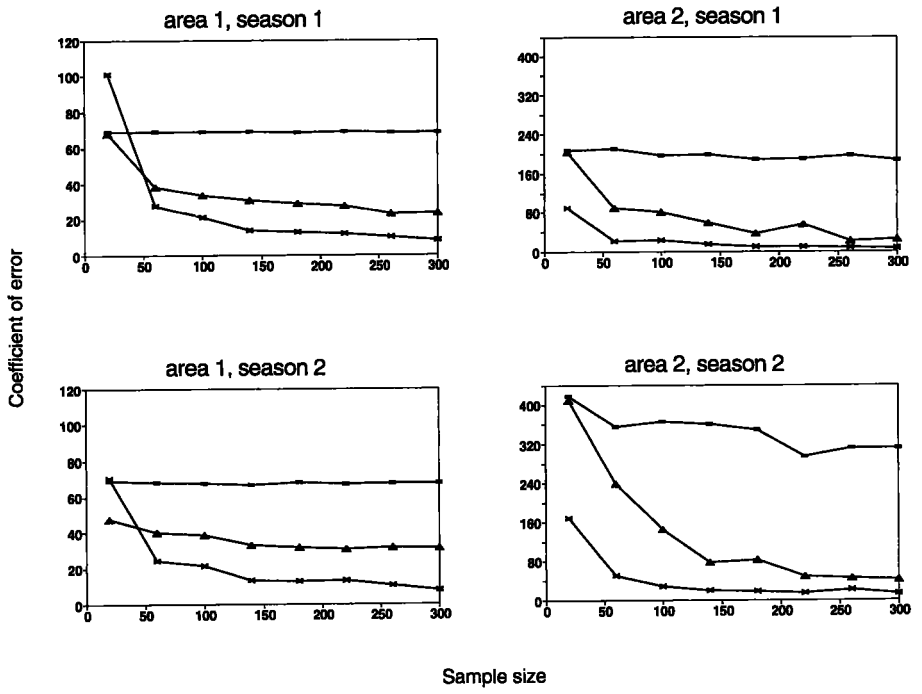

Figure 6

Coefficients of error of the estimates for the parameters of the discrete model under strong diffusivity. The three curves in each graph correspond to zone B recovery probabilities of 0.0 (squares), 0.1 (triangles), and 1.0 (crosses).

based estimates of movement and of certain other parameters, such as fishing mortality, are highly correlated (Hampton, 1991; Porch et al. in press; Aldenberg[1]). A number of competing hypotheses may return similarly low values of the objective function. Trajectory-based methods may prove very useful in this regard by supplying independent estimates of the velocity field that can be fixed in the abundance-based model. This would both reduce the dimensions of the search and eliminate some of the correlation problems. Another possibility might be to combine the abundance and trajectory-based approaches by including both formulations in the objective function.

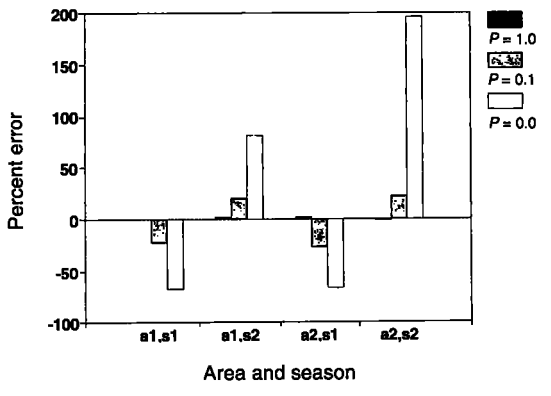

Figure 7

Percent error of the estimates for the parameters of the discrete model under strong diffusivity. The legend refers to the probability (P) of recovering a tag in zone B.

The most important limitation of trajectory-based estimators is that there is no guarantee that they are unbiased unless either the diffusive displacements are negligible relative to the advective displacements or the recovery rates are fairly homogeneous. Fortunately, the validity of the first assumption can be inferred rather easily from the output of the model itself. Estimates of the mean-square dispersion, which reflects the level of velocity variance, can be obtained by using Equation 17. If the square-root of the estimated mean-square dispersion is negligible compared with the actual displacement of the

[1] Aldenberg, T. 1975. Virtual population analysis and migration: a theoretical treatment. ICES Working Document (Counc. mtng.) 1975/F, 32 p.

tag, then the estimated advection field should be relatively accurate. Otherwise the estimates may be biased, either because the velocity variance is large or because the advection model is poorly specified.

The simulation results revealed that the estimators were essentially unbiased when the low level of diffusivity was used in generating the data. The root-mean-square displacements associated with this level of diffusivity were on the order of two percent of the advective displacements. This suggests that random displacements of at least two percent, and perhaps much larger, can be considered "negligible." Simulations that are tailored to specific situations are recommended to determine more accurately the tolerance of any particular application.

Extensions to multiple dimensions with boundaries

The mathematical derivations in this paper were developed in one dimension and without regard to barriers, primarily to simplify the presentation. It may sometimes be convenient to describe tag motion in this manner, such as when the tags are embedded in a major ocean current. Otherwise, the methods can easily be extended to accommodate more complicated scenarios.

Multiple dimensions can be incorporated by constructing dimension specific components in the objective function, e.g.

$$\sum_i \frac{(x_i - \hat{x}_i)^2}{\beta_x T_i} + \frac{(y_i - \hat{y}_i)^2}{\beta_y T_i},$$

where β_x and β_y are the diffusivity parameters in the two-dimensional space spanned by the coordinates x and y. The predicted positions are then obtained by integrating the differential equations describing the advection field in the two-dimensional space. Although multidimensional equations of motion are typically more difficult to solve analytically than their one-dimensional counterparts, they can always be integrated numerically. The other alternative is to use discrete approximations, in which case the motion along each dimension can be treated independently and no further modifications to the methods are necessary. The x and y positions of each tag are then predicted by separate parameterizations of Equations 11 and 12.

Barriers to tag motion, such as coastlines or thermal fronts, tend to preclude analytical solutions to the equations of motion but are relatively easy to handle in a numerical context. The position of each tag is updated at regular intervals by numerically integrating the velocity equations. When the tag encounters the barrier, it reacts according to some prescribed behavior pattern. Subsequently, the numerical integration proceeds as described earlier. The appropriate behavior prescription depends on the type of barrier and the nature of the tagged object. Some common choices include reflecting, absorbing, and sticking barriers—but the suite of possibilities is endless.

Extensions to incorporate variable recovery rates

This part of the article addresses the possibility of modifying trajectory-based estimators to accommodate situations where the diffusive displacements are not negligible and the recovery rates are not homogeneous in time and space. The matter essentially condenses to determining the theoretical probability density of the position of recovered tags so that an appropriate maximum-likelihood solution can be formulated. The predictor is not an issue because it is, by nature, independent of the recovery rates.

The simplest way to approach the problem is in terms of sampling strategies. Each recovered tag can be thought of as a nonrandom selection from the underlying probability density of the tagged population. Tags recovered at any specific location x are therefore misrepresented in the sample by a factor $P_R(x)$, which is the probability of recovering a tag at x. For example, if the underlying probability density for the in situ positions of the tags was the normal distribution with variance βT, then the adjusted objective function would be

$$\sum_i \frac{(x_i - \hat{x}_i)^2}{P_R[x_i] T_i}. \tag{20}$$

The correction factor P_R can be any measure of the relative likelihood of a tag arriving at any given position. In principle, it can be expressed as a function of the parameters of the underlying models of the population dynamics and estimated as part of the overall parameter search. Towards this end, it is important to recognize that the only relevant recovery processes are those that vary among tags. For example, if faster individuals were not significantly more likely to shed their tags than were slower individuals, then tag-shedding would be irrelevant to trajectory-based models regardless of its magnitude. The same would not be true for abundance-based models because tag-shedding would help to determine the total number of recoveries. Thus it should be possible to adjust trajectory-based estimators so that there are fewer parameters than those required by abundance-based estimators.

Bayliff and Rothschild (1974) developed an approximate procedure for adjusting Jones's estimators by the level of fishing effort at the time and place each tag was recovered. A similar procedure could be applied to the estimators developed here by appropriately weighting the objective function. Equation 19, for example, could be modified to read

$$\sum_i \frac{(x_i - \hat{x}_i)^2}{f_i T_i},$$

where f_i is the observed fishing effort in the area where the i'th tag was recovered. Variations in other factors, such as natural mortality and nonreporting, could be treated analogously. Bayliff and Rothschild pointed out that this method of adjustment does not account for the effort in the time-area strata encountered by the tag before its recovery. Even so, such approximate adjustments may be sufficient to reduce the degree of bias to negligible levels. If true, the estimation problem associated with Equation 20 would be simplified considerably. This is an area that deserves more attention, perhaps on an ad hoc basis via simulations.

In some situations it may be possible to circumvent the problem of inhomogeneous recovery rates by dividing the feasible domain into regions where the recovery rates are approximately constant and by estimating the advection field in each region separately. Tags of fish at liberty long enough to have strayed into any of the other regions would be excluded from the analysis.

Acknowledgments

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Appendix

Define a function G such that

$$\int_{x_0}^{x} \frac{dx}{u[x]} = G[x] - G[x_0],$$

where x is the tag's current position in space, x_0 is the tag's initial position, and u is the velocity.

Then

$$\frac{d}{dx}\int_{x_0}^{x} \frac{dx}{u[x]} = \frac{dG[x]}{dx}.$$

From the fundamental theorem of integral calculus

$$\frac{1}{u[x]}\frac{dx}{dx} - \frac{1}{u[x_0]}\frac{dx_0}{dx} = \frac{dG[x]}{dx},$$

which reduces to

$$u[x] = \frac{1}{\frac{dG}{dx}}.$$

On the development of year-class strength and cohort variability in two northern California rockfishes

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Abstract.—We attempt to determine at what point in the early life history year-class strength is established in two species of rockfish, *Sebastes mystinus* and *Sebastes flavidus*. We compare abundance estimates of young-of-the-year rockfish before and after settlement to determine whether this life history transition alters relative year-class strength. Estimates of pelagic juvenile abundance obtained in midwater trawl surveys and indices derived from direct underwater observations of settled juveniles over a common 10-year period (1983–92) were in good agreement (r=0.58–0.86). Trends in rockfish year-class strength were similar, in spite of substantial spatial separation between the trawl and nearshore study areas (50–350 km) and differences in the timing of the surveys (2–4 months). Thus, settlement seems to have little effect on relative year-class strength. Estimates of stage-specific interannual cohort variability show that coefficients of variation (CV's) for five species of late-stage pelagic juvenile rockfish ranged from 0.96 to 2.25. Cohort variability measured at recruitment to the fishery (2–7 years) is much less (CV's=0.60–1.39), suggesting that year-class strength has been determined by the late pelagic juvenile phase. Because cohort variability declines from the recently settled juvenile stage to the age at recruitment to the fishery, some form of compensatory mortality may ameliorate interannual differences in reproductive success.

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Fishery Bulletin 93:710–720 (1995).

Interannual fluctuations in reproductive success lead to substantial recruitment variability in fisheries. Understanding the causes of this variability is an important management issue. However, the problem has yet to be solved despite prolonged, intensive study (Cushing, 1973; Sissenwine, 1984; Rothschild, 1986). A number of investigators have argued that the greatest potential for regulation of year-class size occurs during the larval stage (e.g. Shepherd and Cushing, 1980; Houde, 1987). Likewise, Smith (1985) has shown that in northern anchovy, *Engraulis mordax*, dominant year classes arise only when larval mortality rates are low. Others have suggested that population regulation occurs later in the juvenile period (Beverton, 1984; Sissenwine, 1984; Sissenwine et al., 1984).

To identify at what point during the early life history of fish year-class strength is established, investigators have correlated young-of-the-year abundance measures with later stage recruitment indices. Dementjeva (1964) demonstrated a strong positive correlation between the catch rate (CPUE) of "one summer-old" Caspian bream, *Archosargus rhomboidalis*, in fishery-independent surveys and recruitment indices derived from virtual population analysis (VPA) of the catch. Peterman et al. (1988) tested Lasker's (1975) hypothesis that the annual abundance of northern anchovy recruits is fixed at an early life history stage by comparing abundances of eggs, 4.5-day-old yolk-sac larvae, and 19-day-old larvae, with estimates of age-1 recruits derived from an age-structured analysis of the catch. They found very low correlations (r=–0.09 to 0.07, n=13) and concluded that year-class strength is determined at some point after age 19-day. Similarly, Bailey and Spring (1992) examined the relationship between survey estimates of walleye pollock, *Theragra chalcogramma*, larvae (15 mm SL) and young-of-the-year juveniles (50–130 mm FL) with the numbers of age-2 fish that had recruited to the fishery from a tuned VPA. They reported a good correlation between young-of-the-year juveniles and age-2 fish (r=0.69), but the association between larval abundance and age-2 fish was not significant (r=0.36). Like Smith (1985) they concluded that strong year classes are the result of good larval survival.

Bradford (1992) modeled early life history dynamics and the recruitment process using information assembled from the literature. Owing to poor correlations between the abundance of small larvae and subsequent recruitment, he concluded that year classes are fixed after the early larval period. He also showed that precise predictions of

year-class strength are feasible under a variety of scenarios, if abundance is indexed following juvenile metamorphosis.

The reproductive biology and early life history of *Sebastes* is distinctive (Boehlert and Yamada, 1991). All rockfishes are livebearers, displaying a primitive form of viviparity (Boehlert et al., 1987; Wourms, 1991). Along the west coast of North America, most commercial species of rockfish copulate around September, but fertilization may not occur until weeks, or even months, later (Wyllie Echeverria, 1987). Hatching occurs in the ovary after 25–35 days of embryonic development, and parturition occurs approximately five days later at about the time of yolk-sac absorption (Eldridge et al., 1991; Yamada and Kusakari, 1991). In the central and northern California region, parturition of most commercial species occurs in late fall, winter, and early spring but is most concentrated from January to March (Wyllie Echeverria, 1987; Moser and Boehlert, 1991).

Rockfish larvae typically are found in the upper mixed layer (Ahlstrom, 1961; Ralston et. al.[1]), where they grow slowly until flexion is complete at an age of about 25 days (Laidig et al., 1991). Late larvae (10–20 mm SL) are distributed well offshore (Moser and Boehlert, 1991); at this stage growth rate increases. Late larvae then metamorphose into a pelagic juvenile stage characterized by attainment of mature meristics and pelagic coloration (Moser et al., 1977; Matarese et al., 1989; Moser and Boehlert, 1991). Growth of pelagic juveniles, which feed primarily on copepods and on both larval and juvenile stages of euphausiids (Reilly et al., 1992), can be quite rapid (0.3–0.6 $mm \cdot d^{-1}$) (Woodbury and Ralston, 1991). As pelagic juveniles approach sizes that are competent to settle (30–90 mm SL, depending on the species), they move deeper in the water column (Lenarz et al., 1991) and closer to shore (Larson et al., 1994). These changes in spatial distribution occur at a time of maximum offshore Ekman transport of the ocean's surface layer and onshore recirculation of subsurface waters (Mooers et al., 1978; Largier et al., 1993). Peak settlement to demersal nearshore habitats occurs during the upwelling season from May to July (Carr, 1983; Love et al., 1991), after the fish have spent from 3 to 6 months as plankton and micronekton. Settlement usually occurs in relatively shallow water and, after a period of several months to a year, many species begin to move into adult habitats located in deeper water (Love et al., 1991).

In this study, we attempt to determine at what point in the life history year-class strength becomes fixed in two species of rockfish, i.e. blue rockfish, *Sebastes mystinus*, and yellowtail rockfish, *Sebastes flavidus*. Of particular interest is the influence of settlement on interannual variations in reproductive success. We compare abundance estimates of young-of-the-year juvenile rockfish that were gathered before and after settlement to determine if this life history transition alters relative year-class strength. The comparison is based on two separate fishery-independent surveys conducted over a 10-year period (1983–92). In addition, we examine the relationship between sea-surface temperature (SST) during the larval period and estimates of year-class strength.

For the arguments developed here, we assume that during the study period variation in year-class strength of blue and yellowtail rockfish was due to interannual differences in reproductive success and not to fluctuations in spawning biomass. Given the generally weak relationship between recruitment and spawning stock (Cushing, 1973), this is not an unreasonable assumption, particularly since *Sebastes* are slow-growing species with low rates of natural mortality (Leaman and Beamish, 1984). Nonetheless, yellowtail rockfish have been the focus of a substantial commercial fishery for many years, even though the fishery operates primarily to the north of our study region (Tagart[2]).

Materials and methods

Midwater trawl surveys

Annual trawl surveys designed to estimate the distribution and abundance of pelagic juvenile rockfishes along the central California coast have been conducted aboard the RV *David Starr Jordan* since 1983 (Wyllie Echeverria et al., 1990). Cruises have been conducted during May and June when the pelagic juvenile-stage fish are most susceptible to capture by midwater trawling. These surveys use a modified 26 × 26 m Cobb midwater trawl, with a codend liner of 1.27-cm stretched mesh. Beginning in 1986, three spatially replicated "sweeps" of a series of standard stations were conducted in a study area bounded by Point Reyes and Cypress Point (Fig. 1); from 1983 to 1985 only one sweep was completed per year. As part of the survey design, the area was subdivided

[1] Ralston, S., J. R. Bence, M. B. Eldridge, and W. H. Lenarz. 1993. Estimating the spawning biomass of shortbelly rockfish (*Sebastes jordoni*) in the region of Pioneer and Ascension Canyons using a larval production method. Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Dr., Tiburon, CA 94920. Unpubl. manuscr.

[2] Tagart, J. V. 1993. Status of the yellowtail rockfish resource in 1993, Appendix E. *In* Appendices to the Status of the Pacific Coast groundfish fishery through 1993 and recommended acceptable biological catches for 1994. Pacific Fishery Management Council, 2000 SW First Ave., Suite 420, Portland, OR.

into seven geographical strata, with five to six standard stations located within each stratum. At each station a 15-minute nighttime trawl sample was taken at standard depth (30 m where possible, 10 m at shallow stations). Following the cruise, identification of rockfish specimens was confirmed in the laboratory, standard lengths were measured, and a subsample of otoliths were collected.

Abundance indices for pelagic juvenile rockfish were adjusted to account for interannual differences in the size structure of the catch. After truncating the data to include only the fully vulnerable portion of the catch (i.e. SL ≥25 mm; Woodbury[3]), additional adjustments were performed in a two-step process. Individual fish ages were predicted from standard length [SL] measurements by using linear inverse growth curves (age=f[SL]) that were estimated for each species during the 10-year period from 1983 to 1992. Specifically, the predicted age of species s in year y at standard length l is $\hat{\tau}_{syl} = \alpha_{sy} + \beta_{sy} l$, where the α_{sy} and β_{sy} were estimated by least-squares regressions of age-length data gathered from microscopic examination of otolith daily increments (see Laidig et al., 1991; and Woodbury and Ralston, 1991). If otolith data were unavailable in a particular year, growth parameters were estimated from an analysis of covariance of all the yearly data, by assuming a common slope (days·mm^{-1}) and the mean of interannual intercepts.

For each haul conducted and each species sampled (subscripts not included), abundances of fish of different ages were then adjusted to a common age by using an exponential model with a constant mortality rate (Z), i.e.

$$N_l^* = N_l \exp\left[-Z(\tau^* - \hat{\tau}_{syl})\right],$$

where N_l^* is the adjusted number of individuals of length l, N_l is the unadjusted number, and τ^* is the common age to which abundances were adjusted. In all calculations τ^* was set equal to 100 d, which is generally representative of pelagic juvenile rockfish ages during May–June (Woodbury and Ralston, 1991), and Z was fixed at 0.04 d^{-1}. This latter figure was based on combined estimates of mortality rate for 1) larval shortbelly rockfish, *S. jordani* (Ralston et al.[1]); 2) settled juvenile blue rockfish (Adams and Howard[4]); 3) pelagic juvenile Pacific cod, *Gadus macrocephalus*, and northern anchovy (Bradford, 1992); and 4) pelagic juvenile Pacific whiting, *Merluccius productus* (Hollowed, 1992). The N_l^* were then summed over all lengths occurring within a haul, yielding a haul-specific catch of each rockfish species sampled that was adjusted for variability in length composition.

Final calculation of abundance statistics from our midwater trawl surveys was based upon simple logarithmic transformation of the data, i.e. $y_{jk} = \log_e[x_{jk} + 0.1]$, where x_{jk} is the length-adjusted catch taken in haul j located in stratum k = 1 to 7. We estimated the individual stratum means, variances, and standard errors for each sweep using conventional procedures appropriate to a stratified sampling design (Cochran, 1977). The equally weighted stratified mean was then used as a sweep-specific index of pelagic juvenile abundance. Lastly, because the availability of pelagic juveniles to midwater trawling shows marked seasonal change, the maximum value of the stratified mean (among sweeps completed in a year) was used to estimate relative annual abundance, i.e. year-class strength.

Direct underwater observation surveys

Nearshore assessments were made by underwater observers by using SCUBA at four locations on the northern California coast (Fig. 1). Two of the study sites, Dark Gulch (lat. 39°14'N; long. 123°46'W) and Salmon Point (lat. 39°12'N; long. 123°46'W) in Mendocino County, were monitored since 1983. In 1984, nearshore assessments were initiated at Horseshoe Point (lat. 38°36'N; long. 123°22'W) and at Fisk Mill Cove (lat. 38°35'N; long. 123°21'W) in Sonoma County, 100 km to the south.

Each study site covers approximately 0.5 ha and consists of high-relief rocky reefs surrounded by lower reefs and boulders, interspersed by occasional sand patches. Vertical water clarity was measured from the boat with a white, plastic Secchi disk 20 cm in diameter. Horizontal water clarity at a bottom depth of 10 m was determined by estimating the distance at which rock surfaces could be clearly observed. Counts were not made when conditions were turbulent, nor when visibility was less than 4 m.

Observations for estimating year-class strength began in late July, when settlement of pelagic juveniles was essentially complete, and continued through the end of September. Young-of-the-year fish were distinguished from older cohorts by their size (40–50 mm SL in July), and from other species by characteristic pigment patterns.

Strip-transect counts were made between the hours of 1000 and 1400 by observers using SCUBA over bottom depths of 5–22 m. At each study site,

[3] Woodbury, D. 1993. Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Dr., Tiburon, CA 94920. Unpubl. data.

[4] Adams, P. B., and D. F. Howard. Natural mortality of blue rockfish (*Sebastes mystinus*) during their first year in nearshore benthic habitats. Manuscript submitted to Fishery Bulletin.

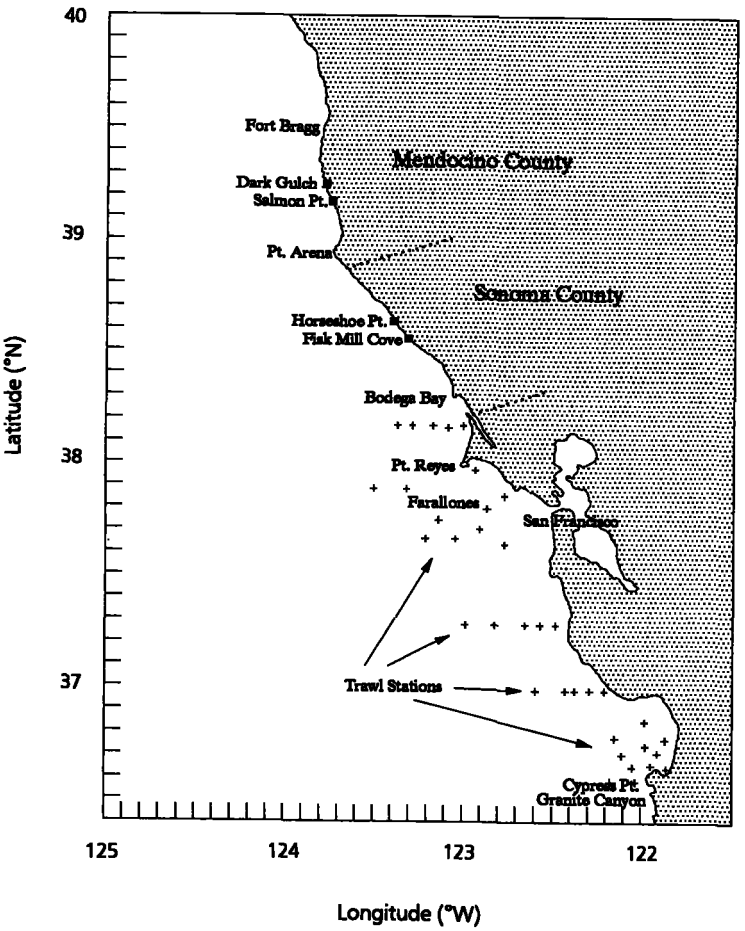

Figure 1

Map of the study area showing the location of trawl stations and diving sites where direct underwater observations of settled juvenile rockfish were made in Mendocino and Sonoma counties (1983–92). Temperature data were collected daily at Bodega Bay, the Farallon Islands, and Granite Canyon.

the abundance of young-of-the-year juveniles was assessed along haphazard transects by a series of timed 1-minute counts that covered approximately 20 m. Observers maintained a constant swimming speed, gazing ahead at all times during the counts. Transects started on the outside edge of the kelp bed and followed a series of arbitrary compass headings covering the offshore portion of the study site. After completing counts in deeper habitats, observers progressed into shallower water.

