Abstract—Age and growth estimates for the blue shark (*Prionace glauca*) were derived from 411 vertebral centra and 43 tag-recaptured blue sharks collected in the North Atlantic, ranging in length from 49 to 312 cm fork length (FL). The vertebrae of two oxytetracycline-injected recaptured blue sharks support an annual spring deposition of growth bands in the vertebrae in sharks up to 192 cm FL. Males and females were aged to 16 and 15 years, respectively, and full maturity is attained by 5 years of age in both sexes. Both sexes grew similarly to age seven, when growth rates decreased in males and remained constant in females. Growth rates from tag-recaptured individuals agreed with those derived from vertebral annuli for smaller sharks but appeared overestimated for larger sharks. Von Bertalanffy growth parameters derived from vertebral length-at-age data are $L_\infty = 282$ cm FL, $K = 0.18$, and $t_0 = -1.35$ for males, and $L_\infty = 310$ cm FL, $K = 0.13$, and $t_0 = -1.77$ for females. The species grows faster and has a shorter life span than previously reported for these waters.

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Age and growth of the blue shark (*Prionace glauca*) in the North Atlantic Ocean*

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The blue shark (*Prionace glauca*) is a large pelagic carcharhinid that is widely distributed in the world's oceans. Throughout its range, it is considered the most abundant species of large shark (McKenzie and Tibbo, 1964; Casey, 1982). In the Atlantic, the blue shark is distributed from Newfoundland to Argentina in the west and Norway to South Africa, including the Mediterranean, in the east (Compagno, 1984). There is strong evidence from tagging data and catch records that blue sharks in the North Atlantic constitute a single stock (Kohler et al., 2002). Moreover, mitochondrial DNA d-loop sequence and nuclear microsatellite analyses indicate no differences between blue sharks from the eastern and western North Atlantic (Shivji[1]).

Distribution and movements of the blue shark are strongly influenced by seasonal variations in water temperature, reproductive condition, and availability of prey (Kohler et al., 2002). Blue sharks make frequent trans-Atlantic movements between the western and eastern regions, utilizing the major North Atlantic current systems (Stevens, 1976, 1990; Casey, 1982, 1985; Kohler et al., 2002). Temporal and geographic patterns of size and sexual segregation have been described for this species, and mating areas and pupping areas are reported to be in the western and eastern regions of the North Atlantic, respectively (Casey, 1982; Kohler et al., 2002). Pregnant females are rare in the western North Atlantic, which is dominated by juveniles of both sexes, adult males, and subadult females (Pratt, 1979; Casey, 1982; Kohler et al., 2002). Catch records from the eastern North Atlantic largely comprised neonates and juveniles of both sexes and adult females (Aasen, 1966; Stevens, 1975, 1976; Connett, 1987; Silva et al., 1996; Kohler et al., 2002).

Although subjected to a number of fisheries, the blue shark is primarily taken as bycatch in longline fisheries throughout the North Atlantic (ICCAT, 2002). Most blue sharks are discarded or only their fins are harvested because of the low palatability of their flesh (Castro et al., 1999). Although incomplete, blue shark landings estimates in the North Atlantic reported to the International Commission for the Conservation of Atlantic Tunas were 25.1 and 24.2 thousand metric tons (t) in 1998 and 1999, respectively (ICCAT, 2002). Domestic longline fisheries in the western North Atlantic rarely land blue sharks, but it was estimated that annual dead discards ranged from 2.8 to 29.3 thousand blue sharks (99.0–1136.3 t) during the period 1987–2000 (Cortés, 2002). The major source of landings in the U.S. has been the recreational fishery, which landed 6.8 thousand blue sharks in 2000 (Cortés, 2002).

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[1] Shivji, M. 2002. Personal commun. Nova Southeastern University, 8000 North Ocean Dr., Dania Beach, FL 33004.

Ecologically, the blue shark is an apex predator of important teleosts and cephalopods (Stevens, 1973; Tricas, 1978; Kohler, 1987). Historical fisheries have shown that sharks are intrinsically sensitive to sustained exploitation (see review by Castro et al., 1999). Slow growth, late ages at maturity, and low fecundities reflect the life history strategies of *K*-selected species; stock size is closely linked to recruitment (Hoenig and Gruber, 1990). Although the current Fishery Management Plan for Atlantic Tunas, Swordfish, and Sharks has established limits on the U.S. commercial and recreational fisheries that impact blue sharks (NMFS, 1999), no international management is currently in place. Given a single North Atlantic stock for this species, any fisheries exploitation, regardless of its coastal origin, may impact the population. Accurate age determinations are necessary for both the assessment and management of the blue shark because they form the basis for calculations of growth and mortality rates, age at maturity, age at recruitment, and estimates of longevity.

Age and growth of the blue shark have been described by a number of studies to varying degrees. In the North Pacific, Cailliet et al. (1983) and Tanaka et al. (1990) used vertebral growth rings and Nakano (1994) used both vertebrae and length-frequency modes to establish growth curves for the blue shark. In the North Atlantic, Aasen (1966) aged the species by assigning ages to length-frequency modes. Later, Stevens (1975), Silva et al. (1996), and Henderson et al. (2001) established growth curves from vertebral growth rings of juvenile blue sharks sampled in the eastern North Atlantic. Low sample sizes, inadequate size ranges, and the lack of age validation limit the utility of these studies for the North Atlantic blue shark population. Skomal (1990) generated growth curves for the blue shark from vertebral growth rings, tag-recaptures, and length-frequency data. In that study, vertebrae from oxytetracycline (OTC) injected recaptured blue sharks were used to validate age estimates. The purpose of the current study is to augment the work of Skomal (1990) with additional tag-recapture data, with corroborative vertebral readings of a different vertebral processing technique, and with more rigorous growth analyses.

Materials and methods

Interpretation of vertebrae

Vertebrae were obtained from blue sharks caught on research cruises, commercial, and recreational fishing vessels, and at sport fishing tournaments between 1966 and 2001. Primary sampling took place between Cape Hatteras, NC, and the Gulf of Maine (NE coast of the United States). To adequately represent the entire size range of the species, small sharks were obtained from the eastern Atlantic from cooperative fishermen and research scientists. When possible, the 15th through 20th vertebrae were excised for the study. When such precision was not possible, this section of backbone was approximated by cutting at the branchial region adjacent to the fifth gill arch. Excess muscle and connective tissue were removed from the vertebrae with a knife. Vertebrae were stored either frozen or preserved in 10% buffered formalin or 70% ethanol.

Only samples that had measured fork length (FL—tip of the snout to the fork in the tail, over the body curvature), total length (TL—tip of 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), or precaudal length (PCL—tip of the snout to the precaudal pit, over the body curvature) were used (Kohler et al., 1995). All lengths reported are in FL unless otherwise noted. TL can be converted to FL by using the regression (Kohler et al., 1995):

$$FL = 0.8313\,(TL) + 1.39 \qquad [n=572\ r^2=0.99].$$

PCL can be converted to FL using the regression (NMFS[2])

$$PCL = 0.9075\,(FL) - 0.3956 \qquad [n=106\ r^2=0.99].$$

One vertebra from each sample was removed for processing. The centrum was sectioned by using a Ray Tech Gem Saw with two diamond blades separated by a 0.6-mm spacer. Each centrum was cut through the middle along the sagittal plane; the resulting bow-tie sections were stored in individual capsules in 70% ethanol. Each section was digitally photographed with a MTI CCD 72 video camera attached to a SZX9 Olympus stereo microscope by using reflected light. All samples were photographed at a magnification of 4×. Band pairs (consisting of one opaque and one translucent band) were counted and measured from the images by using Image Pro 4 software (Media Cybernetics, Silver Spring, MD). Measurements were made from the midpoint of the notochordal remnant of the full bow-tie to the opaque growth bands at points along the internal corpus calcareum. The radius of each vertebral centrum (VR) was measured from the midpoint of the notochordal remnant to the distal margin of the intermedialia along the same diagonal as the band measurements. Specimens previously processed histologically (Skomal, 1990) were used for counts when whole samples for those specimens were not available for reprocessing. Because of the different processing method, histological sections were not used for measurements.

