

Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean

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Abstract Age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, derived from vertebral centra of 258 specimens (118 males, 140 females), ranging in size from 64 to 340 cm fork length (FL) were compared with data from 22 tag-recaptured individuals (74–193 cm FL) and length-frequency data from 1822 individuals (1035 males, 787 females; 65–215 cm FL). Annual band-pair deposition, confirmed by a concurrent bomb radiocarbon validation study, was used as the basis for band interpretation. Validation was further confirmed with a tetracycline-injected male shortfin mako recaptured after being at liberty off South Africa for 1 year and aged at 18 years. Growth rates from tag-recapture analysis (GROTAG) were higher than those derived from vertebral annuli and were only available from sharks up to 193 cm FL at recapture. Modal length-frequency data were used to verify the first four age classes.

Growth curves were fit using both von Bertalanffy and Gompertz models. The 3-parameter version of the von Bertalanffy growth function produced the most biologically reasonable values for males, based on observed data ($L_{\infty} = 253$ cm FL, $K = 0.125$ year $^{-1}$ (estimated longevity = 21 year), and $L_0 = 72$ cm). The 3-parameter version of the Gompertz growth function produced the most biologically reasonable estimates, for females ($L_{\infty} = 366$ cm FL, $K = 0.087$ year $^{-1}$ (estimated longevity = 38 year) and $L_0 = 88$ cm. Males and females were aged to 29 (260 cm FL) and 32 years (335 cm FL), respectively. Both sexes grew similarly to age 11 (207 cm FL, 212 cm FL for males and females, respectively) when the curve leveled in males and continued to rise in females. Age at 50% maturity was estimated at 8 years for males (185 cm FL) and 18 years for females (275 cm FL). The species grows slower, matures later and has a longer life span than previously reported in North Atlantic waters.

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Introduction

Age and growth studies of lamnid sharks have often been confounded by debate over the

periodicity of band-pair formation. Parker and Stott (1965) first suggested that two growth band pairs formed each year (biannual band-pair deposition) in their study of the basking shark, *Cetorhinus maximus*. Pratt and Casey (1983) assumed the same band deposition pattern for the shortfin mako based on consistency with length-frequency and tag/recapture data. Branstetter and Musick (1994) also suggested biannual band-pair deposition for the sand tiger shark, *Carcharias taurus*, based on marginal increment analysis (MIA) and examination of aquarium-reared sharks. Additionally, Chen et al. (1990) proposed biannual band-pair periodicity for the scalloped hammerhead, *Sphyrna lewini*, which was further extended by Anislado-Tolentino and Robinson-Mendoza (2001).

For each species where biannual periodicity has been proposed, an alternate study was performed where annual periodicity was assumed or biannual periodicity refuted. Wintner (unpublished data)¹ is re-aging the basking shark assuming annual periodicity. Goldman et al. (this volume) re-evaluated the age of the sand tiger shark. Using relative MIA and results from two oxytetracycline (OTC)-injected captive sharks they determined that the band pairs are deposited annually. Schwartz (1983) used marginal increments to support annual periodicity in the scalloped hammerhead and Branstetter's (1987) marginal increment data on this species, though limited, also supported annual band-pair deposition. Additionally, while Cailliet et al. (1985) assumed annual periodicity for the white shark, *Carcharodon carcharias* in the Pacific, Wintner and Cliff (1999) could not conclusively validate band periodicity using MIA in this species off the coast of South Africa, but one OTC-injected recapture suggested annual deposition.

Data from Natanson (2001) indicate that Pratt and Casey (1983) overestimated the number of band pairs on vertebral centra of small sharks. Since this was the portion of the growth curve used for comparison with the other methods, the decision to divide their counts in half to make the vertebral growth coincide with the other methods

was unfounded and resulted in vastly overestimating the growth rate in larger fish. Bomb radiocarbon analysis was used to examine the periodicity of the bands on the shortfin mako from the North Atlantic Ocean (Ardizzone et al. this volume; Campana et al. 2002). These data clearly demonstrate that a single band pair per year is formed in sharks with between two and 31 band pairs and that the two band-pair per-year-hypothesis for this species is incorrect.

Annual band periodicity has been validated for the porbeagle, *Lamna nasus*, using OTC, known-age fish and bomb radiocarbon dating (Campana et al. 2002; Natanson et al. 2002). Recently, four studies have been conducted on the age of the shortfin mako in the Pacific, Bishop (2004) assumed annual periodicity based on Cailliet et al. (1983b) and Campana et al. (2002). Using whole vertebrae, annual band-pair deposition was supported by MIA for shortfin makos off Mexico up to approximately 7 years of age (Ribot-Carballal et al. 2005), and in the northwestern Pacific by Hsu (2003), though the results of this latter study were not statistically evaluated. Chan (2001) assumed biannual deposition following Pratt and Casey (1983). Three of the four studies showed distinct differences in growth between males and females (Bishop 2004; Chan 2001; Hsu 2003); the one study that did not (Ribot-Carballal et al. 2005), had very few samples from animals that were larger than the size at male maturity, the point at which the growth begins to diverge between the sexes.

In view of these recent validation studies that contradict the biannual band-pair deposition hypothesis, and the necessity of age information for management, a revision of the age estimates for the shortfin mako from the North Atlantic Ocean using updated techniques and increased sample sizes was undertaken.

Materials and methods

Vertebrae were obtained from shortfin makos caught on research cruises, commercial and recreational fishing vessels, and at sport fishing tournaments between 1962 and 2004. Primary sampling took place between Cape Hatteras, N.C.

