

AGE AND GROWTH OF THE BLUE SHARK, *PRIONACE GLAUCA*, IN THE NORTH ATLANTIC OCEAN

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SUMMARY

Age and growth estimates for the blue shark, *Prionace glauca*, were derived from 411 vertebral centra, and 43 tag-recaptures collected in the North Atlantic. The vertebrae of two oxytetracycline-injected recaptures support an annual spring deposition of growth rings in the vertebrae in sharks up to 192 cm FL. Males and females were aged to 16 and 15 years, respectively. Both sexes grew similarly to age seven when growth rates decreased in males and remained constant in females. Growth rates from tag-recaptures 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 in these waters.

RÉSUMÉ

Des estimations de l'âge et de la croissance du requin peau bleue, *Prionace glauca*, ont été calculées d'après 411 vertèbres et 43 marques récupérées dans l'Atlantique nord. Les vertèbres de deux poissons recapturés piqués à l'oxytétracycline étayaient l'existence d'un dépôt annuel au printemps d'anneaux de croissance dans les vertèbres de requins jusqu'à 192 cm de longueur à la fourche. Les mâles et les femelles avaient respectivement 16 et 15 ans. Les deux sexes avaient grandi de façon similaire jusqu'à 7 ans, âge auquel le taux de croissance avait diminué chez les mâles alors qu'il restait constant chez les femelles. Le taux de capture des poissons recapturés concordait avec celui qui découlait des anneaux de vertèbre chez les petits requins, mais semblait surestimé pour les grands requins. Les paramètres de croissance de von Bertalanffy découlant des données sur la taille à l'âge extraites des vertèbres étaient $L_{\infty} = 282$ cm FL, $K = 0.18$ et $t_0 = -1.35$ pour les mâles et $L_{\infty} = 310$ cm FL, $K = 0.13$ et $t_0 = -1.77$ pour les femelles. La croissance de l'espèce est plus rapide et sa longévité moindre que ce qui avait été signalé auparavant dans ces eaux.

RESUMEN

Las estimaciones de crecimiento y edad para los tiburones azules, *Prionace glauca*, se extrajeron de 411 vértebras centrales y 43 recuperaciones de marcas del Atlántico norte. Las vértebras de dos especímenes recapturados a los que se había inyectado oxytetraciclina respaldan la hipótesis de desarrollo anual, en primavera, de los anillos de crecimiento de en la parte central de las vértebras de los tiburones de hasta 192 cm de longitud a horquilla. Se atribuyó a los machos y a las hembras una edad de 16 y 15 años, respectivamente. Ambos sexos crecieron igual hasta la edad siete, momento en que la tasa de crecimiento descendió en los machos y se mantuvo constante en las hembras. Las tasas de crecimiento de los tiburones marcados y recapturados coinciden con las deducidas de los anillos vertebrales para los tiburones más pequeños, pero parecen presentar una sobreestimación en lo que se refiere a los tiburones más grandes. Los parámetros de crecimiento de von Bertalanffy que se extraen de los datos de longitud por clase de edad extraídos de las vértebras son $L_{\infty} = 282$

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cm FL; K = 0,18 y to = 1,35 para machos y L8 = 310 cm FL; K = 0,13 y to = -1,77 para hembras. La especie crece más rápidamente y tiene una esperanza de vida más corta que la registrada anteriormente en estas aguas.

KEYWORDS

Age determination, Growth curves, Life history, Longevity, Shark fisheries

1. INTRODUCTION

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). Although stock structure in this species remains uncertain, there is evidence to support a single North Atlantic stock. Tagging studies and catch records show that blue sharks exhibit extensive seasonal migrations, which regularly include trans-Atlantic movements (Stevens, 1976; Casey, 1982, 1985). Temporal and geographic patterns of size and sexual segregation have been described in this species (Casey, 1982). Pregnant females are rare in the western North Atlantic, which is dominated by juveniles of both sexes, adult males, and sub-adult females (Pratt, 1979; Casey, 1982). Catch records from the eastern North Atlantic are largely comprised of neonates and juveniles of both sexes and adult females (Aasen, 1966; Stevens, 1975, 1976; Connett, 1987; Silva et al., 1996).

Although subjected to a number of fisheries, the blue shark is primarily taken as bycatch in longline fisheries throughout the North Atlantic. Most blue sharks are discarded or finned due to the low palatability of the flesh (Castro et al., 1999). There is currently no comprehensive international reporting system for Atlantic shark catches and landings, but limited data are available for this species. Domestic longline fisheries in the western North Atlantic rarely land blue sharks, but it was estimated that annual dead discards ranged 7.0-29.3 thousand blue sharks (184.4-1136.3 MT) during the period 1987-1997 (Cramer, 1996; Cramer et al., 1997; Cramer and Adams, 1998). The major source of landings in U.S. Exclusive Economic Zone (EEZ) has been the recreational fishery. The U.S. National Marine Fisheries Service (NMFS) estimates that 10,461 and 4,265 blue sharks were landed by the recreational sector in 1996 and 1997, respectively (NMFS, 1999).