The criterion for what constitutes a band pair (annulus) was based on the contouring of the corpus calcareum in relation to the strength of the band. A clear indentation of the corpus calcareum at the position of an opaque band constituted the consummation of a growth layer within the vertebra and was considered the annulus (Fig. 1). Each layer was considered a temporal growth zone. The first opaque band distal to the focus was defined as the birth mark (BR) and a slight angle change in the corpus calcareum coincided with this mark. In addition, identification of the birth band was confirmed with back-calculation and by comparison of the radius of this band with the radius of vertebrae from young of the year (YOY) and full-term embryos.

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[2] NMFS (National Marine Fisheries Service). 2001. Unpubl. data. Apex Predators Program, 28 Tarzwell Dr., Narragansett, RI 02882.

The relationship between VR and FL was calculated to determine the best method for back-calculation of size-at-age data and to confirm the interpretation of the birth band. Age was calculated for each fish based on a birth date of June 1 (Pratt, 1979), corrected for date of capture. Regressions were fitted to the male and female size-at-age data and an ANCOVA was used to test for difference between the two relationships. The relationship between FL and VR was best described by a polynomial equation; therefore the data were ln-transformed before linear regression. The Fraser-Lee equation of the ln-transformed data was derived for back calculation:

$$ln(FL_a) = b + (ln[FL_c]+b)\ (lnradius_a)\ (lnradius_c)^{-1},$$

where a = age;
b = intercept from the regression; and
c = capture.

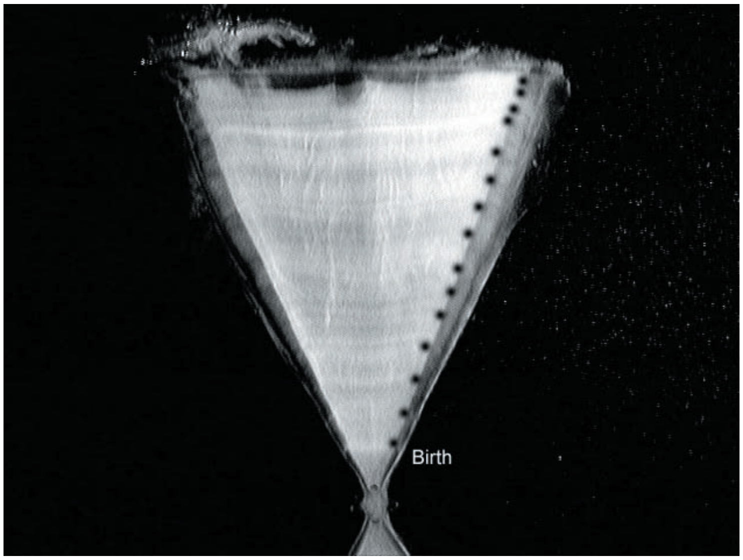

Figure 1

Photograph of a vertebral section from a male blue shark (*Prionace glauca*) estimated to be 14 years old.

Validation

To evaluate the periodicity of band pair formation, vertebrae from OTC-injected and measured tag-recaptured sharks were examined. Over 350 blue sharks of various sizes were measured, tagged, and injected with a 25 mg/kg body weight dose of OTC by scientific personnel aboard research and commercial vessels in the North Atlantic. Upon recapture, vertebrae were removed from injected specimens and stored in 70% ethanol or were frozen. Vertebrae from these sharks were processed, digitally photographed as previously described, and examined for the OTC mark with reflected UV light. The number of band pairs distal to the OTC mark was then compared with the number of years at liberty and expressed as the proportion of the previous complete growth zone.

Data analysis

Aging bias and precision of bands counts were examined by using age-bias plots and the coefficient of variation (Campana et al., 1995). Reader 2 counted 98 sections previously counted by reader 1 (Skomal, 1990). Pairwise comparisons were generated from these data.

Von Bertalanffy growth functions (VBGF) were fitted to length-at-age data by using the following equation (von Bertalanffy, 1938):

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

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

The VBGF was calculated by using the nonlinear regression function in Statgraphics (Manugistics, Inc., Rockville, MD).

Tagging data

From 1963 through 1999, members of the NMFS Cooperative Shark Tagging Program tagged 88,899 and recaptured 4967 blue sharks. Only those sharks reliably measured by biologists or fishermen at both tagging and recapture were used in the analyses. All measurements were converted to FL by using the relationships of Kohler et al. (1995).

The Gulland and Holt (1959) and Francis (1988a) models were used to generate VBGFs from the tag-recapture data. The Gulland and Holt (1959) method uses graphical interpretation of the recapture data to produce estimates of L_∞ and K. Specifically, annualized growth rate (cm/yr) was plotted against average FL (cm) between tagging and recapture to calculate linear regression coefficients. The slope of the line is equal to $-K$ and the x-axis intercept is equal to L_∞.

The Francis (1988a) method (GROTAG) uses maximum likelihood techniques to estimate growth parameters and variability from tagging data. A coefficient of variation of growth variability (v), measurement errors (m and s) and outlier contamination (p) are estimated, as well as growth rates at two user selected lengths (α and β). The reference lengths, α and β, were chosen to lie within the range of tagged individuals. The form of the von Bertalanffy equation becomes

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_a - g_\beta} - L_1\right]\left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta}\right)^{\Delta T}\right].$$

The simplest model, a linear fit with minimal parameters (α and s) was used initially and additional parameters were added to successively increase the model complexity. Significant improvement in the model results were determined by using log likelihood ratio tests in accordance with Francis (1988a). Bootstrapping was used to calculate the 95% confidence intervals for the final parameter estimates. The modeling and bootstrapping were carried out by using a Solver based spreadsheet in MS Excel (Microsoft Corp., Redmond, WA) (Simpfendorfer[3]). The value of t_0 cannot be estimated from tagging data alone, it requires an estimate of absolute size at age, such as size at birth, and was calculated with the VBGF by solving for $t_{0,}$ such that

$$t_0 = t + (1/K)\left[\ln\{L_\infty - L_t / L_\infty\}\right]$$

where L_t = known length at age (size at birth);
K = the von Bertalanffy growth constant; and
L_∞ = the theoretical maximum attainable length from the VBGF.

The t_0 values were calculated based on an average size at birth of 45 cm FL (Pratt, 1979) with $t = 0$.

Longevity

The oldest fish aged from the vertebral method provides an initial estimate of longevity. However, this value is likely to be underestimated in a fished population. Using a teleost species, Taylor (1958) defined life span (A) as the time required to attain 95% of the L_∞ with the following equation:

$$A_{95} = t_0 + \frac{\log_e(1-0.95)}{k}\cdot$$

This equation can be used to determine life span based on 99% of L_∞ by substituting 0.99 for 0.95 in the equation (Taylor, 1958). Fabens (1965) calculated time of >99% of L_∞ using the equation

$$>99\% = 5\frac{(\ln 2)}{k}\cdot$$

Results

Interpretation of vertebrae

Vertebral samples from 411 blue sharks were used in our study: 287 males, 119 females, and five of unknown sex. These samples comprised free-living sharks ranging from 49 cm to 312 cm FL. In addition, vertebrae from seven late-term embryos ranging from 36 cm to 43 cm FL were examined. Blue shark vertebrae did not have consistent prebirth marks; thus, the first distinct opaque band was generally considered the birth mark. The location of the birth band coincided with a slight angle change (Fig. 1).