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and the Gulf of Maine (NE coast of the US), although sampling extended south into the Gulf of Mexico. Vertebrae between the number 15 and 20 were excised from each specimen, except on fish that were commercially dressed, in which samples were obtained closer to the head. The vertebrae were trimmed of excess tissue and stored either frozen or preserved in 10% buffered Formalin or 70% ethanol (ETOH). To determine if the number of growth bands differed along the vertebral column, whole columns from four animals (166–208 cm FL) were removed.

Samples that had measured fork length (FL—tip of the snout to the fork in the tail, over the body-OTB), straight line FL (FL_{SL}), 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—OTB), or total weight (WT) were used. All lengths reported are in OTB FL unless otherwise noted. Conversions used in this study were:

$$\begin{aligned} FL &= 0.9286 (TL) - 1.7101 N = 199r^2 \\ &= 0.99 \text{ (Kohler et al. 1996)} \end{aligned} \quad (1)$$

$$\begin{aligned} WT &= 5.2432 * 10^{-6} * FL^{3.1407} N = 2081r^2 \\ &= 0.96 \text{ (Kohler et al. 1996)} \end{aligned} \quad (2)$$

$$\begin{aligned} OTBFL &= 1.03 (FL_{SL}) - 0.79 N = 30r^2 \\ &= 0.99 \text{ (Bishop et al. 2006)} \end{aligned} \quad (3)$$

in which weights and lengths are expressed in metric units (kg and cm).

One vertebra from each sample and every fifth vertebrae from the whole columns were removed for processing. The centra were sectioned using a Ray Tech Gem Saw² with two diamond blades separated by a 0.6 mm spacer. Each centrum was sectioned through the middle along the sagittal plane, and the resulting bow-tie sections were stored in individual capsules in 70% ETOH. Each section was digitally photographed with an MTI CCD 72 video camera attached to a SZX9 Olympus stereomicroscope using reflected light.

² Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

Band pairs (consisting of one opaque and one translucent band) were counted and measured on 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 intermedia along the same diagonal as the band measurements.

The relationship between FL and VR was used to determine if the vertebrae grew relative to FL and were therefore suitable as an aging structure. Potential differences in vertebral growth between the sexes were tested using the linear interaction model of Neter and Wasserman (1974) to test for statistically significant differences between the sexes.

Vertebral centrum interpretation

Entire vertebral columns were collected from sharks of various lengths to examine the band-pair counts along the column. Band-pair count was plotted against location along the vertebral column for every fifth vertebrae to determine if the counts changed based on location along the vertebral column. Presuming the counts remained the same any vertebrae obtained could then be used for aging.

A band-pair consisted of one opaque and one translucent band. The criteria for designating a band pair were based on broad opaque and translucent bands, each of which was composed of layers of distinct thinner rings (sensu Cailliet et al. 1983a; Martin and Cailliet 1988). A solid broad opaque band through the intermedia and continuing to the corpus calcareum as a translucent band constituted a growth band.

Twenty-one vertebrae from this study had previously been used in bomb carbon age validation studies (Campana et al. 2002; Ardizzone et al. *this volume*). Thus, these samples were considered to be of known age and the criteria for the band pairs were based on the bands identified in sections from these samples.

Validation of annual band periodicity was also obtained through recapture of an OTC-injected

and tagged individual. Shortfin makos of various lengths have been tagged and injected with 25 mg OTC/kg of OTC in both the North Atlantic Ocean and off the east coast of South Africa. A returned vertebra from a recaptured shark from South Africa was examined with reflected UV light for the OTC mark. The number of band pairs distal to the mark was then compared with the number of years at liberty.

The first opaque band distal to the focus was defined as the birth band (BB). A slight angle change in the corpus calcareum coincided with this band. Additionally, the identity of the birth band was confirmed with back-calculation and comparison of the birth band with the vertebral radius from young of the year (YOY).

Data analysis

To ensure that vertebral counts were consistent with those of researchers aging this species in other regions, a three-laboratory intercalibration study was done among researchers at the NMFS Narragansett, RI Laboratory, Moss Landing Marine Laboratories (MLML), Moss Landing, CA and The University of Auckland (UA), Auckland, New Zealand. Digital images of 53 vertebrae were exchanged with MLML and 50 with UA; criteria were discussed and readers counted the bands without prior knowledge the FL of the samples. All counts were made using digital images although the actual samples were available if necessary. Aging bias and precision of bands counts were examined using age-bias plots and the coefficient of variation (Campana et al. 1995).

Once the criteria for the bands were determined using the intercalibration, the first author counted the entire sample twice. Pairwise comparisons of precision and bias were conducted on the two counts. Samples that still did not agree were recounted and then sent to the other laboratories for confirmation of the band number, if a consensus was not reached at that time the sample was discarded.

Von Bertalanffy growth functions (VBGF) were fit to length-at-age data using the original equation of von Bertalanffy (1938) with size at birth L_0 rather than t_0 :

$$L(t) = L_\infty - (L_\infty - L_0)\exp^{-kt} \quad (4)$$

where $L(t)$ = predicted length at time t ;

L_∞ = mean asymptotic fork length;

k = a rate parameter (year^{-1}); and

L_0 = fork length at birth.