The extent to which the blue shark is exploited in the eastern North Atlantic is poorly understood. Although commercial and recreational sectors in several countries harvest, fin, or discard blue sharks, comprehensive catch data are lacking. France and Denmark have reported annual blue shark catches to FAO since 1978. While the latter only reports a few metric tons, landings in France peaked in 1994 at 358 MT (FAO, 1998). In many countries, the meat of the blue shark is consumed fresh, smoked, or dried salted, its hides are used for leather, fins are marketed for shark fin soup, and liver oil and fishmeal are produced as well (FAO, 1998).

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 (Hoenig and Gruber, 1990); stock size is closely linked to recruitment. Although the current Fishery Management Plan for Atlantic Tunas, Swordfish, and Sharks established limits on the U.S. commercial and recreational fisheries that impact blue sharks (NMFS, 1999), no international management is currently in place. Given the likelihood of a single North Atlantic stock, 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 as they form the basis for calculations of growth and mortality rates, age at maturity, age at

recruitment, and estimates of longevity.

Age and growth characteristics have been described for several species of elasmobranchs utilizing size-frequencies, captivity records, tag returns, tooth replacement rates, growth model parameters, and cyclical growth marks on spines and vertebrae. Age is difficult to validate for large elasmobranchs because of poor survivorship in captivity, their highly migratory nature, non-conformity to traditional fish ageing methods, and various sampling constraints. In his review of age and growth studies of elasmobranch species, Cailliet (1990) noted that age validation has been provided for only six species and *P. glauca* was not included.

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 the vertebral growth rings of juvenile blue sharks sampled in the eastern North Atlantic. Low sample sizes and inadequate size ranges, the lack of age validation, and possible inter-population growth differences 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 ring data, tag-recapture data, and length frequency data. In that study, vertebrae from oxytetracycline (OTC) injected recaptures 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, corroborative vertebral readings using a different vertebral processing technique, and more rigorous growth analyses.

2. MATERIALS AND METHODS

2.1 Vertebral Interpretation

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, N.C. and the Gulf of Maine (NE coast of the US). To adequately represent the entire size range of the species, small sharks were obtained from the eastern Atlantic via 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. The vertebrae were cleaned and 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), 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 pre-caudal length (PCL - tip of the snout to the pre-caudal pit, over the body; Kohler et al., 1995) were used. All lengths reported are in FL unless otherwise noted. TL can be converted to FL using the regression (Kohler et al., 1995):

$$FL = 0.8313 (TL) + 1.39 \quad N = 572 \quad r^2 = 0.99$$

PCL can be converted to FL using the regression (NMFS unpub. data³):

$$PCL = 0.9075 (FL) - 0.3956 \quad N = 106 \quad r^2 = 0.99$$

One vertebra from each sample was removed for processing. The centrum was sectioned using a Ray Tech Gem Saw with two diamond blades separated by a 0.6 mm spacer. Each centra was cut

³ 2001. NMFS, Apex Predators Program, 28 Tarzwell Dr., Narragansett, RI 02882. Unpublished data.

through the middle along the sagittal plane; the resulting bow-tie sections were stored in individual capsules in 70% ETOH. Each section was digitally photographed with a MTI CCD 72 video camera attached to a SZX9 Olympus stereo microscope using reflected light. All samples were photographed at a magnification of 4X. Band pairs (consisting of one opaque and one translucent band) were counted and measured from the images using Image Pro 4 software. 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 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 re-processing. Due to the different processing method, histological sections were not used for measurements.

The criteria for a band pair was based on the contouring of the corpus calcareum relative 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 vertebrae (Figure 1). Each layer was considered a temporal growth zone. The first opaque band distal to the focus was defined as the birth mark. A slight angle change in the corpus calcareum coincided with this mark. Additionally, the identity of the birth band was confirmed with back-calculation and comparison of the radius of this band with the radius of vertebrae from young of the year (YOY) and full term embryos.

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. Regressions were fit to the male and female 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, therefore the data were ln-transformed before linear regression. The Fraser-Lee equation of the ln-transformed data was derived for back calculation:

$$\ln(FLa) = b + (\ln[FLc] + b)(\ln radiusa) / (\ln radiusc) - 1$$

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

2.2 Validation

To evaluate the periodicity of band pair formation, vertebrae from oxytetracycline-injected (OTC) 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 frozen. Returned 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 to the number of years at liberty.

2.3 Data Analysis

Ageing bias and precision of bands counts were examined 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 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 fork 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 using the non-linear regression function in Statgraphics.

2.4 Tagging Data

From 1963 through 1999, members of the NMFS Cooperative Shark Tagging Program tagged 88,899 and recaptured 4,967 blue sharks. Only those sharks reliably measured by biologists or fishermen trained by NMFS biologists at both tagging and recapture were used in the analyses. All measurements were converted to FL 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 (a and b). The reference lengths, a and b , were chosen to lie within the range of tagged individuals. The form of the von Bertalanffy equation becomes:

$$\Delta L = \left[\frac{b g_a - a g_b}{g_a - g_b} - L_1 \right] \left[1 - \left(1 + \frac{g_a - g_b}{a - b} \right)^{\Delta T} \right]$$

The simplest model, a linear fit with minimal parameters (a and s) was used initially with additional parameters added to successively increase the model complexity. Significant improvement in the model results were determined using log likelihood ratio tests as per Francis (1988a). Bootstrapping was used to calculate the 95% confidence intervals for the final parameter estimates. The modeling and bootstrapping were carried out using a Solver based spreadsheet in MS Excel (C. Simpfendorfer, pers. comm.⁴). The value of t_0 cannot be estimated from tagging data alone, rather 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:

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

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 FL cm (Pratt, 1979) with $t=0$.