The FL-VR relationship was slightly curvilinear and the ln-transformed data provided a better linear fit (Fig. 2). Therefore, we calculated the regressions based on the ln(FL)-ln(VR) relationship

$$\ln(\mathrm{FL}) = 0.89^{*}\ln(\mathrm{VR}) + 3.10 \qquad [n=392\ r^2=0.97].$$

There was no significant difference between the sexes (ANCOVA, $P>0.10$).

Confirmation of the birth band was made by comparison of the BR of all individuals to the VR of YOY and late-term embryos (Fig 2). The VR of seven late-term embryos (mean VR ±95% CI=2.04 ±0.25) was slightly less than the BR value of the total sample (mean BR ±95% CI=2.70 ±0.03; n=351); the mean VR of 11 early YOY was slightly higher than the BR of the entire sample (49–58 cm FL; mean VR ±95% CI =2.97 ±0.18) (Fig. 2). The location of the birth ring between the VR of both the late-term embryos and the YOY indicated that the birth ring was identified correctly.

Validation

OTC-injected recaptured blue sharks provided evidence for the use of vertebral band pairs as age indicators. Vertebrae from two OTC-injected sharks were returned after 0.7 and 1.5 years at liberty (Table 1). OTC injection produced strong fluorescent marks in the vertebral centra of both these sharks (Fig. 3) and the number of annuli past the OTC mark coincided with the number predicted from time at liberty (Table 1). In OTC-injected recaptured shark (B536), an opaque growth band was deposited just after tagging in May (Fig. 3). In recaptured shark B116452, an opaque growth band was deposited just prior to tagging in June (Fig. 3). These results suggest an annual spring deposition of growth zones within the vertebrae. Thus, vertebral annuli were validated in these two sharks, which were up to 4^+ years of age; the older of these fish (B536) corresponded to this age. Beyond this age, bands were assumed to be annual on the basis of the similar nature of band deposition.

Comparison of counts between two readers indicated no appreciable bias (Fig. 4). The coefficient of variation fluctuated around 15%. This level of precision was considered acceptable; thus, counts generated by both readers and preparation methods were combined for the analyses. The reader maintained quality control by periodically recounting earlier samples and by cross-checking the readings.

Length-at-age data indicated that males and females grow at roughly the same rate. The overlap in observed size-at-age data, as well as the graphical representation of the VBGF curves, indicated that there is little difference in growth for the sexes (Fig. 5). However, the LOWESS (locally weighted regression smoothing) derived curves as well as the VBGF parameters indicated that, theoretically, females grow slower and to a larger overall size than males (Table 2, Fig. 6). The LOWESS curves clearly showed minor differences in growth beginning at approximately seven years of age (Fig. 6), but this was likely an artifact of low female sample size at older ages. Subsequent analyses are presented for each sex and for sexes combined for ease of comparison with previously published studies.

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[3] Simpfendorfer, C. 2000. Personal commun. Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577.

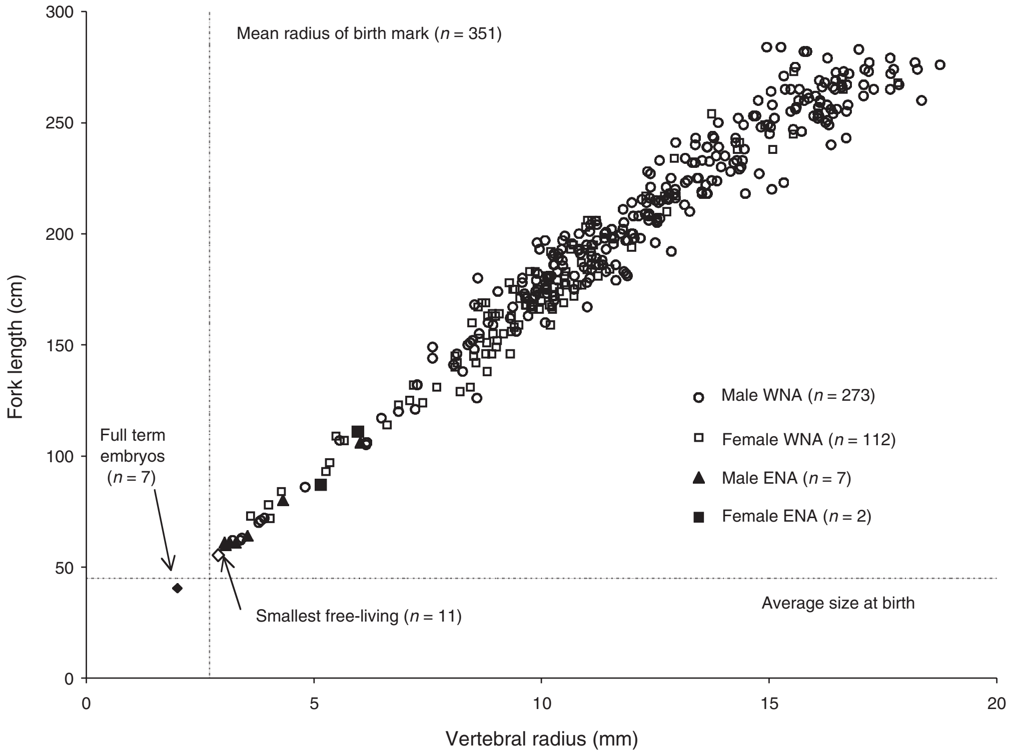

Figure 2

Relationship between vertebral radius and fork length in the blue shark (*Prionace glauca*).

Table 1

Tag-recapture data for OTC-injected recaptured blue shark (*Prionace glauca*). TFL = fork length at tagging, RFL = fork length at recapture.

Sample number	Sex	TFL (cm)	RFL (cm)	Date tagged	Date recaptured	Years at liberty	Growth (cm)	No. of bands after OTC mark
B116452	F	116	162[1]	18 Jun 1987	21 Dec 1988	1.5	33	1.20
B536	M	172	192	9 May 1985	16 Jan 1986	0.7	29	0.68

[1] Calculated from precaudel length.

Tagging data

A total of 43 blue sharks was recaptured with sufficient information for tag-recapture analysis. Data from 18 sharks at liberty >0.9 years were used for Gulland and Holt's (1959) method and all the recaptured sharks were used for the Francis (1988a) method (GROTAG).

The results of the likelihood ratio tests with GROTAG (Francis, 1988a) showed that the more complex nonlinear model with all six parameters was the best fit for these data (Table 3, model 3). The mean annual growth rates are g_{90} = 44.2 cm/yr and g_{180} = 25.5 cm/yr, corresponding to growth rates at a FL= 90 cm and 180 cm, respectively (Fig. 7). Von Bertalanffy estimates from the Gulland and Holt (1959) and GROTAG (Francis, 1988a) methods produced similar von Bertalanffy curves (Table 4, Fig. 8A).

Longevity

The maximum age determined from vertebral band pair counts was 16 and 15 years for males and females, respectively. These ages are likely to be an underestimate of longevity, given the history of fisheries exploitation of this species. Using Taylor's (1958) method, we determined that the age at which 95% and 99% of the L_∞ is reached was 16.5 and 26.1 years, respectively. Fabens (1965) method for >99% longevity produced an estimate of 20.7 years.

Figure 3

Vertebral sections from two OTC-injected blue sharks (*Prionace glauca*). Annuli and birth marks are indicated.

Discussion

Several methods have been employed to validate or verify (or both) age estimates derived from vertebral banding patterns (Cailliet, 1990). Although corroborative verification often comes from the interpretation of length-frequency data, laboratory and field growth studies, and centrum edge analyses, direct age validation for sharks is limited to the interpretation of vertebral banding patterns in OTC-injected fish.