Three variations of the model were used: 3-parameter calculation estimated L_∞ , k and L_0 , 2-parameter method estimated L_∞ and k and incorporated a set $L_0 = 70$ cm FL (H. Mollet unpublished data³), and a 1-parameter method estimated k with observed values for both $L_0 = 70$ cm and $L_\infty = 338.85$ and 267.7 cm females and males, respectively. L_∞ was estimated by taking the mean FL of the three largest specimens from each sex in our sample. These values were considered justified because our sample included all of the largest confirmed measured shortfin makos measured in the sampling area in the past 40 years (N. Kohler unpublished data⁴).

As an alternative to the VBGF analysis, we also used the Gompertz growth function (GGF) as described in Ricker (1979):

$$L(t) = L_0 e^{G(1-e^{(-kt)})} \quad (5)$$

where:

$L_\infty = L_0 e^G$ is the mean maximum FL ($t = \infty$);

k (=g in Ricker 1979) is a rate constant (year^{-1}),

and

L_0 = fork length at birth.

Three variations of this model were also fit to the data as above with either unconstrained parameters and with certain set parameters using the same values as with the VBGF.

All of the growth equations were fit to the length and vertebral band count data using non-linear regression in Statgraphics (Manugistics)[®].² Counts of vertebral band pairs were adjusted for the date of capture assuming a theoretical birthday of 1 March based on the beginning of the estimated period of parturition from Mollet et al. (2000). Thus a specimen with three complete bands caught

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6 months after 1 March would be assigned an age of 3.5 years.

Variable band-pair deposition

Additional growth curves were generated using the assumption that individuals less than or equal to 160 cm FL deposited two band pairs per year and greater than 160 cm FL deposited one band pair per year. Data were sorted based on size and an average band count was calculated for sharks between 150 and 160 cm FL, which was 5 for males and 6 for females. For specimens less than or equal to 160 cm FL, the band count was divided by two to obtain an age estimate. In sharks greater than 160 cm FL, the average band count calculated for the 150–160 cm grouping was subtracted from the total count and the average age of the 150–160 grouping was added to the band count. Thus a 241 cm FL male with a band count of 15 would have an age of 12.5. These data were then used to calculate growth curves using the methods detailed above.

Length-frequency analysis

Length-frequency data were obtained from sharks caught by commercial and recreational fishermen and by biologists operating along the US Atlantic Coast primarily between the Gulf of Maine and Florida Keys between 1961 and 2004. The data set was examined in two ways: combined for all years; and for 20 year groupings based on approximate 20 year generation times: 1961–1980 and 1981–2004, to determine if there were changes over time. Monthly length-frequency histograms separated by sex were initially produced in addition to one with sexes combined. Histograms were plotted in 5-cm intervals using the above three scenarios. The months of June, July and August had the largest samples and were used as comparison to follow the first four age classes.

Tagging data

From 1963 through 2003, members of the NMFS Cooperative Shark Tagging Program tagged 6334 and recaptured 757 shortfin makos. Only those sharks reliably measured by biologists or fishermen

trained by NMFS biologists at both tagging and recapture were used in the analyses.

The Gulland and Holt (1959), Fabens (1965), and Francis (1988a) models were used to generate VBGFs from the tag–recapture data. The Gulland and Holt (1959) model uses graphical interpretation of the recapture data to produce estimates of L_{∞} and k . Specifically, annualized growth rate (cm/year) was plotted against average FL (cm) between tagging and recapture to calculate linear regression coefficients.

$$\frac{d[FL](t)}{dt} = a + b[FL] = k[FL]_{\infty} - k[FL] \quad (6)$$

is the Gulland and Holt (1959) equation where: $\frac{d[FL](t)}{dt}$ is the first derivative of FL as a function of time, i.e. annualized growth rate, $b = -k$ is the slope, $a = k[FL]_{\infty}$ is the growth rate at size 0 (y-axis intercept), and $[FL]_{\infty} = -a/b$ (x-axis intercept) = a/k is the mean maximum size.

$$[FL]_{\text{END}} = [FL]_{\text{INI}} + ([FL]_{\infty} - [FL]_{\text{INI}})(1 - e^{-kT}) \quad (7)$$

is the Fabens (1965) equation where: T is the time between two consecutive measurements $[FL]_{\text{INI}}$ and $[FL]_{\text{END}}$, and the parameters $[FL]_{\infty}$ and k are the same as in the Gulland and Holt (1959) equation. Only sharks at liberty for at least 0.9 years were included in these analyses.

The Francis (1988a) model (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:

$$\Delta L = \left[\beta g_{\alpha} - \alpha g_{\beta} g_{\alpha} - g_{\beta} - L_1 \right] \left[1 - (1 + g_{\alpha} - g_{\beta} \alpha - \beta)^{\Delta T} \right] \quad (8)$$

The simplest model, a linear fit with minimal parameters (α and s) was used initially with additional parameters added to successively increase the model complexity. Significant

improvement in the model results was 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 the Solver add-in in Microsoft Excel® (C. Simpfendorfer personal communication⁵).

Longevity

Three methods were used to estimate 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 due to a decrease in the largest sizes. Taylor (1958) defined the life span of a teleost species as the time required to attain 95% of L_∞ . The estimated age at 95% of L_∞ (= longevity in years) was calculated by solving the VBGF and Gompertz growth functions for t and replacing $L_{(t)}$ with 0.95 L_∞ . For the VBGF we obtained:

$$\text{Longevity} = (1/k) \ln \left[\frac{(L_\infty - L_0)}{L_\infty(1-x)} \right] \quad (9)$$

and for the Gompertz growth curves we obtained:

$$\text{Longevity} = (1/k) \ln \left[\frac{\ln(L_0/L_\infty)}{\ln(x)} \right] \quad (10)$$

with $x = L(t)/L_\infty = 0.95$.