Species and number of juveniles observed each minute were recorded on a plastic slate with the aid of a watch fastened in the upper corner to monitor time. Observers swam 2 m off the bottom and counted young-of-the-year rockfishes within 3 m in any forward direction during the transect. After 1–3 counts the observer made right-angle changes in direction, which resulted in thorough coverage of the study area. The number of daily counts at a site ranged from 10 to 35 ($\bar{x}$=18.8).

Counts were excluded from data analyses when it was obvious that the distribution of juveniles was influenced by unusual conditions. For example, sampling sometimes coincided with a period of convergence when food-rich oceanic waters moved into nearshore surface layers. The distribution of juveniles was very different at these times, as they ascended into the upper 2 m of the water column to feed.

Annual indices of settled juvenile abundance were calculated separately for blue and yellowtail rockfish in Mendocino and Sonoma counties. Because variances increased with the means, individual strip-transect counts were first log-transformed to stabilize the variance. The annual index was then simply calculated as the mean of all counts, e.g.

$$I_{sct} = \frac{1}{n} \cdot \sum_{i=1}^{n} \log_e[C_{isct} + 1],$$

where I_{sct} is the index for species s in county c in year t, and n is the number of counts (C_{isct}) conducted; the sampling precision of the index is given by the standard error of the mean.

Interannual variability in year-class strength

As in many other species, recruitment in rockfish is highly variable and is described well by the log-normal distribution (Bence et al., 1993; Fogarty, 1993). An accepted way to portray relative levels of variation among different sets of data is through use of the coefficient of variation (CV). The CV of the log-normal distribution is unusual, being independent of the mean and equal to $[\exp(\sigma^2) - 1]^{1/2}$, where σ^2 is the variance of logarithms of the log-normally distributed variable (Johnson and Kotz, 1970).

To compare and contrast levels of variation in rockfish year-class strength at specific life history stages, CV's of annual time series were calculated. Because individual annual abundance statistics were usually

estimated with some error, given by the standard error of the mean, and because variance terms are additive, this measurement error was subtracted from the total interannual variance in year-class strength prior to calculation of the CV, i.e.

$$\sigma^2_{CV} = \sigma^2_{TOT} - \sigma^2_{\varepsilon}$$

$$CV = \sqrt{(e^{\sigma^2_{CV}} - 1)}.$$

An estimate of measurement error (σ^2_{ε}) was obtained as the mean of the squared standard error estimates ($s_{It}{}^2$) of the annual index I, averaged over the k years that data were available,

$$\hat{\sigma}^2_{\varepsilon} = \frac{1}{k} \cdot \sum_{t=1}^{k} s^2_{It}.$$

Likewise, the total variance in the index ($\sigma_{TOT}{}^2$) was estimated simply as the sample variance of the index (I_t),

$$\hat{\sigma}^2_{TOT} = \frac{1}{k-1} \cdot \sum_{t=1}^{k} (I_t - \bar{I}_t)^2$$

$$\bar{I}_t = \frac{1}{k} \cdot \sum_{t=1}^{k} I_t.$$

For small sample sizes (k<50) and large CV's (>2.0), there is a positive bias in this estimator (Finney, 1941). We determined the magnitude of the bias by Monte Carlo simulation (Naylor et al., 1966), and we applied a bias correction term to each CV estimated.

Shore station sea-surface temperature

Sea-surface temperature (SST) and salinity are recorded daily at the University of California Bodega Bay Marine Laboratory (BB), the Point Reyes Bird Observatory facility on Southeast Farallon Island (FI), and at the California Department of Fish and Game Laboratory at Granite Canyon (GC) (Walker et al., 1993). SST data from all three sites are generally indicative of hydrographic conditions offshore over the continental shelf (Fig. 1).

Interannual fluctuations in SST within the central California study region were estimated by using an analysis of variance (ANOVA) model applied to the shore station data, i.e.

$$SST_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \varepsilon_{ijk},$$

where SST_{ijk} is the sea-surface temperature recorded at shore station i {i=BB, FI, or GC} on calendar date j {j=1,..., 90} in year k {k=1980,..., 1992}, μ is the population mean SST, and ε_{ijk} is a normally distributed error term. Only the first 90 days of the calendar year were included in the analysis because blue and yellowtail rockfish are winter-spawning species (Wyllie Echeverria, 1987) and a measure of the average SST prevailing from birth to completion of the late larval stage was desired. Year effects (γ_k) in the model were obtained by calculating population marginal means (i.e. least-square means), providing year-specific estimates of SST at average levels of the α_i and β_j (see Searle et al. [1980] for further discussion).

Results

Annual abundance indices of pelagic juvenile blue and yellowtail rockfishes captured by midwater trawl were quite variable (Table 1; Fig. 2). The CV's of these abundance indices were 1.98 and 1.19, respectively, over the 10-year period from 1983 to 1992. Years of high abundance for both species were 1985, 1987, 1988, and 1991, whereas years of low abundance were 1983, 1986, and 1992.

A similar pattern was evident in the data collected by direct underwater observations of recently settled rockfish juveniles in Mendocino and Sonoma Counties (Table 1; Fig. 2), although levels of interannual variation in abundance for these species was somewhat greater. Specifically, estimated CV's ranged

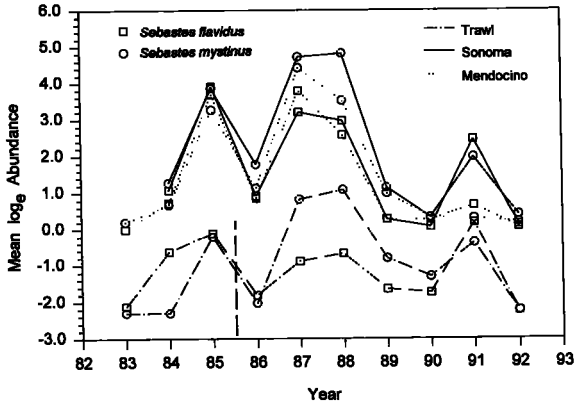

Figure 2

Interannual trends in the abundance of blue (*Sebastes mystinus*) and yellowtail (*Sebastes flavidus*) rockfishes based on trawl surveys of pelagic juveniles and direct underwater observations of settled young-of-the-year fish (1983–92). The dashed vertical line shows when the trawl survey was changed from one to three sweeps. (see Methods section).

Table 1

Coefficients of variation in rockfish year-class strength at selected life history stages. All pelagic and settled juvenile results are based on this study. Within-year measurement error (σ_ε^2) removed for egg, pelagic juvenile, and settled juvenile life history stages (see Methods section).

Species	Young-of-the-year			Entry to fishery
	Egg	Pelagic juvenile	Settled juvenile	
Sebastes mystinus	—	1.98	3.06–3.68	—
Sebastes flavidus	0.10[1]	1.19	2.59–2.69	0.60–0.87[2]
Sebastes entomelas	—	2.25	—	0.82[3]
Sebastes goodei	—	1.49	—	1.39[4]
Sebastes paucispinis	—	0.96	—	0.72[5]

[1] Eldridge and Jarvis (1995).
[2] Tagart (Footnote 2 in the text).
[3] Rogers and Lenarz. 1993. Status of the widow rockfish stock in 1993, Appendix B. *In* Appendices to the status of the Pacific Coast groundfish fishery through 1993 and recommended acceptable biological catches for 1994. Pacific Fishery Management Council, 2000 SW First Ave., Suite 420, Portland, OR.
[4] Rogers and Bence. 1993. Status of the chilipepper rockfish stock in 1993, Appendix D. *In* Appendices to the status of the Pacific Coast groundfish fishery through 1993 and recommended acceptable biological catches for 1994. Pacific Fishery Management Council, 2000 SW First Ave., Suite 420, Portland, OR.
[5] Bence and Rogers. 1992. Status of bocaccio in the Conception/Monterey/Eureka INPFC areas in 1992 and recommendations for management in 1993, Appendix B. *In* Appendices to the status of the Pacific Coast groundfish fishery through 1992 and recommended acceptable biological catches for 1993. Pacific Fishery Management Council, 2000 SW First Ave., Suite 420, Portland, OR.

from 3.06 to 3.68 for blue rockfish and from 2.59 to 2.69 for yellowtail rockfish. The observational data also indicated that 1985, 1987, 1988, and perhaps 1991, were relatively strong years, whereas 1983, 1992, and to some extent 1986, were weak years.

There were highly significant correlations between direct observation counts of settled juvenile rockfish at Mendocino and Sonoma Counties. For blue rockfish the correlation was 0.925 ($P<0.005$) and for yellowtail rockfish it was 0.887 ($P<0.005$). The greatest disparity in abundance between these localities occurred in 1991, when counts of the two species at Mendocino County were low, both in comparison with observations at Sonoma County and with catches in the trawl survey.

The time series of midwater trawl and direct observational data were also well correlated (Fig. 3). For example, results for blue rockfish, *Sebastes mystinus*, showed highly significant ($P<0.005$) positive correlations in excess of 0.80 at both the Mendocino and Sonoma sites. Similarly, the correlation between trawl survey estimates of yellowtail rockfish, *Sebastes flavidus*, abundance and direct counts of this species at Sonoma County ($r=0.799$) was significant ($P<0.01$). The comparison between the trawl data and Mendocino County counts ($r=0.577$) was marginally insignificant ($0.10 \leq P \leq 0.05$). Results were similar when comparisons were restricted to the time period 1986–92, i.e. when three repetitive sweeps of the trawl survey area were completed each year.

Not only were trends in the abundance of individual species at different study sites well correlated; so too were the interspecific abundance patterns of blue and yellowtail rockfish at each of the three specific study sites. For example, the time series of blue rockfish abundance at the Mendocino study site was highly correlated with the yellowtail rockfish series at the same site ($r=0.961$, $P<0.001$). At Sonoma, variations in the abundance of these two species was also closely linked ($r=0.906$, $P<0.001$), substantially more so than in the trawl data ($r=0.589$, $P=0.073$).

The substantial positive correlations among the data for each species (Figs. 2 and 3) suggest that principal component analysis (Green, 1978) would be effective in extracting the primary interannual signal jointly evident in all three time series (i.e. trawl, Mendocino, and Sonoma). Indeed, results for blue rockfish show that the first principal component alone accounted for 89% of the variation present in the three data series. Likewise, for yellowtail rockfish the first component accounted for 87% of the total variation.

Winter SST's along the central California coast, from Bodega Bay to Granite Canyon (Fig. 1), varied greatly during the period 1983–92. Population marginal means for the year factor (γ_k) in the ANOVA temperature model ranged from a low of 10.6°C in 1989 to a high of 13.5°C in 1983, an El Niño year. Typical winter SST's in the study region were 11.5-12.0°C. For the two other factors in the model, the shore station effect (α_i) showed that SST's at Bodega Bay were ~1.0°C cooler than at Southeast Farallon Island and at Granite Canyon, which were quite similar to one another. Likewise, the calendar date effect (β_j) showed clearly the onset of spring transition to upwelling conditions (Strub et al., 1987), evidenced by an abrupt cooling trend that started in mid-March.

Interannual variability in January–March SST's appeared to be related to observed differences in the abundance of pelagic juveniles captured by midwater trawl during May–June and of settled juveniles ob-

served in nearshore habitats in August–September (Fig. 4). For blue rockfish and yellowtail rockfish, it is apparent that the abundance of young-of-the-year juveniles was lowest when winter SST's were highest, as for example in 1983 and 1992. Both years were distinguished by strong El Niño events (Wooster and Fluharty, 1985; Hayward, 1993). There was also the suggestion that cold winter SST's may have adversely impacted survival of these rockfish to the juvenile stage, as evidenced by the data for 1989 and 1990. Conversely, increased numbers of juveniles occurred in years when SST was intermediate, especially in 1987 and 1988. Overall, these findings are consistent with a dome-shaped relationship between larval survival and winter temperature.

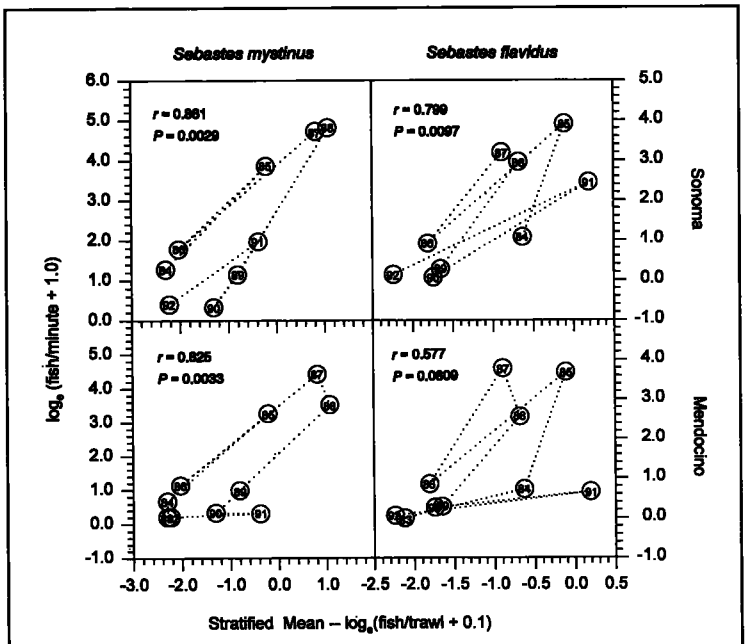

Figure 3

Scattergrams showing the relationship between estimates of year-class strength that are based on trawl surveys of pelagic juveniles (abscissae) and estimates that are based on direct observations of juveniles shortly after settlement (ordinates) for the period 1983–92.

Discussion

Biological synchrony and oceanographic scale

Our results show a broad spatial coherence in the temporal abundance patterns of young-of-the-year juvenile rockfish. The trawl study area is separated from Sonoma and Mendocino Counties by distances of 50–350 km (Fig. 1); yet interannual fluctuations in the abundance of blue and yellowtail rockfish at these sites are closely linked (Figs. 2 and 3). Even so, had there been closer spatial overlap between the trawl and nearshore study areas, the correlations probably would have been even higher. For example, our highest correlations between the annual abundance indices of pelagic and settled juveniles (0.861 and 0.799, Fig. 3) were for Sonoma County, the closer of the two nearshore sites to the trawl survey area.

Not only was there broad spatial agreement in the trends of blue and yellowtail rockfish, abundances of these species were highly correlated with one another. Strong and weak years closely mirrored each other over the 10-year study period (Fig. 2). Other studies have shown marked interannual synchrony among species of pelagic juvenile rockfish, in terms of growth rates and birthdate distributions (Woodbury and Ralston, 1991) as well as shifts in dietary composition (Reilly et al., 1992). These findings indicate that large-scale oceanographic processes are primarily responsible for the extensive interannual fluctuations in the abundance of young-of-the-year juvenile rockfishes.

This conclusion is in agreement with results from Hollowed et al. (1987), who showed extensive inter-

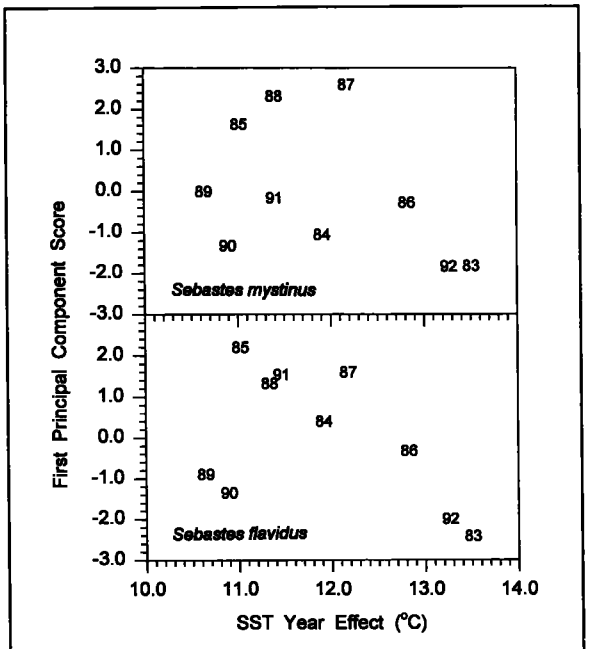

Figure 4

The relationship between interannual variability in sea surface temperature (SST) during the larval period (January to March) and combined estimates of year-class strength for blue (*Sebastes mystinus*) and yellowtail (*Sebastes flavidus*) rockfishes, 1983–92.

specific synchrony in the recruitment patterns of commercially harvested stocks on the west coast of North America, particularly on spatial scales similar to ours. Similar findings had been previously reported from commercial stocks in the northwest Atlantic (Koslow, 1984).

Although there is striking broad-scale synchrony in our data (Fig. 2), there is also reason to believe that in some years mesoscale differences in environmental conditions may strongly influence abundance patterns. For example, results from 1991 seemed to show an uncoupling of the abundance trends of blue and yellowtail rockfish at Mendocino County with those at Sonoma County, as well as with the trawl survey data (Fig. 2). That year was distinctive because northerly distributed species (e.g. *Sebastes emphaeus*, *Sebastes melanops*, and *Sebastes pinniger*) were relatively common in the trawl catches.

Ontogeny and year-class strength

Year-class strength in blue and yellowtail rockfish is apparently established prior to the late pelagic juvenile stage. The strong correspondence between estimates of year-class strength obtained from trawl surveys of pelagic juveniles collected during May–June and from direct observations of settled juveniles in nearshore habitats three months later indicates that reproductive success is governed primarily by events that occur earlier in the life history, presumably during the larval stage (Houde, 1987; Myers and Cadigan, 1993).

This is not to suggest that substantial mortality does not occur after the pelagic juvenile stage. Indeed, over the same time period (1983–92), the among-year variation in nearshore settled juveniles was much greater than that for offshore pelagic juveniles (CV's are presented in Table 1). However, because cohorts maintained their rank in year-class strength through the settlement transition to nearshore habitats (Figs. 2 and 3), the increased variability evident in the Mendocino and Sonoma data is not associated with a reordered strength of year classes.

A possible reason for the greater CV's of recently settled rockfish is that the data collected nearshore are more strongly affected by spatial patchiness in the distribution of young-of-the-year juveniles. Owing to the inherently broader spatial scale of the trawl survey (i.e. each tow covered ~1 km and the survey area extended 200 km in a north-south direction), this latter sampling method would have integrated spatial patchiness on the scale of 10^3–10^5 m. This hypothesis predicts a weakening of the correlation between pelagic and settled juvenile abundances with an increase in the difference in CV's. However, blue rockfish from Sonoma showed the greatest increase in CV through the settlement transition (1.98 to 3.68) and yet had the highest correlation with pelagic juvenile numbers (0.86).

A competing hypothesis to explain the apparent increase in CV's is that of depensatory mortality during settlement. This type of mechanism could further deplete already weak year classes, while having virtually no effect on strong ones. The result would be an increase in interannual variability in abundance without altering relative year-class strength. A logical source of depensatory mortality at settlement is predation by a predator assemblage, which takes a fixed number of settling fish each year. However, Hallacher and Roberts (1985) showed that many kelp-dwelling fishes prey heavily on blue rockfish at the time of settlement but not during the rest of the year (see below). Similarly, recent work by Hobson et al.[5] has shown that three kelp-forest inhabitants that are not highly piscivorous, i.e. *Hexagrammus decagrammus*, *Sebastes melanops*, and *Sebastes mystinus*, feed heavily on recently settled juvenile blue rockfish in years when settlement is strong. These studies indicate that compensation during settlement is more likely than is depensation.

Whatever the cause of the greater CV's of settled juveniles, the strong correspondence between trawl and diver estimates of year-class strength in blue and yellowtail rockfish indicates that reproductive success has been established by the end of the pelagic juvenile stage (see also Myers and Cadigan, 1993). By estimating levels of variability in fecundity, one can infer at a much earlier stage that interannual differences in spawning output are too small to account for fluctuations in recruitment to the fishery (Table 1; see also Shepherd and Cushing, 1980). A seven-year study of weight-specific fecundity in yellowtail rockfish (Eldridge and Jarvis, 1995) yielded an among-year CV of 0.10, after within-year measurement error was removed (see Methods section). This amount of variation is insufficient to account for fluctuations observed at the time rockfish cohorts recruit to the fishery.

Levels of variability at the young-of-the-year juvenile stage, however, are more than adequate. In fact, it would seem that rockfish go through a phase of compensatory mortality, from the settled juvenile stage to the time a cohort enters the fishery (i.e. ages 3–4 in rockfishes). Note that for a log-normal distribution, the CV of year classes recruiting to rockfish fisheries, based on recruitments estimated from

[5] Hobson, E. S., J. R., Chess, and D. F. Howard. 1995. Interannual variations in predation on juvenile *Sebastes* spp. by three northern California predators. Unpubl. manuscr.

catch-at-age analysis in which the stock-synthesis model and other age-structured methods are employed, is typically less than 1.00 ($\bar{x}$=0.84; Table 1). The "Entry to fishery" CV's presented in Table 1 were based on time series of recruitments ranging from 10 (*Sebastes goodei* and *Sebastes paucispinis*) to 25 years (*Sebastes flavidus*), although they did not all span the same time period.

A compensatory mortality source acting from postsettlement until recruitment to the fishery would tend to ameliorate year-class differences observed in the pelagic and recently settled juvenile stages. Two possible agents of compensatory mortality at this stage in life are 1) intraspecific competition for food (Shepherd and Cushing, 1980) or 2) a type-III functional response (sensu Holling, 1959) by predators (i.e. predator switching). Likewise, a rapid numerical response by predators could also lead to compensatory mortality.

There are other data to support this interpretation. Adams and Howard[4] provide data showing that blue rockfish experience compensatory mortality from the time they settle (August–September) until the following spring. They attributed the increased mortality rate experienced by strong year classes to predator switching. Hobson et al.[5] also describe predation on recently settled blue rockfish by *Hexagrammus decagrammus*, *Sebastes melanops*, and *Sebastes mystinus* (i.e. cannibalism), but only in years when settlement was particularly strong (see above). Likewise, Hallacher and Roberts (1985) showed low dietary overlap during the nonupwelling season among a kelp-forest assemblage of six *Sebastes* spp. However, when newly settled young-of-the-year rockfish became abundant during the upwelling season, these species fed heavily on the juveniles, and dietary overlap indices rose sharply. In addition, these authors observed other kelp-forest predator species feeding heavily on juvenile rockfish (*Ophiodon elongatus*, *Anarrhichthys ocellatus*, and *Scorpaenichthys marmoratus*). That a broad suite of predators capable of switching onto juvenile rockfish has been described provides a plausible compensatory mortality mechanism. Similar conclusions regarding the importance of compensatory mortality in recently settled plaice, *Pleuronectes platessa,* living in the North and Wadden Seas have been drawn by Lockwood (1980), Zijlstra et al. (1982), and van der Veer (1986).

It is a widely held precept that stage-specific mortality rates generally decrease with ontogeny, while stage duration increases concomitantly (Miller et al., 1988; Bradford, 1992). Because the total stage mortality is the product of the instantaneous mortality rate and the stage duration ($M \cdot t$), an increase in duration may more than offset a decrease in rate (Shepherd and Cushing, 1980). This has led some to suggest that population regulation may occur during the juvenile phase of the life history (Beverton, 1984; Sissenwine, 1984; Sissenwine et al., 1984). Our findings indicate that rockfish year-class strength is probably determined at some point in the larval phase, which lasts at least 50 days in *Sebastes jordani* (Laidig et al., 1991). Upon completion of the larval stage, however, compensatory density dependence in the settled juvenile phase seems to reduce cohort variability.