2.5 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. Taylor (1958) defined the life span of a teleost species as the time required to attain 95% of the L_{∞} using the equation:

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

⁴ 2000. Colin Simpfendorfer, Mote Marine Laboratory, 1600 City Island Park Sarasota, FL 33577. Unpublished .data.

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) calculation of >99% of L_{∞} using the equation:

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

3. RESULTS

3.1 Vertebral Interpretation

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

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

where $\ln(\text{FL}) = 0.89 * \ln(\text{VR}) + 3.10$ $r^2 = 0.97$, $n = 392$.

There was no significant difference between the sexes (ANCOVA, $p < 0.01$).

Confirmation of the birth band was made through comparison of the BR of all individuals, to the VR of YOY and late term embryos (Figure 2). The VR of seven late term embryos (36-43 cm FL; mean $\text{VR} \pm 95\% \text{ CI} = 2.04 \pm 0.25$) was slightly less than the BR value of the total sample (mean $\text{BR} \pm 95\% \text{ CI} = 2.70 \pm 0.03$; $N = 351$); the mean VR of 11 early YOY was slightly higher than the BR of the entire sample (49-58 cm FL; mean $\text{VR} \pm 95\% \text{ CI} = 2.97 \pm 0.18$) (Figure 2). The location of the birth ring between the VR of both the late term embryos and YOY indicates the birth ring was identified correctly.

3.2 Validation

OTC recaptures returned with vertebrae confirmed the accuracy 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 (Figure 3). In both cases the number of band pairs past the OTC mark coincides with the number predicted based on time at liberty. These results also support an annual spring deposition of growth zones within the vertebrae. Thus, the annual nature of the vertebrae was validated for blue sharks up to 4+ years of age. Past this age, bands were assumed to be annual based on a similar nature of band deposition.

Comparison of counts between two readers indicated no appreciable bias (Figure 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. Quality control was maintained by the reader periodically recounting earlier samples and cross-checking the readings.

Length-at-age data indicate that males and females grow at the same rate. The overlap in observed size at age data as well as the graphical representation of the VBGF curves indicate that there is little difference in growth for the sexes (Figure 5). The LOESS derived curves as well as the VBGF values indicate that females grow slower but to a larger overall size than males (Table 2, Figure 6); the LOESS curves clearly show a difference in growth starting at approximately 7 years of age (Figure 6), but this could be an artifact of low female sample size. Subsequent comparisons are for the sexes separate and combined for ease in comparison to previously published studies.

3.3 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. All data were used for the Francis (1988a) method (GROTAG).

The results of the likelihood ratio tests using GROTAG (Francis, 1988a) show that the more complex non-linear model with all six parameters included 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 (Figure 7). Von Bertalanffy estimates from the Gulland and Holt (1959) and GROTAG (Francis, 1988a) methods produced similar von Bertalanffy curves (Figure 8).

3.4 Longevity

The maximum age based on vertebral band pair counts was 16 and 15 years for males and females, respectively. This is likely to be an underestimate of longevity, given the fishing history. Using Taylor's (1958) method, 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.

4. DISCUSSION

Several methods have been employed to validate and/or verify 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 in oceanic species of 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 coastal carcharhinids: the lemon shark, the sandbar shark, and the Atlantic sharpnose shark. Although more than ten years have transpired since this review, validated growth curves for pelagic sharks are still lacking. In lamnids, direct validation of annual band deposition using OTC has been reported in a single species, the porbeagle shark, *Lamna nasus* (Natanson et al., in press). In coastal carcharhinids, age estimates from vertebral banding patterns have been recently reported for 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), the bronze whaler, *C. brachyurus* (Walter and Ebert, 1991), and the tiger shark, *Galeocerdo cuvier* (Natanson et al., 1999; Wintner and Dudley, 2000), but age interpretations were not validated and vertebral bands were assumed to be annual.

In the current study, we have validated annual band pair deposition in blue sharks up to 4+ years in age using vertebrae from OTC injected fish. These data show that band deposition occurs in the spring. This is further supported by the marginal increment analysis of Skomal (1990), which shows that one band pair is formed annually.

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). The blue shark, however, remains in a discrete temperature regime 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 periodic dives from the surface to depths of 200-600m (Carey and Scharold, 1990).

The ecology of this species may provide a more likely explanation of annulus formation. Kohler (1987) found a seasonal cycle of 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 utilize energy stores during this time for extensive north-south and transatlantic 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 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 (Figure 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. Females enter a distinct subadult phase (Pratt, 1979) at 145 cm FL and 2+ years of age, becoming fully mature by 5 years.