In his review of elasmobranch age and growth studies, Cailliet (1990) found validated growth curves for only six species, which included three carcharhinids: the lemon (*Negaprion brevirostris*); the sandbar (*Carcharhinus plumbeus*); and the Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks. Although more than ten years have transpired since this review, validated growth curves for sharks are still lacking. In lamnids, direct validation of annual band deposition with the use of OTC has been reported in a single species, the porbeagle shark, *Lamna nasus* (Natanson et al., 2002). Although age estimates from vertebral banding patterns have been reported for several carcharhinids, including the oceanic whitetip shark, *Carcharhinus longimanus* (Seki et al., 1998; Lessa et al., 1999), the dusky shark, *C. obscurus* (Natanson et al., 1995; Natanson and Kohler, 1996; Simpfendorfer, 2000), the blacktip shark, *C. limbatus* (Wintner and Cliff, 1995), and the bronze whaler, *C. brachyurus* (Walter and Ebert, 1991), age interpretations were not validated and vertebral bands were assumed to be annual. More recently, Simpfendorfer et al. (2002) validated the annual formation of vertebral banding patterns in *C. obscurus* from Western Australian waters.

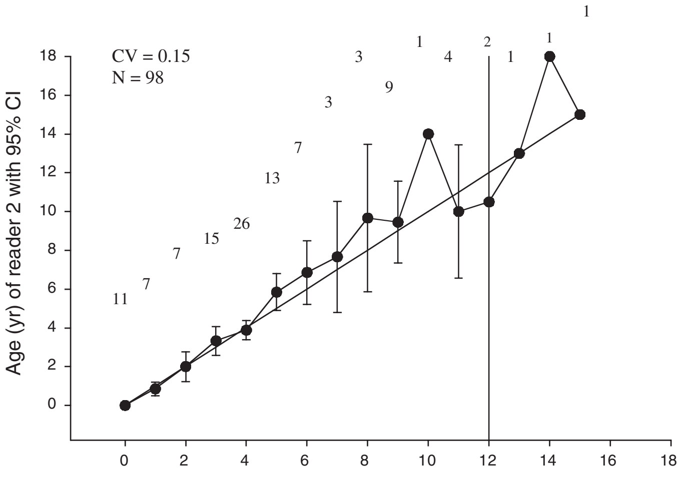

Figure 4

Age bias graph for pair-wise comparison of 98 blue shark (*Prionace glauca*) vertebral counts from two independent readers. Each error bar represents the 95% confidence interval for the mean age assigned by reader 2 to all fish assigned a given age by reader 1. The one-to-one equivalence line is also presented.

In the current study, we have validated annual band pair deposition in *Prionace glauca* up to 4^+ years in age using vertebrae from two OTC-injected fish. These data indicate that annulus formation occurs in the spring. This seasonal formation is further supported by the marginal increment analysis of Skomal (1990), which shows that one band pair is formed annually. However, the low sample size and the lack of OTC-injected recaptured fish over the entire size range of the species do not allow for full age and growth validation. Clearly, the study requires OTC-injected recaptured blue sharks over a broader size range and greater time at liberty—a requirement that is not atypical of age and growth studies on large highly migratory elasmobranchs. Wintner and Dudley (2000) used two OTC-injected recaptured individuals to conclude that growth band deposition is annual in the tiger shark (*Galeocerdo cuvier*). Moreover, Natanson et al. (2002) validated annuli in the porbeagle shark up to 11 years of age by using only two OTC-injected and six YOY recaptured individuals, although the species was aged to 25 years.

The processes that govern vertebral growth have yet to be described in elasmobranchs. The pattern varies from one ring per year in most carcharhinids (Cailliet, 1990), and two rings per year in some lamnids (Parker and Stott, 1965; Pratt and Casey, 1983) to the complete absence of periodicity (Natanson, 1984). Some researchers feel that temperature plays a major role in this process (Stevens, 1975; Ferreira and Vooren, 1991). The blue shark, however, remains within a discrete temperature range year-round (Stevens, 1975; Sciarrota and Nelson, 1977; Casey, 1982). Moreover, acoustic tracking has shown that blue sharks experience large changes in body temperature (up to 7°C) as they routinely pass through the thermocline in their daily periodic dives from the surface to depths of 200–600 m (Carey and Scharold, 1990).

The ecology of this species may provide a more likely explanation of annulus formation. Kohler (1987) found a seasonal cycle for energy storage that correlated with the migratory patterns of the blue shark. In general, blue shark condition was found to be at an annual low in the winter and spring. Blue sharks use energy stores during this time for extensive north-south and trans-Atlantic migrations (Casey, 1985; Kohler, 1987) and periodic deep dives (Carey and Scharold, 1990). It is logical that growth may be depressed during these months, thereby causing a check or annulus in the vertebrae.

Tag-recapture data provide verification of the growth curves derived from vertebral banding. Francis (1988b) suggested that growth curves generated from age-length and length-increment (tagging) data are not directly comparable and that the comparison of growth rates at length was more appropriate. Although VBGF parameters derived from tagging data are noticeably higher, growth rates were similar for both methods (Fig. 7). The higher L_∞ and K can be attributed to the different derivation of the VBGF parameters and the absence of older recaptured sharks in the sample.

Pratt (1979) proposed that maturity in the male blue shark occurs at 183 cm FL and this would coincide with an age of 4–5 years based on the results of the present study. Females enter a distinct subadult phase (Pratt, 1979) at 145 cm FL and 2^+ years of age. Full maturity in females is attained at 185 cm FL (Pratt, 1979), which corresponds to about 5 years of age.

Previous estimates of age and growth of the blue shark in the Atlantic have been determined from vertebral banding patterns, and verification has been made from the interpretation of length-frequency and tagging data (Stevens,1975; Silva et al., 1996; Henderson et al., 2001) (Table 5, Fig. 8). The eastern Atlantic vertebral sample of Stevens (1975) comprised largely females (89%), ranging from 34 cm to 227 cm FL. The resulting growth curve, therefore, largely reflects female growth (Fig. 8C). His use of whole silver-stained centra coupled with the lack of maximum-size fish allowed for the interpretation of only six annuli. From only mean back-calculated lengths at ages two through five, Stevens extrapolated growth of the species with a VBGF to an age of 20 years. Similarly, Silva et al. (1996) and Henderson et al. (2001) investigated age and growth in this species with whole vertebrae from sharks sampled in the eastern North Atlantic. In the former study, vertebral samples from

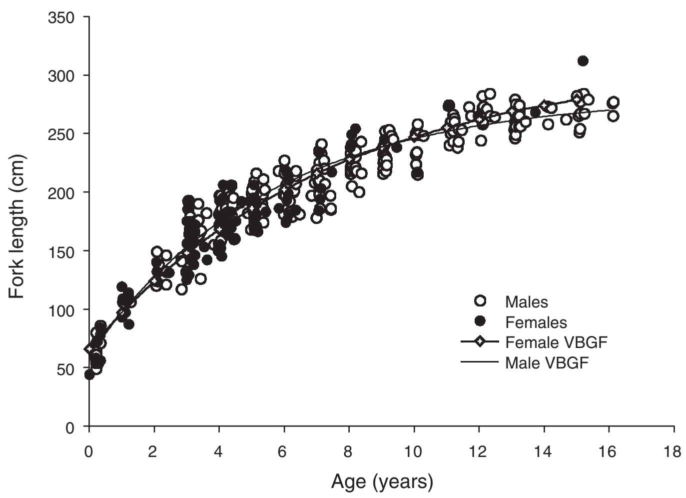

Figure 5

Prionace glauca growth curves and size-at-age data based on vertebral band counts. Von Bertalanffy growth function curves have been fitted to the data by sex.