We have argued that recruitment success in these species of rockfish is governed by large-scale oceanographic processes (see also Mearns et al., 1980). There is evidence that year-class strength depends on the thermal environment at the time of spawning (Fig. 4), although we use SST only as a simple proxy for some complex set of covarying physical variables. However, the association between these variables is nonlinear; apparent year-class failures occur at the extremes of the continuum. This conclusion is supported by the findings of Ainley et al. (1993), who showed that the early summer occurrence of pelagic juvenile rockfish in the diet of a seabird (common murre, *Uria aalge*) was parabolically related to upwelling in January and February. Too little or too much upwelling during the rockfish spawning season had a negative impact on the availability of pelagic juvenile rockfish six months later. Notably, upwelling and SST in that study were inversely correlated. Cury and Roy (1989) have also argued that recruitment success of pelagic fish stocks in upwelling systems is greatest at an intermediate point along the environmental continuum, although they argued that wind speed is the forcing mechanism.

Summary

We argue that events occurring in the larval period are primarily responsible for determining the success or failure of rockfish year classes in central California. Moreover, on the basis of a consideration of intra- and interspecific synchrony and oceanographic scale, physical factors seem to have the greatest impact on larval survival. Consequently, to the extent that recruitment limits stock size in rockfish, population regulation is based on larval dynamics. However, compensatory mortality in the juvenile phase may ultimately limit population growth. Like Myers and Cadigan (1993), we believe that the interplay between stochasticity in the larval period and compensation in the juvenile phase plays a seminal role in structuring rockfish population dynamics.

Acknowledgments

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Description of larval and pelagic juvenile chilipepper, *Sebastes goodei* (family Scorpaenidae), with an examination of larval growth

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Abstract.—Developmental series of larval and pelagic juvenile chilipepper, *Sebastes goodei,* collected off central California were described and illustrated. Pigment patterns were recorded on pre-extrusion larvae through fish in the pelagic juvenile stage, along with the number of dorsal-, anal-, and pectoral-fin rays. The number of gill rakers on the first gill arch, morphometric data, and the development of head spines were also recorded on selected specimens. In addition, otoliths were used to help confirm the identifications of early larvae given the distinctive pre-extrusion optical pattern found in *S. goodei.* For comparison, otoliths were examined on other *Sebastes* spp. commonly found in the region that had pigment patterns similar to, but slightly different from, those of *S. goodei.* Ages were obtained from *S. goodei* and other *Sebastes* spp. otoliths.

Early larvae of *S. goodei* were identified by their lack of pigment on the lower jaw, the cleithral region, and both the caudal and hypural areas, and by the presence of pigment on the cranium and the outer blade of the pectoral fin. Juvenile *S. goodei* were readily identified by their distinctive barred pattern. The distinctive pre-extrusion optical pattern was observed in 96% of *S. goodei* otoliths, as well as a significantly larger extrusion check radius than that in the otoliths of other *Sebastes* spp. Larval growth rates for *S. goodei* calculated from otolith age data appeared to be slower than those previously reported for pelagic juveniles.

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The genus *Sebastes* (family Scorpaenidae) is a diverse group in the eastern Pacific Ocean comprising 72 species (Kendall, 1991), 59 species of which are known to occur off California alone (Eschmeyer et al., 1983). Off California, *Sebastes* spp. form a substantial portion of the groundfish fishery (PFMC[1]). Currently, the preflexion larvae of 51 species occurring off California have been described (Morris, 1956; Westrheim, 1975; Moser et al., 1977; Moser and Ahlstrom, 1978; Moser and Butler, 1981; Stahl-Johnson, 1985; Moser and Butler, 1987; Matarese et al., 1989; Wold, 1991; Moreno, 1993; Laroche[2]), but accurate identification of field-caught larvae is difficult owing to small interspecific differences and relatively large intraspecific variability (Moser et al., 1977; Kendall, 1991; Wold, 1991; Moreno, 1993). Descriptions are usually obtained from laboratory-reared larvae extruded from females of known identity or from a size series of field-caught specimens (Kendall and Lenarz, 1987; Kendall, 1991). Electrophoretic patterns have also been useful in the identification of larval *Sebastes* spp. (Seeb and Kendall, 1991). The ability to readily identify *Sebastes* larvae could facilitate their use in recruitment studies and larval production biomass estimates (Moser and Butler, 1987; Hunter and Lo, 1993; Ralston et al.[3]).

Chilipepper, *Sebastes goodei,* is an important component of the groundfish fishery off California (mainly south of Cape Mendocino) (PFMC[1]). Individuals attain a maximum age of 21 years and a maximum size of 59 cm total length (TL); both males and females reach maturity from 3 to 6 years of age (Wilkins, 1980; Wyllie Echeverria, 1987). Spawning mainly occurs from November through March off northern and central California (Wyllie Echeverria, 1987). Partial descriptions currently exist for recently extruded larvae, 5.7 to 5.8

[1] PFMC (Pacific Fishery Management Council). 1993. Status of the Pacific coast groundfish fishery through 1993 and recommended acceptable biological catches for 1994. Pacific Fisheries Management Council, Portland, OR, 96 p.

[2] Laroche, W. A. 1987. Guide to larval and juvenile rockfishes (*Sebastes*) of North America. P.O Box 216, Enosburg Falls, VT 05450. Unpubl. manuscr., 311 p.

[3] Ralston, S., J. R. Bence, M. B. Eldridge, and W. H. Lenarz. 1993. Estimating the spawning biomass of shortbelly rockfish (*Sebastes jordani*) in the region of Pioneer and Ascension Canyons using a larval production method. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Drive, Tiburon, CA 94920. Unpubl. manuscr., 32 p.

mm notochord length (NL)(Morris, 1956; Moser et al., 1977; Matarese et al., 1989; Laroche[2]), and for a 37.0-mm standard length (SL) pelagic juvenile (Matarese et al., 1989; Laroche[2]).

The purpose of this study is to describe the development of *S. goodei* from pre-extrusion larvae to the pelagic juvenile stage. In addition, the age and growth of early larvae were examined.

Methods

Specimens of larval and pelagic juvenile *S. goodei* were obtained from cruises conducted aboard the NOAA RV *David Starr Jordan* by using bongo nets with 0.505-mm mesh, a 5-m^2 Methot Isaacs-Kidd (MIK) trawl with 2-mm mesh and a 0.505-mm codend, and a 26 m × 26 m mid-water trawl with a 12.7-mm stretched-mesh codend liner. Bongo-net collections were made in February 1991 and 1993, MIK collections in March 1992 and 1993, and mid-water trawl collections in May and June 1992 and 1993. Specimens from bongo and MIK collections were preserved in ethanol (EtOH) (80% for the 1991 bongo collection and 95% for all others), whereas mid-water trawl specimens were frozen. Pre-extrusion larvae were collected from four adult females captured in January 1991 and were preserved in ethanol (initially 80%, but later transferred to 95%). Although preservation in ethanol causes shrinkage (Laroche et al. [1982] observed 3.2% shrinkage in larval English sole, *Pleuronectes vetulus,* preserved in 80% ethanol), the rate of shrinkage decreases with increased fish size (Radtke, 1989). Therefore, while discrepancies in SL due to different preservation methods could have occurred in using the frozen midwater trawl specimens along with the ethanol-preserved MIK trawl specimens, these fish were probably large enough (>24 mm SL) that the shrinkage rate was negligible relative to total size. All samples were collected off central California between Cypress Point (36°35'N latitude) and Salt Point (38°35'N latitude).

A total of 283 fish were examined, including 138 large specimens (>20 mm SL), 130 small specimens (<20.1 mm SL), and 15 pre-extrusion larvae. Large specimens were identified from meristic characters and pigment patterns (i.e. melanophore patterns, because other pigments such as xanthophores are not retained well in ethanol [Matarese et al., 1989]) as described previously in Chen (1986), Matarese et al. (1989), Moreland and Reilly (1991), and Laroche.[2] Small specimens were initially identified by using pigment patterns developed from a size series (Kendall and Lenarz, 1987) based on the pigment patterns of pre-extrusion larvae and on the smallest individuals with complete meristic characters. Pigment patterns were recorded on each specimen examined. Dorsal-, anal-, and pectoral-fin ray counts were recorded on specimens >8.1 mm SL, and the number of gill rakers on the first gill arch were recorded on a subset of 50 large specimens.

Morphometric data, including head length, snout length, snout to anus distance, eye diameter, body depth at the pectoral fin base, body depth at the anus, and pectoral fin length, were taken on 20 specimens (all preserved in 95% ethanol) ranging in size from 5.3 mm NL to 22.0 mm SL. Measurements were recorded in mm by using a dissecting microscope connected to a video camera and computer. Terminology for morphometrics followed Richardson and Laroche (1979).

In order to examine the development of head spines, 20 specimens ranging in size from 6.1 mm NL to 22.0 mm SL were stained with Alizarin Red-S. In addition, because it is often used as a diagnostic character, the presence or absence of supraocular spines was noted in all large specimens. Terminology for head spination followed Richardson and Laroche (1979).

Otolith characters have recently been shown to be helpful in identifying late larval and pelagic juvenile *Sebastes* spp. (Laidig and Ralston, 1995). In particular, the otoliths of *S. goodei* develop a distinctive optical pattern (i.e. a dark inner ring surrounding a dark primordium) during the pre-extrusion larval stage (Laidig and Ralston, 1995). Consequently, otoliths were removed from 50 specimens (4.6 mm NL to 10.7 mm SL) to help confirm the initial pigment-based identifications of larval *S. goodei*. For comparison, otoliths were also removed from 52 larval *Sebastes* of unknown species (3.7 mm NL to 8.2 mm SL) that had pigment patterns similar to, but slightly different from, those of larval *S. goodei*. Otoliths of *S. goodei* and other *Sebastes* spp. were removed from specimens collected at the same sites to determine whether the pigment patterns described in this study were accurately distinguishing *S. goodei* from other *Sebastes* spp. Other *Sebastes* spp. were distinguished from *S. goodei* by one or all of the following characteristics: absence of pigment on the cranium and nape, presence of pigment on the tip of the lower jaw, presence of pigment on the cleithral region, and presence of pigment on the caudal area. *Sebastes jordani* and *S. paucispinis* were not included in the other *Sebastes* spp. category because they were easily identified on the basis of distinctive pigment patterns and morphometrics (Moser et al., 1977). Otoliths were examined under a compound microscope connected to a video camera and computer with a working magnification of 1,250×. The radius of the

extrusion check, the total radius, and the pre-extrusion optical pattern were recorded on all otoliths examined. Pre-extrusion optical patterns (as previously described in Laidig and Ralston, 1995) were recorded as being either "strong," "weak," or "absent." "Strong" patterns were readily visible and required very little focusing for resolution. In "weak" patterns, the dark inner ring surrounding the primordium was not readily visible without fine focusing. "Absent" patterns were devoid of the pre-extrusion optical pattern described for *S. goodei* (Laidig and Ralston, 1995). Ages were recorded only from otoliths with clear, distinct daily rings. Ages were obtained following the methods described in Laidig et al. (1991) and Woodbury and Ralston (1991).

Results

General development

Larval *S. goodei* were extruded at a size of 4.5 to 5.8 mm NL. Notochord flexion began at 5.7 to 6.5 mm NL and was complete at 8.1 to 8.8 mm SL. Meristic counts were similar to those reported by Chen (1986), Moreland and Reilly (1991), and Laroche[2] (Table 1). In late-stage flexion and recently flexed individuals a full complement of pectoral-fin rays was present, while the pelvic, dorsal, and anal fins had begun forming. By 9.0 mm SL, the full complement of pectoral-, pelvic-, dorsal-, and anal-fin rays had developed. Accurate gill-raker counts were obtained only on large specimens (>20 mm SL).

Table 1

Frequency of occurrence of dorsal-, anal-, and pectoral-fin ray, and gill-raker counts in chilipepper, *Sebastes goodei* .

Character	Count	Frequency of occurrence	Percent occurrence
Dorsal-fin rays	13	10	6.6
	14	106	70.2
	15	34	22.5
	16	1	0.7
Anal-fin rays	8	157	90.2
	9	17	9.8
Pectoral-fin rays	16	12	7.8
	17	138	90.2
	18	3	2.0
Gill rakers	33	1	2.0
	34	21	42.0
	35	14	28.0
	36	10	20.0
	37	4	8.0

Changes in body shape in *S. goodei* were related to notochord flexion (Table 2). During flexion, body depth at the pectoral-fin base and at the anus increased substantially (Table 2). Also during flexion, pectoral-fin length increased with the development of the full complement of fin rays (Table 2). In addition, head length, snout length, snout to anus distance, and eye diameter all showed a marked increase during flexion (Table 2).

Head spines first appeared in *S. goodei* at approximately 6.1 mm NL; the pterotic and the second anterior and third posterior preopercular were the first to form (Table 3). During late flexion (approximately 7.5 mm NL), the anterior and the second through fifth posterior preopercular series, the postoculars, and the parietals were evident (Table 3). The parietals were serrate and longer than the nuchals, which developed in postflexion individuals (approximately 8.5 mm SL). The first superior infraorbital also was evident in postflexion individuals (Table 3). The third spine of the posterior preopercular series was always the longest. By 14.0 mm SL, the opercular, inferior infraorbitals, supracleithral, and posttemporal spines had developed and by 20.0 mm SL the nasal and tympanic spines were evident (Table 3). Coronal spines were not observed on any of the specimens (Table 3). Supraocular spines, previously unrecorded in *S. goodei* (Moreland and Reilly, 1991; Laroche[2]), were observed on 11% of the large individuals (>20 mm SL)(Table 4). Specimens with supraocular spines ranged in size from 32.0 to 50.2 mm SL, indicating some variability in the occurrence of this characteristic in the pelagic juvenile stage (Table 4).

Pigment patterns

Pre-extrusion larvae ranging in size from 5.0 to 5.8 mm NL had a group of 6 to 12 melanophores on the cranial region, 2 to 5 melanophores on the nape, pigment on the dorsal region of the gut, and a series of 15 to 25 melanophores lining the ventral body that did not extend anteriorly beyond the third postanal myomere (Fig. 1A).

Recently extruded larvae (1 to 2 days old) ranging in size from 4.5 to 5.7 mm NL had more developed pigment on the cranium and nape than did pre-extrusion larvae and had pigment on the dorsal region of the gut and a series of 13 to 17 melanophores lining the ventral body that did not extend anterior to the fourth postanal myomere (Table 5). Pigment on the cranium persisted throughout development. By 5.7 to 6.1 mm NL (3 to 5 days old), pigment on the outer blade of the pectoral fin became evident (Table 5; Fig. 1B). During flexion, melanophores became

Table 2

Morphometric measurements of chilipepper, *Sebastes goodei*, larvae of various size. All measurements are in mm. Specimens between the dashed lines were undergoing notochord flexion.

SL	Head length	Snout length	Snout to anus distance	Eye diameter	Body depth at pectoral base	Body depth at anus	Pectoral-fin length
5.3	1.06	0.27	1.73	0.39	0.85	0.45	0.35
5.4	1.07	0.28	1.80	0.45	0.90	0.47	0.33
5.6	1.03	0.33	1.83	0.44	0.97	0.43	0.38
5.8	1.05	0.30	1.98	0.47	0.98	0.45	0.41
6.0	1.16	0.32	1.95	0.47	0.98	0.48	0.42
6.1	1.12	0.30	2.03	0.48	1.00	0.44	0.43
6.6	1.40	0.32	2.45	0.49	1.15	0.57	0.74
6.7	1.43	0.36	2.50	0.56	1.16	0.57	0.78
6.8	1.45	0.39	2.50	0.58	1.17	0.59	0.75
7.3	1.80	0.52	2.77	0.67	1.46	0.84	1.01
8.0	2.56	1.00	3.99	0.80	1.99	1.18	1.60
8.1	2.70	1.07	4.20	0.95	2.10	1.60	1.75
8.3	3.00	1.05	4.25	1.01	2.15	1.57	1.88
8.7	3.18	1.13	4.65	1.10	2.51	1.72	1.92
9.1	3.45	1.33	4.75	1.24	2.40	1.90	2.07
9.6	3.61	1.21	5.12	1.38	2.79	2.08	2.28
12.2	4.50	1.35	7.34	1.65	3.16	2.37	3.34
13.9	4.92	1.76	7.97	1.75	3.55	2.72	3.54
20.1	6.50	2.04	10.40	2.40	4.85	3.88	5.28
22.0	8.46	2.73	12.34	2.54	5.71	4.92	6.02

evident on the dorsal surface anterior to the eyes (Table 5). None of the preflexion and flexion larvae were pigmented on the cleithral region or caudal area.

After flexion (>15 days old), pigment lining the ventral body was greatly reduced; approximately 8 melanophores were present either on or near the articulations of the anal-fin rays, and/or on the ventral midline of the caudal peduncle (Fig. 1C). In addition, nape pigment had become imbedded in postflexion individuals. Upon completion of flexion, melanophores had also begun to develop on the pelvic fin and along the posterior portion of the dorsal body surface underlying the soft dorsal fin (Table 5; Fig. 1C).

At 11.0 mm SL (>40 days old), additional melanophores had developed on the dorsal body surface underlying the spinous dorsal fin, and melanophores extended into the fin membranes (Table 5; Fig. 1D). In addition, pigment was evident along the blade of the pelvic fin, had covered the outer half of the pectoral fin, and had begun to develop on the surface of the operculum (Table 5; Fig. 1D). Pigment on the anterior tip of the lower jaw and on the hypural region had begun to occur at 11.8 mm SL, and pigment along the dorsal body surface continued to increase (Table 5).

By 12.0 mm SL, the melanophores lining the dorsal body surface had begun to form the first body bar above the opercular region (Table 5). The first body bar and all subsequent body bars formed initially from the dorsal surface and extended ventrally with development. Pigment along the lateral midline of the body had begun to develop on the caudal region by 14.0 mm SL, and the second body bar had begun to develop underneath the spinous dorsal fin at 14.5 mm SL (Table 5; Fig. 1E). Pigment began to develop along the ventral and posterior regions of the eye orbit at 18.7 mm SL (Table 5).

By 28.0 mm SL, pigment on the ventral and posterior regions of the eye orbit, the dorsal surface anterior to the eyes, the surface of the operculum, the dorsal body surface, the lateral midline of the body, the hypural region, and on the membranes of the spinous dorsal fin were all well developed (Table 5; Fig. 1F). The ventral terminus of the first body bar was projected forward and the second body bar began to develop a similar pattern (Fig. 1F). In addition, the remaining three body bars had begun forming with the first appearance of the third body bar just anterior to the soft dorsal fin, with the fourth body bar directly under the soft dorsal fin, and with the fifth body bar on the caudal region (Table 5). Pectoral- and pelvic-fin pigment had become less prominent by 29.0 mm SL, with melanophores on only the

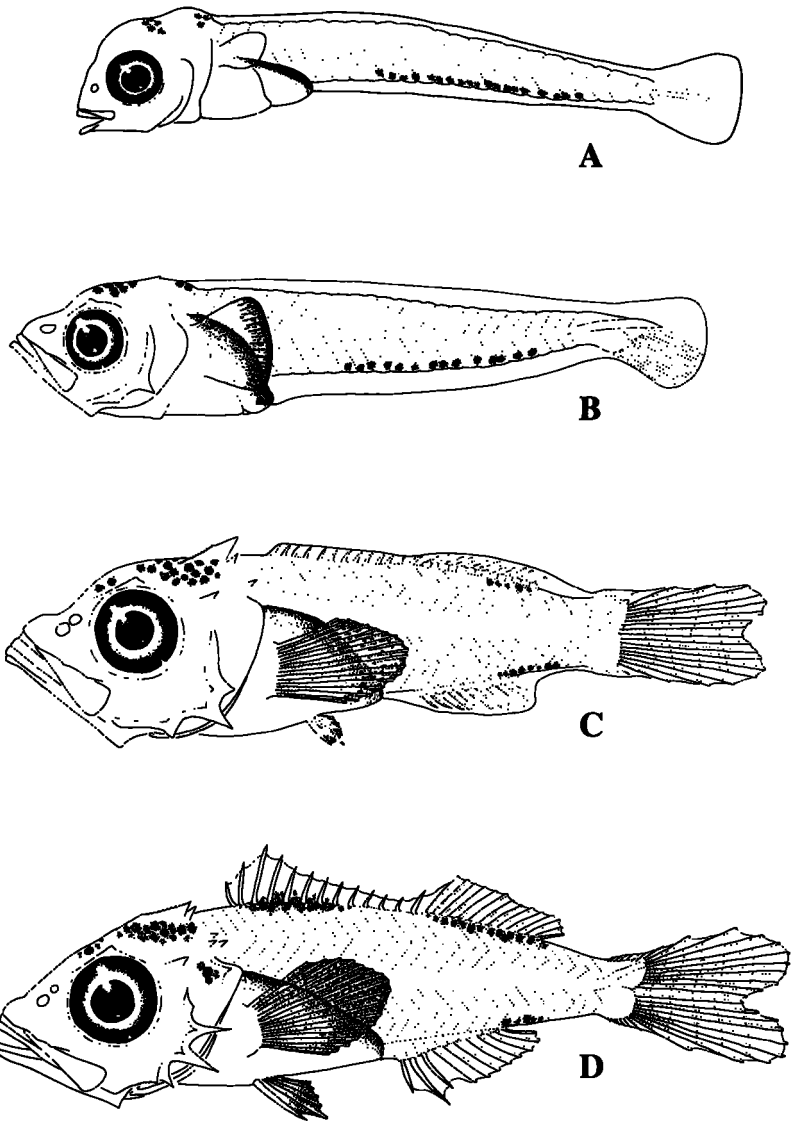

Figure 1

Developmental series of chilipepper, *Sebastes goodei*. (**A**) 5.5-mm pre-extrusion larvae; (**B**) 6.9-mm larvae; (**C**) 9.1-mm larvae; (**D**) 11.1-mm larvae; (**E**) 16.5-mm larvae; (**F**) 26.5-mm pelagic juvenile; (**G**) 35.6-mm pelagic juvenile; and (**H**) 54.3-mm pelagic juvenile.

outer quarter of the pectoral fin. Pigment along the ventral body surface was either absent or occurred sparsely (1 to 7 melanophores) on or near the anal-fin ray articulations and/or on the ventral surface posterior to the anal fin.

At 34.2 mm SL, individuals had begun to lose almost all their pectoral- and pelvic-fin pigment, while the third body bar had become almost fully developed (Fig. 1G). The second and third body bars had developed a forward projecting pattern similar to the

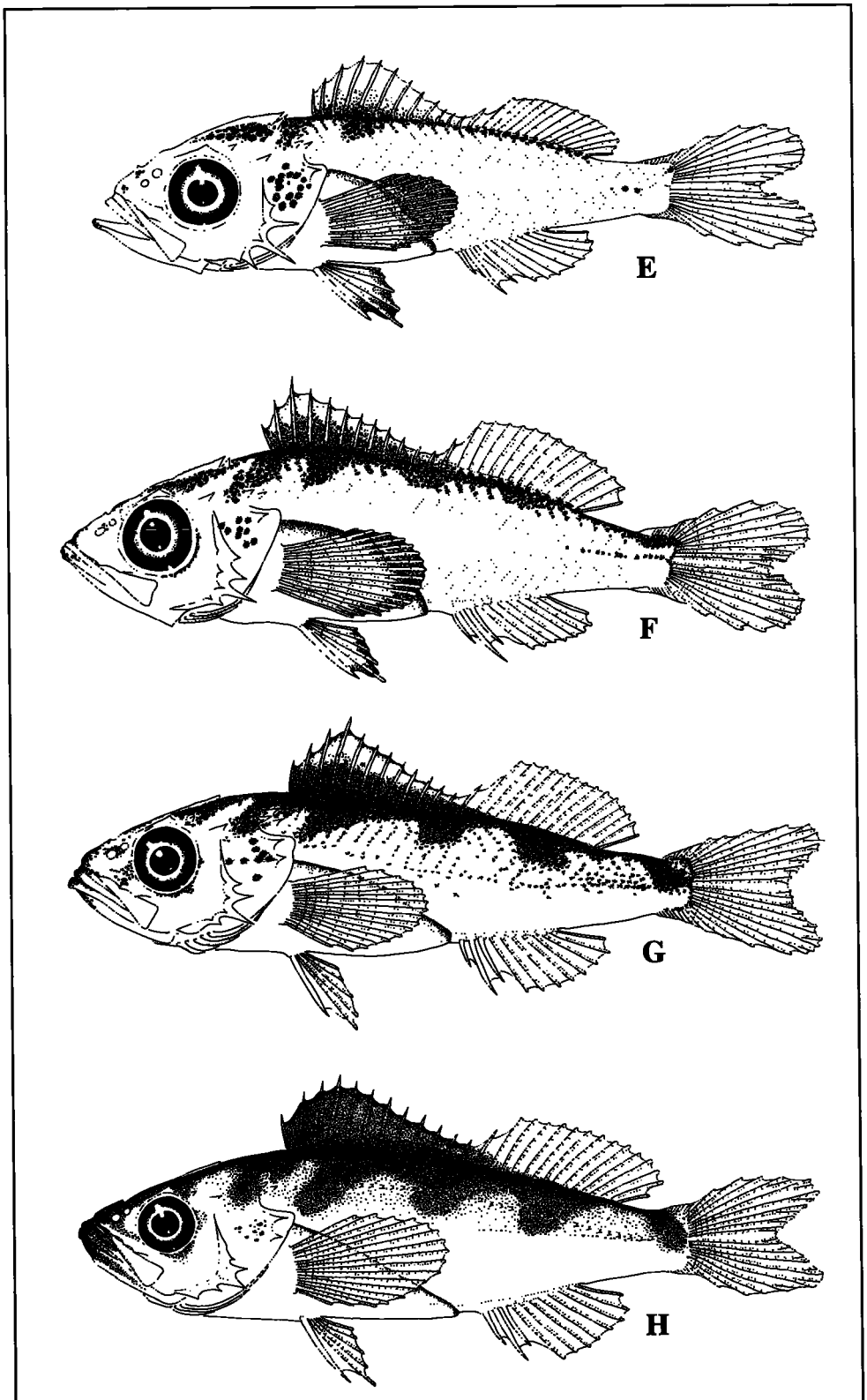

Figure 1 (continued)

Table 3

Development of head spines in chilipepper, *Sebastes goodei*. "1" indicates that spine is present and "0" indicates that spine is absent.