Data from recaptured shortfin makos at liberty for the longest time period in the NMFS Cooperative Shark Tagging Program were tabulated. Ages at tagging were assigned to these fish based on size at tagging, time at liberty was then added to estimate longevity.

Results

Vertebral samples from 290 shortfin makos (64–340 cm) were processed. Additionally, vertebrae from three mid-term embryos ranging in

size from 42.5 to 44.7 cm were processed. Fish with vertebrae taken from the head region, with OTB FL calculated from other measurements, or of unknown sex were not included in the FL/VR analysis reducing the sample size to 236 (108 males, 128 females).

Vertebral centrum interpretation

The FL-VR data was log-transformed and fit with a linear regression (Fig. 1). There was no significant difference between the sexes for intercept ($P = 0.075$) or slope ($P = 0.051$). Therefore, we calculated the power regression for sexes combined. The back-transformed power regression was:

$$\text{FL} = 18.53 \text{ VR}^{0.8927} r^2 = 0.983, n = 236.$$

Examination of the four whole columns revealed that although bands were more difficult to count on smaller vertebrae, counts between vertebrae along the column never differed by more than one. This indicated that vertebrae collected from all regions along the column could be used for counts, though not for band measurements.

Shortfin mako vertebrae did not show consistent pre-birth marks; thus, the first distinct opaque band was defined as the birth band. The

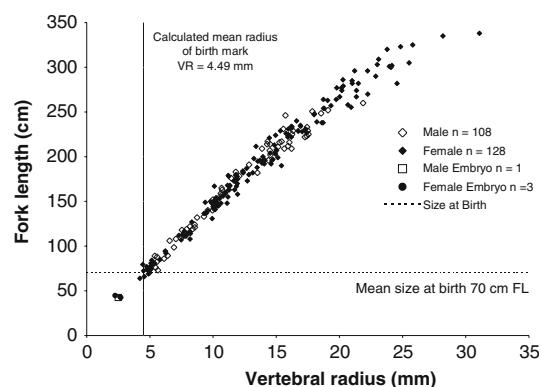


Fig. 1 Relationship between vertebral radius and fork length for male and female shortfin makos. The horizontal dotted line represents the size at birth and the vertical dotted line represents the mean radius of the birth mark

⁵ Colin Simpfendorfer. Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577

location of the birth band (BB) coincided with a slight change in the angle of the corpus calcareum (Fig. 2). The mean BB value of the total sample (mean BB ± 95% CI = 4.49 mm ± 0.04 mm; N = 250) was lower than the mean vertebral radius (VR) of 16 YOY (64–79.5 cm; mean VR ± 95% CI = 4.89 mm ± 0.19 mm) and higher than the mean VR of three mid-term embryos (42.5–44.7 cm; mean VR ± 95% CI = 2.52 mm ± 0.32 mm) (Fig. 1). The location of the BB between the VR of the mid-term embryos and YOY indicates the birth band was identified correctly.

Vertebrae from one OTC-injected shark were returned after 1.04 years at liberty. This shark came from the east coast of South Africa; the estimated size at tagging (212 cm pre-caudal length) was the same as the measured size at recapture (240.7 cm FL OTB) thus the shark showed no growth. The vertebra from this specimen had a distinct OTC mark and one full band pair (the expected number of growth bands after 1 year at liberty) had been deposited between the time of tagging and recapture (Fig. 3). This mature male was aged at 18 years at recapture, which confirms annulus formation at this size and agrees with estimates from bomb radiocarbon dating.

Data analysis

Comparison of counts between readers at the different laboratories indicated that all readers were identifying the same bands. The coefficient of variation between NMFS and MLML (n = 53) varied about a mean of 10.8%, while those between NMFS and the University of Auckland (n = 50) varied about 9.0%. Age bias plots generated for both studies showed variation around the 1:1 plot but no systematic bias.

Comparison of the first and second counts of the first author also indicated no systematic bias (Fig. 4). The individual coefficients of variation fluctuated around the mean at 3.9% and the APE and D were 2.8%. This level of precision was much lower than for the porbeagle (15%) (Natanson et al. 2002) and was thus considered acceptable; and the second count was used for those counts that differed by one band (64%). A third count was completed on those that differed by two or more bands, if the third count did not agree with either of the first two, the vertebrae were sent to the other labs for confirmation and discarded if no consensus was reached (3%). Quality control was maintained by periodically recounting earlier samples and cross-checking the readings. Eighteen additional samples were discarded due to questionable length

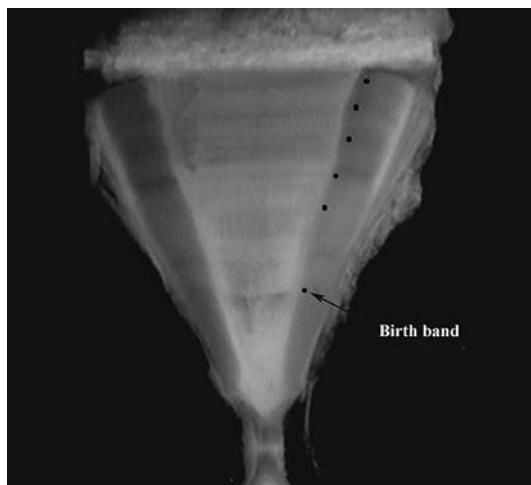


Fig. 2 Photograph of a vertebral section from a 151 cm fork length (FL) female shortfin mako estimated to be 5 years old. The birth band (BB) is indicated and band pairs are marked with a dark circle. Vertebral radius = 10.2 mm