Table 2

Von Bertalanffy growth function parameters and 95% confidence intervals calculated by using vertebral and tag-recapture methods for the blue shark (*Prionace glauca*). n = number of sharks in sample.

Method		L_∞	K	t_0	n
Vertebral	Combined	286.8	0.17	−1.43	411
	CI	±7.32	0.01	0.20	
	Male	282.3	0.18	−1.35	287
	CI	±7.15	0.02	0.23	
	Female	310.8	0.13	−1.77	119
	CI	±34.8	0.03	0.50	
Tag-recapture					
GROTAG	Combined	302.4	0.23	−0.69	43
Gulland and Holt (1959)	Combined	331.7	0.19	−0.77	18
	CI	±80.0	0.12		

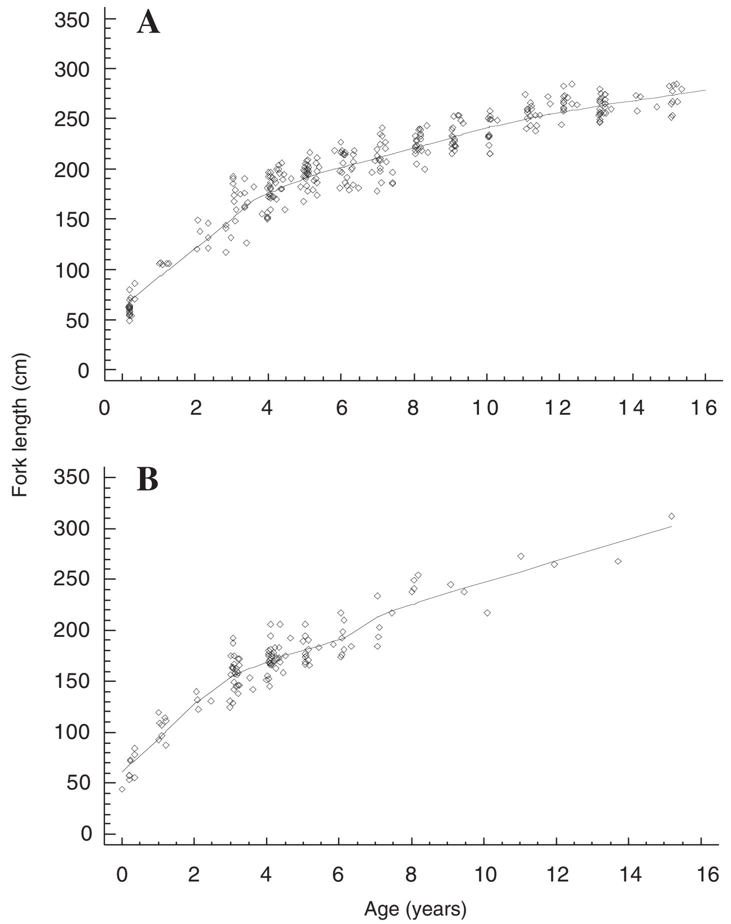

Figure 6

Prionace glauca growth curves and size-at-age data based on vertebral band counts. LOWESS (locally weighted regression smoothing) curves have been fitted to the data by sex: (**A**) males and (**B**) females.

308 juvenile blue sharks collected in the Azores were used to model early growth in this species. Silva et al. (1996) calculated an annual growth rate of 30 cm/yr for the first five years of life and aged the samples to seven years. More recently, Henderson et al. (2001) used 159 vertebrae sampled from blue sharks taken from oceanic waters off Ireland. Like the previous two studies, the size range of samples was limited to juvenile fish less than 191 cm FL and the estimated ages ranged from 1 to 6 years.

Stevens (1975), Silva et al. (1996), and Henderson et al. (2001) modeled blue shark growth with the VBGF. These curves are similar to each other (Silva et al., 1996, Henderson et al., 2001), yet show slower growth than the current study (Fig. 8) despite the fact that we used criteria similar to those of Stevens (1975) for vertebral interpretation. This result is not surprising in light of the fact that these three studies share common methods and sample biases. All three of the previous studies were performed on juvenile sharks from the eastern North Atlantic, the vast majority of which were between 100 and 184 cm FL. Because of the lack of samples from very small fish, one study (Silva et al., 1996) included vertebral readings from full-term embryos in the growth curve. It is well documented that embryonic growth is not comparable to postnatal growth (Casey et al., 1985; Pratt and Casey, 1990) and, therefore, embryos should not be included in a postnatal growth curve. The lack of large and small specimens in the calculations of these growth curves is particularly problematic because validation of the first growth increment is essential as it forms the basis of further counts. Moreover, the smallest and largest of the specimens are the most influential in the estimation of growth (Campana, 2001).

All three of the previous studies used similar whole centrum vertebral processing techniques and band count criteria, which would lead to corroborating counts, yet not necessarily to accurate counts (Campana, 2001). Whole vertebrae simply do not allow for high band resolution in older slower growing fish. Therefore, counts from whole

Table 3

Log-likelihood function values and parameter estimates for three growth models fitted to *Prionace glauca* tagging data using GROTAG (Francis 1988a). For a significant ($P<0.05$) improvement in fit, the introduction of one extra parameter must increase λ by at least 1.92 (Francis 1988a). * indicates fixed parameters. Model 3 shows 95% confidence intervals.

		Model		
Parameter	Symbol (unit)	1	2	3
Log likelihood		–197.29	–176.91	–174.61
Mean growth rates	g90 (cm/yr)	21.53	39.04	44.18 (35.37–54.33)
	g180 (cm/yr)	10.92	21.90	25.46 (19.29–33.41)
Growth variability	v	0*	0.46	0.27 (0.06–0.44)
Measurement error	s (cm)	1.06	1.37	5.39 (2.25–7.40)
	m (cm)	0*	0*	–2.03 (–5.37–2.10)
Outliers	p	0.83	0.28	0.18

vertebrae generally underestimate ages in larger individuals. The counts obtained in the three eastern Atlantic studies may be accurate because they are from juvenile sharks where vertebral bands are not compressed. In fact, juvenile growth from our size-at-age data overlaps the growth curves from these studies. However, the VBGF growth curves and resulting estimates of growth rate and age at maturity from the eastern Atlantic studies are suspect because of the lack of fish at the lower and upper end of the curve. The general lack of maximum-size fish in these studies resulted in the estimation of an artificially inflated L_∞ and, therefore, a lower growth rate (K) for this species (Table 5). Vertebral band deposition was assumed to be annual in these studies, but low sample sizes, sample bias, and lack of validation limits the utility of this previous work. In the current study, the use of sections and the adequate representation of the entire size range for both sexes yielded more accurate age estimates of 16 and 15 years for males and females, respectively.

Age and growth estimates of the blue shark in the North Pacific have been determined by using vertebral bands and length-frequency data (Cailliet et al., 1983; Tanaka et al., 1990; Nakano, 1994). Although the VBGF was used to model growth based on vertebral interpretation, the resulting parameters differed greatly among studies (Table 5). In general, Cailliet et al. (1983) reported a male growth rate similar to that in our present study, but a much smaller L_∞ (Table 5). For females, the latter holds true, but the growth coefficient is much higher (0.25) than reported in our study. Tanaka et al. (1990) found a similar growth trend in the western North Pacific with females growing faster than males, but the VBGF parameters were very different with higher L_∞ and lower K values. When compared to our study, the VBGF parameters of Tanaka et al. (1990) yield slower growth and a greater maximum size for males and a similar growth rate and smaller maximum size for females. Tanaka et al. (1990) attributed these intra- and inter-oceanic differences to the different methods used. More recently, Nakano (1994) sampled blue sharks across the North Pacific and derived VBGF growth parameters that were similar to those of Tanaka et al. (1990), but estimated growth rate to be slower than that of our present study. It is difficult to ascertain whether interoceanic differences in growth are real or are an artifact of method. Although Tanaka et al. (1990) presented data to support the latter within the North Pacific, the much larger maximum size attained by this species in the North Atlantic (Strasburg, 1958; Tanaka, 1984) cannot be overlooked in relation to interoceanic growth differences.

