Abstract.—Otolith microstructure analysis was applied to sagittae from 18 larvae (5–10 mm notochord length) and 77 juvenile, young adult, and adult (4.3–212 cm lower jaw fork length, LJFL) Atlantic blue marlin *Makaira nigricans* for estimation of age and growth rate. Contingency table analyses indicated that a periodicity of one increment per day was most consistent with the seasonal distribution and peaks of back-calculated spawning dates of the aged samples (May to November), and with information on spawning reported in the literature. Microstructural features of larval blue marlin sagittae were indistinguishable from those in the otoliths of other tropical pelagic species where conclusive age validation has verified daily increment deposition rates. Average percent error of the counting method (precision) for the aged samples of juveniles and young adults/adults was 1.6%.

Estimated ages of larvae ranged from 9 to 12 days while estimated ages of juveniles, young adults, and adults ranged from 21 to 495 days (1.4 years). Otolith microstructure analysis could not be applied with confidence to blue marlin older than 1.4 years. Allometric equations for the length-weight relationship of immature (≤140 cm LJFL) and mature male and female blue marlin (>140 cm) are presented. Sexual dimorphic growth (weight only) in Atlantic blue marlin appears to begin at 140 cm LJFL.

Both the maximum (~16 mm/day at 50 days) and sustained (~10 mm/day) growth rates in length during the first 100 days indicate that Atlantic blue marlin are one of the fastest growing of all teleosts in the early stages of development. An attempt to determine the periodicity of presumed annual marks on otoliths from adult blue marlin (213–367 cm LJFL) by evaluating microstructural characteristics and increment counts between annuli was unsuccessful.

Estimating Age and Growth of Young Atlantic Blue Marlin *Makaira nigricans* from Otolith Microstructure

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Published reports on age determination for billfishes (Istiophoridae) are rare compared with those available for other fishes (Lee 1989). Moreover, data providing validated ages for this family are almost nonexistent (Prince et al. 1987), yet age and growth data are important for stock assessment of fish populations (Beamish and McFarlane 1983).

Age determination of Atlantic blue marlin *Makaira nigricans* is probably more difficult than for most other teleosts because of numerous aspects of the marlin fishery and their life history, including the facts that (1) their life cycle does not lend itself to artificial propagation or survival in captivity, (2) they are a very large, highly mobile, solitary, comparatively rare, and sparsely distributed predator with an extensive geographical range, making them inaccessible for routine scientific study and increasing the costs and difficulty of obtaining samples, (3) they occupy different climatic areas during the same calendar year, making interpretations of bands on hard structures less certain because they may not form with great regularity or uniformity, (4) while incidental catches from longline fisheries form the largest part of their harvest, the logistics of sampling longline operations have hindered collection and examination of large numbers for scientific study, (5) in comparison with almost all other teleosts, their otoliths are exceptionally small and fragile, making them difficult to extract and expensive to prepare and analyze, (6) specimens less than 34 kg (75 lb) are extremely rare, due in part to the apparent exceptionally rapid growth rate in juveniles, (7) extremely low tag-recapture rates (0.4% in the Atlantic; Scott et al. 1990) make acquisition of hard structures from long-term recaptures or oxytetracycline injected blue marlin highly unlikely, and (8) long-lived species are more difficult to age and preliminary indications suggest that blue marlin are long lived, attaining ages of 25–30 years or more (Hill et al. 1989).

Recognizing these difficulties, the National Marine Fisheries Service's (NMFS) Southeast Fisheries Science Center (SEFSC) began a long-range plan in 1980 to collect samples for age determination and an evaluation of ageing methods of blue and white

marlin *Tetrapturus albidus*. An initial report (Prince et al. 1984) indicated that otoliths and dorsal spines were the most promising structures examined, but the best approach for determining the accuracy of these two ageing methods was unclear. Marginal increment analysis (MIA) of 328 dorsal spine sections (Prince et al. 1987) failed to provide evidence of the temporal periodicity (i.e., regularity) of annulus formation, due in part to the large amount of variability in these measurements.

Estimates of age and growth rates of young fish are generally more reliable than for adults because microstructural increments on otoliths of fast-growing juveniles are fewer in number and are often easier to count or measure accurately (Casselman 1983, Prince et al. 1987, Summerfelt and Hall 1987). In addition, otolith microstructural analysis for ageing young fish is inherently more precise than counts of annual marks on structures of adults since errors in counting increments are made in days, not years. Following the recommendations of Prince et al. (1987), otolith microstructural analysis of young blue marlin was selected as the method of choice for improving knowledge of age and growth of this species. The small otoliths, narrow increment widths, and longevity of blue marlin (25–30 years) were expected to limit the microstructural method to the first few years of life. A few researchers, however, have reported success in counting microstructural increments between presumed annual marks on sagittae from older adult temperate and tropical species (Pannella 1971, Radtke 1984, Brothers and Mathews 1986) as a means of determining their periodicity in older fish.

Objectives of this study were to (1) estimate the age and growth of young Atlantic blue marlin from otolith microstructural analysis, (2) determine the periodicity of increment formation by (i) comparing the distribution of back-calculated spawning dates with the spawning season of Atlantic blue marlin reported in the literature, and by (ii) comparing microstructure characteristics of increments on larval blue marlin otoliths with those found in other species where increment deposition rate has been established, (3) determine the precision of the ageing method, (4) fit the ageing data to an appropriate growth equation(s) so daily growth rates could be compared with other fast-growing species, and (5) determine whether counts of microstructural increments between presumed annuli in otoliths of adult blue marlin are consistent with the hypotheses that microstructural increments are deposited daily and gross zonation is annual.

Methods

Data used in this study cover several distinct life-history stages, i.e., larvae, juveniles, young adults, and adults. Although our life-history partitions are somewhat arbitrary, they are defined here to minimize confusion related to their use in various analyses described below. All references to length for juvenile, young adult, and adult blue marlin in the remainder of the paper are lower jaw fork length (LJFL), while length for larvae are notochord (NL) or standard length (SL). Adults were separated from younger stages at about 110 cm, based on changes in form of the length-at-age relationship (discussed later). All planktonic blue marlin larvae in our sample were <11 mm. Juvenile blue marlin 4.3–110 cm were always sexually immature and did not have the full array of adult morphological characters. A few young adult blue marlin >110–140 cm had the full array of adult morphological characteristics but most in this size range were sexually immature. Sexually mature adult blue marlin were nearly all over 140 cm and had the full array of adult morphological characteristics.

Data collection

Juveniles, young adults, adults   During 1980–83, juvenile through adult Atlantic blue marlin were collected directly by NMFS samplers from taxidermists, commercial and recreational fishermen, and at billfish tournaments or ports in the Gulf of Mexico, Caribbean Sea, and northwestern Atlantic Ocean. All size categories were initially targeted and 3–5 hard structures, including sagittae, were collected from each specimen. After 1983, a special "save it for science program" was developed (Prince 1984) to obtain extreme size categories, since blue marlin under 100 pounds (45 kg) and over 900 pounds (409 kg) are very rare in the northwestern Atlantic Ocean (Prince et al. 1984).

Most blue marlin specimens used in this study were caught on hook-and-line, but dipnets were also used for smaller size categories. In addition, some specimens were obtained from the stomachs of larger predators. Fish samples were preserved by freezing or immersion in 95% ethanol to reduce deterioration of the otoliths.

When possible, the following supplemental data were collected from each fish: (1) lower jaw fork length, (2) round weight, (3) sex, and (4) date of capture. Length measurements along the contour of the body were made to the nearest centimeter (cm). Weight was measured to the nearest pound and later converted to kilograms (kg). Sex was determined by visual inspection or histological examination (M.J. Wolfe, Dep. Avian and Animal Medicine, Cornell Univ., Ithaca, NY

14853-6401, pers. commun., 14 Aug. 1987). When sex could not be determined, specimens were designated as unknown sex. Otoliths (sagittae) were removed from the craniums using extraction procedures of Radtke (1983a).

Larvae Istiophorid larvae were collected 25–26 August 1982 at 14 stations off Miami, Florida, during a two-day cruise of the *RV Virginia Key*. Surface tows were made at the western edge and in the axis of the Gulf Stream using either a 1m conical plankton net or a 1×2m neuston sampler, both with 0.947-mm mesh size. Larval istiophorids were separated from the other plankton, and their numbers represented about 5% of the fish in the samples. All larval samples were preserved in 95% ethanol.

Preserved istiophorid larvae were soaked in water for several minutes before measurements were recorded and otoliths extracted. This reduced some of the shrinkage caused by the alcohol and tended to straighten and soften the bodies. Theilacker (1980) reports that shrinkage of larvae caused by net-handling decreases with size while that due to preservation alone is constant. Since all the larvae were nearly the same size (5–10mm), we assumed shrinkage to be an undetermined constant proportion.

Larvae were measured with a dissecting scope to the nearest 0.1mm from the tip of the lower jaw to the tip of the notochord (NL), or to the developing hypural plate (SL). Otoliths were removed from larvae using the methods of Brothers and McFarland (1981). Istiophorid larvae were then cleared and stained according to methods of Potthoff (1986) so vertebral counts could be made. The blue marlin larvae were distinguished from the *Istiophorus–Tetrapturus* group based on vertebral counts.

