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

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

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

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

Daily growth increments on otoliths of juvenile scombrids (skipjack, *Euthynnus pelamis*, and yellowfin tuna, *Thunnus albacares*, bluefin tuna, *T. thynnus*, black skipjack, *Euthynnus lineatus*, Atlantic mackerel, *Scomber scombrus*, and southern bluefin tuna, *Thunnus maccoyii*) have been tentatively validated (Uchiyama and Struhsaker, 1981; Radtke, 1983; Wild and Foreman, 1980; Brothers et al., 1983; D'Amours et al., 1990; Jenkins and Davis, 1990; Wexler, 1993). However, no published study has been directed at the validation of daily growth increments on the otoliths of Spanish mackerel.

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

Manuscript accepted 22 November 1996.
Fishery Bulletin: 530–539 (1997).

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

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

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

Methods

Collection and treatment of specimens

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

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

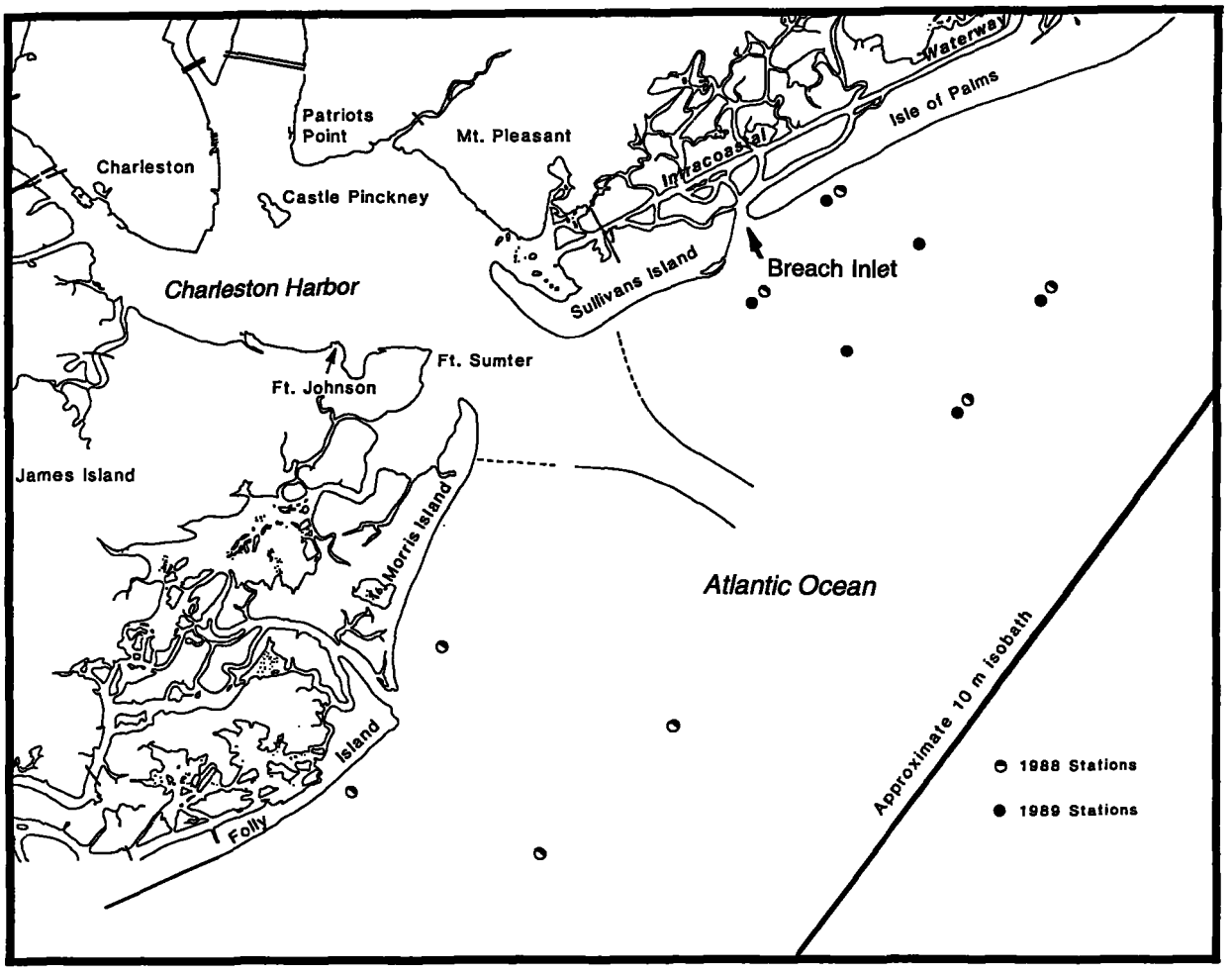

Figure 1

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

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

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

Marginal increment analysis

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

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

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

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

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

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

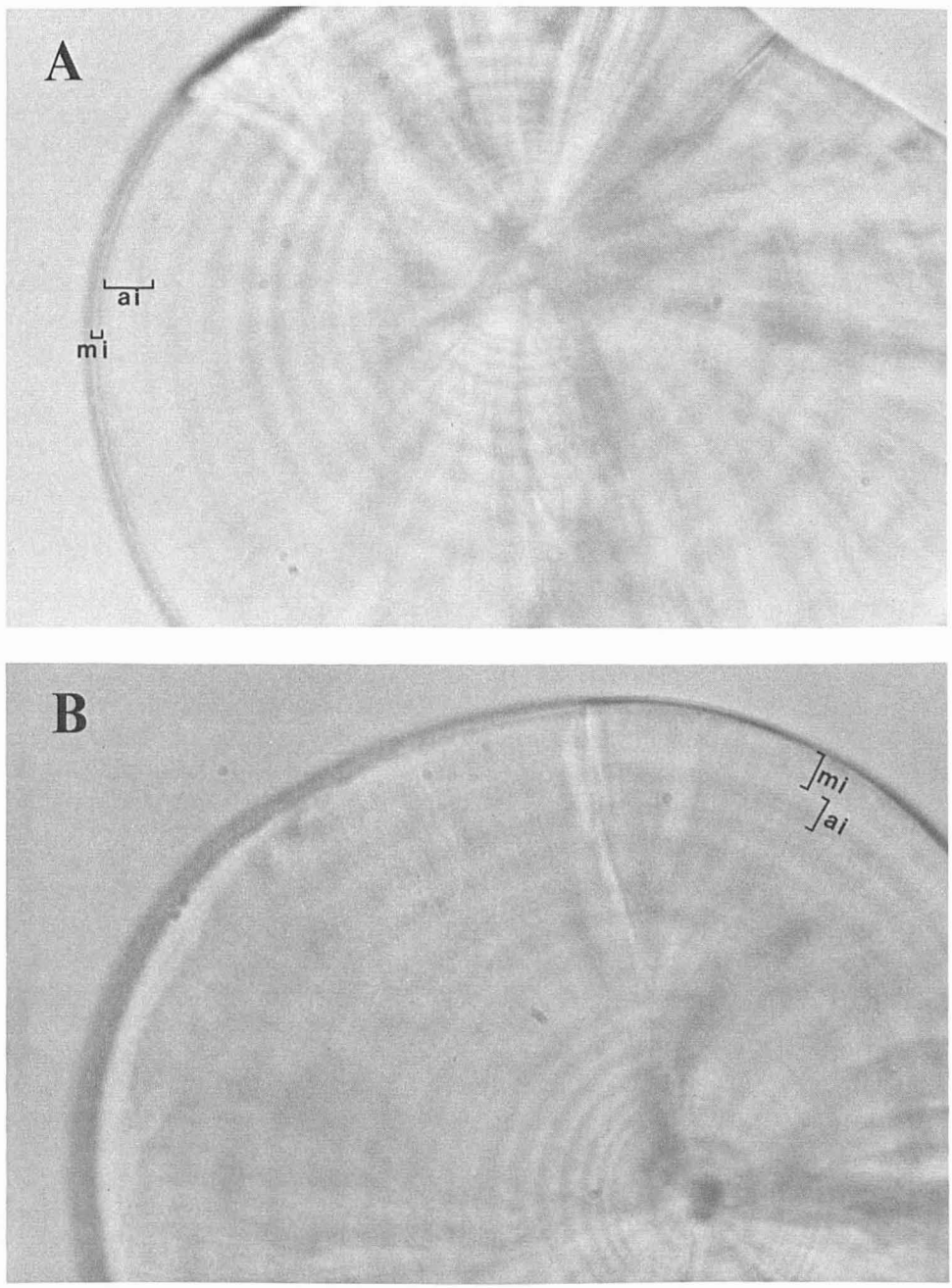

Figure 2

(**A**) Lapillus from a Spanish mackerel juvenile (SMI=0.3) captured at Breach Inlet between 0309 h and 0830 h EDT. (**B**) Lapillus from a Spanish mackerel juvenile (SMI=0.9) captured at Breach Inlet between 1613 h and 2211 h. Incomplete marginal increment (mi), and adjacent fully formed increment (ai) are indicated.