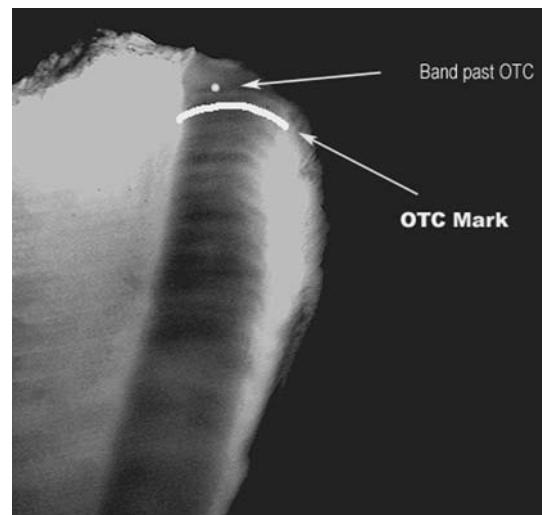


Fig. 3 Vertebra from an oxytetracycline (OTC) injected 240.7 cm 18-year-old male shortfin mako showing location of the OTC mark. Magnification = 8×

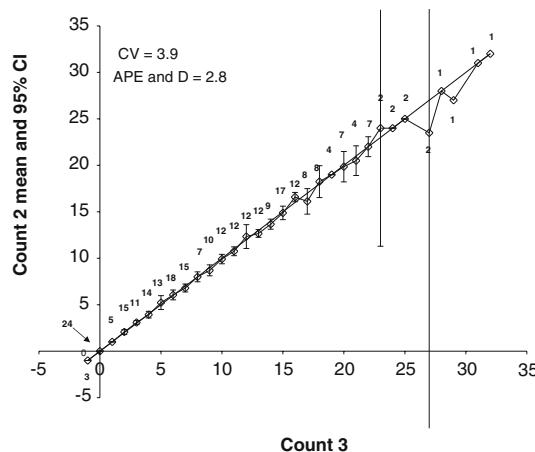


Fig. 4 Age bias graph for pair-wise comparison of 290 shortfin mako vertebral counts from two independent age readings by the first author. Each error bar represents the 95% confidence interval for the mean age assigned in reading 2 to all fish assigned a given age in reading 1. The one to one equivalence line is also presented

data or poor sectioning, the remaining 264 (118 male, 140 female and 6 of unknown sex) were used for the age analyses.

All the growth curves fit the data over the observed size ranges (Fig. 5a, b). However, comparison of the estimates from the VBGF and GGF parameters showed that the VBGF 3-parameter function provided the most reasonable estimates of maximum size and size at birth for males, while the GGF 3-parameter provided the most reasonable estimates of the parameters for females based on observed values of size at birth and maximum size (Table 1, Fig. 6). For females, estimates of maximum size and size at birth from the VBGF were substantially higher than observed values. Additionally, the low K estimates resulted in high longevity values, while the GGF predicted lower estimates of maximum size and longevity, closer to observed values. Size at birth and maximum size estimated by the 3-parameter GGF, while slightly high, were more reasonable than those estimated using the other methods. Additionally, longevity estimated using the 3-parameter GGF was consistent with the actual aged values. The largest female in our sample (366.2 cm FL) was estimated to be 20 years, which is clearly an underestimation. In addition, the shark was not measured by the authors and

the length could not be confirmed, thus this data-point was not included in the calculations (Fig. 6).

In contrast, the growth for males was better represented by the VBGF, as the GGF predicted lower values for maximum size and longevity and a higher size at birth (Table 1, Fig. 6). The L_{∞} estimated for the males by all of the methods was lower than the largest known male, thus underestimating longevity. The 3-parameter VBGF fit the male data well with the exception of the largest male shark (289 cm) collected from the Gulf of Mexico (Fig. 6). The age estimate for this shark seems to fit better within data from the females (Fig. 6). This fish was not measured by us and the length is unconfirmed, thus it was not included in calculations. The data from the OTC-injected male shark fit well on the growth curve.

Length-at-age data indicate that males and females grow at similar rates until approximately 11 years (207–212 cm). After this point, which is close to the length-at-maturity of males, there is a dramatic difference between the sexes, as indicated by the lack of overlap in observed size at age data (Fig. 6). Males growth starts to level out after the size at 50% maturity (185 cm FL), whereas growth of females continues to rise. Subsequent comparisons are for the sexes separate.

Variable band-pair deposition

Growth functions for the variable band deposition scenario produced lower values of L_{∞} and higher values of K than those for annual band deposition alone, showing the faster initial growth as would be expected assuming two bands per year during a portion of the lifetime (Table 1). Corresponding estimates of longevity, and size at maturity, for both sexes, were lower than those derived from annual band deposition, yet higher than the Pratt and Casey (1983) values.