Previous estimates of age and growth of the blue shark in the Atlantic have utilized vertebral banding patterns with verification from the interpretation of length frequency and tagging data (Stevens, 1975; Silva et al., 1996; Henderson et al., 2001). The eastern Atlantic vertebral sample of Stevens (1975) was comprised largely females (89%), ranging from 34 cm to 227 cm FL. His use of whole silver stained centra coupled with the lack of maximum size fish allowed for the interpretation of only six annuli. Based solely on 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, the studies of Silva et al. (1996) and Henderson et al. (2001) investigated age and growth in this species with whole vertebrae from blue sharks sampled in the eastern North Atlantic. In the former study, vertebral samples from 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 (Figure 8a,b,c) despite the fact that we utilized similar criteria to those of Stevens (1975) for vertebral interpretation. This result is not surprising in light of the fact that these three studies share common methodologies 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 -184 cm FL. Due to the lack of samples from smaller fish, one study (Silva, 1996) included vertebral readings from full term embryos in the growth curve. It is well documented that embryonic growth is not comparable to post-natal growth (Casey et al., 1985; Pratt and Casey, 1990) and therefore embryos should not be included in a post-natal growth curve. The lack of the 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 sample 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, yet not necessarily accurate counts (Campana, 2001). Whole vertebrae simply do not allow for high band resolution in larger slow growing fish. Therefore, counts from whole vertebrae generally underestimate ages in larger individuals. The counts obtained in the three eastern Atlantic studies may be accurate because they are from small 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 due to the lack of small and large samples. 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 of the Pacific blue shark has been conducted based on 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 the current 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 here. 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 this study, the VBGF parameters of Tanaka et al. (1990) yield slower growth and 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 methodology. 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 the current study. It is difficult to ascertain whether inter-oceanic differences in growth are real or are an artifact of methodology. Although Tanaka et al. (1990) present data to support the latter within the Pacific, the much larger maximum size attained by this species in the Atlantic (Strasburg, 1958; Tanaka, 1984) cannot be overlooked relative to inter-oceanic growth differences.

Longevity estimates for the blue shark indicate that they may live for 26 years when Taylor's (1958) method was 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 based on 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 in the North Atlantic. Of the 4,967 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 former shark 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 of 1+ years of age which would correspond to a maximum age of 10+ years at recapture. The latter fish, 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 (Figure 5).

The occurrence of sexual differences in growth is well documented in elasmobranchs, with females usually growing larger. In the blue shark, there is little evidence that females attain a larger size. Maximum size male and female specimens in this study, 284 cm FL and 312 cm FL, respectively, represent 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 while 288 cm FL and 279 cm FL females are 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 oceans (Suda, 1953; Tucker and Newnham, 1957; Aasen, 1966; McKenzie and Tibbo, 1964; Dragonik and Pelzarski, 1983; Stevens, 1984). In the Pacific, the maximum size of 254 cm FL has been reported (Strasberg, 1958; Cailliet et al., 1983). 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, and/or avoid longline and sport fishing gear. In this study the VBGF parameters (Table 5) and our largest sample show that females 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 utilizing 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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Table 1. Tag/recapture data for the OTC and known age recaptures with vertebrae.
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)	# of Bands after OTC Band
<i>OTC</i>	116452	F	116		06/18/87	12/21/88	1.5	33	1.20
	107725	M	172	162* 192	05/09/85	1/16/86	0.7	29	0.68

*Calculated from PCL.

Table 2. VBGF parameters and 95% confidence intervals calculated by using vertebral and tag/recapture methods.

<i>Method</i>		L_{∞}	K	t_0	N
Vertebral	Combined	285.4	0.17	-1.41	410
	CI	+7.18	0.01	0.20	
	Male	282.3	0.18	-1.35	287
	CI	+7.15	0.02	0.23	
	Female	286.8	0.16	-1.56	118
	CI	+30.2	0.04	0.46	
GROTAG	Combined	302.4	0.23	-0.69	43
Gulland Holt (1959)	Combined	331.7	0.19	-0.77	18
	CI	+80	0.12		
Stevens (1975)		353*	0.11	-1.04	82
Cailliet et al. (1983)		222*	0.22	-0.80	130

*Converted to FL

Table 3. Log-likelihood function values and parameter estimates for three growth models fitted to blue shark tagging data using GROTAG (Francis 1988a). For a significant ($P < 0.05$) improvement in fit, the introduction of one extra parameter must increase χ^2 by at least 1.92 (Francis 1988a)* indicates fixed parameters. Model 3 shows 95% confidence intervals.

Parameter	Symbol (unit)	Model		
		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)
	s (cm)	1.06	1.37	5.39 (2.25-7.40)
Measurement error	m (cm)	0*	0*	-2.03 (-5.37-2.10)
	p	0.83	0.28	0.18
Outliers				

Table 4. Size at age for the blue shark, *Prionace glauca*, calculated from von Bertalanffy equations based on tag/recapture and vertebral methods.

Age	Vertebral Method	Gulland Method
0	60.7	45
1	95.8	94
2	125.3	135
3	150.3	169
4	171.3	197
5	189.1	220
6	204.1	240
7	216.8	255
8	227.5	269
9	236.5	
10	244.1	
11	250.5	
12	256.0	
13	260.5	
14	264.4	
15	267.7	
16	270.4	

Table 5. VGBF parameters and maximum age derived from vertebral bands in the blue shark, *Prionace glauca*.