Otolith preparation and microstructural analysis

The general approach of Brothers et al. (1983) for otolith microstructure analysis of larval and juvenile bluefin tuna was adopted for this study. Otolith mass for all blue marlin ≥4.3cm was measured on a microbalance to the nearest 0.01mg. The extremely small size of sagittae from blue marlin ≤4.3cm precluded measurements of otolith mass for this size category. The transparency and shape of otoliths from larvae and small juveniles (≤23cm) allowed their examination, without further preparation, with a compound light (polarized) microscope adapted for video viewing. Because of the change in mass and configuration of

sagittae from larger fish (≥23cm), preparation of these otoliths included breaking them along the sulcus by light pressure with a scalpel. The medial surface of the dorsal lobe was ground on a glass plate with a mineral oil slurry of 600-grit silicon dioxide to slightly thin the fragment and give it a flat surface on which to rest. The distal surface was then ground with the 600-grit to a point just short of reaching the core region of the otolith. Fine emery paper or diamond compound (3μm) was then used to polish the surface.

The best counting paths were found to be on either the anterior (antirostrum) or posterior axis of the dorsal lobe (Fig. 1A). Counts and photographs of the video image of "primary" microstructural increments (Geffen 1987) are from the dorsal lobe and, where possible, along the anterior axis (Figs. 1B–D). Alternatively, due to lack of specimen clarity or poor preparation, counts were made along the posterior axis. Counts started at the first visible increment outside the core (Fig. 1C) and continued to the margin of the structure (Fig. 1D). Increment counts and measurements were made at magnifications ranging from 100 to 2500×.

Increment counts for larval, juvenile, and young adult/adult blue marlin otoliths include only primary increments. Fine increments, provisionally identified as "subdaily" (Figs. 2A,B), were often observed in the otolith region corresponding to larval and early juvenile growth. These subdaily increments were easily identified by their vague appearance and regular clustering within the more prominent primary units (Fig. 2), and were not tallied.

Counts were not corrected for age at first increment formation because known age larvae were not available. Back-calculated spawning dates were computed by subtracting the total count of primary increments for each sample from the date of capture.

Preparation of otolith sections for scanning electron microscope (SEM) examination followed methods described by Brothers et al. (1983), Brothers and Mathews (1986), Brothers (1987), and Jones and Brothers (1987). Some otoliths were sectioned and rough polished according to the methods of Wilson (1984). The majority of increment counts were made on lateral views of whole otoliths or broken sagittae, but a limited number of samples (9) were available in which counts could be made from transverse sections and whole sagittae from the same fish.

Otoliths that were found to be overground, eroded, decalcified, or which had an irregular, disrupted, or unusual microstructural record were excluded from the ageing analysis.
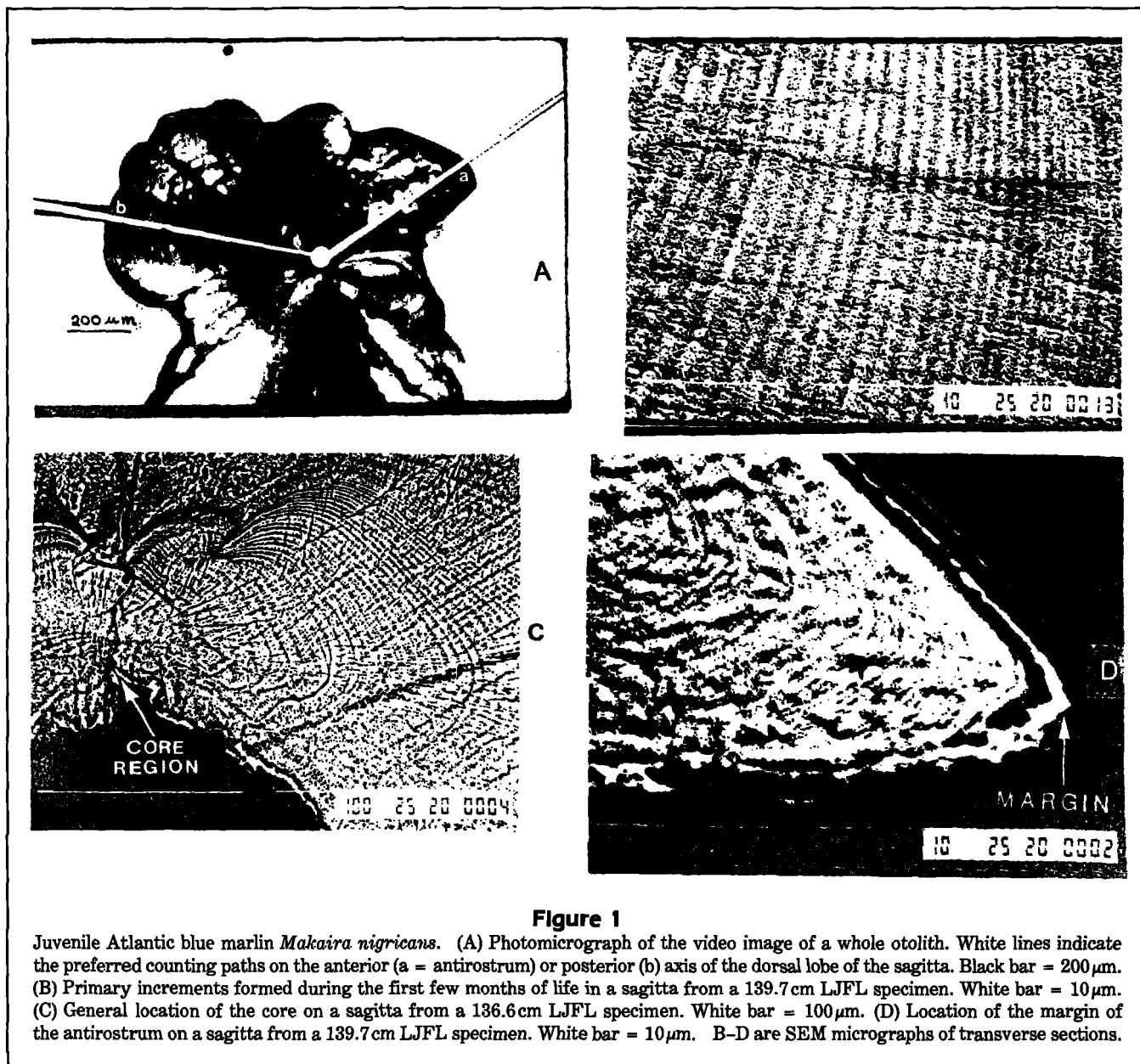
Figure 1

Juvenile Atlantic blue marlin *Makaira nigricans*. (A) Photomicrograph of the video image of a whole otolith. White lines indicate the preferred counting paths on the anterior (a = antirostrum) or posterior (b) axis of the dorsal lobe of the sagitta. Black bar = 200 μm. (B) Primary increments formed during the first few months of life in a sagitta from a 139.7 cm LJFL specimen. White bar = 10 μm. (C) General location of the core on a sagitta from a 136.6 cm LJFL specimen. White bar = 100 μm. (D) Location of the margin of the antirostrum on a sagitta from a 139.7 cm LJFL specimen. White bar = 10 μm. B–D are SEM micrographs of transverse sections.

Precision of age-determination technique

The repeatability or precision of otolith microstructural analysis applied to juveniles and young adults/adults (for increment counts 21–495) was assessed using the average percent error (APE) approach of Beamish and Fournier (1981). Three nonconsecutive blind counts were made by the same reader. Computation of APE for individual samples was:

$$APE = 100 \left(1/R \left(\sum_{i=1}^{R} |X_{ij} - X_j| / X_j \right) \right) \qquad (1)$$

where X_{ij} = the ith count for the jth fish, X_j = the average count for the jth fish, and R = the number of counts for each fish.

The index of APE for all fish in this sample (N 77) using a single reader was:

$$APE = 100 \left(1/N \left(\sum_{i=1}^{N} \left(1/R \left(\sum_{i=1}^{R} |X_{ij} - X_j| / X_j \right) \right) \right) \right) \qquad (2)$$

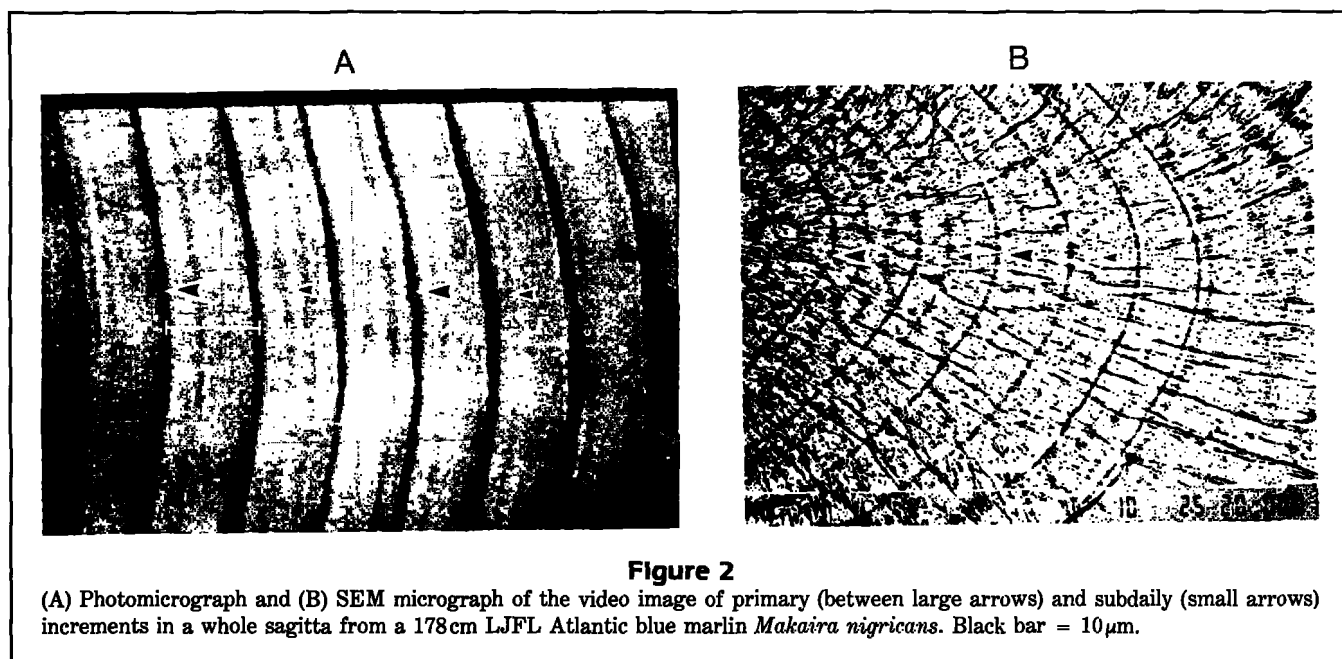where N = the total number of juvenile and young adults/adults aged.