Table 4

Size at age (cm) for the blue shark (*Prionace glauca*) calculated from von Bertalanffy equations based on tag-recapture and vertebral methods.

	Vertebral method			Tag-recapture GROTAG method
Age (yr)	combined	male	female	
0	61.0	60.9	66.1	45
1	95.8	97.4	97.0	99
2	125.2	127.8	124.0	141
3	150.1	153.3	147.6	175
4	171.2	174.5	168.2	201
5	189.0	192.3	186.2	222
6	204.1	207.1	201.9	239
7	216.8	219.5	215.7	252
8	227.6	229.8	227.7	263
9	236.7	238.5	238.2	
10	244.4	245.7	247.4	
11	251.0	251.7	255.4	
12	256.5	256.8	262.4	
13	261.1	261.0	268.5	
14	265.1	264.5	273.9	
15	268.4	267.4	278.5	
16	271.3	269.9		

Longevity estimates for the blue shark indicate that they may live for 26 years when Taylor's (1958) method is employed. On the other hand, Fabens' (1965) method for >99% longevity produced an estimate of 20.7 years, which may be more realistic. The maximum age determined from vertebral band-pair counts was 16 and 15 years for males and females, respectively. An analysis of maximum times at liberty for tagged blue sharks supports the notion that this species does not live as long as previously reported for the North Atlantic. Of the 4967 blue sharks recaptured to date, 99% were at liberty for less than five years. The maximum times at liberty are 9.1 and 8.5 years, despite the 39-year history of the tagging program. The shark at liberty for 9.1 years was a male tagged at an estimated 122 cm FL; size at recapture was not reported. According to our growth curve, the shark was tagged at 1^+ years of age, which would correspond to a maximum age of 10^+ years at recapture. The shark at liberty for 8.5 years, also a male, was estimated to be 198 cm FL at tagging, which would correspond to 5^+ years of age. Therefore, at recapture, this fish would be a maximum age of 13.5 years, although its measured FL at recapture actually corresponds to 11 years on our growth curve. The largest long-term recapture was a male, 244 cm FL at tagging and 266 cm FL at recapture 6 years later. This would correspond to an estimated age of 10 years at tagging and 16 years at recapture, which falls well within the values of directly aged vertebrae (Fig. 5).

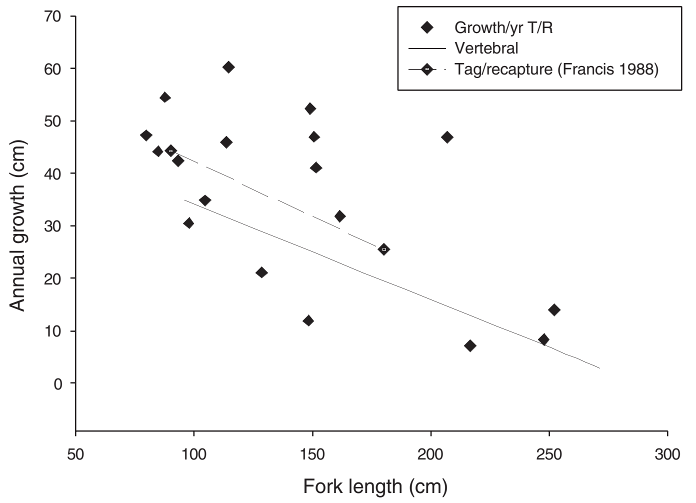

Figure 7

Comparison of the annual growth rates of the blue shark (*Prionace glauca*) derived from multiple aging methods.

The occurrence of sexual differences in growth is well documented in elasmobranchs; females usually grow larger than males (Cortés, 2000). Although the largest blue shark in our study was a 312-cm-FL female, there is little evidence that large females are highly abundant in the North Atlantic. Maximum size male and female specimens in our study, 284 cm FL and 312 cm FL, respectively, represented the largest reliably measured blue sharks from the North Atlantic, with the exception of a 320-cm-FL specimen (sex unspecified) examined by Bigelow and Schroeder (1953). Indeed, a thorough review of the literature reveals that although 288-cm-FL and 279-cm-FL females were reported by Gubanov and Grigor'yev (1975) from the Indian Ocean, males are consistently cited as being very much larger than females in the world's

Table 5

Van Bertalanffy growth function parameters and maximum age derived from vertebral bands in the blue shark (*Prionace glauca*) separated by location and sex.

Sex	Ocean	Region	*n*	L_∞	*K*	T_0	Max. age	Authors
Male	North Atlantic	All	287	282.3	0.18	–1.35	16	Current study
		East	112	309.0	0.12	–1.07	5	Silva et al. (1996)
	North Pacific	East	38	246.7	0.18	–1.11	9	Cailliet et al. (1983)
		West	43	308.1	0.10	–1.38	7	Tanaka et al. (1990)
		All	148	319.5	0.13	–0.76	10	Nakano (1994)
Female	North Atlantic	All	119	286.8	0.16	–1.56	15	Current study
		East	82	353.0	0.11	–1.04	6	Stevens (1975)
		East	170	382.0	0.09	–1.19	5	Silva et al. (1996)
	North Pacific	East	88	202.6	0.25	–0.80	9	Cailliet et al. (1983)
		West	152	254.1	0.16	–1.01	8	Tanaka et al. (1990)
		All	123	268.9	0.14	–0.85	10	Nakano (1994)
Combined	North Atlantic	All	411	285.4	0.17	–1.41	16	Current study
		East	336	284.0	0.14	–1.08	5	Silva et al. (1996)
		East	159	314.4	0.12	–1.33	6	Henderson et al. (2001)
	North Pacific	East	130	222.1	0.22	–0.80	9	Cailliet et al. (1983)

oceans (Suda, 1953; Tucker and Newnham, 1957; Aasen, 1966; McKenzie and Tibbo, 1964; Dragonik and Pelzarski, 1983; Stevens, 1984; Francis et al., 2001). Although the largest blue shark reported from the North Pacific was only 254 cm FL (Strasburg, 1958; Cailliet et al., 1983), individuals up to 331 cm FL have been reported from the South Pacific and the largest sharks were all males (Francis et al., 2001). The paucity of females exceeding 225 cm FL in the current study and the complete lack of these specimens in the Stevens (1975), Silva et al. (1996), and Henderson et al. (2001) samples indicate that these fish are rare, inhabit unknown or unfished areas of the Atlantic, or possibly avoid fishing gear. In our study, the VBGF parameters (Table 5) show that females theoretically attain larger sizes than males. However, the low number of large females in this and previous studies may indicate that natural mortality prevents them from attaining these lengths. The occurrence of severe lacerations on female blue sharks incurred during courtship is well documented (Stevens, 1974; Pratt, 1979). Although highly speculative, the long-term cumulative effects of such behavior may act as a source of increased mortality in females of the species, shortening their life-span and limiting the number that reach the larger sizes.

Through an integrated approach incorporating vertebral banding, OTC injection, and tagging data, it has been shown that the blue shark grows faster and lives a shorter life than previously thought in the North Atlantic. We believe that the validated vertebral interpretations generated during this study for the first four years of growth, combined with the vertebral counts and longevity estimates from tag-recapture data, provide vigorous estimates of age and growth for a large pelagic carcharhinid, the blue shark.