Region	Sex	N	Lmax	K	to	Maximum Age	Authors
North Atlantic	Male	287	282.	0.18	-	16	Current study
Eastern North Atlantic	Male	112	3	0.18	1.35	7	Silva (1996)
Eastern North Pacific	Male	38	309.	0.18	-	9	Cailliet et al. (1983)
Western North Pacific	Male	43	0	0.10	1.07	7	Tanaka et al. (1990)
North Pacific		148	246.	0.13	-	10	Nakano (1994)
			7		1.11		
			308.		-		
			1		1.38		
			319.		-		
			5		0.76		
North Atlantic	Female	118	286.	0.16	-	13	Current study
Eastern North Atlantic	Female	82	8	0.11	1.56	6	Stevens (1975)
Eastern North Atlantic	Female	170	353.	0.00	-	7	Silva (1996)
Western North Pacific	Female	88	0	1	1.04	9	Cailliet et al. (1983)
North Pacific	Female	152	382.	0.25	-	8	Tanaka et al. (1990)
		123	0	0.16	1.11	10	Nakano (1994)
			202.	0.14	-		
			6		0.80		
			254.		-		
			1		1.01		
			268.		-		
			9		0.85		
North Atlantic	Combine	410	285.	0.17	-	16	Current study
Eastern North Atlantic	d	336	4	0.14	1.41	7	Silva (1996)
Eastern North Atlantic	Combine	159	284.	0.12	-	6	Henderson et al. (2001)
Western North Pacific	d	130	0	0.22	1.08	9	Cailliet et al. (1983)
North Pacific	Combine		314.		-		
	d		4		1.33		
	Combine		222.		-		
	d		1		0.80		

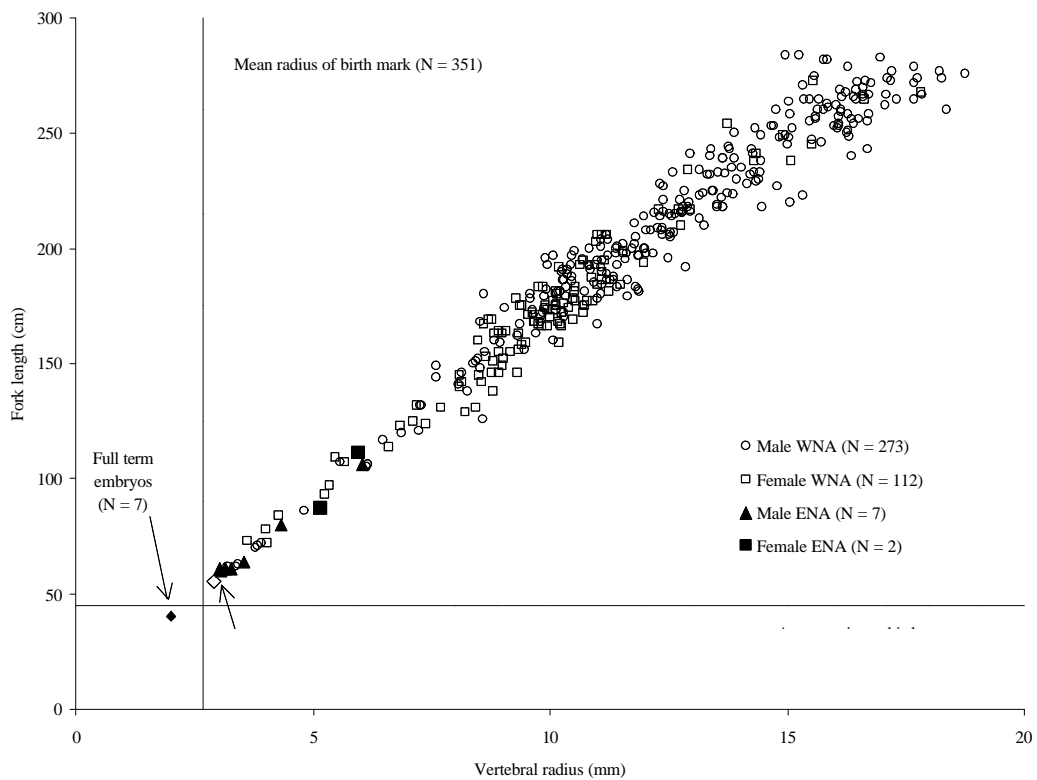
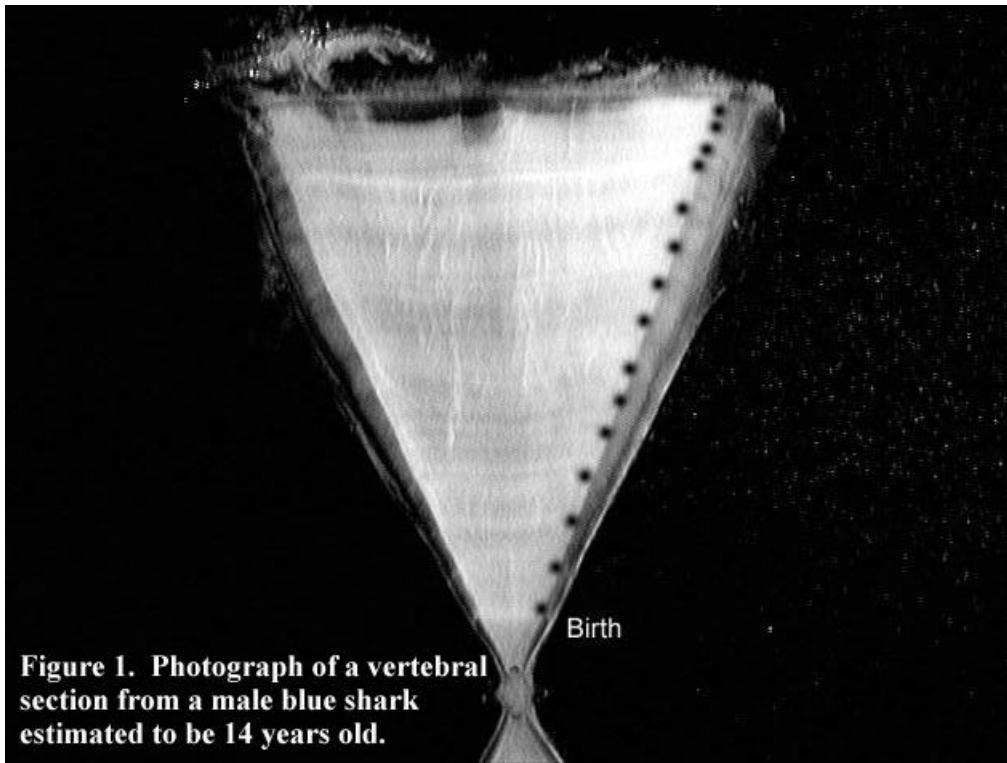