Figure 2

(A) Photomicrograph and (B) SEM micrograph of the video image of primary (between large arrows) and subdaily (small arrows) increments in a whole sagitta from a 178 cm LJFL Atlantic blue marlin *Makaira nigricans*. Black bar = 10 μm.

Computations of APE were not made for the 18 larval blue marlin because only one count was made for each of these samples.

Statistical procedures

Length-at-age The growth trajectory for the age range in our sample, as summarized in Table 1, is asymmetric and S-shaped, with growth rates increasing up to about 40–50 cm and declining thereafter. Richards (1959) described the relationship between this inflection point (relative to the maximum or asymptotic size) and the most common growth equations. The von Bertalanffy equation has no inflection point and those for the Gompertz and logistic equations are at 3/8 and 1/2 of the maximum size, respectively. In addition, the logistic equation is symmetric around the point of inflection.

The Gompertz equation was appropriate for modeling growth of younger fish (i.e., it had an inflection point and was asymmetric). Assuming an inflection point of 40 cm and dividing by 3/8, we estimated a maximum size of 107 cm for this growth phase. In order to obtain a better estimate of limiting size for this growth stanza, we included data up to 113 cm (111 days) and fit the Gompertz equation

$$L = P_1 * \exp\{-P_2 * \exp[-P_3 * t]\} \qquad (3a)$$

to data for young fish. This procedure allowed us to assess the upper and lower limits of each growth equation (i.e., above and below 110 cm).

We used the von Bertalanffy equation

$$L = P_1 * \{1 - \exp[P_2 * (t - P_3)]\} \qquad (3b)$$

for older fish, including data down to 95 cm (96 days), since no inflection point was evident in this range. Results using the two equations differed by less than 2 cm at 110 cm body length, and growth rates were nearly the same at this length. Therefore, data were separated at 110 cm for subsequent analyses. Combining these two equations provides continuous estimates of size-at-age and daily growth rates for the age range in our data.

Generic parameter labels (P for length, Q for weight) are used in growth equations to indicate that no physical or biological meaning should be ascribed. In general, growth equation parameters are highly intercorrelated and, in addition, are highly correlated with the size range of the data. Our data covers only the initial phase of adult growth, so the usual biological and temporal interpretations are unwarranted. For the same reason, the use of generalized or multicycle equations did not seem appropriate.

Least-squares estimates of the parameters of the von Bertalanffy and Gompertz equations were obtained using Marquardt's (1963) algorithm and the methods of Conway et al. (1970). Because the size range in our data covers fish from 5 mm to over 212 cm, the natural log transformation was used to minimize proportional rather than absolute differences.

Table 1

Summary of results of the otolith microstructure method applied to sagittae of Atlantic blue marlin *Makaira nigricans*. Range in estimated age (days), sample size (*n*), mean increment count (days), mean observed and estimated (in parentheses) lower jaw fork length (LJFL, cm), average growth rate (cm/day), LJFL range (cm), mean observed and estimated (in parentheses) round weight (kg), and round weight range (kg) are given for each age category. Estimated lengths and weights were computed from growth equations described in text.

Range in estimated age (days)	Sample size (*n*)	Mean increment count (days)	Mean LJFL (cm)	Average growth rate (cm/day)	LJFL range (cm)	Mean round weight[1] (kg)	Round weight range (kg)
1-20	18	10	[2]0.6 (0.7)	0.1	[2]0.5-1.0	—	—
21-30	1	21	4.3 (3.9)	0.3	4.3	[3]0.6 (0.4)	[3]0.6
31-60	1	40	23.0 (23.1)	1.0	23.0	0.1 (0.1)	0.1
61-90	1	89	95.3 (91.3)	1.5	95.3	4.3 (4.7)	4.3
91-120	7	105	103.3 (102.3)	0.5	88-118	6.2 (6.6)	3.5-10.0
121-150	3	141	114.7 (119.0)	0.3	100-126	9.6 (12.1)	8.4-11.4
151-180	5	169	128.5 (129.5)	0.5	116-136	13.5 (15.1)	10.9-17.5
181-210	9	193	143.9 (137.2)	0.7	129-173	17.5 (17.9)	12.7-21.8
211-240	7	229	147.4 (147.6)	0.1	139-152	24.5 (22.6)	19.5-39.0
241-270	4	254	161.8 (153.9)	0.6	150-172	30.5 (26.1)	20.0-43.1
271-300	5	292	158.8 (162.3)	-0.1	153-173	30.7 (31.9)	22.7-45.8
301-330	7	317	156.9 (167.3)	-0.1	140-170	30.1 (36.1)	24.0-36.3
331-360	4	341	170.6 (171.4)	0.6	149-180	43.6 (39.9)	38.5-47.2
361-390	9	373	172.4 (176.4)	0.1	160-193	40.5 (45.5)	30.8-58.0
391-420	3	411	199.8 (181.4)	0.7	196-207	62.5 (52.0)	51.7-72.4
421-450	8	432	183.1 (184.0)	-0.8	154-196	49.7 (55.8)	35.4-58.0
451-480	2	454	190.9 (186.3)	0.4	173-209	56.1 (59.6)	40.0-72.2
481-510	1	495	212.1 (190.1)	0.5	212.1	83.9 (66.6)	83.9

[1] Mean weight was averaged for males and females >110 days.
[2] Notochord length
[3] Grams

Length-weight relationships Significant changes in body form usually occur at or near sexual maturity for most teleosts. The smallest mature male blue marlin reported in the literature is about 166 cm long (Erdman 1968). However, we established the upper length limit for immature fish at 140 cm because the length-weight relationship of fish between 140 and 166 cm in our sample appeared to be closer to that for larger fish.

Differences in the slopes and Y-intercepts of the length-weight relationships for each sex category (i.e., males, females, and unknown sex) were tested using covariance analysis. Mature fish in our age analysis are a small and size-selected subsample of those available, since a majority of the adult blue marlin population is over 200 cm. To maximize the amount of information for length-weight analysis of mature adults (>140 cm long), we used all available length and weight data collected by the SEFSC recreational billfish survey program from 1972 to 1988 (1969 males, 3260 females). Covariance analysis was used for fish in the common length range 140-277 cm (maximum length of males in the sample) to compare the length-weight relationship of mature male and female blue marlin. Separate

length-weight equations were developed for the entire mature size range of both sexes, and a single length-weight equation was used for immature fish (≤140 cm).

Weight-at-age The variability of weight-at-age in our data was large and sample sizes for each sex were small, a common occurrence in marlin studies. Since variability in length is much less than for weight and our length-weight relationships are based upon large numbers of fish, we estimated weight-at-age by converting individual lengths to weights. For larvae and juveniles, we converted parameters of the Gompertz length-at-age equation directly using equations 4a-d below.

From equation 3a and using the allometric equation

$$\ln W = a + b \ln L,$$

we obtain

$$\ln W = a + b * \ln P_1 - b * P_2 * \exp[-P_3 * t]$$

which allows us to derive the weight-at-age equation

$$W = Q_1 * \exp \{Q_2 * \exp [-Q_3 * t]\} \qquad (4a)$$

where

$$Q_1 = \exp (a) * P_1 * * b \qquad (4b)$$

$$Q_2 = b * P_2 \qquad (4c)$$

and

$$Q_3 = P_3. \qquad (4d)$$

Gompertz equations were used to describe the age-weight relationship for all sizes of blue marlin in this study. For larvae and juveniles, we converted the length parameters (P) to weight parameters (Q) directly using equations 4a–d. For adults, we first converted individual lengths to weights using either the equation for immature fish for young adults (see Results) or the sex-specific equations (see Results) for fish larger than 140 cm and then fit the Gompertz equation (4a) to obtain a continuous young adult/adult weight-at-age relationship.

Increment counts Spearman's rank correlation (SRC; Conover 1971) was used to evaluate the association of total increment count with LJFL, otolith weight, and round weight. Chi-square contingency table analyses (Snedecor and Cochran 1980) were used to determine whether the distribution of back-calculated spawning dates was independent of predicted deposition rates (with periodicities (P) of 0.1–0.9, 1, and 2 increments per day) and days to first increment formation. Fractional periodicity values are interpreted as the proportion of increments actually counted; i.e., true age is underestimated. Multiple increments per day would correspond to overestimates of age, possibly due to counting subdaily increments. To minimize the effect of small sample sizes in a cell, spawning dates were tallied by calendar quarters for each periodicity (P) value. Because all larvae were collected within a 48-hour time period, only the average larval age and length were used in these calculations.

Results

Limitation of the ageing method

Otolith analysis Sagittae from 155 juvenile, young adult, and adult blue marlin, ranging in length from 4.3 to 369 cm LJFL, and 18 larvae, 5–10 mm NL, were used to test for diel periodicity of increment deposition. References here to increments, primary increments, or daily increments generally imply daily deposition (see Discussion).