Age and growth analysis

Whole lapilli from 415 larval and juvenile Spanish mackerel were examined. For larvae and juveniles <100 mm SL, otolith radius was measured from the center of the primordium to the margin of the otolith along a consistent axis. Measurements were made with an ocular micrometer at magnifications of 100× or 400× depending upon the size of the otolith. Presumed daily increments on the lapilli were counted on a video monitor under 1,000× magnification. Two independent counts of presumed daily increments

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

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

Results

Several features of increment deposition were observed to be consistent among the otoliths examined. Two diffuse and poorly defined increments (core increments) surrounded the primordium (Fig. 3). Mean core width was 11.4 mm and there was little variation with fish length (SD=0.54 mm, n=40, length range=9.0–300.1 mm). Although these increments were counted as daily, the nature of their deposition was clearly different from that of subsequent rings. This finding indicated that they were formed during a separate developmental stage. The absence of fish younger than 9 days precluded precise determination of the time period represented by these two increments. Subsequent increments were clearly defined on most lapilli and were easily discernible in whole otoliths examined under a light microscope without any special preparation (grinding or polishing). Subdaily increments occurred, particularly in older juveniles, and were discernible from the daily increments (Fig. 4).

Marginal increment analysis

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

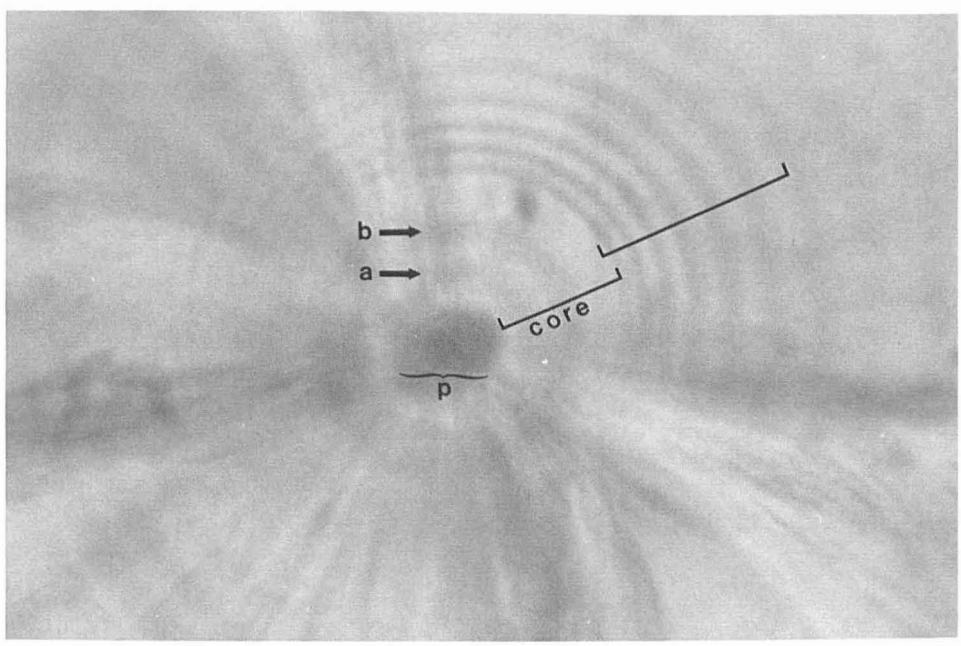

Figure 3

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

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

Age and growth

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

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

No significant difference was found between increment counts for left and right lapilli (paired t-test, P=0.190). Therefore, if left and right counts differed, the otolith whose increments were more clearly defined, or which was in better condition, was used to assign an age to the fish. Growth in young Spanish mackerel was quite variable within age classes, particularly in juveniles older than 23 days (Fig. 6). Nonlinear regression analysis provided the following growth equation:

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

Table 1

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

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

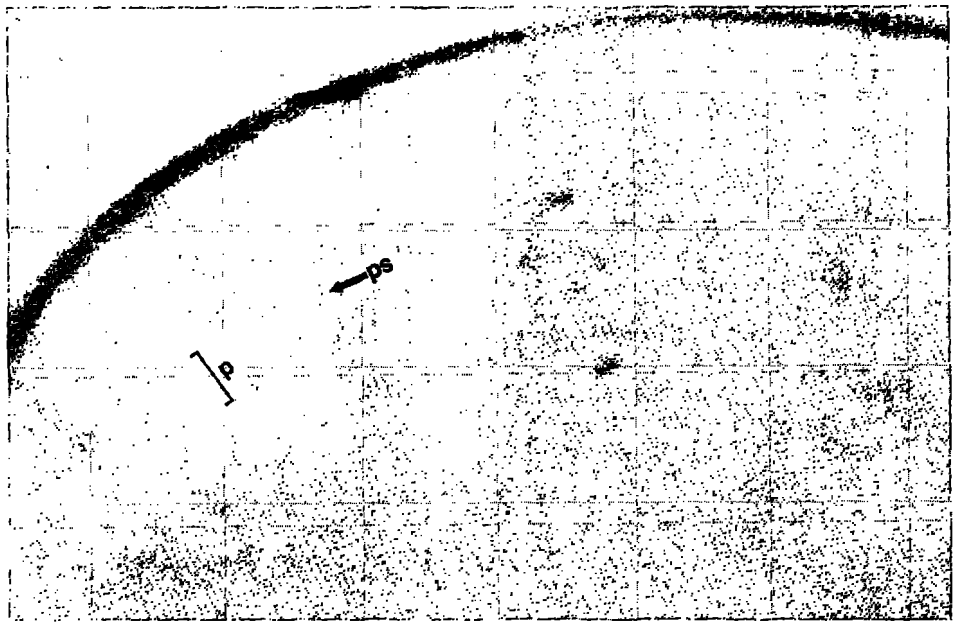

Figure 4

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

Based on this growth equation, predicted absolute growth rate (predicted SL/age in days) was 2.4 mm/day for the first 150 days of life. Early growth was characterized by relatively slow growth for the first 23 days of life (1.9 mm/day) followed by a surge of rapid growth from 23 to 40 days, during which growth rates approached 5.0 mm/day. Predicted absolute growth of older juveniles (40–150 days) was 2.0 mm/day.

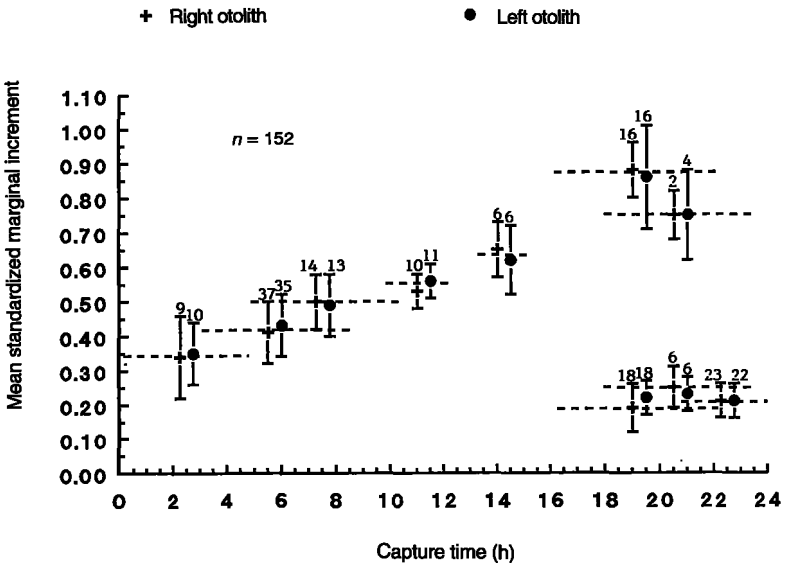

Figure 5

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

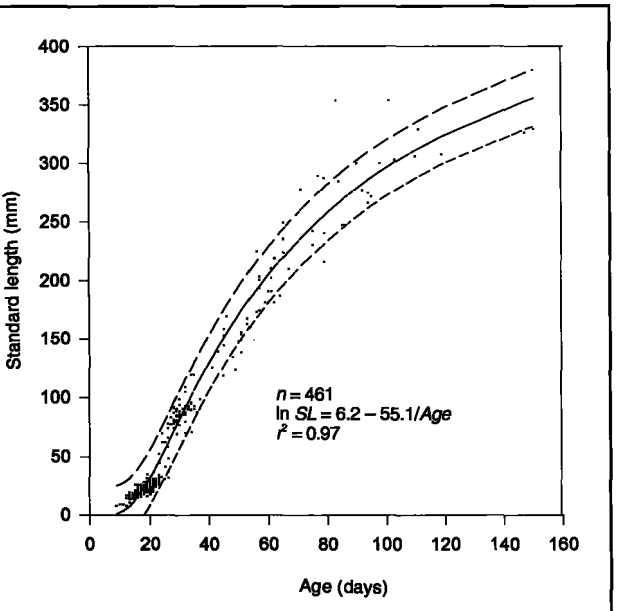

Figure 6

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

Discussion

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

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

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

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

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

Age and growth

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

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

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

Acknowledgments

We would like to express sincere thanks to Mark Collins, Robert Johnson, George Sedberry, and Bruce Stender for their assistance and advice. For their assistance in field sampling we would like to thank Shirelle Brown, Scott Van Sant, Byron White, Paula Keener-Chavis, Pete Richards, and Vince Taylor. We would also like to thank Bruce Stender, Charles Barans, William Roumillat, and SEAMAP for providing many of the specimens used in this study. Financial support and equipment for this study were provided by the South Carolina Department of Natural Resources, the University of Charleston's Grice Marine Laboratory, and the Slocum-Lunz Foundation.

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