Figure 2. Relationship between vertebral radius and fork length for male and female blue sharks. The open triangle is the mean vertebral radius of the smallest free-living specimens (n=11), the hexagram is the mean vertebral radius of the largest embryos (n=7). The horizontal line represents the size at birth and the vertical line represents the mean radius of the birth mark.

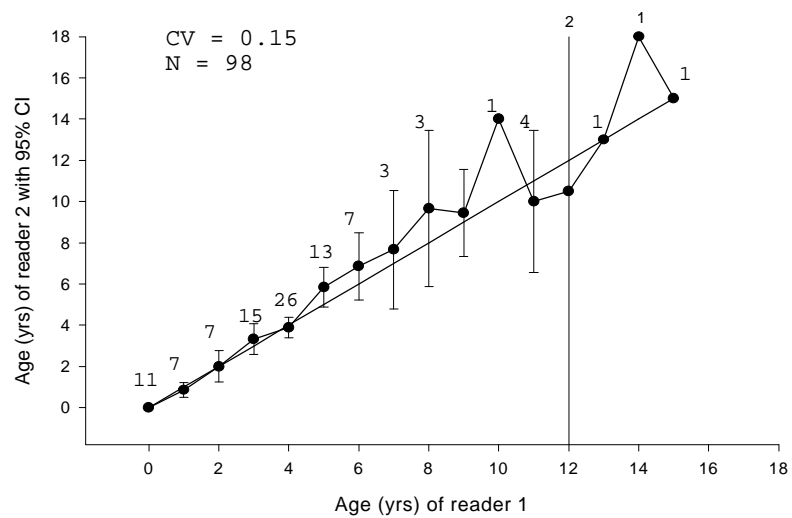
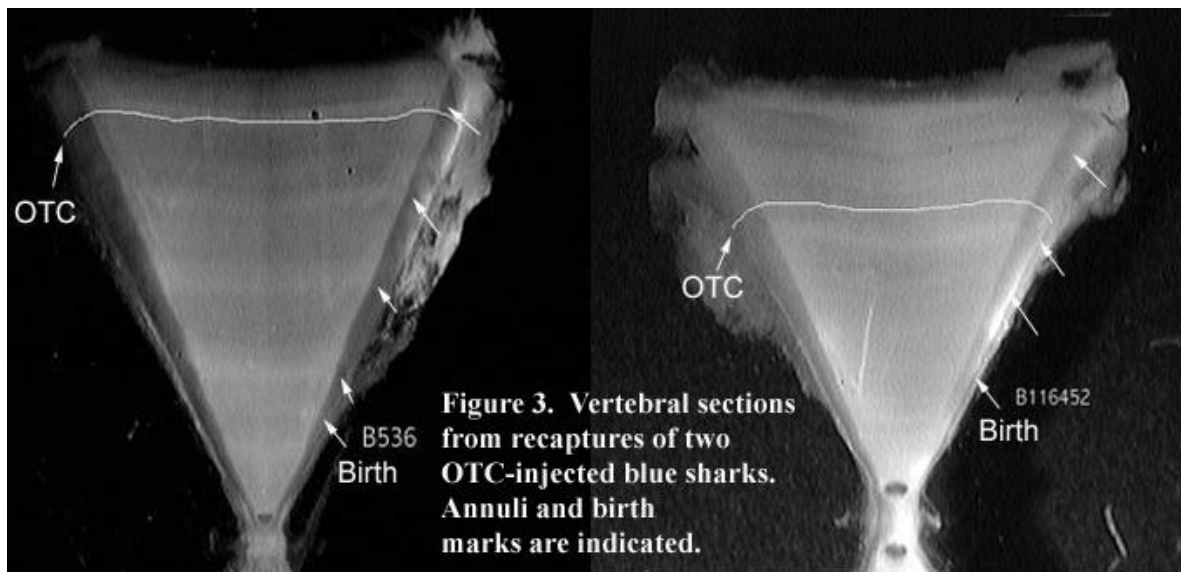