The decision to analyze increment counts using the whole otolith method (except for the 18 larval otoliths) was based on our evaluation where both the whole and sectioned otoliths were available from nine specimens. Counts using the whole otolith method were higher in eight out of the nine (88%) sagittae samples analyzed. We felt that the differences were due to the compressed incremental record on sectioned sagittae, and as a result we concluded that section counts consistently underestimated the total increment count. Therefore, we used whole sagittae counts in our analysis.

The otolith microstructure method could not be applied with confidence to whole sagittae from fish longer than 212 cm because of the limitations of light microscopy and difficulties in discriminating finely-spaced increments of less than about 1 μm. Discontinuities of the microstructural record usually occurred at counts of about 400–500 along the antirostrum dorsal lobe counting path. The SEM micrograph in Figure 1B and the entire microstructural record from a 23-cm juvenile illustrated in Figure 3 are examples of the undisrupted incremental record observed on whole sagittae in young fish.

Otolith microstructural analysis was successfully applied to 18 larvae and 77 juvenile and young adult/adult blue marlin. Forty additional blue marlin <212 cm in length (30%) could not be aged using the otolith microstructural method. These samples included otoliths broken or lost during preparation and poorly sectioned otoliths from another study. Therefore, the 30% rejection rate is conservative in estimating the expected yield of useful counts and age data from a fresh set of samples.

Range in estimated age Estimated ages, based on counts on the whole sagittae of the 18 larval blue marlin, ranged from 9 to 12 days (Table 1); 66% of the larvae had either 10 or 11 increments. The range in estimated ages of the 77 juvenile and young adult/adult blue marlin was 21–495 days (a maximum of 1.4 years, Table 1). Correlations between total increment count and round weight (SRC = 0.915), otolith weight (SRC = 0.895), and LJFL (SRC = 0.893) for juvenile and young adult/adult blue marlin were similar or the same.

Periodicity of increment formation

Otolith microstructure Otolith microstructure of larval blue marlin (Fig. 4A) was indistinguishable from that of frigate mackerel *Auxis thazard* and other pelagic species of similar size (Figs. 4B–D). For some species, daily increments have been validated by rearing experiments, otolith marking, or other methods (Brothers et al. 1976, Wild and Foreman 1980, Brothers et al. 1983).
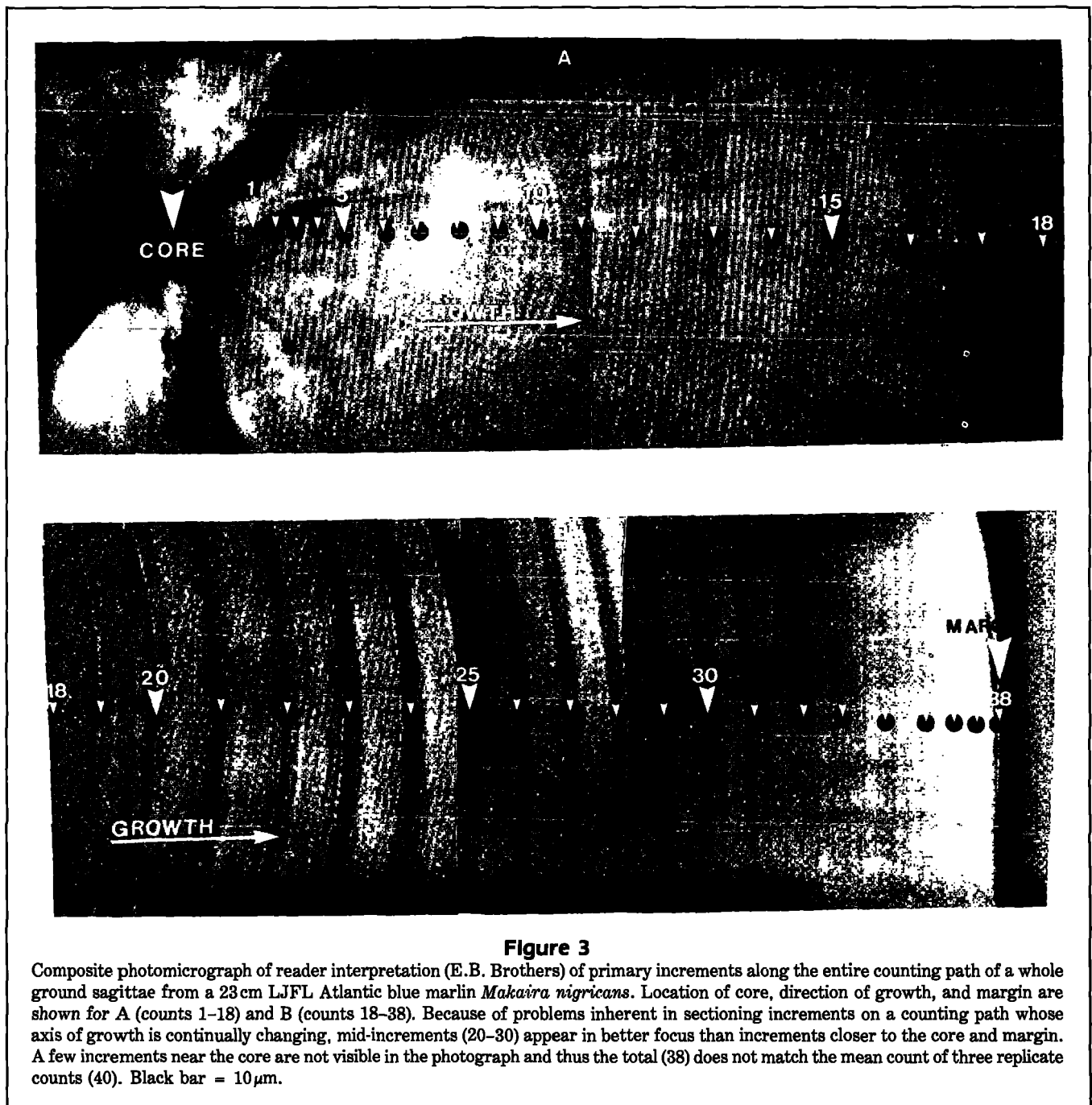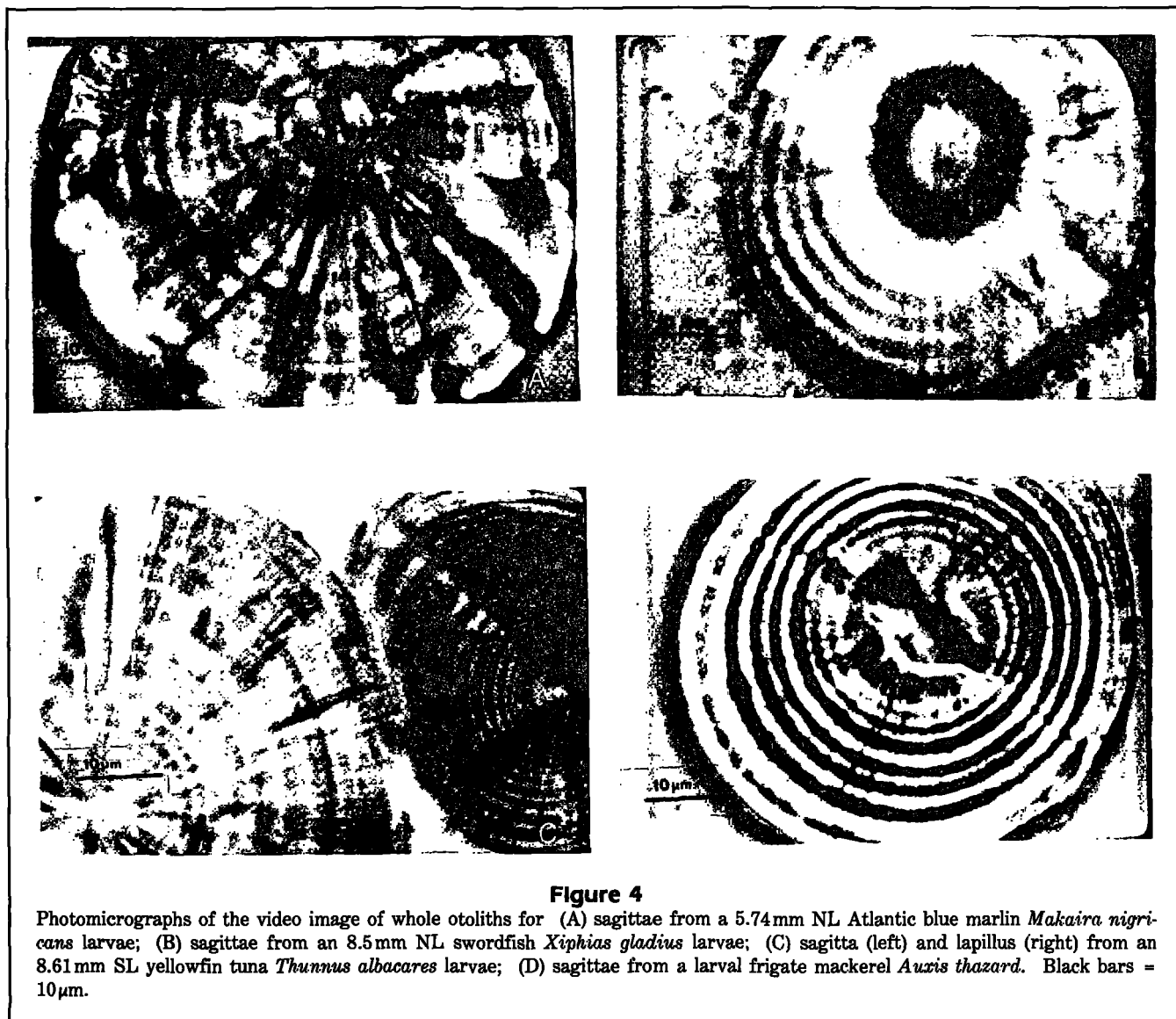
Figure 3
Composite photomicrograph of reader interpretation (E.B. Brothers) of primary increments along the entire counting path of a whole ground sagittae from a 23 cm LJFL Atlantic blue marlin *Makaira nigricans*. Location of core, direction of growth, and margin are shown for A (counts 1-18) and B (counts 18-38). Because of problems inherent in sectioning increments on a counting path whose axis of growth is continually changing, mid-increments (20-30) appear in better focus than increments closer to the core and margin. A few increments near the core are not visible in the photograph and thus the total (38) does not match the mean count of three replicate counts (40). Black bar = 10 μm.