	Standard length (mm)																			
Spine	6.1	6.3	7.5	7.7	8.2	8.5	9.2	9.6	10.0	10.7	11.7	12.2	13.4	13.8	14.1	16.8	18.8	19.4	21.5	22.0
Pterotic	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Preoperculars																				
1st Anterior	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2nd Anterior	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3rd Anterior	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1st Posterior	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2nd Posterior	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3rd Posterior	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4th Posterior	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
5th Posterior	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Preocular	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Supraocular	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Postocular	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Parietal	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Infraorbitals																				
1st Inferior	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
2nd Inferior	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
3rd Inferior	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1
1st Superior	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2nd Superior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
3rd Superior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4th Superior	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Nuchal	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Postemporals																				
Inferior	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Superior	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Supracleithral	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Operculars																				
Inferior	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Superior	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Nasal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Tympanic	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Coronal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

first body bar (Fig. 1G). By 38.3 mm SL, the fourth and fifth body bars were fully developed but did not develop the forward projecting pattern of the first three body bars (Table 5). In addition, pectoral- and pelvic-fin pigment had disappeared (Table 5).

The largest individual examined was 58.3 mm SL, which had all 5 body bars fully developed and well-developed pigment on the anterior tip of the lower jaw, the ventral and posterior region of the eye orbit, the dorsal surface anterior to the eyes, the hypural region, the entire dorsal body surface, and the spinous dorsal fin (Table 5; Fig. 1H). Pigment on the lateral midline surface had become indiscernible owing to the increased pigmentation of the lateral surface. The barred pattern had become slightly obscured by mottling over the dorsal lateral surface. Pectoral- and pelvic-fin pigments were recorded for a few of the larger individuals, but these were a result of 1 to 4 solitary melanophores located usually on one fin only (Table 5). Cheek bars and pigment on the anal fin were not observed on any of the specimens examined (Table 5).

Otolith analysis

The extrusion check radius in *S. goodei* otoliths was significantly larger than that of other *Sebastes* spp. (*S. goodei* mean=14.84 μ, SD=0.577; other *Sebastes* spp. mean=12.03 μ, SD=0.869; t=19.29, df=89, P=0.0001) (Fig. 2). In addition, "strong" patterns were observed in the majority of *S. goodei* specimens, which provided confirmation of the initial pigment-based identifications but which occurred in only a small minority of other *Sebastes* spp. (Table 6). The extrusion check radius of the other *Sebastes* spp. otoliths with "strong" patterns ranged from 11.6 to 12.4 μ, which was much smaller than the extrusion check radius range of 13.7 to 16.5 μ observed for *S. goodei*.

An exponential model provided a good fit for SL versus total otolith radius with no discernible pattern in the residuals (r^2=0.933)(Fig. 3), whereas a linear model was used to regress SL on age (r^2=0.909)(Fig. 4). The slope of the linear regression indicated a growth rate of 0.135 mm·day^{-1} (Fig. 4). The model's estimate of size at age 0 was 5.1 mm, which closely approximates the observed sizes of pre-extrusion (5.0 to 5.8 mm NL) and recently extruded

Table 4

Frequency of occurrence of supraocular spines in chilipepper, *Sebastes goodei*.

Supraocular spine	Frequency of occurrence	Percent occurrence
Neither side	119	88.0
One side	14	10.4
Both sides	1	0.7

Table 5

Proportions of chilipepper, *Sebastes goodei*, with melanophores present at various pigment loci averaged over 2.0-mm size bins (range of +/− 1.0 mm). SL = standard length in mm. FLEX = flexion stage where "0" indicates preflexion, "1" indicates undergoing flexion, and "2" indicates that flexion is complete. n = number of specimens examined. Definitions of pigment loci are as follows: LJ = anterior tip of the lower jaw; EYE = posterioventral edge of the eye orbit; HEAD = cranial surface (including nape pigment); FACE = dorsal surface anterior to the eyes; OPER = operculum; CHK = radiating cheek bars; DORS = dorsal body surface; VENT = ventral body surface; MID = along the lateral midline; HYP = hypural region; DFIN = spinous dorsal fin; AFIN = anal fin; PEC = blade of the pectoral fin; PEL = pelvic fin; B1 = first (most anterior) body bar; B2 = second body bar; B3 = third body bar; B4 = fourth body bar; and B5 = fifth body bar (on peduncle).

SL	FLEX	n	LJ	EYE	HEAD	FACE	OPER	CHK	DORS	VENT	MID	HYP	DFIN	AFIN	PEC	PEL	B1	B2	B3	B4	B5
4	0	11	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6	1	54	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
8	2	21	0.0	0.0	1.0	0.4	0.0	0.0	0.4	1.0	0.0	0.0	0.0	0.0	1.0	0.2	0.0	0.0	0.0	0.0	0.0
10	2	16	0.0	0.0	1.0	0.9	0.0	0.0	0.6	1.0	0.0	0.0	0.0	0.0	1.0	0.5	0.0	0.0	0.0	0.0	0.0
12	2	15	0.3	0.0	1.0	0.9	1.0	0.0	1.0	1.0	0.2	0.3	0.9	0.0	1.0	1.0	0.3	0.0	0.0	0.0	0.0
14	2	8	0.6	0.0	1.0	1.0	1.0	0.0	1.0	1.0	0.4	0.3	1.0	0.0	1.0	1.0	0.6	0.3	0.0	0.0	0.0
16	2	2	0.5	0.0	1.0	1.0	1.0	0.0	1.0	1.0	0.5	1.0	1.0	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
18	2	2	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	0.5	1.0	1.0	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
20	2	5	0.6	0.6	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0
22	2	13	0.6	0.9	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0
24	2	5	0.8	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0
26	2	6	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.2
28	2	8	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.5	0.3	0.5
30	2	6	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.8	0.8	1.0	1.0	1.0	0.7	0.7
32	2	6	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.8	1.0	1.0	1.0	1.0	0.8	1.0
34	2	6	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.8	0.8	1.0	1.0	1.0	0.7	1.0
36	2	6	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.7	0.8	1.0	1.0	1.0	1.0	1.0
38	2	7	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.4	0.6	1.0	1.0	1.0	1.0	1.0
40	2	3	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	1.0
42	2	3	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	1.0
44	2	7	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	1.0
46	2	13	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	1.0
48	2	9	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	1.0
50	2	11	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	1.0
52	2	16	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.3	0.0	1.0	1.0	1.0	1.0	1.0
54	2	5	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.4	0.0	1.0	1.0	1.0	1.0	1.0
56	2	2	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.5	0.0	1.0	1.0	1.0	1.0	1.0
58	2	2	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.5	0.5	1.0	1.0	1.0	1.0	1.0

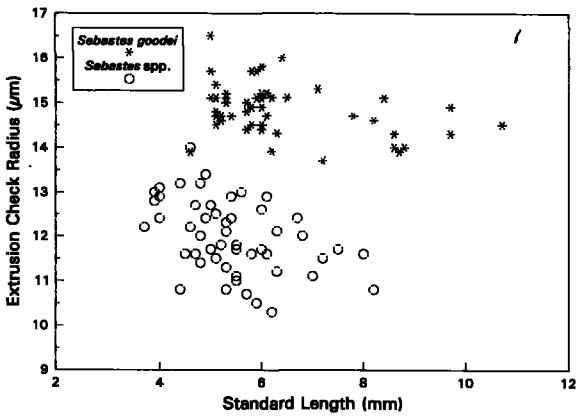

Figure 2

Comparison of standard length versus extrusion check radius between chilipepper, *Sebastes goodei*, and other *Sebastes* spp.

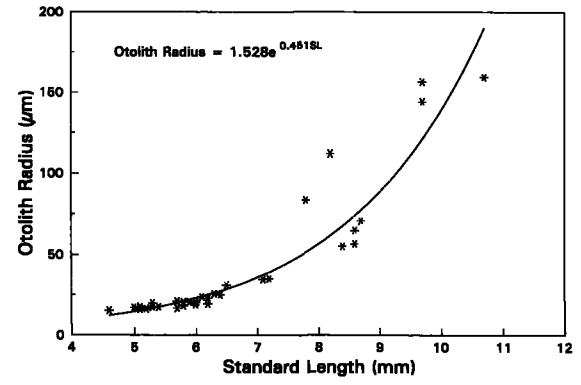

Figure 3

Model of otolith radius (otolith growth) versus standard length for chilipepper, *Sebastes goodei*. Predicted values of the growth curve (exponential function) are represented by a solid line.

(4.5 to 5.7 mm NL) larvae. In comparison to the other *Sebastes* spp., *S. goodei* was significantly larger at any given age (ANCOVA, df=1, 99, P=0.0001)(Fig. 4).

Discussion

The ability to identify larval and juvenile *S. goodei* can potentially lead to future studies on the spatial and temporal extent of spawning and the estimation of larval production biomass for this species based on larvae and juveniles collected in standard plankton studies (Moser and Butler, 1987; Ralston et al.[3]). Preflexion *S. goodei* larvae can be distinguished from other *Sebastes* spp. off central California by the presence of pigment on the cranium and nape (evident even in pre-extrusion larvae), and by the absence of pigment on the dorsal midline surface, the tip of the lower jaw, the caudal area, and the cleithral region (Fig. 1, A and B). In general, extrusion and pre-extrusion larvae of other *Sebastes* spp. that have been described in the literature either lack pigment on the cranium and the nape and/or possess pigment on at least one of the other areas described above (Morris, 1956; Moser et al., 1977; Moser and Ahlstrom, 1978; Moser and Butler, 1981, 1987; Stahl-Johnson, 1985; Kendall and Lenarz, 1987; Matarese et al., 1989; Wold, 1991; Moreno, 1993; Laroche[2]), Based on a cluster analysis by Wold (1991) and existing descriptions of early larvae (Westrheim, 1975; Moser et al., 1977; Stahl-Johnson, 1985; Moser and Butler, 1987; Matarese et al., 1989; Wold, 1991; Moreno, 1993; Laroche[2]), other *Sebastes* spp. commonly found in the study region with larval pigment patterns similar to *S. goodei* include *S. entomelas, S. flavidus, S. melanops, S. mystinus, S. pinniger, S. ruberrimus,* and members of the subgenus *Sebastomus*, which includes *S. chlorostictus, S. constellatus, S. helvomaculatus,* and *S. rosaceus*. Otolith analysis showed that other *Sebastes* spp. with similar pigmentation had otolith characters significantly different from those of *S. goodei* (Fig. 2; Table 6) indicating that *S. goodei* could be accurately identified solely on the basis of pigment patterns described in this study (Fig. 1, A and B). It should be noted that pigment on the cleithral region has not always been documented, because it may be partially obscured by the operculum in some specimens and, therefore, overlooked. To avoid identification problems, the operculum should be lifted to reveal the pigment on the cleithral region.

Juvenile *S. goodei* can be distinguished from other *Sebastes* spp. off central California by their distinctive barred pigment pattern (Fig. 1, G and H)(Matarese et al., 1989; Moreland and Reilly, 1991; Laroche[2]). The forward projecting pattern of the first three body bars readily distinguishes *S. goodei* from other barred *Sebastes* spp., such as *S. saxicola* and *S. caurinus*, in which the body bars do not project forward (Matarese et al., 1989; Laroche[2]). Meristic characters can also be used to distinguish *S. goodei* from these other barred *Sebastes* spp. because the modal anal-fin-ray count in *S. goodei* is 8, whereas the modal counts for *S. saxicola* and *S. caurinus* are 7 and 6 respectively (Chen, 1986; Matarese et al., 1989; Moreland and Reilly, 1991). Although the majority of *S. goodei* did not possess supraocular spines,

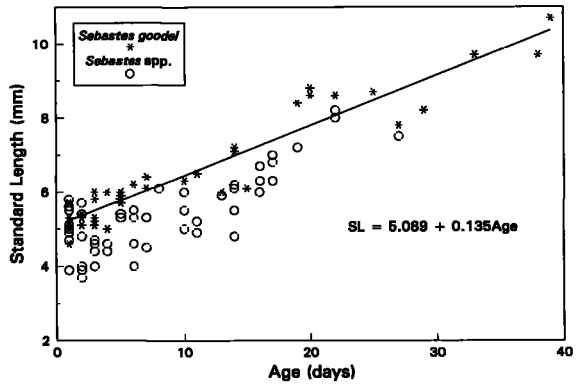

Figure 4

Comparison of age at length for chilipepper, *Sebastes goodei*, and other *Sebastes* spp. The solid line represents the predicted values of the growth curve (linear regression) for larval *Sebastes goodei* alone.

this characteristic is variable (Table 4). Such variability has been reported in other species, including *S. entomelas, S. flavidus, S. melanops,* and *S. mystinus* (Laroche and Richardson, 1981), and should be taken into account when using this characteristic in the identification process.

The identification of *S. goodei* larvae, initially based on pigment patterns, can be confirmed by using otolith characters, given the distinctive optical pattern and the relatively large extrusion check radius (Fig. 2; Table 6). The mean extrusion check radius of 14.84 μ (SD=0.577) in larvae from this study is similar to the mean extrusion check radius of 15.15 μ (SD=0.89) in pelagic juveniles reported by Laidig and Ralston (1995). Although the use of otoliths is more labor intensive than the use of pigment patterns or meristic characters, otoliths can provide relatively accurate identifications when pigment patterns and meristic characters yield dubious results or when pigment patterns and meristic characters are compromised (e.g. in identification of specimens from stomach contents). Studies have shown that otolith characters can be used to separate both species (Hecht and Appelbaum, 1982; Victor, 1987; Gago, 1993;) and stocks (Messieh, 1972; McKern et al., 1974; Rybock et al., 1975). Laidig and Ralston (1995) have found distinctive otolith characters in *S. auriculatus, S. flavidus, S. goodei, S. jordani, S. mystinus,* and *S. paucispinis.* Therefore, the use of otolith characters may be very useful in the identification of other species.

It appears that *S. goodei* grows slower during the larval stage (Fig. 4) than during the juvenile stage (Woodbury and Ralston, 1991). The growth rate of

Table 6

Frequency of occurrence of the pre-extrusion optical pattern in chilipepper, *Sebastes goodei,* otoliths and its occurrence in the otoliths of other *Sebastes* spp. with similar larval pigment patterns.

Species	Optical pattern	Frequency of occurrence	Percent occurrence
S. goodei	Strong	38	76.0
	Weak	10	20.0
	Absent	2	4.0
Other *Sebastes* spp.	Strong	4	7.7
	Weak	14	26.9
	Absent	34	65.4

0.135 mm·day^{-1} for larvae during the first 40 days in this study (Fig. 4) is relatively slow in comparison with the 0.399 to 0.555 mm·day^{-1} growth rates reported by Woodbury and Ralston (1991) for *S. goodei* juveniles 35 to 170 days old. Laidig et al. (1991) observed a similar trend of slow growth during the larval stage and accelerated growth during the juvenile stage in *S. jordani.* During the first 20 days of life, *S. jordani* had a growth rate of approximately 0.165 mm·day^{-1}, whereas at 35 to 165 days, the growth rate was 0.53 mm·day^{-1}. Laidig et al. (1991) also indicated that owing to notochord flexion, early larval growth in *S. jordani* was slightly sigmoidal rather than linear. Growth for *S. goodei* probably follows a similar pattern, but because of the small sample size in this study, such a pattern could not accurately be discerned.

Acknowledgments

We would like to thank the officers and the crew of the RV *David Starr Jordan* and all the scientists who participated in the collection of samples. Special thanks to Ralph DeFelice for his illustrations and to Stephen Ralston for his assistance in the otolith analysis. Geoffrey Moser, Arthur Kendall, and William Lenarz made helpful suggestions on early versions of the manuscript.

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Abstract.—A flow and survival relationship, based on 1970's research, for juvenile chinook salmon, *Oncorhynchus tshawytscha,* that migrate through the Snake and Columbia Rivers is the foundation of many fishery managers' recommendations for modifications to the hydropower system to stem the decline of populations recently listed under the Endangered Species Act. However, a review of the 1970's data found that estimated fish survivals through the hydropower system reflected conditions that no longer exist and that between 1977 and 1979 these estimated survivals were negatively biased. Debris entrained in front of, and throughout, the fish collection system of the uppermost dam on the Snake River resulted in fish descaling and most likely poor fish survival. Under the lowest flow conditions, decreased survival due to increased travel time was exacerbated by sporadic or less than optimal turbine operations, or both, which further delayed fish passage through the dams and, at the uppermost dam, subjected fish to debris for longer periods of time. Use of flow and survival relationships based on yearly estimates of juvenile migrant survival in the 1970's will probably not accurately predict survival of spring-migrating juvenile chinook salmon under present conditions. This is particularly true for survival predictions during low-flow conditions.

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A review of flow and survival relationships for spring and summer chinook salmon, *Oncorhynchus tshawytscha,* from the Snake River Basin

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The Columbia River watershed historically has produced more chinook salmon, *Oncorhynchus tshawytscha,* than any other river system in the world (Netboy, 1980). The majority of the spring chinook salmon originated in the Snake River Basin (Fulton, 1968). In the early 1880's, spring and summer chinook salmon provided commercial fisheries in the lower Columbia River with average annual catches of 17.7 million kilograms (Craig and Hacker, 1940). Heavy exploitation by these fisheries, however, caused a substantial depletion of the dominant summer stock; the fisheries, therefore, concentrated on the spring and fall stocks (Craig and Hacker, 1940; Gangmark, 1957). Summer chinook salmon populations from the mid- and upper Columbia River continued to decline such that by 1964 the commercial fishery for all summer fish was closed. By this time, Snake River Basin spring and summer chinook salmon accounted for approximately 78 percent of the remaining upper river populations (Fulton, 1968).

The primary causes of stock declines in the early years were overfishing, habitat destruction, and damming of tributaries for water withdrawal and small-scale hydropower (Craig and Hacker, 1940). Concern about the potential impacts on upstream salmonid migration and the loss of downstream migrant juveniles passing through turbines at mainstem hydropower projects was expressed even before construction of Bonneville Dam (Fig. 1)(Griffin, 1935). Because the river flow during the time of the juvenile migration generally far exceeded the capacity of the powerhouse turbines, most fisheries research related to migrant salmonid passage was directed toward adults and the development of adequate upstream passage facilities for them at dams. However, some research on juvenile salmonid survival through turbines was conducted in the early 1940's[1] after construction of Bonneville Dam and in 1954 after construction of McNary Dam (Schoeneman et al., 1961).

The first comprehensive program to study of juvenile salmonid migrants in the mainstem Columbia and Snake Rivers was initiated in 1961 by the Secretary of the U.S. Department of Interior. The program was instigated by construction of the high-head Brownlee Dam

[1] Holmes, H. B. 1952. Loss of salmon fingerlings in passing Bonneville Dam as determined by marking experiments. U.S. Fish Wildl. Serv. Unpubl. manuscr., 62 p.

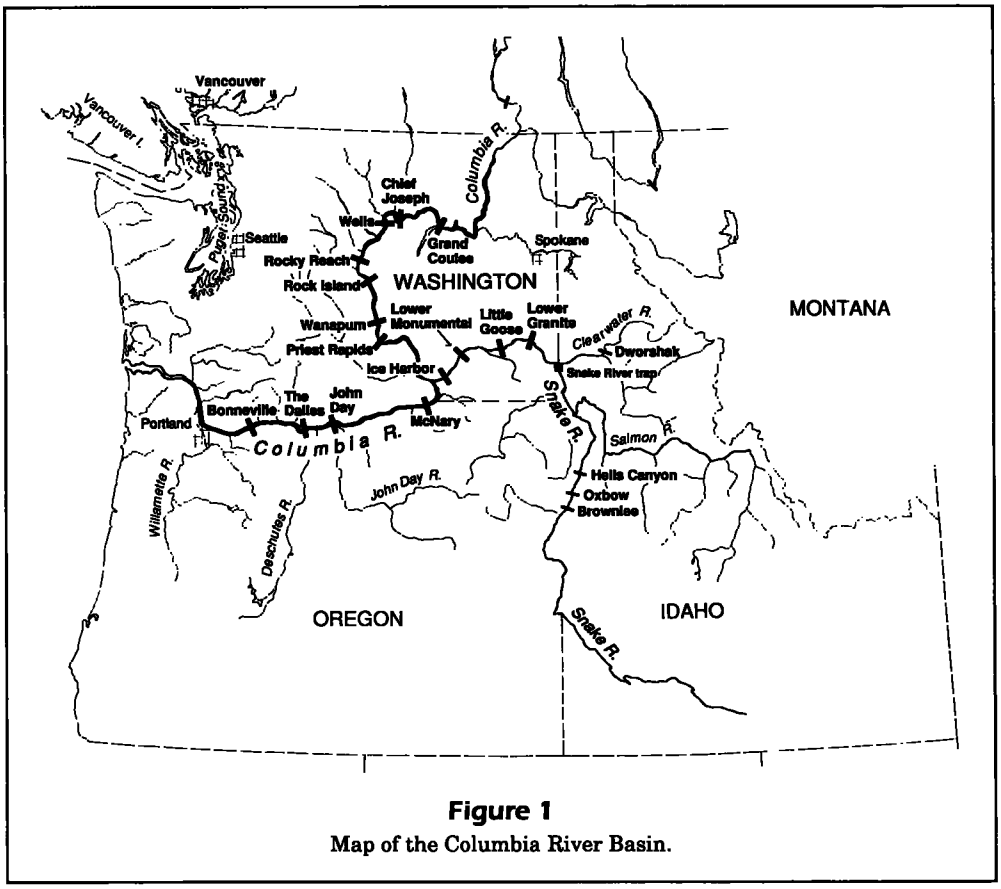

Figure 1
Map of the Columbia River Basin.

on the middle Snake River (Hells Canyon area) in 1958 and in anticipation of low-head dams authorized, but not yet constructed, for the lower Snake River (the stretch from its confluence with the Columbia River upstream to the confluence of the Clearwater River). As part of these efforts, one group of researchers from the Bureau of Commercial Fisheries (now the National Marine Fisheries Service [NMFS]) began studies with juvenile chinook salmon from the Snake River Basin to determine migration rates in relation to flow through areas of impounded and unimpounded stretches of the Snake and Columbia Rivers (Raymond, 1968). As the Lower Snake River dams and John Day Dam on the Lower Columbia River were completed, NMFS expanded these studies to estimate, in addition, the survival of fish passing through these impoundments. Raymond (1979) summarized the results of research from 1964 through 1975; results from 1976 through 1983 were detailed in a number of unpublished contract reports to the U.S. Army Corps of Engineers (COE).[2]

[2] Sims, C. W., W. W. Bentley, and R. C. Johnsen. 1977. Effects of power peaking operations on juvenile salmon and steelhead trout migrations—progress 1976. Report to U.S. Army Corps of Engineering, Portland, OR, 44 p. Northwest Fish. Sci. Cent., NMFS.

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Sims, C. W., A. E. Giorgi, R. C. Johnsen, and D. A. Brege. 1984. Migrational characteristics of juvenile salmon and steelhead in the Columbia River Basin—1983. Report to U.S. Army Corps of Engineering, Portland, OR, 31 p. Northwest Fish. Sci. Cent., NMFS.