Figure 4. Age bias graph for pair-wise comparison of 98 blue-shark vertebral counts from two independent age readers. Each error bar represents the 95% confidence interval for the mean age assigned by reader 2 to all fish assigned a given age by the reader 1. The one to one equivalence line is also presented

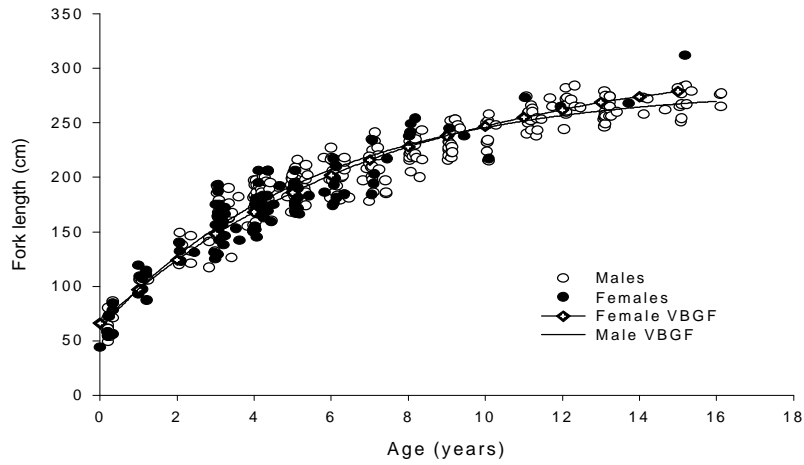


Figure 5. Blue shark growth data based on vertebral band counts. VBGF curves have been fitted to the data by sex. Open circles are males, closed circles are females.

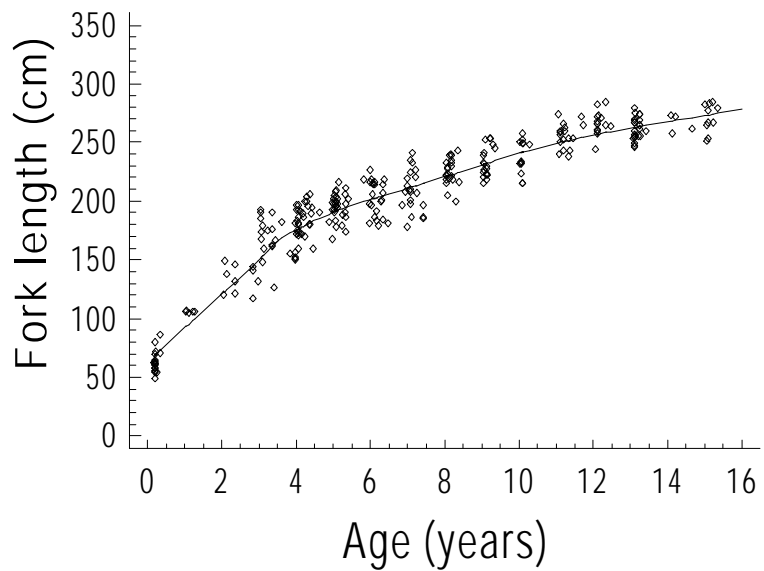
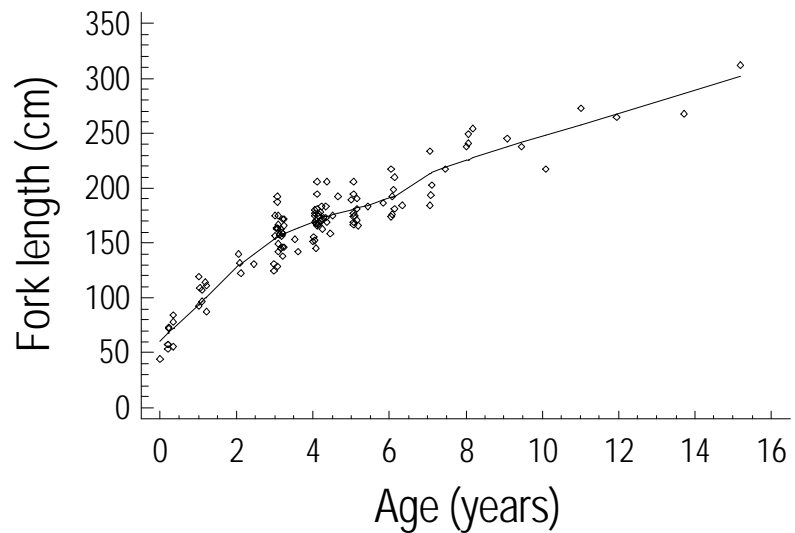


Figure 6. Blue shark growth data based on vertebral band counts. LOESS curves have been fitted to the data by sex: A) males and B) females