An optically dense region (primordium) about 5 μm in diameter comprises the center of blue marlin sagittae and is usually encircled by one or two diffuse, optically dense layers. Well-defined growth increments surround this region. We refer to the area circumscribed by the first clear growth increment as the core (Fig. 1C).

Subunits (optically light and dark rings) of primary increments are of about equal thickness for the first two or three increments. Thereafter the optically translucent subunit becomes progressively wider relative to the denser subunit (Fig. 3). As in other species (Figs. 4A-D), increments on larval blue marlin otoliths appear visibly distinct in nature for most specimens and are structurally analogous to the daily growth increments seen in many other species, including some tropical pelagic species (Brothers 1979, Pannella 1980). Subdaily increments were also observed in blue marlin

Figure 4
Photomicrographs of the video image of whole otoliths for (A) sagittae from a 5.74 mm NL Atlantic blue marlin *Makaira nigricans* larvae; (B) sagittae from an 8.5 mm NL swordfish *Xiphias gladius* larvae; (C) sagitta (left) and lapillus (right) from an 8.61 mm SL yellowfin tuna *Thunnus albacares* larvae; (D) sagittae from a larval frigate mackerel *Auxis thazard*. Black bars = 10 μm.

otoliths, and have been noted in acetate replicas and SEM preparations of many species, including other oceanic pelagics (Brothers et al. 1983).

Back-calculated spawning dates The primary back-calculated spawning dates (i.e., two or more individuals in a monthly interval) were from May through November (Fig. 5A). Except for the 18 larvae which were all sampled in the month of August, the distribution of back-calculated spawning dates did not appear to be associated with the dates of capture (Fig. 5B). The large variation in age of the juveniles and young adults/adults (about 3–16 months) suggests that calculated spawning dates are not a simple reflection of the distribution of capture dates of size selected fish.

To examine the effect of various increment deposition rates on the distribution of back-calculated spawning dates, we used a contingency table analysis of numbers of spawning dates by season for periodicities (P) of 0.5, 1, and 2 increments per day (Fig. 6A). The distribution of back-calculated spawning dates depends strongly upon the periodicity assumption (χ^2 76.88, df 6, $P<0.0001$). A deposition rate of one increment per day was the only periodicity of those examined that resulted in most spawning occurring in the summer and fall (Fig. 6A). To examine if substantial undercounting of increments occurred, periodicities ranging from 0.1 through 1.0 increments per day were tested (Fig. 6B). Chi-square test for independence (χ^2 85.778, df 24, $P<0.0001$) was highly significant. Only at periodicities

Figure 5

(A) Back-calculated spawning dates for 18 larvae and 77 juvenile and young adult/adult Atlantic blue marlin *Makaira nigricans*. Total increment count on the otolith (sagittae) and date of capture were used to back-calculate spawning month. (B) Distribution of capture dates for 18 larvae and 77 juvenile and young adult/adult Atlantic blue marlin collected 1980–88.

Figure 6

(A) Seasonal distribution of spawning (%) of Atlantic blue marlin *Makaira nigricans* predicted from chi-square contingency table analyses for increment deposition rates of 0.5, 1.0, and 2.0 increments per day, and (B) for deposition rates of 0.8, 0.9, and 1.0 increments per day. Summer and fall spawning is most closely predicted in (A) and (B) by a periodicity of 1.0 increments per day.

of ≥0.8 do high levels of spawning shift from the second to the fourth quarter (Fig. 6B). A periodicity of 1 increment per day agrees most closely with the qualitative information available for blue marlin spawning activity.

To determine whether the lack of information on the time of first increment formation affected our interpretation of increment deposition rate, we constructed a contingency table of seasonal spawning versus first increment formation of 1–7 days (using a periodicity of 1.0). The Chi-square statistic (χ^2 1.42, df 18, $P >$ 0.999) showed that for P = 1.0, a range of 1–7 days for first increment formation does not significantly alter the back-calculated spawning distribution.
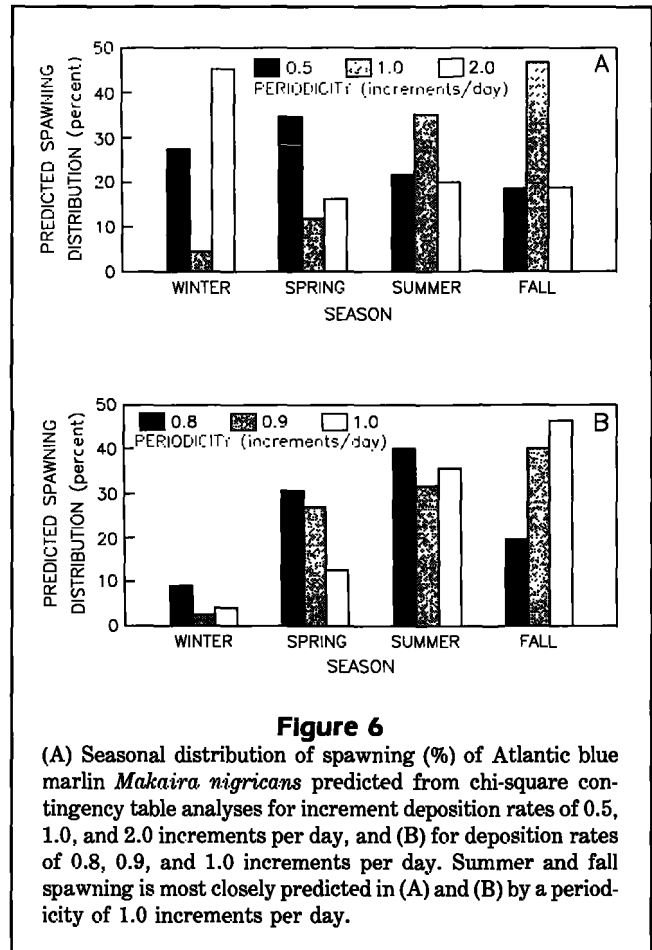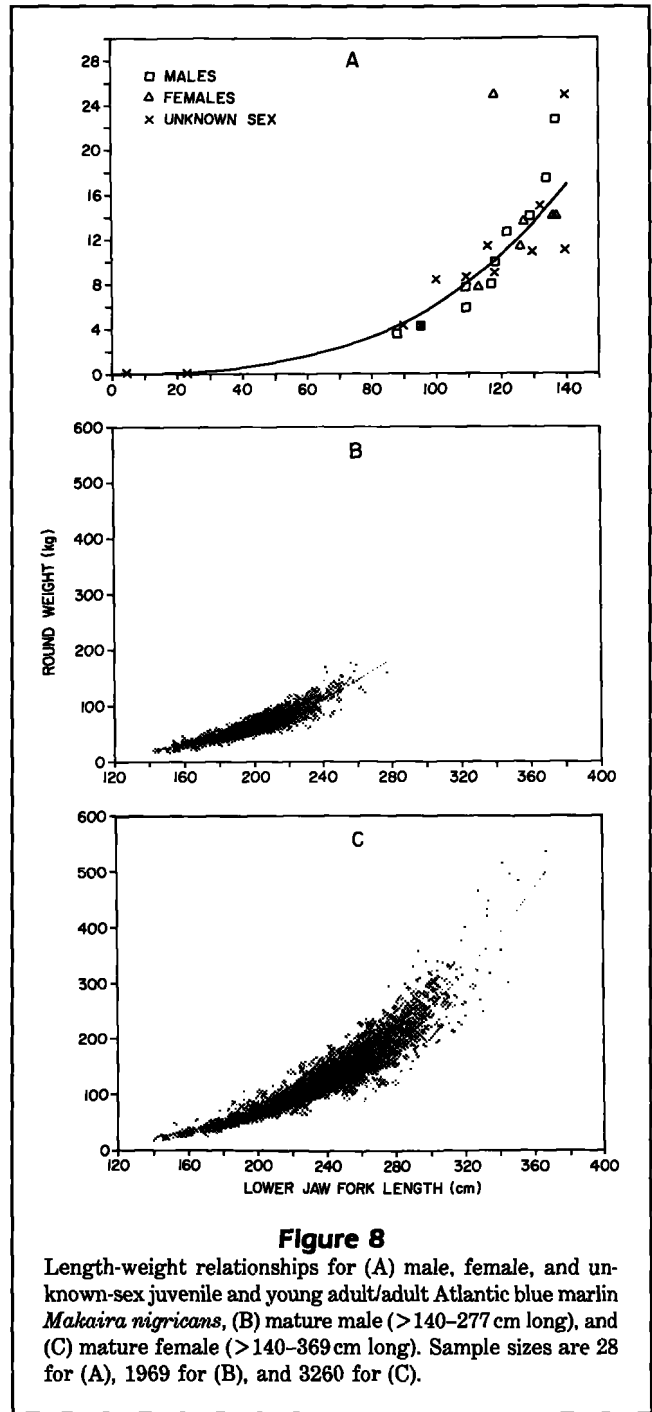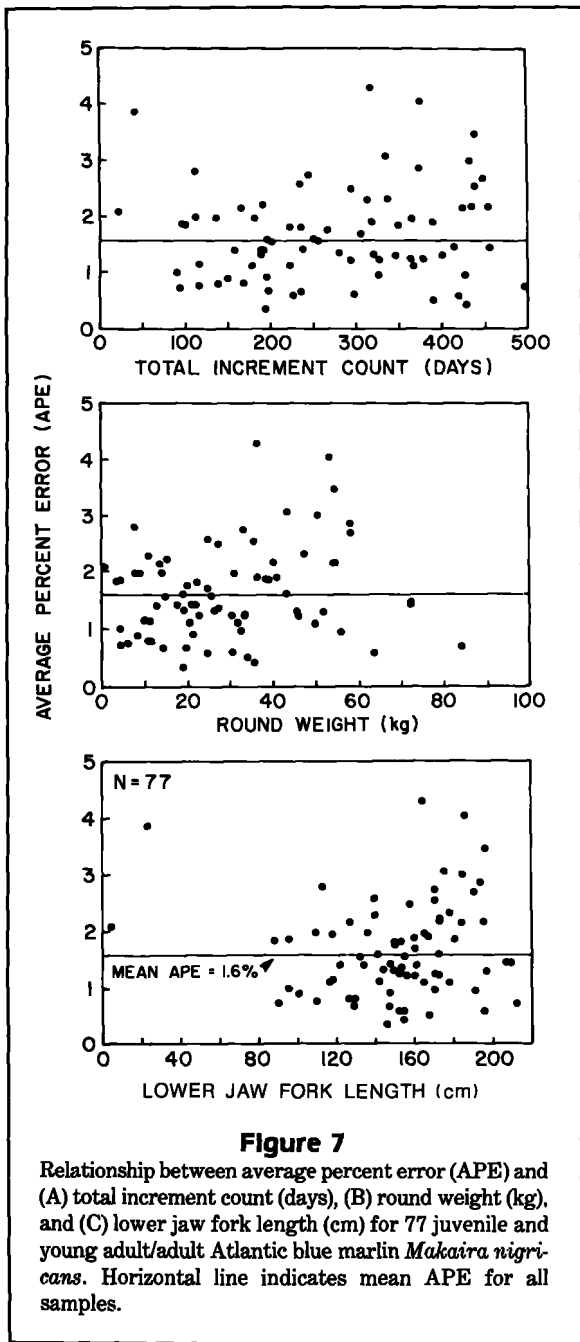
Precision