Length-frequency

Data from 3374 shortfin makos (1575 female, 1799 male) obtained between 1961 and 2004 were examined for length-frequency modes (Fig. 7). No visual differences were observed in the modes between the two 20-year time periods thus all the data were combined. Though the first few modes

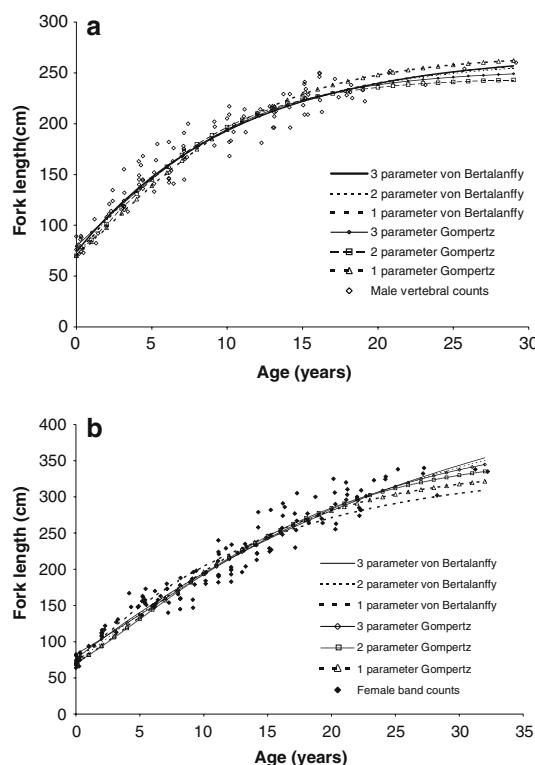


Fig. 5 Comparison of von Bertalanffy and Gompertz growth curves generated using 3, 2, and 1 parameter estimation for each model for the shortfin mako. (a) male, (b) female

in the summer months were quite clear, the later modes became obscured and it was decided to use only juveniles (up to 215 cm, higher than male maturity of 185 cm) so that the entire last mode of immature males was included in the final plots. Since juvenile growth in this species is similar, the sexes were combined. The majority of the samples were collected in June ($n = 1822$), and four distinct modes are visible (Fig. 7). Additionally a small mode is visible at 100 cm, but it blends into the next mode by August and becomes indistinct; thus it was not considered to be a true mode. Based on the modal analysis sharks grow 40 cm in the first year, 35 cm in the second and 30 cm in the third year.

Tagging data

A total of 22 shortfin mako was recaptured with sufficient information for tag/recapture analysis. Time at liberty ranged from 0.08 to 2.56 years and

size at tagging ranged from 74 to 137 cm. Data from 14 sharks at liberty >0.9 years were used for Gulland and Holt's (1959) and Fabens' (1965) methods whereas all individuals were used for GROTAG (Francis 1988a).

None of the tag/recapture methods produced biologically reasonable values for maximum size and longevity (Table 1). The different models of the likelihood ratio tests using GROTAG (Francis 1988a) all produced the same results (Table 2). The mean annual growth rates are $g_{85} = 47.5 \text{ cm year}^{-1}$ and $g_{130} = 29.5 \text{ cm year}^{-1}$, corresponding to growth rates at FL = 85 cm and 130 cm, respectively. The Fabens (1965) and GROTAG results were quite similar to each other but had a lower L_∞ and a higher K than Gulland and Holt (1959) (Table 1). All of the plotted curves looked similar but GROTAG better fit the data and was considered a more reliable curve due to its use of all available data. However, as previously stated due to limited number of samples, size range and times at liberty, the growth predicted from the tag/recapture data could be questioned, particularly in light of the high confidence intervals around the parameter estimates and lack of a strong relationship between the Gulland and Holt (1959) parameters (Fig. 8).

While direct comparison of the growth curves using the vertebral, length-frequency and tag/recapture generated growth curves is misleading, it can be useful to compare the growth rates at set sizes (Francis 1988b). The tag/recapture curves and the length-frequency modes indicate a much faster growth for the young mako sharks than the vertebral growth indicates (Table 2).

Longevity

The maximum age based on vertebral band-pair counts was 29 and 32 years, for males and females, respectively. The calculated longevity estimate of 21 years for males is an underestimate and was lower than that obtained directly; while for females, the calculated longevity (38 years) was older than that obtained using vertebral counts.

The maximum ages of 21 for males and 32 for females calculated using the tag/recapture analysis are close to the ages obtained by vertebral counts. None of the long-term recaptures were

Table 1 von Bertalanffy growth function parameters and 95% confidence intervals calculated by using vertebral and tag/recapture methods

Method		L_∞	K	L_0	n	Longevity
von Bertalanffy—3 parameter	Male	253.3	0.125	71.6	118	21.3
	CI \pm	8.3	0.016	5.9		
	Female	432.2	0.043	81.2	140	65.8
	CI \pm	54.8	0.011	7.4		
von Bertalanffy—2 parameter	Male	252.1	0.128		118	20.8
	CI \pm	7.1	0.011			
	Female	393.1	0.054		140	51.6
	CI \pm	31.5	0.009			
von Bertalanffy—1 parameter	Male		0.109		118	24.8
	CI \pm		0.004			
	Female		0.074		140	37.3
	CI \pm		0.003			
Gompertz—3 parameter	Male	241.9	0.191	76.7	118	16.3
	CI \pm		0.020	5.3		
	Female	365.6	0.087	88.4	140	38.1
	CI \pm		0.013	6.6		
Gompertz—2 parameter	Male	238.3	0.212		118	15.0
	CI \pm		0.013			
	Female	331.3	0.118		140	28.9
	CI \pm		0.010			
Gompertz—1 parameter	Male		0.159		118	20.5
	CI \pm		0.007			
	Female		0.113		140	30.2
	CI \pm		0.004			
Tag/recapture						
Gulland and Holt (1959)	Combined	281.7	0.24		14	11.4
	CI \pm	95.7	0.05			
Fabens (1965)	Combined	199.41	0.58		14	4.5
	CI \pm	46.65	0.51			
GROTAG	Combined	203.9	0.51		22	5.1