The methods used by NMFS researchers to estimate migration rates, timing, and survival were detailed by Raymond (1979). In brief, unique batch marks were applied by some combination of freeze brands and fin clips to yearling (stream-type migrants which were offspring of spring and summer stocks) wild or hatchery chinook salmon collected at hatcheries, from scoop traps and purse-seines, and/or at hydroelectric dams. The marked chinook salmon were then released from the collection sites and recaptured at downstream scoop-trap or purse-seine sites, or from gatewells or collection facilities at dams.

The estimated population of chinook salmon passing a capture site was derived from the formula $\hat{N} = n/\hat{CE}$, where $\hat{N}$ = the estimate of the total number of chinook salmon passing (either for the unmarked population as a whole or for specific mark groups); n = the number of chinook salmon collected (unmarked or marked); and $\hat{CE}$ = the collection efficiency. Collection efficiency was determined from separate groups of chinook salmon that were collected semiweekly at each capture site from the unmarked population of fish that was passing each capture site and subsequently marked uniquely for semiweekly upstream releases at each capture site. Estimates of collection efficiency for each site were derived from the formula $\hat{CE} = (r/(R-10\%R)) \times 100\%)$, where $\hat{CE}$ = the collection efficiency; R = the number of chinook salmon marked and released upstream specifically for collection efficiency estimates; and r = the number of chinook salmon recaptured from collection efficiency (R) releases. The number of chinook salmon released was decreased by 10% to account for suspected mortalities due to handling, marking, release procedures, and migration between the upstream release site back to the capture site. These methods also assumed that any adverse effects of handling, marking, and/or release procedures were equal for all release groups (Raymond, 1979).

Collection efficiency generally decreased as river flow increased. At Ice Harbor Dam, collection efficiency curves were fitted by regression techniques to paired data sets of individual collection efficiency estimates with the corresponding mean river flow during the period the estimates were made (Raymond, 1979). These curves were then used in future years to predict collection efficiency under various flows. At other capture sites, the data were considered too variable to develop reliable collection efficiency curves. In these cases, real-time estimates of collection efficiency were continually obtained during the period when fish were captured at the site.

The population estimate (N) was made in the following manner: if 15 marked chinook salmon of a particular group or 2,000 unmarked chinook salmon were captured at a collection site during a 24-hour period when the CE = 2%, then the estimated number of marked chinook salmon or the total number of unmarked chinook salmon which passed the collection site during the period would have been 750 (15/0.02) or 100,000 (2,000/0.02). Total population estimates were the sum of daily population estimates over the period of time when a specific, marked group of fish passed the site or over the period when the unmarked population passed.

Travel time of marked fish between two sites was determined by subtracting the date of release from a collection site (or the median passage date of fish at one capture site) from the median date of passage at a downstream capture site. Migration rates of fish were determined by dividing the distance between two sites by the travel-time estimate between the two sites. Survival estimates were made by dividing the population estimate at a downstream capture site by either the number of fish released at an upstream collection site or the population estimate at a capture site.

Nearly all fish used for marking in the first study years were products of natural spawning. The percentage of hatchery chinook salmon varied with hatchery output each year, but 100% of the Snake River stock was wild before 1966. Raymond (1988) estimated that from 1966 to 1969 hatchery fish represented about 15% of the chinook salmon migration that reached the upper dam (Ice Harbor Dam, 1966–68; Lower Monumental Dam, 1969) on the lower Snake River. According to his estimates, this percentage increased to 45–55% from 1970 to 1976 (the upper dam was Little Goose Dam, 1970–74; Lower Granite Dam, 1975–present) and averaged greater than 80% from 1981 to 1984.

The 1973–79 NMFS yearly point estimates of survival (Fig. 2) (1973–75 in Raymond [1979]; 1976–79 [see Footnote 2]) were used by NMFS researchers[3] to indicate the effects of the recently completed Snake River hydropower dams on juvenile fish survival. Particularly low juvenile fish survivals were observed under the low-flow conditions in 1973 and 1977, whereas survival estimates did not vary much under a broad range of higher flows. In the early 1990's, computer models were developed by the Northwest Power Planning Council, state fishery agencies, and tribes in the Pacific Northwest to predict survivals of juvenile fish migrating from Lower Granite Dam

[3] Sims, C. W., and F. J. Ossiander. 1981. Migrations of juvenile chinook salmon and steelhead trout in the Snake River from 1973 to 1979, a research summary. Final Report to U.S. Army Corps of Engineering, Portland, OR, 31 p. Northwest Fish. Sci. Cent., NMFS.

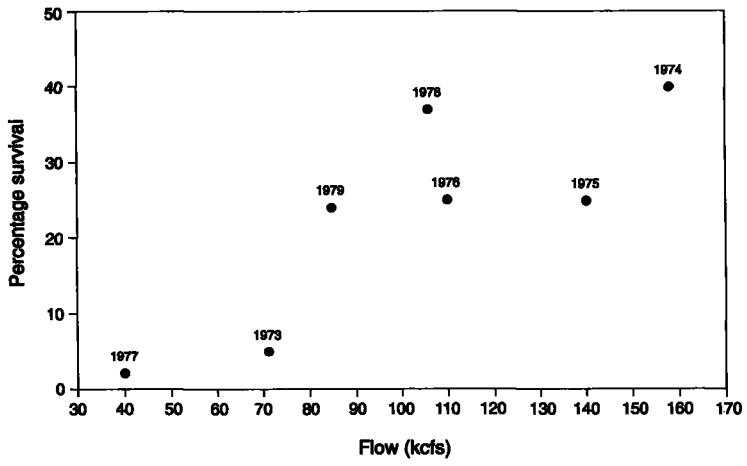

Figure 2

Survival estimates for juvenile spring and summer chinook salmon, *Oncorhynchus tshawytscha*, migrating through the upper dam (Little Goose Dam, 1973–74; Lower Granite Dam, 1975–79) on the lower Snake River to either John Day Dam (1976–79) or The Dalles Dam (1973–75) compared with the average river flow at Ice Harbor Dam during the period (±7 days) of peak migration for the years 1973 through 1979 (data from Sims and Ossiander [1981][see Footnote 3]).

to Bonneville Dam under present river conditions. To calibrate the models, they were fitted to the 1970's NMFS flow and survival data (after altering them to represent the turbine, bypass, and spill conditions that existed in the 1970's).

However, present river conditions and dam operations differ substantially compared with those in the 1970's. Further, detections in recent years of marked fish that migrated through the Snake River to McNary Dam under relatively low flows indicate that juvenile fish survive at a rate substantially higher than that which would be predicted from flow and survival relationships derived from the 1970's data. Because recent information is not in agreement with past data, but because the 1970's data are the foundation of some of the present computer models, we initiated a critical review of the NMFS data from the 1970's to determine whether these data were still relevant.

We initially reviewed all the NMFS data files from which estimates of survival were reported. These included original NMFS field notes, analyses of mark and recapture data, and yearly research summaries. We also reviewed field notes and data summaries from other concurrent NMFS research that documented the condition of fish collected at dams. On reviewing the original data, we determined that the lowest estimates of survival within the hydropower system (1973 and 1977) were mainly a result of low survival in the Snake River. Although the low flows increased travel time, more significantly, the entire migrant fish population was subjected to debris problems at the uppermost Snake River dam. Additionally, as a result of low flows, turbine operations were cut dramatically during nighttime hours (when fish normally pass dams) so that fish were delayed further and thus subjected to the effects of the debris for longer periods. We then compared the low 1970's survival estimates with some Snake River survival estimates of recent years.

Data review

Effects of dam operations and debris on fish condition

Juvenile salmon mortality for Snake River migrants was initially somewhat minimized because when the dams were first built, they were equipped with only three operating turbine units. This limited the amount of flow through the powerhouses to approximately 1,840–1,980 $m^3 \cdot s^{-1}$ (65–70 thousand cubic feet per second [kcfs]). From 35 to 75% of the total river flow (and a presumed equal percentage of the fish population) passed over the spillways during the spring seaward migration. Except under conditions where high atmospheric gas supersaturation decreased survival (Ebel and Raymond, 1976), survival of juvenile migrant fish through spillways was generally estimated at greater than 97% (Raymond, 1988). Three additional turbines were added to Ice Harbor Dam in 1975, to Little Goose and Lower Granite Dams in 1978, and to Lower Monumental Dam in 1979. This led to progressively less uncontrolled spill in the Snake River and a concomitant increase in fish passing through turbine intakes. To decrease fish mortality in the turbines, many of the fish that passed into turbine intakes at Little Goose and Lower Granite Dams were diverted to bypass and collection facilities (Smith and Farr, 1975; Matthews et al., 1977). However, the potential benefit of these bypass systems in decreasing the mortality of fish entering turbine intakes was compromised primarily because of debris that had collected at the dams.

With the exception of Ice Harbor Dam (which had a debris boom installed), huge amounts of woody debris began to accumulate at the upstream face, in

the forebay, and on the trashracks of the dams as the Lower Snake River dams were constructed. Most of the debris accumulated at the uppermost dam in any given period. With periods of high spill, some debris passed downstream through spillways, but as the volume of spill decreased, the trash load at the upper dam increased. By 1979 at Lower Granite Dam, debris extended upstream from the dam approximately 1 km (Fig. 3). The debris that collected at Little Goose and Lower Granite Dams after their construction provided a continual supply of woody material that clogged trashracks, accumulated in the gatewells, and collected throughout the fish facilities. Gatewell orifices and all other components of the bypass systems were continually obstructed by debris. Although debris was constantly in the forebays, attempts were made to remove it from the trashracks. However, the rakes that were used to clear the trashracks were ineffective and instead, large, heavy-steel beams were occasionally lowered down the trashracks in an attempt to push impinged debris to the bottom. As judged by water levels and turbulence in the gatewells, this procedure met with limited success.

To compound problems, when first constructed the fish facilities at Lower Granite and Little Goose Dams had undersized plumbing systems and other poorly designed components through which fish moved. Lower Granite Dam had only 20.3-cm diameter orifices to the bypass system which were often plugged and required continual efforts (usually futile) by fish workers to remove debris to maintain unobstructed flows. During peak collection periods at the collection facilities, workers often required 1 hour, and at times up to 3 hours, to transfer fish from one of the five raceways into a fish transport barge. Occasionally, the 6-inch transfer lines would completely plug with debris and fish. The effect of debris throughout the bypass and collection systems was to increase fish injury, descaling, and ultimately mortality from dam passage (Table 1). Total mortalities at Lower Granite Dam were often so high (personal observations by the authors) that individual dead fish could not be counted. Most often, we kept volumetric estimates (buckets full) of dead fish dipnetted from tail-screens in raceways. The fish not collected at the uppermost dam passed through either the spillway or through the trashracks and then the turbines. Although not measured, the mortality of fish that were not collected at the uppermost dam, but which passed through the debris on the trashracks and then the turbines, probably was higher than that at downstream dams where debris on the trashracks was much less of a problem. For example, in 1979, fish sampled from the gatewells at Little Goose Dam showed far less descaling (a reduction of 50%) after the trashracks at Lower Gran-

Figure 3
Debris in the forebay of Lower Granite Dam, 1979.

Table 1

Average facility-caused descaling and delayed mortality for groups of unmarked and marked Snake River spring and summer chinook salmon, *Oncorhynchus tshawytscha*, smolts collected at Little Goose or Lower Granite Dams from 1972 through 1990. Smolts were held approximately 48 hours before or after truck transport to an area below Bonneville Dam.

Year	Dam	Facility-caused descaling (%)	Unmarked-fish delayed mort. (%)	Marked-fish delayed mort. (%)
Not Transported				
1972	Little Goose	19.6	<1.0; 17.6	21.8
1978	Lower Granite	7.5	20.6	13.8
1979	Lower Granite	5.3		5.0
1980	Lower Granite	4.0	2.2	
1986	Lower Granite	3.7		0.3
1987	Lower Granite	3.3		1.1
1989	Lower Granite	2.3		1.1
1990	Lower Granite	3.6		1.3
Transported				
1972	Little Goose	16.0	12.2	10.0
1973	Little Goose	19.6	15.3	17.2
1975	Lower Granite	13.0		11.5
1976	Little Goose	11.5	3.2	6.1
	Lower Granite	7.0	4.1	4.7
1977	Little Goose	23.9	21.3	42.5
	Lower Granite	26.0	31.4	30.0
1978	Little Goose	20.0	12.7	13.1
	Lower Granite	7.5	11.2	17.1
1979	Little Goose	8.1	19.8	
	Lower Granite	5.3	10.0	
1980	Lower Granite	4.0	1.9	

ite Dam were partially cleared of debris with the steel beam.[4]

Fish passage conditions were particularly bad at Little Goose Dam in 1973 and Lower Granite Dam in 1977 because river flows were so low that little (1973) to no (1977) spill occurred at Snake River dams. Thus, nearly all fish had to pass through trashracks at dams into either the turbines or the debris-laden bypass systems. Additionally, it was not unusual for one or more turbines to operate at full or nearly full capacity for relatively short periods during the evening peak load and then shut down for relatively long periods (authors' personal observations). At other times, one or two turbines were operated at partial capacity for relatively long periods. The slowing or stopping of turbines probably delayed dam passage by reducing or stopping the flow into each turbine and, thus, fish were not attracted to the bypass.

Under these conditions in 1977, 10–14% of spring and summer chinook salmon smolts within 140 m of the forebay at Lower Granite Dam were descaled (a fish was considered descaled if it was missing 10–100% of its scales), whereas fish sampled 400 m to 2 km upstream showed no descaling.[5] These observations suggest that fish were delayed at the dam and that they swam in and out of the debris-covered trashracks, possibly while loads were adjusted or when velocities were insufficient to draw fingerlings completely into the bypasses or through the turbines. For fish that passed into the collection facility, an average of 26.0% were descaled. Under similar conditions at Little Goose Dam, the percentage of fish descaled averaged 19.6 and 23.0% in 1973 and 1977, respectively, probably because they hit something during passage through the trashracks or bypass system. (The high level of descaling observed in 1977 most likely resulted from the fact that fish had previously passed Lower Granite Dam.) When debris partially occluded openings through which fish passed, it not only provided objects that the fish hit but caused increased water velocity through the remaining open area. Thus, fish hit the debris with more force as the amount of debris increased. A fish with external injury, such as descaling, would likely have had internal injury as well. To determine the relationship between descaling percentage (as a measure of total injury) and mortality within a short time period, random samples of bypass fish were collected during some years and held in tanks with flow-through river water. The rate of mortality during approximately 48 hours of holding was measured, and the extent to which this was dependent upon descaling percentage was evaluated. Facility-caused descaling was highly positively correlated with delayed mortality for marked untransported fish (R=0.94, $P \leq 0.002$) and unmarked transported fish (R=0.90, $P \leq 0.007$), whereas it was fairly

[4] Smith, J. R., G. M. Matthews, L. R. Basham, S. Achord, and G. T. McCabe. 1980. Transportation operations on the Snake and Columbia Rivers, 1979. Report to U. S. Army Corps of Engineering, Walla Walla, WA, 28 p. Northwest Fish. Sci. Cent., NMFS.

[5] Park, D. L., J. R. Smith, E. Slatick, G. M. Matthews, L. R. Basham, and G. A. Swan. 1978. Evaluation of fish protective facilities at Little Goose and Lower Granite Dams and a review of mass transportation activities, 1977. Report to U.S. Army Corps of Engineering, Portland, OR, 60 p. Northwest Fish. Sci. Cent., NMFS.

positively correlated for marked transported fish (R=0.77, $P \leq 0.075$) (Table 1). Too few unmarked untransported groups were observed to examine the correlation. Further, we did not use the limited data because the <1.0% delayed mortality measured in one of the 1973 tests is inexplicable (the NMFS annual report[6] for the year stated that the results were "somewhat surprising," considering that migrants passing the dam suffered, in actuality, a 50% mortality). Although not evident from the summary table (Table 1), in the 1970's most of the descaled fish were missing considerably more than 10% of their scales as compared with present conditions where highly descaled fish are the exception rather than the rule.

Annual survival estimates were lowest for 1973 and 1977 (Fig. 2), the two years with the lowest river flows and the highest levels of descaling at the upper dam. The relatively low survivals may well have been greatly influenced by debris-related problems at the upper dams and were compounded by the low river flows in these two years.

In 1980, the COE began removing debris from the Lower Granite Dam forebay, and in 1981 a permanent debris rake was installed and used for the first time to remove debris from the trashracks (effective rakes to remove debris from trashracks were also built during the 1980's for other dams). In 1983, a temporary boom was placed upstream from Lower Granite Dam to divert new debris away from the powerhouse. The temporary boom was replaced by a permanent structure in 1984. Debris is now diverted away from the powerhouse and removed from the river, and trashracks are systematically cleaned. Additionally, the bypass systems at Lower Granite and Little Goose Dams have been substantially modified and improved. For example, pipe and orifice sizes have been increased so that what little debris enters the systems does not cause problems. Fish and debris separators have been modified so that fish are separated under water and they exit after separation via large flumes rather than small pipes. Descaling and 48-hour delayed mortality in recent years have been much less than those observed in the 1970's (Table 1), even under "relatively" low-flow conditions such as occurred in 1987.

To verify improved migratory conditions for chinook salmon smolts after debris problems had been eliminated or greatly controlled in the Snake River, we compared historic with recent Snake River survival estimates. Survival estimates in the 1970's over a 2- or 3-dam stretch under moderate to high river flows ranged from 33 to 50% (Raymond, 1979). Over a comparable 2-and 3-dam stretch in 1993 and 1994, survival estimates were 77%[7] and 66%[8], respectively. For low-flow conditions, we estimated survival of PIT-tagged (passive-integrated-transponder-tagged) (Prentice et al., 1990) chinook salmon smolts from Little Goose Dam to McNary Dam in 1992 by using Raymond's (1979) techniques for comparing populations of fish that passed both dams. We used 50 and 75% collection efficiency estimates for the two dams, respectively. Flows were similar in 1973 and 1992 (Fig. 4); however, our 1992 survival estimate (which covered three dams and reservoirs, but not the most upstream dam) was 81% compared with 12% for two dams and reservoirs in 1973 (Raymond, 1979).

Discussion and conclusions

The argument for a flow-survival relationship for juvenile salmonid migrants, based on the 1973–79 NMFS yearly point estimates of inriver survival (Fig. 2), is heavily influenced by the low survivals estimated for 1973 and 1977 under low-flow conditions. Low survival of river migrants (both above and through the hydropower system) certainly occurred during the 1973 and 1977 low-flow years. However, the estimated low fish survivals within the hydropower system resulted more likely from fish encounters with debris at dams (encounters which were increased because of low flows and exacerbated by sporadic turbine operations) than from river discharge. Data collected in the past few years on PIT-tagged fish that migrated under low to moderately-low flow conditions, comparable to those in the 1970's, indicated a substantially higher survival of juvenile smolts.

Under present conditions, low flows during the spring migration may not lead to direct losses of migrant fish as high as those in the 1970's within the

[6] Ebel, W. J., R. W. Krcma, and H. L. Raymond. 1973. Evaluation of fish protection facilities at Little Goose Dam and review of other studies relating to protection of juvenile salmonids in the Columbia and Snake Rivers, 1973. Report to U.S. Army Corps of Engineering, Portland, 52 p. Northwest Fish. Sci. Cent., NMFS.

[7] Iwamoto, R. N., W. D. Muir, B. P. Sandford, K. W. McIntyre, D. A. Frost, J. G. Williams, S. G. Smith, and J. R. Skalski. 1994. Survival estimates for the passage of juvenile chinook salmon through Snake River dams and reservoirs. Report to the Bonneville Power Admin., Portland, OR, 140 p. Northwest Fish. Sci. Cent., NMFS, and Univ. Washington.

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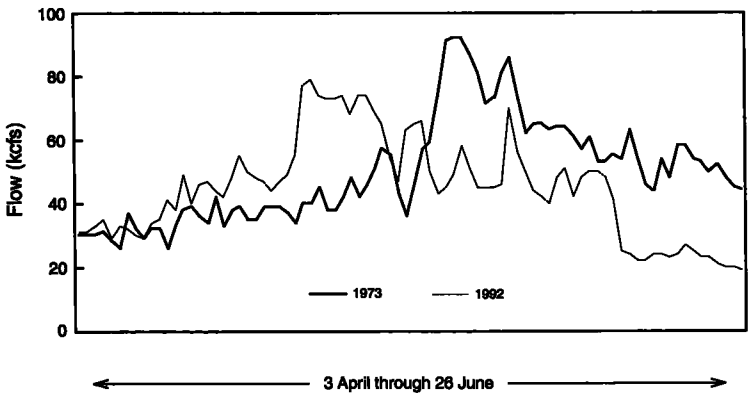

Figure 4

Comparison of 1973 and 1992 Snake River flows during the spring juvenile salmonid seaward migration.

Table 2

Changes in average runoff (in thousands of cubic feet per second) in the Columbia River at The Dalles Dam.

	May	June	July
1926–58	283	353	224
1959–75	250	344	211
1976–91	206	199	132

hydropower corridor, but past research definitely showed that low flows increased travel time (Raymond, 1979). Certainly adult returns of spring and summer chinook salmon have been greatly reduced in most years since the mid-1970's (Matthews and Waples, 1991). This poor return has coincided with a substantial decrease in lower Columbia River flows during the late spring and early summer smolt migrations as a result of completion of storage reservoirs in the upper Columbia River Basin (Table 2). The decreased volume of freshwater entering the estuary and ocean may have delayed entry of fish to the ocean or may have changed the ecology of the system sufficiently to affect predator-prey interactions above and below the trophic level of the juvenile migrant fish and, thus, their survival.

The 1970's juvenile survival estimates made by NMFS in average-to-high flow years also reflected the effects of debris for the proportion of the population that passed through the juvenile collection and bypass systems. These survival estimates are probably lower than those for present passage conditions, even when one accounts for the installation of new bypass systems at dams where they did not exist in the 1970's. Thus, they do not apply to present-day migrants in the Snake and Columbia River hydropower system, and we recommend they not be used by modelers, unless substantial modifications are made to adjust for the errors that we have discussed. We also recommend continued emphasis on research to provide up-to-date survival estimates under present system conditions, because the data gathered to date do not cover a wide range of flows.

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A decline in the abundance of harbor porpoise, *Phocoena phocoena*, in nearshore waters off California, 1986–93

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Harbor porpoise, *Phocoena phocoena*, have been caught incidentally in set gill nets off the central California coast since at least 1958 (Norris and Prescott, 1961). The annual mortality of harbor porpoise caught in gill nets in this region peaked in the mid-1980's and then gradually declined (Barlow and Forney, 1994) as fishing effort decreased following the implementation of restrictions and area closures in order to protect marine mammals, sea birds, and sport fisheries (Barlow et al., 1994). In 1986, a series of aerial line-transect surveys was initiated jointly by the California Department of Fish and Game and the National Marine Fisheries Service to monitor trends in abundance of the central California harbor porpoise population. Harbor porpoise in this region are managed separately from animals found off northern California and Oregon, because movement of animals along the U.S. West Coast appears limited, and fishery-induced mortality is restricted to central California (Barlow and Hanan, in press). An analysis of covariance model applied to the first five annual surveys (1986–90) failed to detect a significant trend in abundance (Forney et al., 1991); however, simulations revealed that statistical power to detect trends, given the level of variability observed in the time series, was low with only five survey years. A minimum of ten survey years was estimated as necessary to provide sufficient power.

Additional surveys utilizing the same methodology were conducted in 1991 and 1993, completing an eight-year time series. In updating the analysis of trends in central California harbor porpoise abundance for the period 1986–93, I anticipated either that 1) no significant trend would be identified because of low power, or 2) an increase in abundance might be detected because the population was expected to be recovering after the reduction in fishery-induced mortality. However, a declining trend in central California harbor porpoise abundance was identified for the period 1986–93. Because of the surprising nature of this result and because of the management implications, this report presents the updated 1986–93 analysis and includes additional data from the 1989–1993 aerial surveys in northern California for the first time.

Methods

A complete description of both field and analytical methodology can be found in Forney et al. (1991), and only a brief summary of the methods used is provided here.