Average percent error for the aged samples of juvenile and young adult/adult blue marlin (N 77) was 1.6% (Fig. 7). This level of precision is either less than or equal to APE values reported for other species and various ageing methods (Table 2). No obvious trends in APE with the increment count or round weight were evident (Fig. 7). Average percent error generally increased with increases in body length (Fig. 7), except for outliers in the first two lengths of the measured range (4.3 and 23.0 cm).

Length-weight relationships

The length-weight relationship for all immature blue marlin (≤140 cm; sexes pooled, Fig. 8A), is represented by the allometric equation

$$\ln W = -11.950 + 2.9921 (\ln LJFL); \quad R^2 = 0.98. \quad (5)$$

The length-weight relationships for mature adult blue

Figure 7

Relationship between average percent error (APE) and (A) total increment count (days), (B) round weight (kg), and (C) lower jaw fork length (cm) for 77 juvenile and young adult/adult Atlantic blue marlin *Makaira nigricans*. Horizontal line indicates mean APE for all samples.

Figure 8

Length-weight relationships for (A) male, female, and unknown-sex juvenile and young adult/adult Atlantic blue marlin *Makaira nigricans*, (B) mature male (>140–277 cm long), and (C) mature female (>140–369 cm long). Sample sizes are 28 for (A), 1969 for (B), and 3260 for (C).

marlin >140 cm (Figs. 8B, C, respectively) are given by the allometric equations

males:
$$\ln W = -12.568 + 3.1583 \ (\ln \text{LJFL}); \ R^2 = 0.87 \quad (6)$$

females:
$$\ln W = -13.121 + 3.2734 \ (\ln \text{LJFL}); \ R^2 = 0.92. \quad (7)$$

Covariance analysis indicated that the slopes of

length-weight regressions for male and female blue marlin in the common length range of 140–277 cm were significantly different (P 0.0001).

Growth

Observed and estimated length and weight-at-age are shown in Table 1, and all length-at-age data are shown

Table 2

Comparison of the precision of various ageing methods and structures for Atlantic blue marlin *Makaira nigricans*, bluefin tuna *Thunnus thynnus*, lemon shark *Negaprion brevirostris*, and little tunny *Euthynnus alletteratus* based on the average percent error approach of Beamish and Fournier (1981).

Species	Study	Age range (Ageing structure)	Units of ageing method	Average percent error Mean (Range)
Blue marlin	This study	0.024–1.4 years (otoliths)	days	1.6% (0.3–4.0%)
Bluefin tuna	Prince et al. (1985)	1–28 years (vertebrae)	years	none (0.3–6.3%)
Lemon shark	Brown (1988)	0.42–21 years (centrum)	months	3.4% (0–14%)
Blue marlin	McGowan et al. (1987)	2–10 years (spines)	years	none (0.02–0.09%)
Little tunny	Cayre and Diouf (1983)	1–8 years (spines)	years	10.5% (none)

in Figure 9 for males, females, and unknown sex combined. Length and weight-at-age, absolute growth rates (AGR, cm or kg/day), and relative growth rates (RGR, percent body length or weight/day) were computed for the first 495 days using the appropriate growth equation (Table 3). The maximum AGR for blue marlin (sexes combined, 1.66 cm/day) occurred at a length of 39 cm and an estimated age of about 50 days (Table 3). The AGR then decreased continuously to about 0.09 cm/day at 495 days. Relative growth rates decreased continuously from about 21% at 10 days to 0.04% at 495 days (Table 3).

The change in length-weight relationships which we detected at about 140 cm occurred later than the change in form of the length-at-age relationship (about 110 cm). Thus, our weight-at-age curves for fish >110 cm are composites derived from lengths of mostly immature fish (110–140 cm) where no differences in length-weight relationships were found, and adults where sexual dimorphism was evident. As a result, they show a small difference in growth rates for young males and females in the length range 110–140 cm, even though the data in this range do not indicate significant differences in either length-at-age or the length-weight relationship.

Our results show a slight decrease and then increase in AGRs for weight from 80 to 150 days, but this is probably an artifact of the estimation procedure. Parameter estimates are very highly correlated, indicating that growth in weight is essentially linear beyond the maximum relative growth rate for weight which occurs at about 70 days.
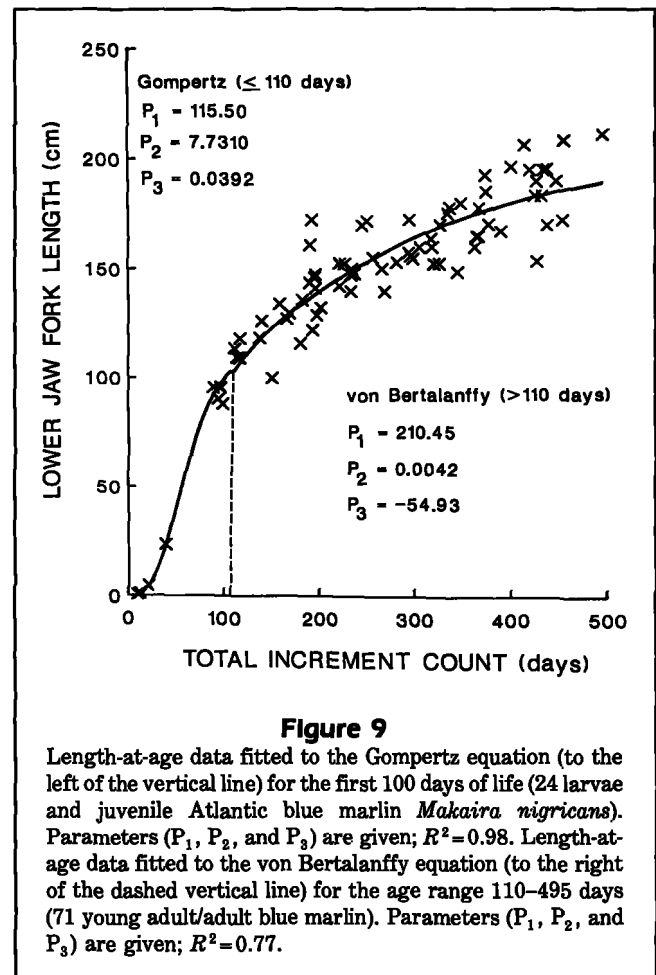

Figure 9

Length-at-age data fitted to the Gompertz equation (to the left of the vertical line) for the first 100 days of life (24 larvae and juvenile Atlantic blue marlin *Makaira nigricans*). Parameters (P_1, P_2, and P_3) are given; R^2=0.98. Length-at-age data fitted to the von Bertalanffy equation (to the right of the dashed vertical line) for the age range 110–495 days (71 young adult/adult blue marlin). Parameters (P_1, P_2, and P_3) are given; R^2=0.77.

Table 3

Growth of Atlantic blue marlin *Makaira nigricans* predicted by the Gompertz and von Bertalanffy equations[1] based on analysis of otoliths for the first 495 days of life. Estimated lower jaw fork length (LJFL, cm) are given for ages 10–495 days for all sexes combined, as well as estimated weights (kg) for males and females. Absolute growth rates (AGR) are given in cm or kg per day, and relative growth rates (RGR) are calculated as 100*AGR divided by length or weight.