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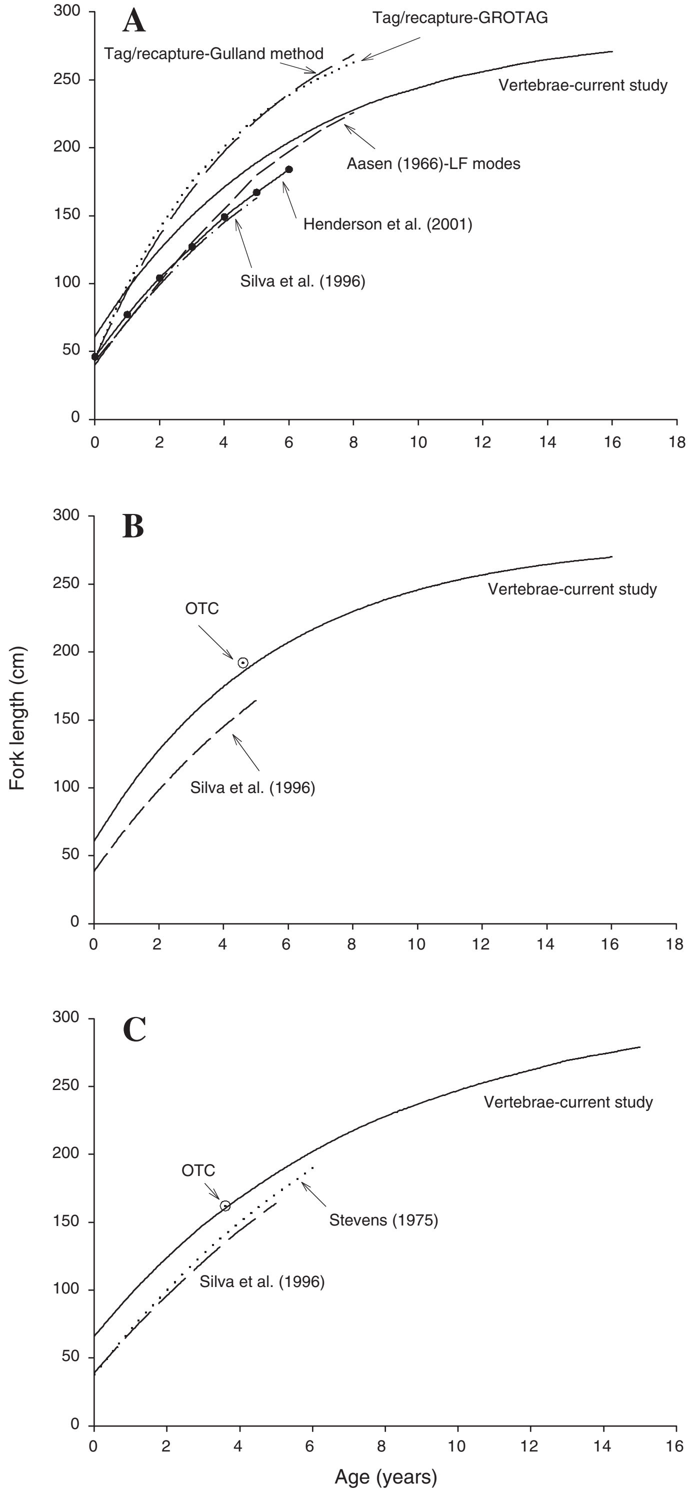

Figure 8

Von Bertalanffy growth curves generated from vertebral and recapture data for (**A**) sexes combined, (**B**) male, and (**C**) female *Prionace glauca*, as compared to OTC-injected recaptured blue sharks; included for comparison are the von Bertalanffy growth curves of other North Atlantic studies.

Literature cited

Aasen, O.
1966. Blahaien, *Prionace glauca* (Linnaeus, 1758). Fisken og Havet 1:1–15.

Bigelow, H.. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine, 577 p. U.S. Dep. Int., Fish and Wildl. Serv., Fish. Bull. 53.

Cailliet, G. M.
1990. Elasmobranch age determination and verification: an updated review. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics, and status of the fisheries (H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi, eds.), p. 157–165. U.S. Dep. Commer., NOAA Tech. Rep. 90.

Cailliet, G. M., L. K. Martin, J. T. Harvey, D. Kusher, and B. A. Welden.
1983. Preliminary studies on the age and growth of blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. *In* Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks (E. D. Prince and L. M. Pulos, eds.), p. 179–188. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.

Campana, S. E.
2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish. Biol. 59:197–242.

Campana, S. E., M. C. Annand, and J. I. McMillan.
1995. Graphical and statistical methods for determining the consistency of age determinations. Trans. Amer. Fish. Soc. 124:131–138.

Carey, F. G., and J. Scharold.
1990. Movements of blue sharks (*Prionace glauca*) in depth and course. Mar. Biol. 106:329–342.

Casey, J. G.
1982. Blue shark, *Prionace glauca*. Species synopsis. *In* Ecology of the Middle Atlantic Bight fish and shellfish—Monograph 15—fish distribution (M.D. Grosslein and T. Azarovitz, eds.), p. 45–48. MESA New York Bight Atlas, NY Sea Grant, Albany, NY.
1985. Trans-Atlantic migrations of the blue shark: a case history of cooperative shark tagging. *In* World angling resources and challenges; proceedings of the first world angling conference (R. H. Stroud, ed.), p. 253–267. Int. Game Fish Assoc., Ft. Lauderdale, FL.

Casey, J. G., H. L. Pratt Jr., and C. E. Stillwell.
1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 42(5):963–975.

Castro, J. I., C. M. Woodley, and R. L. Brudek.
1999. A preliminary evaluation of the status of shark species. FAO Fisheries Technical Paper 380, 72 p. FAO, Rome.

Compagno, L. J. V.
1984. FAO species catalogue. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. FAO Fish Synop. 125, vol. 4, 250 p. FAO, Rome.

Connett, S.
1987. Blue sharks studied in the eastern Atlantic. *In* The shark tagger: 1987 summary (J. Casey, H. L. Pratt Jr., N. E. Kohler, and C. E. Stillwell, eds.), p. 8–10. Newsletter of the Cooperative Shark Tagging Program. U.S. Dep. Commer., NOAA, NMFS, Narragansett, RI.

Cortés, E.
2000. Life history patterns and correlations in sharks. Rev. Fish. Sci. 8(4):299–344.
2002. Catches and catch rates of pelagic sharks from the northwestern Atlantic, Gulf of Mexico, and Caribbean. Col. Vol. Sci. Pap. ICCAT 54(4):1164–1181.

Dragonik, B, and W. Pelzarski.
1983. The occurrence of the blue shark, *Prionace glauca* (L.), in the North Atlantic. Rep. Sea Fish. Inst. 19:63–77.

Fabens, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Ferreira, B. P., and C. M. Vooren.
1988a. Age, growth, and structure of the vertebrae in the school shark *Galeorhinus galeus* (Linnaeus, 1758) from southern Brazil. Fish. Bull. 89:19–31.

Francis, R. I. C. C.
1988a. Maximum likelihood estimation of growth and growth variability from tagging data. NZ J. Mar. Freshwater Res. 22:43–51.
1988b. Are growth parameters estimated from tagging and age-length data comparable? Can. J. Fish. Aquat. Sci. 45: 936–942.

Francis, M. P., L. H. Griggs, and S. J. Baird.
2001. Pelagic shark bycatch in the New Zealand tuna longline fishery. Mar. Freshwater Res. 52(2):165–178.

Gubanov, Ye. P., and V. N. Grigor'yev.
1975. Observations on the distribution and biology of the blue shark *Prionace glauca* (Carcharhinidae) of the Indian Ocean. J. Ichthyol. 15:37–43.