Field methods

Aerial line-transect surveys were conducted from late summer to early fall (15 August through 15 November) of the years 1986–91, and 1993. In each survey year, a set of 26 transects between Point Conception and the Russian River (Fig. 1A) was replicated as often as weather permitted (generally 4–8 times) to monitor the central California harbor porpoise population. Beginning in 1989, a set of 17 additional transects between the Russian River and the California-Oregon border (Fig. 1B) was surveyed 1–3 times per field season to monitor the northern California population. The transects followed a zigzag pattern designed to survey systematically between the coast and the 92-m (50-fathom) isobath, which is the depth range in which the majority of harbor porpoise are expected to be found in this region (Barlow, 1988). The only deviation from this design occurred outside San Francisco Bay, where the 92-m (50-fathom) contour is located too far offshore for safe operation of the survey aircraft; in this region, the transect lines extended only to the 55-m (30-fathom) contour. Total transect length was 916 km, and under good weather conditions all transects could be surveyed in two days. The survey platform was a high-wing, twin-engine Partenavia P-68 aircraft outfitted with two bubble windows for lateral viewing and with a belly port for downward viewing. The survey team consisted of three observers (situated left, right, and belly) and one data recorder. Line-transect methods were followed with sighting distances calculated from the angle of declination to the sighting (obtained with a hand-held clinometer) and from the aircraft's altitude. Surveys were flown at about 167–185 km/hr (90–100 knots) airspeed and 213 m

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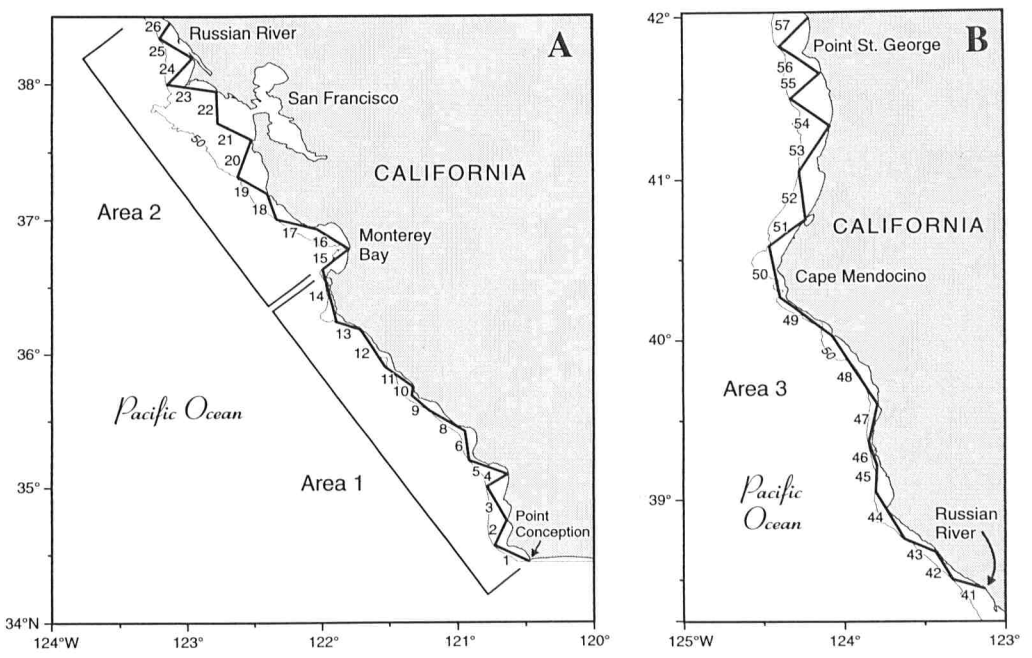

Figure 1

Flight transects and defined areas for aerial surveys for harbor porpoise, *Phocoena phocoena*, in (**A**) central California (transects 1–26; areas 1 and 2) and (**B**) northern California (transects 41–57; area 3). Transect 7 was combined with transect 8 after 1986 and is not shown.

(700 ft) altitude. Flights were conducted only when weather conditions were good (Beaufort sea states 0–3, mostly with clear or partly cloudy skies). Sighting information and environmental conditions were recorded and updated throughout the survey by using a laptop computer connected to the aircraft's LORAN navigation system.

Analytical methods

The number of porpoise observed per kilometer of search effort was used as a measure of relative abundance. These data were stratified by Beaufort sea state (0–1, 2, and 3), area (transects 1–14 and 15–26 in central California, and 41–57 in northern California; see Fig. 1), and percent cloud cover (<25%; ≥25%). After log-transformation, a stepwise selection procedure was used to construct an analysis of covariance model of the form:

$$P = \mu + \alpha_1 + \alpha_2 + \ldots + \delta(y - \bar{y}) + \varepsilon, \qquad (1)$$

where P is the log-transformed value of the number of porpoise seen per kilometer + 0.001; μ is the mean value of P; the α's are factors influencing apparent porpoise abundance (such as sea state); δ is the coefficient for the covariate year (y); $\bar{y}$ is the mean year; and ε is a random error term. This additive model for the log-transformed data is equivalent to a multiplicative model for the actual data (stratification variables such as sea state are expected to change the fraction of animals observed, and thus have a multiplicative effect). Variability caused by unequal survey coverage in each combination of sea state, percent cloud cover, and geographic area was included in the model by weighting by the number of kilometers flown. The analysis was done separately for central California alone (transects 1–26) and for both central and northern California (transects 1–26 and 41–57). Previous simulations (Forney et al., 1991) indicated that power would still be low with this eight-year time series; therefore, the critical value for type-I error was set at $\alpha = 0.10$. This was expected to provide a power of approximately 60% to detect a large change in abundance of ±10% per year but would still have low power (approximately 25%) to detect trends on the order of ±5% per year.

Results

A summary of survey coverage (total kilometers surveyed, percent surveyed under good conditions) and

Table 1

Summary of harbor porpoise, *Phocoena phocoena,* aerial survey data collected 1986–1993 in central and northern California. Areas 1, 2, and 3 correspond to transects 1–14, 15–26, and 41–57, respectively (see Fig. 1). "% good conditions" is defined as 100 times the total kilometers surveyed with Beaufort sea states 0–2 and <25% cloud cover, divided by the total number of kilometers flown in all conditions. "—" = no surveys were flown; SD = standard deviation.

		Year						
Area		1986	1987	1988	1989	1990	1991	1993
1	no. of sightings	36	28	15	22	18	12	9
	no. of porpoise	62	47	20	44	29	20	17
	mean group size ± SD	1.72 ± 0.91	1.68 ± 1.79	1.33 ± 0.49	2.00 ± 1.41	1.61 ± 1.04	1.67 ± 0.65	1.89 ± 0.93
	km surveyed	1,767	1,618	1,834	1,653	1,887	1,066	1,941
	% good conditions	56.4%	66.7%	31.3%	32.4%	60.3%	56.5%	68.7%
2	no. of sightings	63	44	88	60	57	43	69
	no. of porpoise	104	76	154	134	126	76	149
	mean group size ± SD	1.65 ± 1.17	1.73 ± 1.11	1.75 ± 1.18	2.23 ± 1.51	2.21 ± 1.47	1.77 ± 1.11	2.24 ± 1.61
	km surveyed	1,282	1,463	2,086	1,607	1,751	669	1,919
	% good conditions	55.9%	34.3%	36.0%	42.1%	32.0%	58.9%	59.9%
3	no. of sightings	—	—	—	44	173	87	143
	no. of porpoise	—	—	—	76	296	166	246
	mean group size ± SD	—	—	—	1.73 ± 1.21	1.71 ± 1.27	1.91 ± 1.02	1.72 ± 1.40
	km surveyed	—	—	—	804	1,084	612	966
	% good conditions	—	—	—	34.1%	67.3%	77.9%	88.0%

sighting information (number of sightings, number of porpoise, and mean group size) is provided in Table 1 for each year and region. Survey coverage was comparable in most years, but owing to poor weather throughout the 1991 field season, only about half of the usual replication was obtained during this year. Differences also occurred in the proportion of survey effort obtained under good sighting conditions, defined as Beaufort sea states 0–2 and as less than 25% cloud cover. Consistent differences in encounter rates, measured as the number of porpoise observed per kilometer surveyed, are apparent between the three defined areas (Fig. 2). Substantially higher encounter rates occurred in northern California than in central California, and the lowest encounter rates occurred south of Monterey Bay, in the southern end of this population's range.

The best model obtained by the stepwise selection procedure for central California data included area, Beaufort sea state, and cloud cover as categorical variables, and year as the covariate (Table 2). All four factors were significant at $\alpha = 0.10$, with probabilities ranging from 0.0001 to 0.0798 (Table 3). With the exception of the inclusion of the covariate year in the model, these results are qualitatively the same as those for the analysis of the first five years of data (Forney et al., 1991).

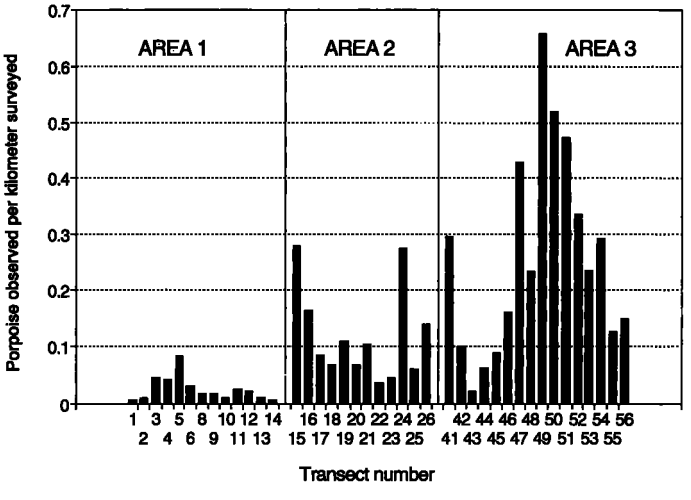

Figure 2

Mean number of harbor porpoise, *Phocoena phocoena,* observed per kilometer on each of the surveyed transects. Only data obtained under good survey conditions (Beaufort sea state 0–2, <25% cloud cover) are included. Transect and area numbers correspond to those shown in Figure 1.

Table 2

Stepwise model building procedure for the 1986–93 central California aerial survey data. Parameters marked in bold indicate variables that were included in the model at each step. P=ln(porpoise/km + 0.001); μ = mean value of P; BF = Beaufort sea state; AR = area; CL = cloud cover, and YR = year. Interaction effects are represented with an asterisk between the variables.

	Step number and base model				
	1	2	3	4	5
	$P = \mu$	$P = \mu + AR$	$P = \mu + AR + BF$	$P = \mu + AR + BF + CL$	$P = \mu + AR + BF + CL + YR$
Probability value for tested additional variables	BF: 0.0183 **AR: 0.0001** CL: 0.0379 YR: 0.4606	**BF: 0.0009** CL: 0.0013 YR: 0.3514	**CL: 0.0003** YR: 0.5508 BF*AR: 0.7567	**YR: 0.0798** BF*AR: 0.8043 BF*CL: 0.8981 CL*AR: 0.1344	BF*AR: 0.7823 BF*CL: 0.9131 CL*AR: 0.1640 YR*AR: 0.2783 YR*BF: 0.7010 YR*CL: 0.7943

Table 3

Results of analysis of covariance for central California and combined central and northern California aerial survey data. The complete model simultaneously includes all variables marked in bold in Table 2. SE = standard error.

	Central California			Central and northern California		
Source	df	F	P	df	F	P
Model	5	15.70	0.0001	6	22.64	0.0001
Area	1	52.75	0.0001	2	48.30	0.0001
Beaufort sea state	2	8.71	0.0004	2	11.26	0.0001
Cloud cover	1	17.18	0.0001	1	18.91	0.0001
Year	1	3.16	0.0798	1	3.04	0.0850
Error	73			85		
r^2		0.5182			0.6151	
Year coefficient (SE)		−0.098	(0.055)		−0.087	(0.050)
Annual rate of change		9.3%			8.3%	

The important difference is that the five-year time series did not reveal a trend in abundance, whereas the analysis including the new (1991 and 1993) data indicated a decline in harbor porpoise abundance in central California during the eight-year period 1986–93. To investigate the possibility that animals may have moved northward into northern California, the analysis was repeated with northern California as a third area stratum. The results were essentially the same: the year effect was slightly less pronounced but still significant at $\alpha = 0.10$ (Table 3). Figure 3 shows a plot of relative abundance (porpoise observed per kilometer) in each of the three defined areas for the period 1986–93, adjusted for the effects of sea state and cloud cover (based on the parameters of the best-fitting model). The combined relative abundance for all of central California, calculated as an average of the values of porpoise per kilometer for areas 1 and 2, weighted by the proportion of the total study area encompassed by each (33.6% for area 1; 66.4% for area 2), is indicated by a dashed line in Figure 3.

Discussion

The indication of a declining trend in abundance is somewhat surprising, given that the central California population of harbor porpoise was expected to be recovering from impacts of heavy fishery-related mortality prior to about 1987 (Barlow and Forney, 1994). The point estimate for the decline corresponds to a 9.3% per year decrease (coefficient of variation, CV=0.56) in harbor porpoise abundance for central California (or 8.3%, CV=0.56, if northern California surveys are included in the analysis); however, the confidence in this value is low because of the low power of the test. There are a number of possible explanations for the observed decline, including 1) statistical error, 2) movement of animals out of the study area, 3) effects of fishery-related mortality, and 4) change in natural mortality and net reproduction. Each of these possibilities will be discussed separately below.

Statistical error

It is possible that the results of the test are incorrect, that is, an α-error (detecting a trend although

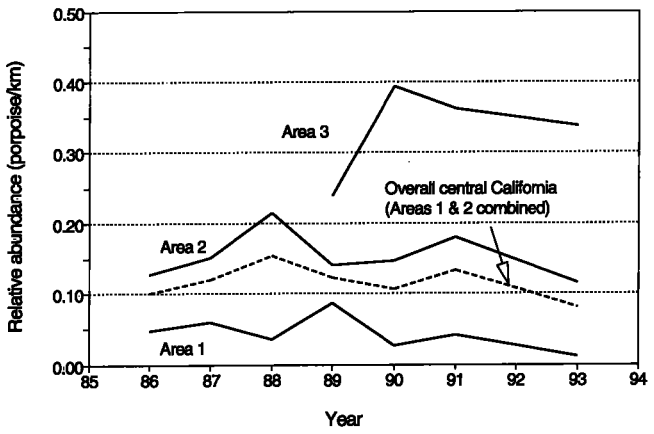

Figure 3

Relative abundance of harbor porpoise, *Phocoena phocoena,* for the period 1986–93. Relative abundance is defined as the number of porpoise observed per kilometer surveyed, adjusted for the effects of sea state and cloud cover on sighting rates. Areas correspond to those shown in Figure 1. The combined relative abundance for all central California was calculated as an average of the adjusted values of porpoise per kilometer for areas 1 and 2, weighted by the proportion of the total study area encompassed by each (33.6% of the total study area was in Area 1; 66.4% was in area 2).

in fact the population is stable) or γ-error (detecting a decline when the population is in fact increasing; Forney et al., 1991) has occurred. The latter is expected to be virtually zero for this eight-year time series (Forney et al., 1991). The former was set at 0.10 a priori in order to increase power. Assuming symmetry, this should have resulted in a 5% probability of detecting a decline if the population were in fact stable.

Movement of animals out of the study area

In recent years, an increasing body of evidence indicates that long-term changes have occurred in the California Current during the last few decades, including an increase in surface water temperature and sea level height (Roemmich, 1992), a decrease in zooplankton abundance (Roemmich and McGowan, 1995), and changes in the size of seabird populations (Ainley et al., 1994). There has also been a dramatic increase in the abundance of short-beaked common dolphins, *Delphinus delphis,* off California (Barlow, 1995; Forney et al., 1995), possibly due to a northward shift in the distribution of this tropical and warm-temperate species (Anganuzzi and Buckland, 1994). A northward range extension into central California has also been documented for another tropical and warm-temperate species, the bottlenose dolphin, *Tursiops truncatus,* following the El Niño event of 1982–83 (Wells et al., 1990). This species now is seen regularly in nearshore waters off central California, within the range of the harbor porpoise.

Similarly, harbor porpoise in central California may have shifted their distribution out of the study area (either to the north or farther offshore) in response to environmental changes, causing an apparent decline in abundance in the nearshore region. Unfortunately, no detailed data on harbor porpoise distributions and oceanographic conditions are available to test this hypothesis. However, it is noteworthy that the relative abundance of harbor porpoise in central California (dashed line in Fig. 3) exhibits a significant negative correlation (α=0.05, Pearson correlation coefficient r=–0.79, P=0.035) with 1986–93 September sea-surface temperature anomalies off Monterey Bay,[1] despite the coarse nature of these two measurements. Thus, in years when sea-surface temperatures were warmer, the relative abundance of harbor porpoise (a temperate species) was lower, and vice versa. This may be indicative of movement of harbor porpoise in relation to changes in sea-surface temperature (or to other environmental factors that are correlated with sea-surface temperature), but it is not known whether harbor porpoise move northward or offshore in response to such environmental changes.

Studies of pollutant ratios in animals along the U.S. West Coast suggest that harbor porpoise do not move frequently between central and northern California (Calambokidis and Barlow, 1991). Consistent with these observations, a shift of animals from central to northern California is not indicated in the analysis of this aerial survey series because the declining trend is still significant when northern California data are included. However, power to detect trends reliably in the northern portion of the study area is probably low, given only four surveys in this region. Additional surveys will improve the ability to detect a northward shift within California, if one is present. It is important to note, however, that harbor porpoise off northern California show a continu-

[1] The sea-surface temperature anomaly is defined as the deviation of the mean monthly sea-surface temperature in a given year from the long-term mean for that month. Thus positive anomalies indicate warmer than average months and vice versa. Oceanographic Monthly Summary, U.S. Dep. Commer., NOAA, National Ocean Service, available from NOAA/NOS, Ocean Products Branch, 5200 Auth Road, Room 100, Camp Springs, MD 20746.

ous distribution into waters off Oregon (Barlow, 1988; Barlow et al., 1988), where they are managed separately because of jurisdictional boundaries. Without simultaneous surveys in Oregon, a more widespread shift in distribution cannot be ruled out.

Alternatively, harbor porpoise may have changed their distribution in relation to distance from shore or water depth. The surveys extended only to approximately the 92-m (50-fathom) depth contour. Although the majority of harbor porpoise are expected to be found inshore of this depth (Barlow, 1988), an increase in the proportion of animals found in deeper waters could cause an apparent decline within the 0–92 m (0–50 fathom) study area. This hypothesis cannot presently be tested because detailed surveys for harbor porpoise in waters deeper than 92 m have not been conducted off California, and inferences for offshore areas cannot readily be drawn on the basis of distribution patterns inshore of 92 m depth.

Effects of fishery-related mortality

If the detected decline in harbor porpoise abundance along the California coast is a real phenomenon, then one possible cause for the decline may be incidental mortality of this species in California set gillnet fisheries. Although annual mortality is thought to have gradually declined from about 200–300 animals per year in 1980–87 to about 30–50 animals annually in the last few years (Barlow and Forney, 1994), there was no observer program to monitor mortality in set gillnet fisheries from April 1987 to June 1990. Total mortality estimates for these unmonitored years are based on kill rates for the 1990–91 fishing season and on estimated 1987–90 fishing effort (Perkins et al.[2]). These estimates are accurate only if the mortality observed in the 1990–91 fishing season is representative of 1987–90 rates. If fishery-related mortality of harbor porpoise was in fact higher during 1987–90, this may have contributed to a decline in abundance greater than is apparent from the mortality estimates (see Perkins et al.[2]).

Absolute abundance estimates for central California harbor porpoise have recently been updated on the basis of pooled data from the 1988–93 aerial surveys, yielding an estimate of 4,120 (CV=0.22) harbor porpoise (Barlow and Forney, 1994). Assuming an otherwise stable population, 9.3% of the population, or roughly 350–450 animals, would have had to be removed during each year of the study period in order to cause the decline indicated by the analysis for central California. The fishery-related mortality estimates range from 12 animals in 1993 to 197 animals in 1986 and have large standard errors, but the upper 95% lognormal confidence limits of the mortality estimates are lower than 9.3% of the population estimate in all years since 1984 (derived from data in Perkins et al.[2]; Hanan et al.[3,4]; Konno[5]; Julian[6,7]). Although these mortality estimates assumed fishing effort was known without bias, when in fact it may have been underestimated (Julian[7]), fishery-related mortality alone does not appear to be responsible for the decline in harbor porpoise abundance within the central California study area. However, potential effects of age or sex bias in harbor porpose mortality and potential time lags in the impact of such takes are unknown.

Change in natural mortality and net reproduction

An increase in natural mortality (e.g. due to increased predation, disease, or a reduced food supply) could contribute to a decline in abundance. Natural mortality rates for harbor porpoise are not known. The small size of harbor porpoise may make them vulnerable to shark and killer whale predation, but there is no evidence (i.e. from strandings) to suggest that predation rates may have been higher during the past eight years than in prior time periods. Harbor porpoise appear to be opportunistic feeders: market squid, *Loligo opalescens*, spotted cusk eel, *Chilara taylori*, and northern anchovy, *Engraulis mordax*, are known to be prominent components of their diet in the Monterey Bay region (Sekiguchi, 1987; Dorfman, 1990); however, both studies indicate that the northern anchovy is the most important of these prey

[2] Perkins, P., J. Barlow, and M. Beeson. 1994. Report on pinniped and cetacean mortality in California gillnet fisheries: 1988–90. Admin. Rep. LJ-94-11. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., P.O. Box 271, La Jolla, CA 92038.

[3] Hanan, D. A., S. L. Diamond, and J. P. Scholl. 1986. An estimate of harbor porpoise mortality in California set net fisheries April 1, 1984 through March 31, 1985. Admin Rep. SWR-86-16, 38 p. Available from Southwest Region, 300 S. Ferry St., Terminal Island, CA 90731.

[4] Hanan, D. A., S. L. Diamond, and J. P. Scholl. 1987. An estimate of harbor porpoise mortality in California set net fisheries April 1, 1985 through March 31, 1986. Final rep. to National Marine Fisheries Service, Southwest Region, 300 S. Ferry St., Terminal Island, CA 90731.

[5] Konno, E. S. 1990. Estimates of sea lion, harbor seal and harbor porpoise mortalities in California set net fisheries for the 1987–88 fishing year. Draft rep. available from California Department of Fish and Game, P.O. Box 271, La Jolla, CA 92038.

[6] Julian, F. 1993. Pinniped and cetacean mortality in California gillnet fisheries: preliminary estimates for 1992. Int. Whaling Comm. Working Paper SC/45/O22, 29 p.

[7] Julian, F. 1994. Pinniped and cetacean mortality in California gillnet fisheries: preliminary estimates for 1993. Int. Whaling Comm. Working Paper SC/46/O11, 28 p.

items. In recent years, California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys have revealed a decline in California anchovy populations (Jacobsen et al., 1994), and the occurrence of this species in the diet of California sea lions, *Zalophus californianus,* off southern California has decreased markedly since 1991.[8] Based on these considerations, an alternate hypothesis for the observed decline in harbor porpoise abundance is that the population has been affected by a decline in a major food source, the northern anchovy. However, too few stranded or incidentally caught harbor porpoise have been available recently for examination of food habits (Peltier et al., 1993, 1994; Lennert et al., 1994;), and data are presently insufficient to test the possibility of such a relationship.

Conclusions

Despite a reduction in fishery-related mortality, the harbor porpoise population in nearshore waters off central California appears to have declined between 1986 and 1993. Potential causes of this decline are poorly understood, and further studies are imperative. Recent restrictions on coastal gillnet fisheries have substantially reduced harbor porposie mortality in central California. If the decline was caused primarily by fishery-related mortality, then the population should exhibit a stable or increasing trend over the next several years. Continuation of the aerial-survey time series will provide a means of detecting such a trend. Additional research should also address possible relationships between the density and distribution of harbor porpoise and environmental conditions (such as water temperature and prey availability).

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Seasonal influences on statolith growth in the tropical nearshore loliginid squid *Loligo chinensis* (Cephalopoda: Loliginidae) off Townsville, North Queensland, Australia

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Information is currently accumulating on age, growth, and maturity rates of squids, with a number of studies focusing on tropical and warm water species (eg. Jackson, 1990, a and b; Arkhipkin and Mikheev, 1992; Bigelow, 1992; Jackson and Choat, 1992; Arkhipkin and Nekludova, 1993; Jackson, 1993; Laptikhovsky et al., 1993; Young and Mangold, 1994; see also Jackson, 1994, for review). The interpretation of growth phenomena in squids is complicated owing to the high degree of temperature dependency in growth (O'Dor and Wells, 1987; Forsythe and Hanlon, 1989). Moreover, growth is highly variable even within particular temperature regimes (Lipinski, 1986; Natsukari et al., 1988). The use of validated daily increments in statoliths is a convincing tool for determining both the rate of growth and its variance. However, there is also the potential that temperature-induced variation in growth rates might be reflected in statolith growth rates.