Estimated age (days)	All sexes combined			Males only[2]			Females only[2]		
	LJFL length (cm)	AGR	RGR	Weight (kg)	AGR	RGR	Weight (kg)	AGR	RGR
10	0.62	0.13	20.49	0.00	0.00	0.00	0.00	0.00	0.00
15	1.58	0.27	16.84	0.00	0.00	0.00	0.00	0.00	0.00
20	3.39	0.47	13.84	0.00	0.00	0.00	0.00	0.00	0.00
25	6.36	0.72	11.37	0.00	0.00	0.01	0.00	0.00	0.01
30	10.66	1.00	9.35	0.01	0.00	0.02	0.01	0.00	0.02
35	16.30	1.25	7.68	0.03	0.01	0.04	0.03	0.01	0.04
40	23.10	1.46	6.31	0.08	0.02	0.06	0.08	0.02	0.06
45	30.77	1.60	5.19	0.18	0.03	0.09	0.18	0.03	0.09
50	38.95	1.66	4.27	0.37	0.05	0.12	0.37	0.05	0.12
55	47.27	1.66	3.51	0.66	0.07	0.15	0.66	0.07	0.15
60	55.42	1.60	2.88	1.07	0.09	0.17	1.07	0.09	0.17
65	63.17	1.50	2.37	1.58	0.11	0.18	1.58	0.11	0.18
70	70.34	1.37	1.95	2.17	0.13	0.18	2.17	0.13	0.18
75	76.84	1.23	1.60	2.83	0.14	0.18	2.83	0.14	0.17
80	82.62	1.09	1.31	3.52	0.14	0.17	3.52	0.14	0.17
85	87.70	0.95	1.08	4.20	0.14	0.16	4.20	0.14	0.16
90	92.11	0.82	0.89	4.87	0.13	0.14	4.87	0.13	0.14
95	95.90	0.70	0.73	5.49	0.12	0.13	5.49	0.12	0.13
100	99.13	0.60	0.60	6.06	0.11	0.11	6.06	0.11	0.11
105	101.87	0.50	0.49	6.58	0.10	0.10	6.58	0.10	0.10
110	104.17	0.42	0.41	7.04	0.10	0.09	7.04	0.10	0.09
115	106.11	0.44	0.42	8.88	0.08	0.08	9.77	0.09	0.08
120	107.72	0.44	0.41	9.18	0.08	0.08	10.09	0.09	0.08
135	116.59	0.40	0.34	11.04	0.09	0.09	12.06	0.10	0.08
150	122.39	0.37	0.31	12.48	0.10	0.08	13.60	0.11	0.09
165	127.83	0.35	0.28	14.01	0.11	0.08	15.25	0.11	0.09
180	132.93	0.33	0.25	15.64	0.11	0.08	17.01	0.12	0.09
195	137.72	0.31	0.23	17.36	0.12	0.09	18.88	0.13	0.09
210	142.21	0.29	0.20	19.17	0.12	0.09	20.87	0.14	0.10
225	146.43	0.27	0.19	21.05	0.13	0.09	22.96	0.14	0.10
240	150.39	0.26	0.17	23.01	0.13	0.09	25.15	0.15	0.10
255	154.10	0.24	0.16	25.04	0.14	0.09	27.44	0.16	0.10
270	157.58	0.23	0.14	27.12	0.14	0.09	29.83	0.16	0.10
285	160.84	0.21	0.13	29.27	0.14	0.09	32.30	0.17	0.10
300	163.91	0.20	0.12	31.45	0.15	0.09	34.85	0.17	0.11
315	166.78	0.19	0.11	33.67	0.15	0.09	37.48	0.18	0.11
330	169.48	0.17	0.10	35.93	0.15	0.09	40.18	0.18	0.11
345	172.01	0.16	0.10	38.21	0.15	0.09	42.94	0.19	0.11
360	174.39	0.15	0.09	40.50	0.15	0.09	45.76	0.19	0.11
375	176.62	0.14	0.08	42.80	0.15	0.09	48.62	0.19	0.11
405	180.67	0.13	0.07	47.41	0.15	0.09	54.46	0.20	0.11
435	184.23	0.11	0.06	51.97	0.15	0.08	60.40	0.20	0.11
465	187.37	0.10	0.05	56.45	0.15	0.08	66.39	0.20	0.11
495	190.14	0.09	0.05	60.81	0.14	0.08	72.38	0.20	0.11

[1]Parameter estimates are shown below. Definitions for P_1, P_2, and P_3 are given in text.

Variable	Age interval	Equation	P_1	P_2	P_3
Length	<110 days	Gompertz	115.506	7.731	0.039
Length	>110 days	Bertalanffy	210.453	0.004	−54.933
Weight	<110 days	Gompertz	9.581	23.132	0.039
Weight (M)	>110 days	Gompertz	118.428	3.820	0.004
Weight (F)	>110 days	Gompertz	179.862	4.064	0.003

[2]The AGR and RGR for male and female weight are the same for 10 to 110 days.

B

Figure 10
(A) Photomicrograph of the video image of the whole otolith show-
ing a medial view of the ventral lobe of a sagittae from a 258.0 cm
LJFL male Atlantic blue marlin *Makaira nigricans*. White arrows
show location of opaque zones of presumed annual increments. Black
bar = 200 µm.   (B) Scanning electron micrographs of the transverse
section of the sagittae from a 140.5 cm LJFL male Atlantic blue
marlin. White arrows on section (bottom) showing entire otolith and
on the enlargements (middle and bottom) indicate approximate loca-
tion of presumed annual zones identified in photomicrograph. White
bars represent 1000 µm, 100 µm, and 100 µm from top to bottom,
respectively.

A
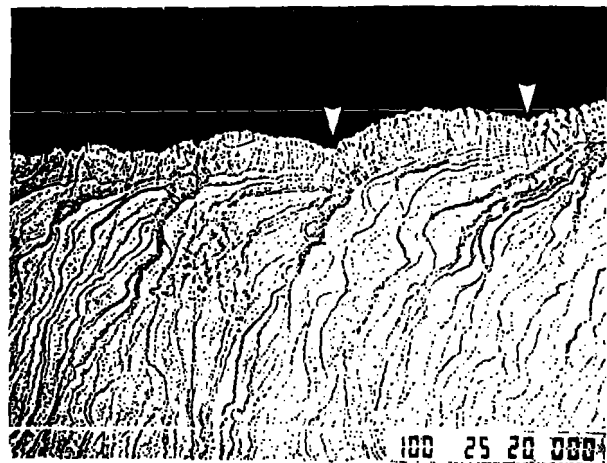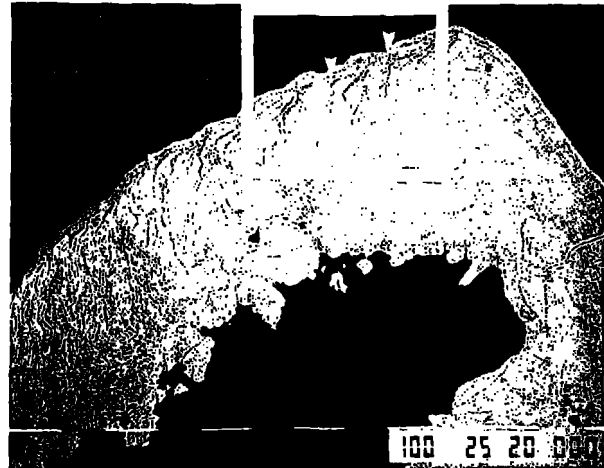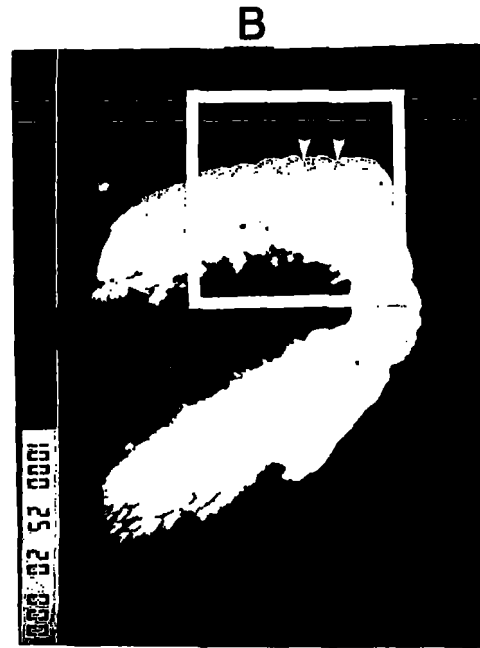
Discussion

Limitation of the ageing method

Within the age range of 9 to 495 days, reliability of the ageing method decreased progressively with increasing age. An upper limit for optical resolution of primary increments occurred at a body length of about 212 cm. Beyond this length, depositions of individual increments were too close together to distinguish, and we did not feel that accurate counts could be made. Therefore, based on otolith appearance and increment spacing at the margin, we did not apply the otolith microstructure method to fish larger than 212 cm. While this limit is arbitrary and perhaps conservative, the practical application of this technique for Atlantic blue marlin will certainly be restricted to no more than the first 2 years of life.

Because of the morphology of blue marlin otoliths, the SEM technique is only practical for transverse sections. Although the microstructural record could sometimes be read for several hundred days longer than with a light microscope preparation, other limitations, such as irregularity in the ventral lobe, made this a difficult and impractical approach (see Fig. 10). The dorsal lobe has a very regular and easily read early-growth record (up to about 1.4 years), but has a very uneven margin. Incremental growth is greatly compressed and probably interrupted to varying degrees, depending on which particular radius is intersected by the section. Furthermore, the extremely small size of blue marlin otoliths (i.e., a maximum dorsal lobe radius of about 2 mm), combined with a probable maximum age exceeding 25 years (Hill et al. 1989), means that increments will average about 0.2 μm if a complete record is present. Counting such fine increments requires optimal sectioning, polishing, and etching and an otolith crystalline structure that will allow such fine structures to be seen. Increments of this width have been reported (Radtke 1984, Brothers and Mathews 1986); however, it is not clear whether such fine increments can always be seen.