measured, however, the estimated lengths combined with the times at liberty gives information on longevity. Three recaptured sharks were at liberty longer than 10 years. The male with the longest time at liberty (12.7 year) was estimated at 183 cm (corresponding to 7.9 years) at tagging and 21 years at recapture. The longest time at liberty for a female was 12.4 years. The shark was estimated at 100 cm (3 year) at tagging and 15.4 years at recapture. Another female, at liberty 10.5 years was estimated to be 274 cm at tagging corresponding to 21.3 years and 31.8 years at recapture.

Discussion

In 1983, Pratt and Casey, in aging the shortfin mako in the North Atlantic Ocean, put forth the

hypothesis that this species deposits vertebral bands twice per year. Although the two-band-per-year hypothesis was brought into doubt several times since its inception (Cailliet and Bedford 1983; Natanson 2001; Natanson et al. 2002), there has been no evidence that this hypothesis is erroneous until recently. Recent advances in the validation of the periodicity of bands using bomb carbon techniques have been used to confirm that bands in this species are deposited annually (Campana et al. 2002; Ardizzone et al. this volume; Cailliet and Goldman 2004). Additionally, the results from one recaptured male after OTC-injection supports annual band periodicity at 18 years. Thus, the previous ages for the shortfin mako using the two-band-per year hypothesis (Pratt and Casey 1983) were underestimated. Biannual band-pair deposition has also been suggested in other shark species, including the sand

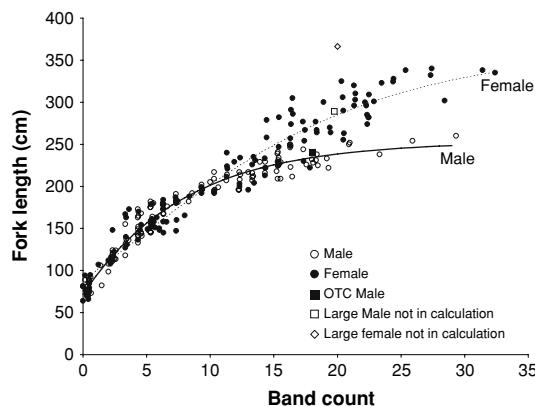


Fig. 6 Shortfin mako growth data based on vertebral band counts. Growth curves have been fitted to the data by sex the 3-parameter Von Bertalanffy growth functions (VBGF) for males and the 3-parameter Gompertz for females. Open circles are males, closed circles are females. Closed square is oxytetracycline (OTC) injected male, open square is largest male [289 cm fork length (FL)] not included in the growth curve calculation, open triangle is largest female (366 cm FL) not included in the growth curve calculation. Modes from length-frequency analysis are also presented for comparison

tiger (Branstetter and Musick 1994), basking shark (Parker and Stott 1965), and scalloped hammerhead (Chen et al. 1990; Anislado-Tolentino and Robinson-Mendoza 2001). Goldman et al. (this volume) validated annual periodicity in the sand tiger, using OTC. The data for the assumption of biannual deposition for the other two species were

inconclusive and the studies lacked the appropriate supporting evidence. There are therefore no validated studies proving biannual band-pair deposition for any species.

In the present study, there was no difference in band-pair counts in vertebrae along the vertebral column. Bishop (2004) also found no difference using vertebral columns of three shortfin makos of varying size. This factor is important in the present study as many samples were taken from the head region from fish that were processed for sale. However, Hsu (2003) found a distinct difference in the vertebral counts along the column. Band counts are expected to vary between techniques, oceans and readers. The authors in the present study intercalibrated with Bishop (2004) and coordinated efforts to use the same methodology for processing, measuring and counting, thus it is not surprising that the results of these studies agreed. The discrepancy with the Hsu (2003) study could be attributed to the use of whole vertebrae versus sections and thus technique. Counts on whole vertebrae often underestimate those in sections because of compression of the last bands. In a smaller vertebra, such as those at the extreme head or tail, it would be difficult to distinguish between bands in a whole vertebra which might be clear in a section. Although it has yet to be investigated, it is also possible that the differences between the Hsu (2003) and other studies represent a real difference in the populations of the species.

Fig. 7 Length-frequency modes for juvenile shortfin mako caught in June

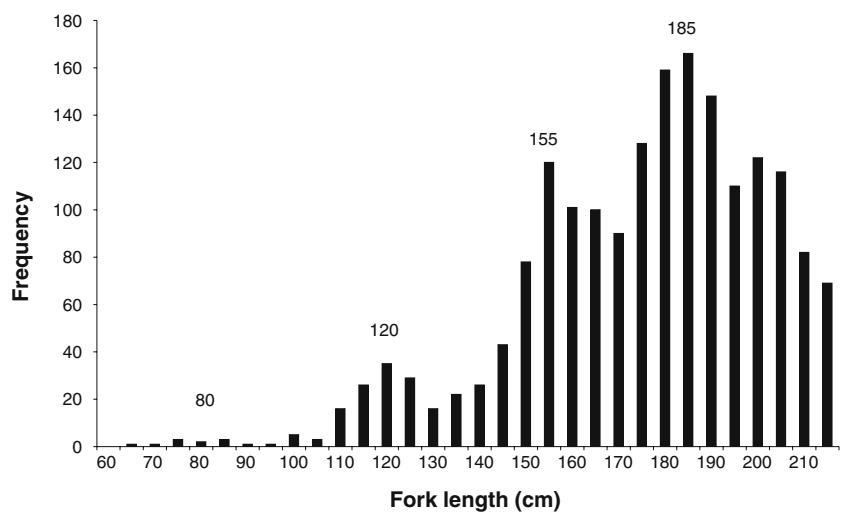


Table 2 Log-likelihood function value and parameter estimates for Growth rates from tag-recapture analysis (GROTAG) (Francis 1988a) growth model fitted to shortfin mako tagging data