Recent work on the uncoupling between otolith size and fish size (see Campana and Jones, 1992) has indicated that individual variation in growth rates can have profound effects on soma-otolith relationships. While such features make analysis such as back calculation of individual size less than straightforward (Campana, 1990), they do provide a mechanism for detecting past growth histories (or perhaps even past environmental histories) to which a fish has been exposed. For example, if two similar-sized fish of the same species show considerable disparity in otolith size, it suggests that the individual with the larger otolith has grown slower (e.g. Reznick et al., 1989; Wright et al., 1990). Lipinski et al. (1993) have also documented substantial uncoupling in squid statolith growth and in growth of the mantle in *Todaropsis eblanae* and *Todarodes angolensis* off southern Africa.

Statolith increments are produced daily in *Loligo chinensis* (Jackson, 1990b) as well as in other loliginid squids such as *Alloteuthis subulata* (Lipinski, 1986), *Loligo opalescens* (Yang et al., 1986), *Loliolus noctiluca* (Jackson, 1990b), and *Sepioteuthis lessoniana* (Jackson, 1990a; Jackson et al., 1993). However, compared with fish otolith analysis in which there is a substantial number of ageing and increment validation studies (e.g. Campana and Neilson, 1985; Stevenson and Campana, 1992), much of the work with statolith ageing and validation is still preliminary in nature. However, evidence does support daily periodicity in statolith increment production in many species (Jackson, 1994) although there is an ongoing need for further validation and ageing studies. Because age and population information is already available for *Loligo chinensis*[1] (Jackson, 1990b, 1993; Jackson and Choat, 1992), this study was undertaken to see if seasonal differences in growth rate are reflected in statolith-size:body-size relationships in this tropical nearshore squid.

Materials and methods

Individuals of *Loligo chinensis* were captured by using paired otter trawls (each net consisted of an 11-m gape and 3.8-cm mesh). Trawls were towed for approximately 20 minutes at a speed of 2–2.5 knots. Samples were taken in Cleveland Bay (19°15'S,146°50'E) in water <20 m deep off Townsville, North Queensland. Statoliths were obtained from squid caught during two seasonal periods, 12 January 1989 (austral summer, n=35) and 13 July 1989 (austral winter, n=33). Squid were preserved in 10% buff-

[1] It is now known that the species *Loligo chinensis* which is found in shallow tropical waters off North Queensland is a distinct species from *L. chinensis* which is found elsewhere in the tropical Indo-Pacific. J. Yeatman. 1993. James Cook Univ. of North Queensland. Personal commun. Furthermore, all *Loligo* species in Australian waters will probably be referred to as *Photololigo* in the future. Until this is resolved, I have referred to the species of this study as *Loligo chinensis* which is the same species referred to as *Photololigo* cf. *chinensis* (east coast form) in Dunning et al. (1994) and *Photololigo* sp. 3 in Yeatman and Benzie (1994).

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Fishery Bulletin 93:749–752 (1995).

ered seawater formalin and subsequently transferred to 70% ethanol. Mantle length (ML) measurements (nearest mm) were taken on the preserved individuals. Statoliths were removed shortly after preservation and mounted in Crystal Bond thermoplastic cement.

Total increment number was determined (with a camera lucida attached to an Olympus BH compound microscope) as the mean of three consecutive counts that differed less than 10% from the mean (see also Jackson and Choat, 1992; Jackson, 1993). Statolith length (to the nearest 10 μm) was measured with an eyepiece micrometer (with an Olympus BH compound microscope) along the longest axis from the dorsal dome to the tip of the rostrum.

Results

For the summer population, the relationship between statolith length and mantle length as well as statolith length and age was curvilinear. However, both relationships were linear for the winter population (Fig. 1; Table 1). Because all relationships were not linear, an analysis of covariance could not be applied to these data sets. However, a paired t-test was used to compare statolith lengths of similar-sized males and females (mantle lengths between 90 and 110 mm, n=24) from both January (summer) and July (winter). Squid statoliths from the July sample were significantly longer than statoliths from the January sample (P<0.05).

The relationship between statolith length and mantle length (Fig. 1A) suggested that somatic growth was greater than statolith growth as size increases (i.e. in larger squids the mantle was increasing in length faster than was the statolith). Moreover, in general, for any given length, a winter squid had larger statoliths than its summer counterpart.

There were also considerable seasonal differences in the growth of the statolith with age (Fig. 1B). There was a rapid increase in statolith length in summer over a relatively short period from 60 to 100 days. In contrast, statolith growth was much slower in the winter; the statolith gradually increased in length from 80 to 170 days. However, statoliths eventually reached a greater length in the older, winter-population squids. This feature was a factor of age because winter squids were not longer than summer squids. In comparing similar-aged squids between seasons, for any given age, a summer squid generally had a larger statolith than its winter counterpart.

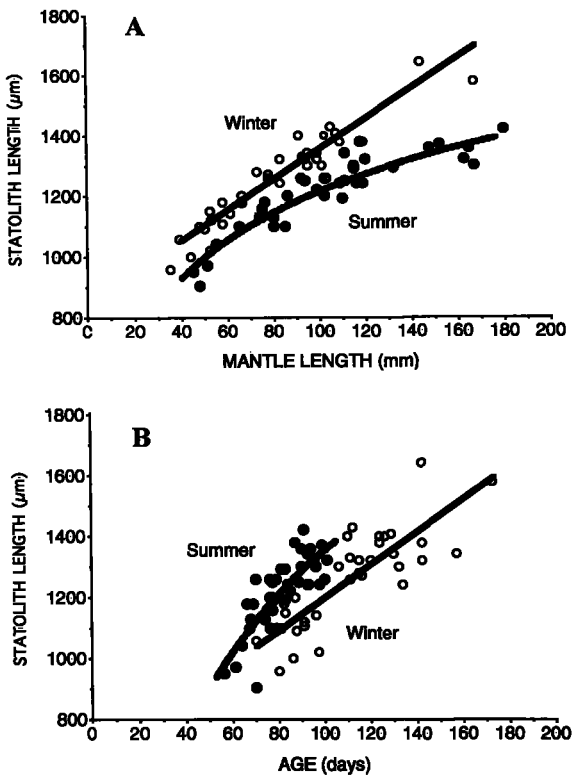

Figure 1

The relationship between (**A**) statolith length and mantle length and (**B**) statolith length and age for summer (January) and winter (July) samples of *Loligo chinensis*.

Discussion

Current research on fish somatic-otolith growth relationships provides a background for the possible mechanisms underlying somatic-statolith growth relationships for *L. chinensis*. The relationship between both statolith length and mantle length and statolith length and age shows striking similarities to otolith length versus fish length and age studies. Mosegaard et al. (1988), Secor and Dean (1989), Reznick et al. (1989), Wright et al.(1990), and Mugiya and Tanaka (1992) have shown that slower-growing fish have larger otoliths than similar-sized, faster-growing fish. Furthermore, for striped bass, *Morone saxatilis*, and Atlantic salmon, *Salmo salar*, slower-growing fish have larger otoliths at any given size, although faster-growing fish have larger otoliths at any given age (Secor and Dean, 1989; Wright et al., 1990). A similar relationship is evident between statolith length and both mantle length and age for *L. chinensis*.

These teleost studies provide insights into the growth dynamics of squid. The slower growing individuals of *L. chinensis* (winter population) had larger

Table 1

Regression equations for the relationship between mantle length and statolith length and for age and statolith length for individuals of *Loligo chinensis* collected in both summer and winter. ML = mantle length. All regressions were highly significant ($P \leq 0.001$).

Season	Relationship	n	Equation	r^2
Summer	ML vs. statolith length	38	$y = -238.4 + 731.2 \log x$	0.84
Summer	Age vs. statolith length	38	$y = -1585.8 + 1470.6 \log x$	0.63
Winter	ML vs. statolith length	33	$y = 849.4 + 5.03x$	0.91
Winter	Age vs. statolith length	33	$y = 672.7 + 5.3x$	0.67

statoliths because they were in reality much older than similar-sized, faster-growing squids (summer population). Alternatively, when statolith length and individual age were compared, faster-growing squids had larger statoliths than slower-growing squids for a given age because the individual itself was considerably larger (e.g. in the summer, squids were reaching adult sizes at around 80 days whereas in the winter, 80-day squid were still juveniles).

Morris and Aldrich (1985) have suggested that statolith length may be a better indicator of squid age than increment number because they observed less variation in the mantle length:statolith length relationship than in the mantle length:age relationship in *Illex illecebrosus*. However, the seasonal difference in the relationship between the statolith and the soma of *L. chinensis* suggests that this technique should be used cautiously until further research into temperature effects is conducted (see also Campana, 1990; Lipinski et al., 1993). On the basis of laboratory observations, Forsythe and Hanlon (1989) and Forsythe (1993) have suggested that even fairly small variations in ambient temperature can have a marked effect on somatic growth rates. Temperature has also been shown to be an important influence on growth rates of *Sepia australis* in the field (Roeleveld et al., 1993). This preliminary study with *L. chinensis* suggests that temperature variation will not only greatly influence somatic growth but statolith growth as well. The uncoupling of statolith growth and somatic growth in squid is certainly an area that deserves further research (see Lipinski et al., 1993).

Statoliths are structures which have accentuated both the differences and similarities between cephalopods and fish. The increment structure and the growth of the statolith in relation to the squid soma are remarkably similar to that of the otolith in fish. In contrast, the enumeration of growth increments in both otoliths and statoliths have accentuated very different growth strategies and life histories (e.g. Jackson and Choat, 1992; Alford and Jackson, 1993) of two organisms that are biologically very different but nevertheless show many similarities.

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A comparison of Steller sea lion, *Eumetopias jubatus*, pup masses between rookeries with increasing and decreasing populations

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The Steller sea lion, *Eumetopias jubatus*, population in Alaska has decreased by 62% since the late 1970's (Merrick et al., 1987; Loughlin et al., 1992; Sease et al., 1993). Declines occurred at all 33 rookeries in the Gulf of Alaska and Aleutian Islands, although numbers at five rookeries in Southeast Alaska and Oregon increased. The severity of the declines at affected rookeries led the National Marine Fisheries Service (NMFS) to list the species as threatened throughout its range under the Endangered Species Act (1990). The proximate cause for the decline appears to be chronically reduced juvenile (ages 0–3 yr) survival. After the early 1980's, juveniles were in far lower abundance on rookeries than in the 1970's (Merrick et al., 1988; NMFS[1]).

During the summers of 1987–88, 424 female pups were marked at the Alaska rookery on Marmot Island. According to the life table constructed for the area from data collected in the 1970's (York, 1994; Calkins and Pitcher[2]), close to 90 females should have survived to 1994. Biologists returning to the site from 1991 through 1994 have relocated less than 25 animals (NMFS[1]). York (1994) found that changes in the population size and the age structure of adult females were consistent with a decrease in juvenile survival. Also, the mass of juvenile animals in the 1980's was significantly less than that found in the 1970's (Calkins and Goodwin[3]).

The age when juvenile survival decreases remains unknown. One hypothesis is that early pup survival has decreased. Although numbers of pups observed dead on the rookeries have been consistently low during and immediately after the pupping season (NMFS[1]), it is difficult to measure early survival of Steller sea lion pups because carcasses rapidly disappear from rookeries (due to storms, tides, and scavengers). An alternative approach to counting dead pups is to study the potential survival of live pups found on the rookeries.

Pup mass provides useful information on juvenile survival because of the presumed relationship between mass and survival. Heavier juvenile mammals have a higher probability of survival than do lighter individuals for a variety of species including grey seals, *Halichoerus grypus*, wolves, *Canis lupus*, humans, *Homo sapiens*, Columbian ground squirrels, *Spermophilus columbianus*, and northern fur seals, *Callorhinus ursinus* (Coulson and Hickling, 1964; van Ballenberghe and Mech, 1975; Terrenato et al., 1981; Murie and Boag, 1984; Baker and Fowler, 1992). Weighing pups also has advantages over measurements of general condition (e.g. blood-based indices)—it is noninvasive, has minimal impacts on rookeries, and can provide a large, widespread

[1] National Marine Mammal Laboratory, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115. Unpubl. data, 1994.

[2] Calkins, D. G., and K. W. Pitcher. 1982. Population assessment, ecology, and trophic relationships of Steller sea lions in the Gulf of Alaska. *In* Environmental assessment of the Alaskan continental shelf, p. 455–546. Final Rep. 19 to OCSEAP (Outer Continental Shelf Environment Assessment Program).

[3] Calkins, D. G., and E. Goodwin. 1988. Investigations of the decline of Steller sea lions in the Gulf of Alaska. Unpubl. rep., 76 p. Available from National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

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sample size at minimal cost (when incorporated into other research).

Our hypothesis was that if the cause of the decline affected the health of pups, then pups should be smaller at rookeries with declining populations than at rookeries with increasing populations. We examined this hypothesis by comparing the masses of pups weighed during 1987–94 at rookeries documented as having either increasing (Oregon and Southeast Alaska) or decreasing (Gulf of Alaska and Aleutian Island) populations (NMFS[4]). In this note, we present our analyses of sex-based and temporal variability in pup masses, compare masses obtained from the two groups of rookeries, discuss potential sources of bias in the mass measurements, and conclude with a comment on the possible source(s) of the observed differences in pup masses.

Methods

Data collection

Steller sea lion pupping is synchronous from central California to the Aleutian Islands (Bigg, 1985; Merrick, 1987). The median pupping date is 12–13 June; viable births begin in late May and continue through the end of June. We weighed pups from 26 June to 8 July, before pups were sufficiently mobile to escape into the water, as part of pup censuses conducted at the rookeries. Pups aggregated into small pods (10–20 pups each) after adult animals had been cleared from the rookery during the census. Individuals in a pod were captured by hand, sexed, tagged on both foreflippers, bagged into a hoop net, and weighed to the nearest kilogram. Lengths were not measured because of the difficulty in obtaining precise measurements from pups that have not been anesthetized. The first pod selected was typically at the fringe of the rookery and subsequent pods were selected from areas progressively closer to the center of the rookery. Pods were sampled until the desired sample size (usually 50 pups per site) was reached.

A total of 1,245 Steller sea lion pups (616 females and 629 males) were weighed at twelve rookeries (Table 1; Fig. 1) in four areas during 1987–94 in Oregon, Southeast Alaska, the Gulf of Alaska, and the Aleutian Islands. During 1987–94, populations at the Oregon and Southeast Alaska sites increased 5–15%, whereas populations at the Gulf of Alaska and Aleutian Island sites decreased 20–50% (Table 1) (Loughlin et al., 1992; Sease et al., 1993; NMFS[4]).

Data analysis

Differences in mean mass by sex of pup were analyzed for each site separately and then for the whole data set. All subsequent analyses were performed separately for each sex.

Short-term interannual variation (during 1987–94) in mean pup mass was tested separately for one rookery in each of three geographic areas—Rogue Reef (Oregon), Marmot Island (Gulf of Alaska), and Ugamak Island (Aleutian Islands). For each of these sites the weight of pups was measured on roughly the same day for two or three years (Table 1). Long-term interannual variation was tested separately for the Sugarloaf and Marmot Island rookeries by comparing their 1992–93 masses with data collected by

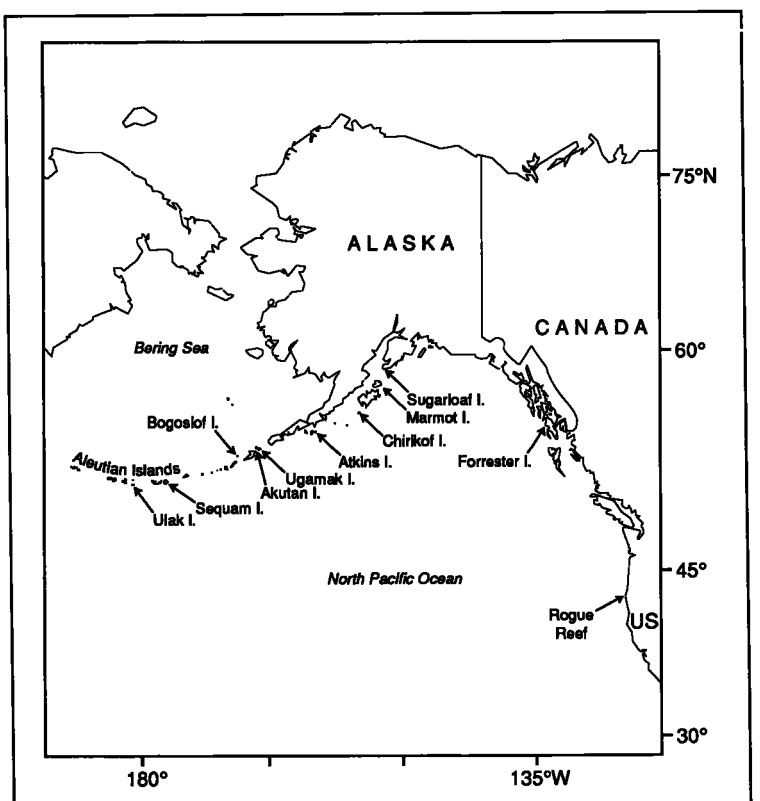

Figure 1

Steller sea lion, *Eumetopias jubatus*, rookeries at which pups were weighed during 1965–94.

[4] NMFS. 1995. Status review of the Steller sea lion (*Eumetopias jubatus*). Unpubl. rep, 120 p. Available from National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

Table 1

Steller sea lion, *Eumetopias jubatus*, mean pup masses (kg) by date, sex, and rookery, collected during 1987–94. *n* indicates number of pups weighed, and SD indicates standard deviation of the mean value. *T*-value represents the Student's *t* calculated for the comparison of male and female masses for the site and year combination. All *t*-tests were significant at $P<0.01$.

		Female mass			Male mass			
Site	Weighing date	*n*	Mean (kg)	SD	*n*	Mean (kg)	SD	*t*-value
Oregon								
Rogue Reef	30 Jun 1987	56	20.70	3.39	44	24.90	3.33	6.20
	29 Jun 1888	46	20.00	3.38	54	23.40	3.66	4.79
	7 Jul 1990	20	21.38	2.90	25	23.88	3.85	2.41
SE Alaska (Forrester Island Complex)								
North Rock	28 Jun 1990	56	24.10	3.03	49	26.40	4.69	3.02
Cape Horn Rock and Lowrie	29 Jun 1990	64	25.70	3.31	70	29.60	4.89	5.36
Gulf of Alaska								
Sugarloaf	1 Jul 1992	23	23.30	3.57	27	27.30	3.88	5.84
Marmot	30 Jun 1987	89	25.40	3.68	60	29.20	4.20	2.81
	30 Jun 1988	29	26.40	4.05	21	29.70	4.16	3.54
	8 Jul 1993	19	29.70	5.51	32	35.60	5.89	3.77
Chirikof	26 Jun 1990	27	22.20	3.18	34	28.00	4.60	5.50
Atkins	30 Jun 1991	24	28.40	3.70	26	31.60	4.60	2.70
Aleutian Islands								
Ugamak	2 Jul 1990	28	27.40	3.70	22	32.50	6.70	3.42
	3 Jul 1991	25	30.30	3.60	25	36.40	4.30	5.44
	3 Jul 1993	15	28.10	4.05	35	33.90	5.57	3.63
Akutan	7 Jul 1992	20	31.80	4.72	30	37.80	5.75	3.87
Bogoslof	5 Jul 1990	23	28.70	3.90	27	36.00	5.60	5.26
Seguam	27 Jun 1994	27	26.98	5.00	23	35.51	4.96	6.01
Ulak	3 Jul 1994	25	30.44	4.28	25	38.50	5.53	5.79

Alaska Department of Fish and Game (ADF&G[5]) in 1965 and 1975 (Table 2; ADF&G). To our knowledge, these are the only data on pup size that have been collected prior to our study.

Variation in mean pup mass within the 26 June–8 July weighing period was analyzed for Oregon, the Gulf of Alaska, and the Aleutian Islands by using a linear regression of the natural log of mean mass from a weighing against weighing day. Significance and equality of slopes of the regressions were tested with a Student's *t*-statistic.

Mean pup masses collected for the 26–30 June period were compared for the Oregon, Southeast Alaska, and Gulf of Alaska regions by using Student's *t*-statistic. Means and standard errors were calculated for each area's weighings by treating each weighing as a separate strata; calculations were performed by methods of stratified random sampling (Cochran, 1977). Mean pup masses obtained from the Gulf of Alaska and Aleutian Islands were compared by using an analysis of covariance (with weighing day as the covariate) because of the 14-day spread in weighing days at these locations. Note that to use an analysis of covariance, the slopes of the regression of mass against weighing date were first compared for the Gulf of Alaska and Aleutian Islands to ensure homogeneity of slopes.

Results

Male pups ($\bar{x}$=30.5 kg, standard error [SE]=0.3) were significantly heavier (t=318.8, $P<0.01$) than female pups ($\bar{x}$=26.2 kg, SE=0.212) for all sites combined. Males were also significantly heavier at all individual rookeries in all years sampled (Table 1; $P<0.01$).

The only significant interannual variation in mean pup masses for 1987–94 was for female pups at Ugamak Island (F=4.15, P=0.04). No significant inter-

[5] Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518. Unpubl. data, 1976.

annual differences were found in mean female mass at the other three sites or in male masses at any site. Both female (F=8.6, P<0.01) and male (F=12.9, P<0.01) pups weighed at Marmot Island in 1993 were significantly heavier than pups weighed at the rookery in 1975, though the weighings occurred a week later in 1975. Mean mass of pups weighed at Sugarloaf Island in 1965, 1975, and 1992 were not significantly different for either female (F=3.1, P=0.1) or male (F=1.3, P=0.5) pups. However, two of the 1965 and 1975 weighings were conducted two weeks later than the 1992 weighing.

Table 2

Steller sea lion, *Eumetopias jubatus*, pup masses (kg) by date, sex, and rookery, collected during 1965 and 1975 at Sugarloaf and Marmot Islands in the Gulf of Alaska. *n* indicates number of pups weighed, and SD indicates standard deviation of the mean value.

		Female mass			Male mass		
Site	Weighing date	*n*	Mean (kg)	SD	*n*	Mean (kg)	SD
Sugarloaf	1 Jul 1965	7	19.70	2.27	13	24.90	2.73
	14 Jul 1965	9	23.80	3.13	11	29.30	5.83
	13 Jul 1975	16	23.90	3.04	35	27.40	6.99
Marmot	17 Jul 1975	21	25.30	3.92	29	30.80	4.35

Mean male mass increased significantly in the Gulf of Alaska during the 26 June–8 July weighing period (t=2.9, P=0.05, r^2=0.68). However, there was not a significant relationship between weighing day and mean mass for males in Oregon or the Aleutian Islands, nor for females in any of the three geographic areas. The slopes of the regression of mean pup mass against weighing day were not significantly different for the Gulf of Alaska and Aleutian Islands for female (t=0.26, P>0.5) and male (t=0.57, P>0.5) pups.

Mean mass increased significantly for both sexes from Oregon to Southeast Alaska to the Gulf of Alaska and Aleutian Islands. Oregon female (t=105.1, P<0.01) and male (t=79.3, P<0.01) pups were significantly lighter than their counterparts in Southeast Alaska (Fig. 2). Mean mass of Southeast Alaska female (t=29.4, P<0.01) and male (t=36.9, P<0.01) pups was significantly less than that of Gulf of Alaska pups. Gulf of Alaska female and male pups were both significantly lighter than Aleutian Island female (F=6.0, P=0.03) and male (F=16.3, P<0.01) pups.

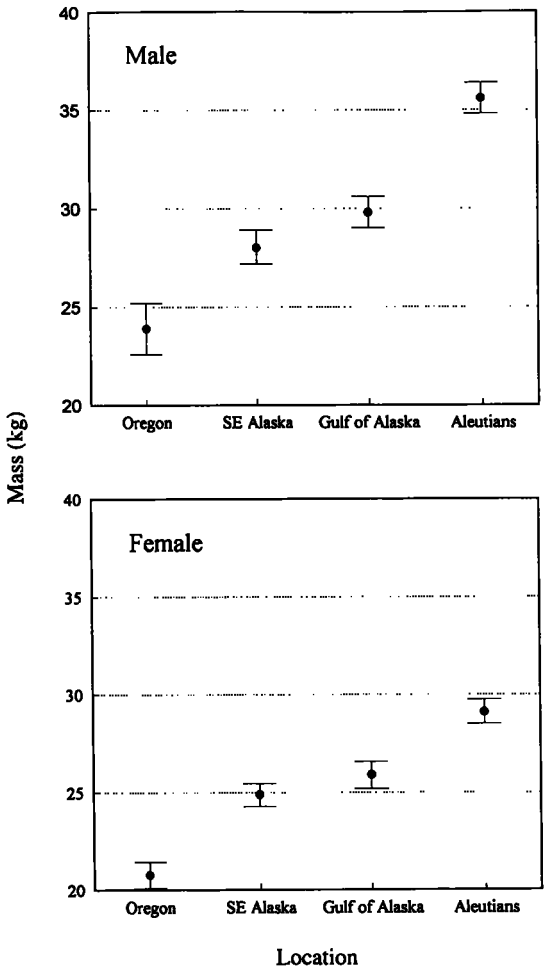

Figure 2

Steller sea lion, *Eumetopias jubatus*, mean pup masses (kg) by sex and area during 1987–94. Error bars represent 95% confidence intervals around the mean.