The problem of increment resolution in larger/older blue marlin may have resulted in an underestimate of age and overestimated growth rate. Campana and Neilson (1985) state that apparent non-daily increment formation reported for some species (Geffen 1982) could be due to limited instrument resolution, as well as variable otolith preparation and retarded growth due to environmental conditions during deposition. We minimized these potential effects by rejecting hard-to-analyze samples and by using increment counts on lateral or sagittal views instead of transverse sections. The SEM examination of sagittal and transverse sec-

tions also helped confirm that errors of underestimating increments were minimized using the light microscope counting procedure. In addition, the chi-square contingency table analyses confirmed that significant errors in undercounting increments did not occur, assuming that the qualitative description of spawning in the literature is accurate.

Under optimal conditions, increments separated by less than 0.2 μm cannot be resolved with the light microscope. In practice, our observation is that with moderately thick sections and the complex three-dimensional morphology of istiophorid otoliths, the resolution limit is two or three times this value. Thus, otolith growth zonations narrower than about 0.5 μm will be underrepresented in the increment count. Since all increments in blue marlin sagittae were much larger than 0.5 μm (for fish ≤ 1.4 years of age), we feel this problem did not affect the results of this study. Although subdaily increments were commonly observed (Fig. 2), these features were easily distinguished from the primary increments (Figs. 2, 3) and thus overestimation of total increment count was probably not a source of error in this study.

Periodicity of increment formation

Back-calculation of spawning dates and descriptions of otolith microstructure are inherently less desirable for determining the periodicity of increment formation than direct approaches such as rearing fish of known age in captivity or chemical labeling (e.g., oxytetracycline, Geffen 1987). Geffen (1987) reviewed seven methods of age validation and rated each method according to levels of reliability for providing evidence of daily ring deposition. The otolith microstructure approach was characterized as providing a medium level of reliability, allowing only limited inferences for validation of daily ring deposition. Conversely, Geffen (1987) rated the estimation of hatching dates as a medium-to-highly-reliable method for evaluating the strength of assuming daily ring formation in teleost otoliths. Therefore, the results of our study should be tempered accordingly.

Otolith microstructure Our examination of microstructural features of blue marlin otoliths identifies and characterizes the primordium, core, primary increments, subdaily increments, and increment spacing. These microstructural features in larval blue marlin sagittae were indistinguishable from the same characteristics described in the sagittae of related teleost species, some of which had definitive age validation based on rearing experiments.

Back-calculated spawning dates There are several potential sources of error in the back-calculated spawning dates reported in this study. Since istiophorids have never been reared in captivity, we had no basis for correcting for the time of initial growth-increment formation in blue marlin sagittae. However, increment deposition has generally been reported to start within the first week after hatching in most teleosts, and in the majority of studies the first ring usually forms during the first 3 days after hatching (Brothers 1979, Brothers et al. 1983, Radtke 1983b). Therefore, this type of error probably did not bias our estimates of spawning dates by more than 7 days. In addition, we feel that the precautions taken to minimize underestimates of increment counts (discussed earlier) avoided major errors of this type.

Mahon and Mahon (1986) summarized existing data on spawning of blue marlin in the northwestern Atlantic (Erdman 1968, Eschmeyer and Bullis 1968, Yeo 1978) and reported that the spawning season occurs from April through November. Peak spawning is thought to occur primarily in midsummer (Erdman 1968), but a smaller peak in the fall has also been reported (Yeo 1978).

Our data on back-calculated spawning dates (Fig. 5A) agree with the qualitative data on spawning season reported by Mahon and Mahon (1986) and the peaks of spawning documented by Erdman (1968) and Yeo (1978). Back-calculated spawning dates are based on a wide range of fish age and dates of capture (Fig. 5B). As shown in Figure 6, periodicities other than 1 allocate substantial numbers of back-calculated spawning dates and peak spawning to months outside the reported spawning season. The results of the chi-square contingency table analyses and the observations of otolith microstructure are both consistent with the hypothesis that the increments in sagittae from young Atlantic blue marlin are formed once each day.

Precision

Blue marlin are considered to be a long-lived species (Hill et al. 1989) and thus potentially have many age-classes in the fishery. The APE method of evaluating the precision of a set of age determinations, described by Beamish and Fournier (1981), is not independent of age and thus appeared well-suited for blue marlin. Mean APE values (ranging from 0.3 to 4.0%) for blue marlin, in the age range 21–495 days, are well within the range published for other species (Table 2) using annual or monthly ageing methods. The APE values for these ageing techniques are not directly comparable to daily ageing methods (i.e., errors in daily increment methods obviously have a smaller effect on age estimation than errors from annual ageing methods). Never-

theless, the overall mean APE, 1.6% (as well as the range in APE values), indicates that the otolith microstructure method applied to young blue marlin clearly meets the requirement (<10%) described by Powers (1983) for an acceptable level of precision for use of an ageing technique in stock assessment.

Growth

The maximum absolute growth in length (1.66 cm/day at 39 cm LJFL) we report for young Atlantic blue marlin exceeds that estimated from length frequencies by de Sylva (1957) for Atlantic sailfish *Istiophorus platypterus* for the second month of life (1.10 cm/day for the length range 18–51 cm total length). De Sylva (1957) estimates that 6-month-old (180-day) sailfish attain a modal total length of 142.2 cm (~113.9 cm LJFL), while we found that blue marlin reach the same size in about 130 days. Also, while blue marlin and sailfish are almost the same size at the end of the first month, our average relative growth rate (5.7%) computed for the same size range as sailfish (RGR = 3.9%, 18–51 cm total length or about 10–38 cm LJFL) is nearly 1.5 times larger during the second month.

Growth rates are very rarely constant for extended periods of time during early life cycles, i.e., periods of rapid growth are usually followed by periods of declining growth giving rise to the S-shaped or asymptotic growth curves. Thus, it is almost certain that growth rates exceed the first 100-day average of 1 cm per day somewhere during this period. Both the magnitude and location of the estimated maximum depend to some extent upon the validity of the choice of the growth equation.

Our data suggest that blue marlin is one of the most rapidly growing teleosts in terms of absolute growth rates, but that larval, juvenile, and young adult/adult growth are not particularly exceptional measured on a relative scale. For example, maximum growth of the common dolphin *Coryphaena hippurus* does not exceed 0.5 cm/day for the first year of life (Pew 1957; C. Brownell, The Oceanic Inst., P.O. Box 25280, Honolulu, HI 96825, pers. commun., 6 Sept. 1988), but the species attains a maximum length of 1.5 m, compared with 4.5 m for blue marlin, one of the largest North Atlantic teleosts (Norman and Fraser 1948). Conversely, Atlantic bluefin tuna attain a maximum weight similar to Atlantic blue marlin (over 454.5 kg), yet the maximum growth rate of bluefin tuna for the first year is similar to dolphin and varies from 0.1 to 0.6 cm/day (Brothers et al. 1983). Similarly, as shown in Table 3, the relative growth rate (17%) for 1.5-cm LJFL blue marlin postlarvae is only slightly above that (13%) reported by Hunter and Kimbrell (1980) for Pacific mackerel *Scomber japonicus* postlarvae averaging 1.5 cm SL.

Interspecific comparisons of linear growth rates can be misleading if differences in body shape and resultant patterns of growth in body weight are not considered. Juvenile blue marlin are very elongate fishes, and the very high rates of growth in length correspond to only moderate rates of increase in weight. For example, the maximum calculated relative growth rate is 1.8% body weight per day at an age of about 70 days. This value is well within the typical range exhibited by teleosts (Weatherley 1972). Extraordinary consumption rates or conversion efficiencies would not be required to support the growth rates predicted in this study. Furthermore, since swimming speed usually increases with body length, this early growth period no doubt is advantageous for survival and sets the stage for the fast-swimming and wide-ranging capabilities of adults.

While sexual dimorphism in linear growth was not evident from our samples (perhaps due to small sample size), significant differences in the length-weight relationships were found above 140 cm. Our weight-at-age equations indicate small differences in growth rates between sexes for both length and weight may begin at about 110–120 cm.

Ageing adults

In order to evaluate the usefulness of the ageing methods used in this study on adult blue marlin (213–367 cm LJFL), SEM and light microscope analysis of the microstructural increments between presumed annual marks were examined on whole otoliths and transverse sections of 23 fish. Although the presumed annual marks (as described by Wilson 1984) were clearly visible in both the dorsal and ventral lobes of sagittae in adult fish over 300 cm LJFL (Fig. 10), the microstructural increments between these marks could not be clearly distinguished for accurate counts. Conversely, the presumed annual marks could not be distinguished on sagittae from the largest young adults (200–212 cm LJFL) while the microstructural increments were still visible. Therefore, this approach could not offer conclusive evidence for validating either daily or annual periodicities in blue marlin otolith deposition.

Incidental observations of relative otolith size (dimension and mass) in Atlantic and Pacific blue marlin indicate that individuals with relatively larger otoliths also have many more presumptive annuli in their otoliths compared with similar-sized fish (Wilson 1984, Hill et al. 1989). The coefficients of determination for linear regressions of these parameters are strong (range in R^2, 0.70–0.91; Wilson 1984). Further exploration of the relationships between fish size, otolith size, and increment counts coupled with validated ages for

younger fish could lead to more robust regression techniques (Boehlert 1985) to estimate the age of adult blue marlin.

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