Gulland, J. A., and S. J. Holt.
1959. Estimation of growth parameters for data at unequal time intervals. J. Cons. Int. Explor. Mer 25:47–49.

Henderson, A. C., K. Flannery, and J. Dunne.
2001. Observations on the biology and ecology of the blue shark in the North-east Atlantic. J. Fish. Biol. 58: 1347–1358.

Hoenig, J. M., and S. H. Gruber.
1990. Life history patterns in the elasmobranchs: implications for fisheries management. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics, and status of the fisheries (H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi, eds), p. 1–16. U.S. Dep. Commer., NOAA Tech. Rep. 90.

ICCAT (International Commission for the Conservation of Atlantic Tunas).
2002. ICCAT data preparatory meeting for Atlantic shark stock assessment. Col. Vol. Sci. Pap. ICCAT, 54(4): 1064–1106.

Kohler, N. E.
1987. Aspects of the feeding ecology of the blue shark in the western North Atlantic. Ph.D. diss., 163 p. Univ. Rhode Island, Kingston, RI.

Kohler, N. E., J. G. Casey, and P. A. Turner.
1987. Length-weight relationships for 13 species of sharks from the western North Atlantic. Fish. Bull. 93:412–418.

Kohler, N. E., P. A. Turner, J. J. Hoey, L. J. Natanson, and R. Briggs.
2002. Tag and recapture data for three pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. Col. Vol. Sci. Pap. ICCAT 54(4):1231–1260.

Lessa, R., F. M. Santana, and R. Paglerani.
1999. Age, growth and stock structure of the oceanic whitetip shark, *Carcharhinus longimanus*, from the southwestern equatorial Atlantic. Fish. Res. 42:21–30.

McKenzie, R. A., and S. N. Tibbo.
1964. A morphometric description of the blue shark (*Prionace glauca*) from the Canadian Atlantic waters. J. Fish. Res. Board Can. 21:865–866.

Nakano, H.
1994. Age, reproduction and migration of blue shark in the North Pacific. Bull. Nat. Res. Inst. Far Seas Fish. 31:141–256.

Natanson, L. J.
1984. Aspects of age, growth, and reproduction of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. M.A. thesis, 71 p. San Jose State Univ., San Jose, CA.

Natanson, L. J., J. G. Casey, and N. E. Kohler.
1995. Age and growth of the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic. Fish. Bull. 93: 116–126.

Natanson, L. J., and N. E. Kohler.
1996. A preliminary estimate of age and growth of the dusky shark *Carcharhinus obscurus* from the south-west Indian Ocean, with comparisons to the western North Atlantic. S. Afr. J. Mar. Sci. 17:217–224.

Natanson, L. J., J. J. Mello, and S. E. Campana.
2002. Validated age and growth of the porbeagle shark, *Lamna nasus*, in the western North Atlantic. Fish. Bull. 100:266–278.

NMFS (National Marine Fisheries Service).
1999. Final fishery management plan for Atlantic tunas, swordfish, and sharks., 1162 p. Highly Migratory Species Management Division, Silver Spring, MD.

Parker, H. W., and F. C. Stott.
1965. Age, size and vertebral calcification in the basking shark, *Cetorhinus maximus* (Gunnerus). Zool. Meded. 40(34):305–319.

Pratt, H. L., Jr.
1979. Reproduction in the blue shark, *Prionace glauca*. Fish. Bull. 77:445–470.

Pratt, H. L., Jr., and J. G. Casey.
1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. Can. J. Fish. Aquat. Sci. 40(11): 1944–1957.
1990. Shark reproductive strategies as limiting factors in directed fisheries, with a review of Holden's method of estimating growth parameters. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics, and status of the fisheries (H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi, eds), p. 97–110. NOAA Tech. Rep. 90.

Sciarrotta, T. C., and D. Nelson.
1977. Diel behavior of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. Fish. Bull 73:519–528.

Seki, T., T. Taniuchi, H. Nakano, and M. Shimizu.
1998. Age, growth and reproduction of the oceanic whitetip shark from the Pacific Ocean. Fish. Sci. 64(1):14–20.

Silva, A. A., H. M. Silva, and K. Erzini.
1996. Some results on the biology of the blue shark, *Prionace glauca*, in the North Atlantic based on data from a research cruise of the R/V *Arquipelago* in Azorean waters: a summary paper, 9 p. Universidade dos Acores, Horta, Acores, Portugal.

Simpfendorfer, C. A.
2000. Growth rates of juvenile dusky sharks, *Carcharhinus obscurus* (Lesueur, 1818), from southwestern Australia estimated from tag-recapture data. Fish. Bull. 98:811–822.

Simpfendorfer, C. A., R. B. McAuley, J. Chidlow, and P. Unsworth.
2002. Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters. Mar. Freshwater Res. 53:567–573.

Skomal, G. B.
1990. Age and growth of the blue shark, *Prionace glauca*, in the North Atlantic. M.S. thesis, 82 p. Univ. Rhode Island, Kingston, RI.

Stevens, J. D.
1973. Stomach contents of the blue shark (*Prionace glauca* L.) of southwest England. J. Mar Biol. Assoc. U.K. 53: 357–361.
1974. The occurrence and significance of tooth cuts on the blue shark (*Prionace glauca* L.). J. Mar. Biol. Assoc. U.K. 54:373–378.
1975. Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). J. Mar. Biol. Assoc. U.K. 55:657–665.
1976. First results of shark tagging in the northeast Atlantic, 1972–1975. J. Mar. Biol. Assoc. U.K. 56: 929–937.
1984. Biological observations on sharks caught by sportfishermen off New South Wales. Aust. J. Mar. Freshwater Res. 35:573–590.
1990. Further results from a tagging study of pelagic sharks in the Northeast Atlantic. J. Mar. Biol. Assoc. U.K. 70: 707–720.

Strasburg, D. W.
1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. Fish. Bull. 58:335–361.

Suda, A.
1953. Ecological study of the blue shark (*Prionace glauca* Linne'). South Sea Area Fish Res. Lab. Rep. 26:1–11.

Tanaka, S.
1984. Present status of fisheries biology. *In* Elasmobranchs as fishery resources (T. Taniuchi and M. Suyama, eds.), p. 46–59. Jpn. Soc. Sci. Fish., Fish. Ser. 49.

Tanaka, S., G. M. Cailliet, and K. G. Yudin.
1990. Differences in growth of the blue shark, *Prionace glauca*: technique or population? *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics, and status of the fisheries (H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi, eds.), p. 177–187. U.S. Dep. Commer., NOAA Tech. Rep. 90.

Taylor, C. C.
1958. Cod growth and temperature. J. Cons. Int. Explor. Mer 23:366–370.

Tricas, T.
1978. Relationships of the blue shark, *Prionace glauca*, and its prey species near Santa Catalina Island, California. Fish. Bull. 77:175–182.

Tucker, D. W., and C. T. Newnham.
1957. The blue shark *Prionace glauca* breeds in British seas. Ann. Mag. Nat. Hist., Series 12, 10:673–688.

von Bertalanffy, L.
1938. A quantitative theory of organic growth (inquiries on growth laws II). Hum. Biol. 10:181–213.

Walter, J. P., and D. A. Ebert.
1991. Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae) from southern Africa, with a review of some life history parameters. S. Afr. J. Mar. Sci 10:37–44.

Wintner, S. P., and G. Cliff.
1995. Age and growth determination of the blacktip shark, *Carcharhinus limbatus*, from the east coast of South Africa. Fish. Bull. 94:135–144.

Wintner, S. P., and S. F. J. Dudley.
2000. Age and growth estimates for the tiger shark, *Galeocerdo cuvier*, from the east coast of Africa. Mar. Freshwater Res. 51:43–53.