Discussion

Our expectations in this study were either that there would be no significant differences in mean pup mass between rookeries or that pups at rookeries with declining populations would be smaller than pups at rookeries with increasing populations. Considerable research by scientists at NMFS, ADF&G, and other research facilities has focused on comparing the condition of pups between Southeast Alaska and the Gulf of Alaska, because it has been assumed that the opposing population trends in the two areas were a result of some limiting factor (e.g. lack of food or disease) affecting only the Gulf of Alaska population,

and that this factor could be expressed in the condition of the pups.

We were surprised to find that pups were heavier at rookeries with decreasing populations (i.e. in the Gulf of Alaska and Aleutian Islands) than at rookeries with increasing populations (i.e. in Southeast Alaska and Oregon). We were also surprised to find that mean pup mass at Marmot and Sugarloaf Island in 1992–93 was equal to or greater than that of pups weighed at the sites in 1965 and 1975 (prior to the onset of the decline).

The implications of these findings to the search for the ultimate cause of the Alaskan Steller sea lion population decline are twofold. First, the large size of pups in the areas of declining population suggests that pup condition is not compromised in the first month postpartum and that the factor reducing juvenile survival acts after the neonatal period. Second, the larger pup size in declining populations implies that pregnant and early postpartum females in those populations are not having difficulty finding prey.

We have considered possible biases that could have influenced these results (Trites, 1991). Some bias may be associated with the unknown birth date of the pups weighed. To obtain masses of known-age animals, it is necessary to capture pups soon after birth. The cost of obtaining a large, geographically representative sample by such an approach is prohibitive. Such an approach would increase the mortalities of weighed pups (due to abandonment), would greatly disrupt the rookeries (days of repeated captures would be necessary), and would be very expensive. Because pupping is synchronized throughout the range, a random selection of pups from each site during the same time period should provide samples that are representative of the same age structure.

A biased sample could also result if pups were not selected at random. Lighter pups have been selected from pup pods by handlers in some studies of northern fur seal pups (Roppel et al.[6]). However, all pups from a pod were weighed in our study. A bias could still remain if pup mass varied systematically through the rookery (e.g. smaller pups aggregated at the periphery, larger pups in the center), or if pups aggregated by size within the rookery. We selected pups from pods at both the periphery and the center of rookeries. In addition, pups at the time of the weighings had not yet begun to group together. The lack of significant interannual variation during this study indicates that the bias was (if present) consistent over time.

The variation in mean pup mass at rookeries and between the 1970's and the present appears to be real and could be explained in several ways. First, the increase of two years in the average age of Gulf of Alaska adult females since 1976–78 (York, 1994) has probably increased the average size of reproducing female sea lions (Calkins and Pitcher[2]). Northern fur seal data suggest that larger females produce larger pups (NMFS[4]). If Steller sea lions are similarly affected, then the increase in mean size of pups in the Gulf of Alaska since 1976–78 would be partly due to the increased average size of reproducing females. There are no data on female age or size from Southeast Alaska or Oregon with which to evaluate the contribution of this factor to differences between geographic areas. In addition, the larger size of pups in the Gulf of Alaska to Aleutian Island area could be a phenotypic expression of the genetic differences found between this area and the Southeast Alaska to Oregon area (Bickham et al., in press). Finally, the greater mass of pups at rookeries with reduced populations could be a density-dependent response to reduced competition among adult females for food. Studies of the foraging effort of postpartum females currently being conducted in Southeast Alaska and the Gulf of Alaska will be useful in testing this hypothesis.

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Fertilization of the second clutch of eggs of snow crab, *Chionoecetes opilio*, from females mated once or twice after their molt to maturity

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Females of the commercially important genus *Chionoecetes* (Brachyura: Majidae) copulate and extrude eggs for the first time soon after a terminal molt to maturity (Watson, 1972; Adams, 1982). Females preparing for the molt to maturity are termed "pubescent," those bearing a first clutch are "primiparous," and those bearing a second or subsequent clutch are "multiparous." Spermathecae allow females to store sperm that is not expended at spawning (Watson, 1970; Adams and Paul, 1983; Beninger et al., 1988).

The importance of sperm stored from the first mating to reproductive output is partially documented for the Tanner crab, *Chionoecetes bairdi* (Adams and Paul, 1983; Paul and Paul, 1992), but remains largely unknown for the snow crab, *Chionoecetes opilio* (Elner and Beninger, 1992). Watson (1970) observed that some female *C. opilio* hatched a clutch and then extruded a new clutch of fertilized eggs without remating. Assuming that copulation occurs only at the molt to maturity, he concluded that female *C. opilio* can produce more than one batch of fertile eggs from a single mating (also see Watson, 1972). Subsequently, field and laboratory studies have shown that multiparous females of *C. opilio* and of *C. bairdi* can, and often do, mate before extruding a new clutch (Adams, 1982; Paul, 1984; Taylor et al., 1985; Conan and Comeau, 1986; Hooper, 1986; Claxton et al., 1994; Moriyasu and Conan[1]). Because the female *C. opilio* that Watson observed spawning were of unknown reproductive history (i.e. number of matings and clutches), the conclusion that one mating is sufficient to produce more than one viable clutch is suspect and warrants further investigation.

In *C. bairdi*, the viability of stored sperm apparently decreases over time, and some multiparous females may fail to spawn or may extrude unfertilized eggs when isolated from males for more than one breeding season (Paul, 1984). Furthermore, in laboratory experiments with *C. bairdi*, Paul and Paul (1992) found that 10 out of 11 females did not receive enough sperm at the first mating to fertilize more than one clutch. These investigators suggested that this may also be the case for *C. opilio*. However, Sainte-Marie and Lovrich (1994) estimated that primiparous *C. opilio* usually have enough stored sperm to fertilize at least one additional clutch. Therefore, we compared the size of the second clutch and the proportion of divided (i.e. fertilized) eggs for female *C. opilio* mated only at the molt to maturity with those values obtained for females with access to males at a second spawning.

Materials and methods

Males and pubescent females were collected in Baie Sainte-Marguerite (ca. 50°06'N, 66°35'W), northwest Gulf of Saint Lawrence, from September through October 1991, and in March 1992. Carapace width (CW) of females and males, and right chela height (CH) of males, were measured to the nearest 0.1 mm as described in Sainte-Marie and Hazel (1992). Males >40 mm CW were classified on the basis of chela allometry into either of two sperm-producing forms (Comeau and Conan, 1992), designated adolescent or adult following terminology in Sainte-Marie et al. (in press). (Other investigators have used the terms "small-clawed," "morphometrically immature," or "juvenile" to designate adolescent males, and "large-clawed" or "morphometrically mature" to designate adult males.) Classification was initially done by visual comparison of individual male measurements with scatterplots of CH on CW for a large sample of males from the source site, and verified a posteriori by using a site-appropriate discriminant function from Sainte-Marie and Hazel (1992).

Crabs were segregated by sex in tanks of either 1,400 or 2,000 L with flowing seawater. The mean temperature of seawater over the year following the first mating of females was 1.5°C, and monthly

[1] Moriyasu, M., and G. Y. Conan. 1988. Aquarium observation on mating behavior of snow crab, *Chionoecetes opilio*. Int. Counc. Explor. Sea C.M. (Council meeting) 1988/k:9, 14 p.

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means ranged from a low of 0.1°C in March 1992 to a high of 3.0°C in August 1992 (daily records: low of –0.3°C and high of 6.5°C). Photoperiod was controlled to correspond to natural light rhythms. Individual crabs were identified by a plastic tag tied around the basipodite of one of the fourth or fifth pereiopods. Crabs were fed frozen shrimp (*Pandalus borealis*) semiweekly. Beginning in January 1992, tanks were checked twice daily for molting individuals.

Less than 12 hours after molting to maturity, each female was placed in a 120-L tank that was either empty or contained one male. Male mates were hard-shelled adult crabs in either of three size categories, 40–60, 80–100, and 120–140 mm CW, or hard-shelled adolescent crabs of 80–100 mm CW. Actual size ranges were 48.6–59.8, 82–99.4, and 120.3–138.3 mm CW for adult males, and 80.1–99.8 mm CW for adolescent males. The female was left in the tank until either eggs were extruded or 24 hours had elapsed. The female was then allowed to harden her shell for 5–6 days in isolation and was monitored daily to detect delayed egg extrusion. Finally, the female was retagged and transferred to a communal holding tank for females. Males were used once only and then held in communal tanks for up to 14 months after mating, to determine whether they would moult.

Egg color of each primiparous female was monitored at least every 2–3 months in order to evaluate development of the clutch. About one month before the anticipated period of hatching, i.e. May to June 1993, females bearing ripe eggs were isolated in either 90- or 120-L tanks with flowing seawater. One hard-shelled adult male of 78.8–119.5 mm CW was introduced into the tanks of randomly selected females in each of two groups, representing those females that had initially mated either with adolescent (3 females remated) or with adult (17 females remated) males. The tanks were monitored once a day to detect the onset of hatching and, where appropriate, mating behavior.

Ten to 12 weeks after the second clutch was extruded, a sample of at least 25 eggs was taken at the base of each of the eight pleopods of 58 females. Pleopods on the right-hand side were assigned numbers 1 to 4, and those on the left-hand side were assigned numbers 5 to 8, from front to rear. During sampling, females did not shed or lose more than ≈50 eggs in excess of those removed by the observer. Samples of eggs from each pleopod were fixed and stained to reveal nuclear DNA by means of a technique adapted from Dubé et al. (1985) and Dufresne et al. (1988). Eggs were fixed for one hour in a solution of 97% glucamine-acetate (GA) buffer, 2% formaldehyde, and 1% Triton, and then rinsed in GA buffer. The GA buffer was composed of 250 mM N-methyl glucamine, 250 mM potassium gluconate, 50 mM Hepes, and 10 mM EGTA, adjusted to pH 7.4 with glacial acetic acid. Eggs were then stained for one hour in a solution of 0.5 µg Hoescht dye per mL of GA buffer and were then rinsed twice and preserved in GA buffer at 4°C. The numbers of divided and undivided eggs in each pleopod sample were determined by epifluorescent microscopy.

Females were examined to evaluate clutch size one week after eggs were sampled from second clutches. Female abdomens were indexed for repleteness with eggs on a scale of 0 (empty) to 4 (very full). The index of clutch size is similar to the more refined percent clutch statistic, where actual clutch size is rated as a percentage of the largest clutch a female decapod of a given size can hold (Blau, 1986). The egg repleteness index and the percent clutch statistic both correlate significantly with the actual number of eggs held by a female decapod (Shields et al., 1990; Sainte-Marie, unpubl. data).

Results and discussion

Females molted to maturity from 8 January to 12 April 1992 and ranged in size from 49.7 to 74.4 mm postmolt CW. Only females that survived until August 1993 were analyzed in this study. Overall mortality of females from time of maturity molt until August 1993 was 50.3% (of 155) but was unrelated to mating status (mated or unmated) or to the mate's identity (maturity, CW). Of the 11 adolescent males that were mated, eight molted 3–57 days ($\bar{x}$=30 d) after mating, one molted 384 days after mating, and two died within 14 months of mating. No adult male molted over the 14-month period, consistent with the hypothesis that adult males are in anecdysis (O'Halloran, 1985; Conan and Comeau, 1986).

Of the nine females that were initially unmated, only four extruded a first clutch (Table 1) four or more days after their molt to maturity. All of the 68 females that initially mated extruded a first clutch: 56 did so while in the presence of their mate and 12 extruded later, i.e. 1–5 days after separation from their mate. First clutches did not develop and hatch on the four females that were unmated and on the 12 females that were mated but slow to spawn. Sainte-Marie and Lovrich (1994) reported that delayed spawning occurred in *C. opilio* when few or no sperm were delivered to females at mating. These authors hypothesized that females can gauge the contents of their spermathecae and, when insufficiently inseminated, postpone extrusion in expectation of a more fecund mate. By comparison, only two females that extruded eggs while in the presence of their mate failed to hatch their first clutch. Clutches

Table 1

Mating and spawning history of female snow crab, *Chionoecetes opilio*, that were not paired with a male after their molt to maturity or that were paired with a male but lost their first clutch. Male mates were adolescent or adult. Median and range (in parentheses) for clutch size and percentage of divided eggs are given for the second clutch. Clutch size is based on a 0 (empty) to 4 (very full) scale for abdomen repleteness with eggs. Calculation of median clutch size includes females with no eggs (scored as 0). The percentage of divided eggs is followed by the number of clutches examined, in superscript.

Male after molt	Total number of females	Females with first clutch	Male at second spawning	Females with second clutch	Second clutch	
					Size	% Divided eggs
No	9	4	No	2	0.0 (0–3)	—
Adolescent	3	3	No	2	2.5 (1–4)	$0.0^{n=1}$
			Adult	1	2.0	$97.5^{n=1}$
Adult	11	11	No	6	1.0 (0–4)	$4.2\ (0–56.7)^{n=4}$

carried by the 18 unsuccessful primiparous females started to show signs of degradation about 2–4 months after spawning as many or all eggs changed from bright to pale orange and eventually became almost white, and clutches were sloughed or lost within 8–10 months of spawning. The relatively high, 20.6%, incidence of first clutch loss recorded for mated females may be a laboratory artifact resulting from the 24-hour time limit for mating and noncompetitive mating context.

We examined 516–1,769 eggs from each second clutch of six females that lost their first clutch and of 52 females that hatched their first clutch, for a combined total of 54,808 eggs. Divided eggs were at the 128- or 256-cell stage. In 24 out of 55 females that carried at least some divided eggs, the ratio of divided eggs to total number of eggs in the pleopod sample was not independent of pleopod position (χ^2 test, $P<0.05$). One female had 89.5–100% divided eggs on pleopods 1–7, but no egg was divided on pleopod 8. Eggs from this female were sampled a second time to confirm the observation. The heterogeneous distribution of divided eggs in some clutches was not expected and to our knowledge has not yet been documented. Most previous studies contain little or no information on methods for sampling and determining viability of eggs. The reason for the contagious distribution of divided eggs is unknown. Perhaps attachment of eggs to individual pleopods is orderly and follows an extrusion hierarchy, and sperm in the fertilization chamber is temporarily or permanently depleted during extrusion. Nevertheless, our finding underscores the importance of sampling eggs from throughout the clutch when assessing fertilization success. We estimated the overall proportion of divided eggs in a clutch as the mean of proportions of divided eggs on each of the eight pleopods.

Among females that lost their first clutch, 38.9% did not spawn a second time (Table 1), and the remainder extruded second clutches from February to March 1993. In the latter group, second clutches contained 0–56.7% divided eggs when females had no access to males or 97.5% divided eggs in the case of one female that was paired with a male at the second spawning (Table 1).

Most females that were initially mated with adult males and then hatched a first clutch of eggs produced a large second clutch with a high percentage of divided eggs without remating (Fig. 1; Table 2). Of the 34 successful primiparous females that mated only at the molt to maturity, only two (5.9%) did not spawn a second time, whereas two others produced second clutches with <60% divided eggs (Fig. 1). There was no significant difference in the size of the second clutch (Kruskal-Wallis test, $H=4.60$, $P=0.10$) or in the percentage of divided eggs in the second clutch ($H=2.50$, $P=0.29$) among groups of females mated only at the molt to maturity by adult males with CW's of 40–60 mm (median clutch size: 3.0, median percentage divided eggs: 88.9%, $n=13$), 80–100 mm (4.0, 96.0%, $n=8$), or 120–140 mm (3.0, 94.6%, $n=8$). These data are consistent with the number of sperm cells stored by female *Chionoecetes* after the first spawning being unrelated to male CW (Adams and Paul, 1983; Sainte-Marie and Lovrich, 1994). Similarly, our data, although limited, indicate that stored sperm from adolescent males also resulted in the production of a large second clutch containing a high proportion of divided eggs, and was as effective as stored sperm from adult males (Fig. 1; Table 2). Although virgin females mated with adolescent males store as many sperm as those mated with adult males, Sainte-Marie and Lovrich (1994) speculated that the longevity of adolescent sperm might be less than that of adult sperm because of a higher sperm-cell to seminal-plasma ratio in ejaculate. However, this was not apparent after one year of storage.

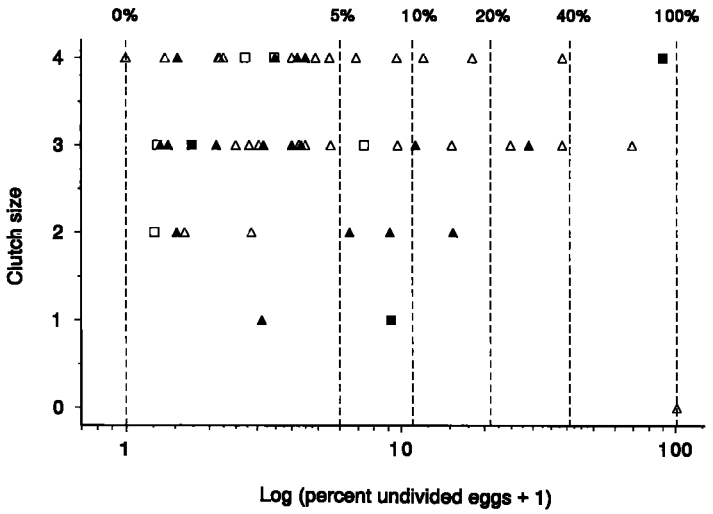

Figure 1

Scattergram of clutch size and percentage undivided eggs for second clutches of female snow crab, *Chionoecetes opilio*, that hatched their first clutch. Females were mated either with adolescent (squares) or adult (triangles) males after their molt to maturity and were subsequently prevented (open symbols) or allowed (solid symbols) to mate with an adult male at second spawning. The open triangle in the lower right corner of the scattergram represents two females with no clutch.

Among successful primiparous females, there was no significant difference in the size of the second clutch (Kruskal-Wallis test, H=2.45, P=0.12) or in the percentage of divided eggs (H=0.44, P=0.51) between those with (median clutch size: 3.0, median percentage divided eggs: 96.9%, n=20) and those without (3.0, 96.3%, n=34) access to males at second spawning (also see Table 2). It is likely that remating occurred in a majority of females with access to males at second spawning because we observed precopulatory embraces in 18 of 20 pairs and copulation in five pairs. Although the proportion of divided eggs in second clutches was high for females isolated from males, one might have expected an even higher proportion in females paired with males owing to the potential for acquiring additional, fresh sperm. However, it was hypothesized for *C. opilio* that stored sperm can be evacuated from the spermathecae by the second mate using his gonopods (Beninger et al., 1991; Elner and Beninger, 1992). If this or any other mechanism to prevent a rival's sperm from fertilizing eggs (see for example Diesel, 1990) exists in *C. opilio*, then successive matings would not contribute additively to the pool of sperm available to fertilize a new clutch. Nevertheless, our results indicate that the viability and number of sperm remaining in spermathecae after one year of storage were not limiting for the fertilization of a second clutch in females mated only at the molt to maturity.

The success of female *C. opilio* in fertilizing a second clutch of eggs with stored sperm and the contrasting failure of female *C. bairdi* (Paul and Paul, 1992) can probably be explained by the ≈10-fold greater number of sperm cells stored after the first spawning by *C. opilio* (Sainte-Marie and Lovrich, 1994). Moreover, mean size and fecundity of females are less in *C. opilio* than in *C. bairdi* (Haynes et al., 1976); therefore, fewer sperm cells are mobilized to fertilize a clutch in the former species.

Table 2

Median and range (in parentheses) of clutch size and percentage of divided eggs for second clutches of female snow crab, *Chionoecetes opilio*, that were paired with a male after their molt to maturity and that hatched their first clutch. First male mates were adolescent or adult; all second male mates were adult. Clutch size is based on a 0 (empty) to 4 (very full) scale for abdomen repleteness with eggs. Calculation of median clutch size includes females with no eggs (scored as 0). The Kruskal-Wallis test was used to compare clutch size and percentage of divided eggs for females in different experimental treatments: H-statistic and probability level (P) are shown.

Male after molt	Adult male at second spawning	n	Second clutch	
			Size	% Divided eggs
Adolescent	No	5	3.0 (2–4)	98.3 (93.6–99.7)
	Yes	3	3.0 (1–4)	91.8 (11.2–99.3)
Adult	No	29	3.0 (0–4)	95.5 (0.0–100.0)
	Yes	17	3.0 (1–4)	97.0 (72.1–99.7)
			H = 2.50	H = 5.15
			P = 0.48	P = 0.16

Although our laboratory findings suggest that sperm stored at the first mating is effective for fertilizing the second clutch in *C. opilio*, these findings cannot be indiscriminately extrapolated to the field, for at least two reasons. First, the importance of sperm stores in wild *Chionoecetes* females might fluctuate interannually (Beninger et al., 1988; Paul and Paul, 1992). In the northwest Gulf of Saint Lawrence, the intensity of recruitment to the first benthic instar of *C. opilio* varies among years in an apparently recurrent pattern: five consecutive, moderate-to-strong year classes alternate with three consecutive, weak year classes (Sainte-Marie et al., in press, and unpubl. data). Given that adult snow crab are anecdysic and that there exist marked differences between the sexes in size and age at adulthood, recruitment pulses cause adult sex ratios and characteristics of breeding males to change considerably over time (Ennis et al., 1990; Comeau et al., 1991; Sainte-Marie et al., in press). Thus, in some years, the number or quality, or both, of males available for mating with pubescent females might be limiting and this could conceivably result in a decrease in the proportion of primiparous females having received enough sperm to fertilize a second clutch. Second, our laboratory experiments pertain only to a one-year reproductive cycle. However, under some natural conditions female *C. opilio* incubate their eggs for 24–27 months (Kanno, 1987; Mallet et al.[2], 1993; Sainte-Marie, 1993), instead of the ≈12-month duration observed in our laboratory and inferred for many wild populations (e.g. Ito, 1967; Watson, 1969; Kon, 1980). Mallet et al.[2] suggested that this difference is due to temperature: in the Gulf of Saint Lawrence, egg development would take two years for females in their usual deep-water habitat (–1° to 1°C year-round), but only one year for females that stayed for some time in warmer shallow waters. In the former case, effective fertilization of the second clutch in which stored sperm was used would thus depend on sperm surviving in sufficiently high numbers over a 2-year period. Clearly, a better understanding of the interrelations between population and reproductive dynamics, sperm delivery, sperm longevity (viability), and the duration of sperm storage is necessary before any general statement can be made about the importance of stored sperm to reproductive output in *C. opilio*.

[2] Mallet, P., G. Y. Conan, and M. Moriyasu. 1993. Periodicity of spawning and duration of incubation time for *Chionoecetes opilio* in the Gulf of St. Lawrence. Int. Counc. Sea C.M. [council meeting] 1993/K:26, 19.

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Publication Awards, 1994

National Marine Fisheries Service, NOAA

The Publications Advisory Committee of the National Marine Fisheries Service is pleased to announce the awards for best publications authored by NMFS scientists and published in the Fishery Bulletin for Volume 92 and in the Marine Fisheries Review for Volume 55. Eligible papers are nominated by the Fisheries Science Centers and Regional Offices and are judged by the NMFS Editorial Board. Only articles that significantly contribute to the understanding and knowledge of NMFS-related studies are eligible. We offer congratulations to the following authors for their outstanding efforts.

Fishery Bulletin, Volume 92

Outstanding Publication

Prager, Michael H.

A suite of extensions to a nonequilibrium surplus-production model. Fish. Bull. 92:374–389.

Outstanding Publication

Jacobson, Larry D., Nancy C. H. Lo, and J. Thomas Barnes.

A biomass-based assessment model for northern anchovy, *Engraulis mordax*. Fish. Bull. 92:711–724.

Marine Fisheries Review, Volume 55

Outstanding Publication

Nitta, Eugene T., and John R. Henderson.

A review of interactions between Hawaii's fisheries and protected species. Mar. Fish. Rev. 55(2):83–92.

Honorable Mention

Pooley, Samuel G.

Hawaii's marine fisheries: some history, long-term trends, and recent developments. Mar. Fish. Rev. 55(2)7–19.

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