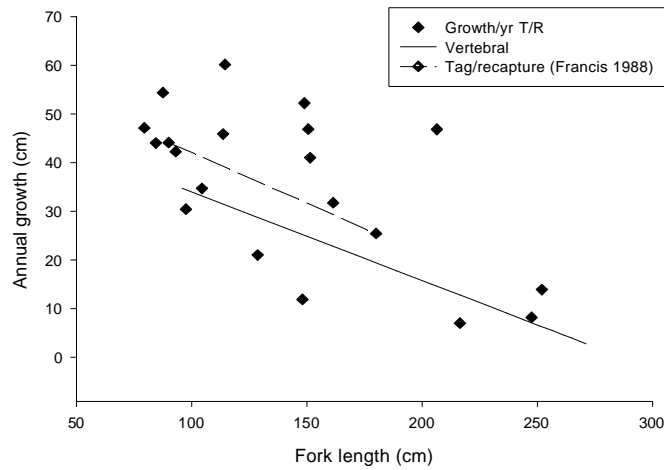


Figure 7. Comparison of the annual growth rate of the blue shark using multiple aging methods.

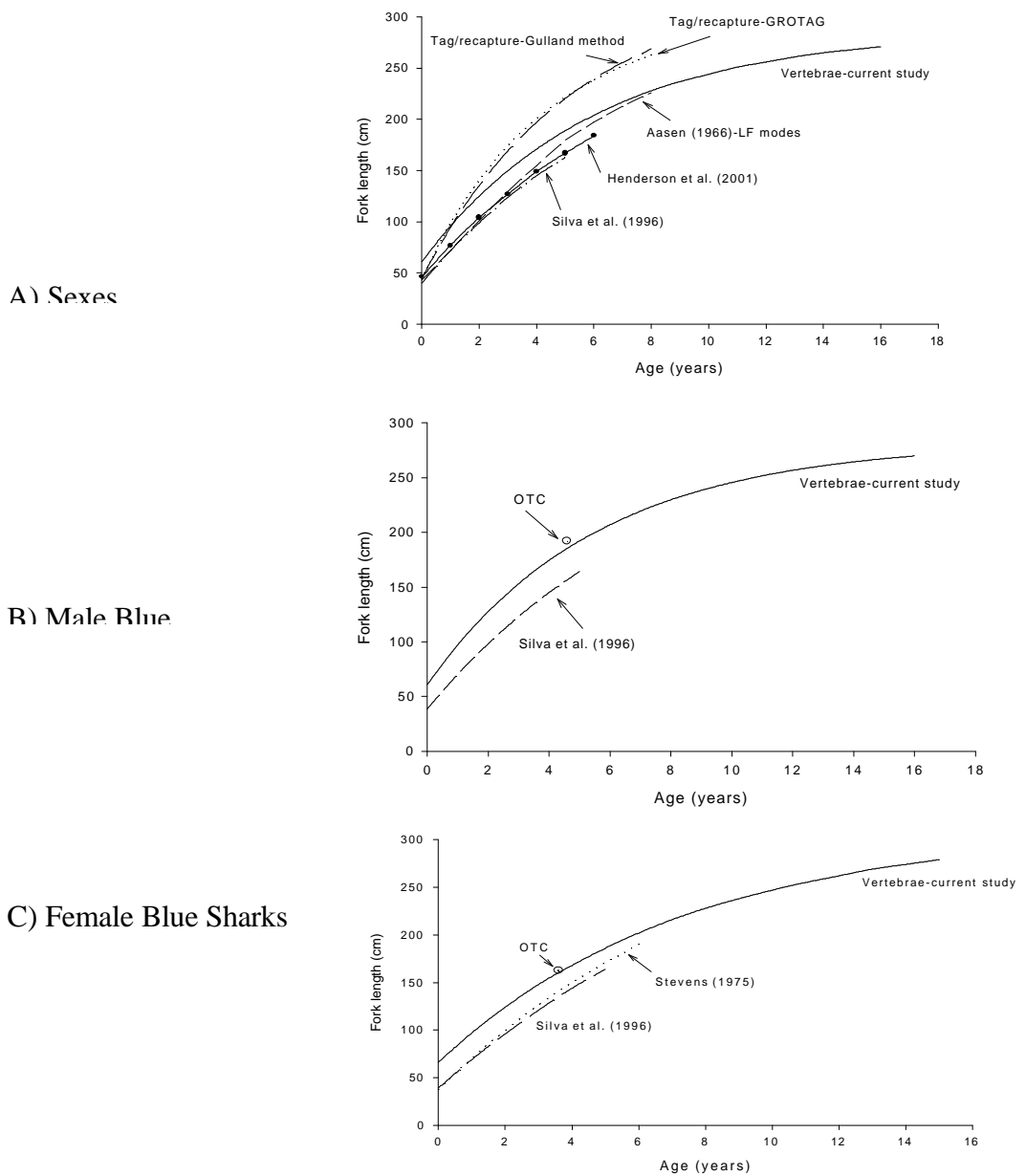


Figure 8. Von Bertalanffy growth curves generated from vertebral and recapture data for A) sexes combined, B) male and C) female blue sharks, as compared to OTC recaptures. Included for comparison are the von Bertalanffy growth curves of other North Atlantic studies.