Parameter	Symbol (unit)	Values	Growth vertebral	Growth length- frequency
Log likelihood λ		-86.89		
Mean growth rates	g_{85} (cm/year)	47.5	17.4	42.5
	g_{130} (cm/year)	29.5	13.1	36.1
Measurement error	s (cm)		11.01	

Vertebral growth based on male growth curve

The band counts from Natanson (2001) support Pratt and Casey's (1983) original band counts on sharks greater than 150–160 cm FL but disagree with their assigned age estimates. Conversely, band counts from Natanson (2001) on sharks less than 150 cm FL disagree with the bands counts from the 1983 study but agree with the assigned age estimate and also correspond to the growth estimates based on Pratt and Casey's (1983) other three methods. Direct comparison of age-length and length-increment-derived growth curves has been shown to be inappropriate since the publication of the Pratt and Casey (1983) study (Francis 1988b). In the present study, we also used juvenile length-frequency and tag/recapture data to independently estimate growth. The current results based on increased sample sizes and improved data analysis techniques are very similar to the Pratt and Casey (1983) results in that the growth rates predicted by the juvenile length-frequency modes and the tag/recapture

data are higher than that of the vertebral analysis. In the present study, however, the vertebral bands pairs are validated from age two to 31 (Ardizzone et al. *this volume*) and the vertebral growth curve cannot be manipulated to agree with the other methods; rather those methods need to be examined.

The high estimates for L_∞ and K from GROTAG can be attributed to the different derivation of the VBGF parameters, small sample size and the absence of older recaptured sharks in the sample. Additionally, the tag/recapture growth data examined graphically using Gulland and Holt (1959) shows no relationship and a large variation in growth rate of these individuals (Fig. 8). The length-frequency modes are primarily applicable to the young size classes and may be a better indicator of growth for those sizes. Both tag-recapture and length-frequency show similar fast growth in the younger fish as compared to the vertebral method. However, the data from these methods is only slightly above the length at age data from the vertebrae (Fig. 6). The fast initial growth represented by the data is not reflected in the growth curves as they are unable to handle rapid initial growth. The tag-recapture growth curves approach L_∞ faster than those derived from vertebral analyses and asymptote at a lower size than biologically reasonable due to the dependence on the younger size classes. The difference between these methods is not entirely unexpected and was also seen in the shortfin mako in Bishop (2004). Size-mode analysis in the porbeagle was also quite distinct in the first year but also showed a much faster growth rate than the vertebral growth curve (Natanson et al. 2002). Since the assigned ages in this study were based on validated counts, the more rapid growth, as seen in modal analysis, is difficult to interpret. Perhaps the modes coalesce at younger ages than was previously presumed due to the large variation of size at age combined with the rapidity of the growth. This effect was seen in one mode, which appeared in July at 100 cm and blended into the next by August.

The vertebral results provide an estimate of growth for the entire size range of the species and thus are more likely to reflect species growth than methods based on juveniles alone. Male

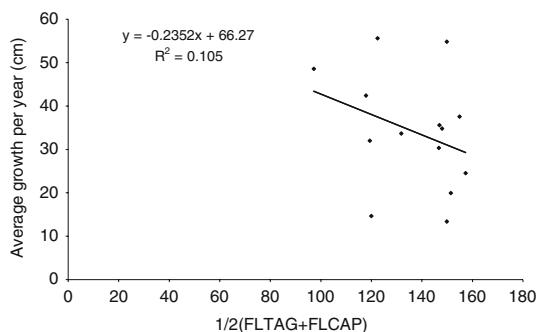


Fig. 8 Gulland and Holt (1959) tag-recapture graph for 14 recaptured shortfin makos. The negative slope equals estimated K and the x -intercept equals L_∞

Table 3 Growth function parameters and 95% confidence intervals calculated by using vertebral ages adjusted for deposition rate of two band pairs per year until 160 cm FL followed by one band-pair per-year deposition

Method		L_{\max}	K	L_0	n	Longevity
von Bertalanffy—3 parameter	Male	240.2	0.18	84.8	118	13.9
	CI \pm	8.11	0.03	6.64		
	Female	388.9	0.06	90.7	140	43.7
	CI \pm	37.07	0.01	7.00		
von Bertalanffy—2 parameter	Male	232.5	0.24		118	11.2
	CI \pm	5.99	0.02		140	30.9
	Female	347.0	0.90			
	CI \pm	20.48	0.01			
Gompertz—3 parameter	Male	234.4	0.25	89.8	118	11.7
	CI \pm		0.04	6.33		
	Female	388.9	0.11	97.3	140	29.5
	CI \pm		0.02	6.47		
Gompertz—2 parameter	Male	225.0	0.37		118	8.5
	CI \pm		0.03			
	Female	315.3	0.16		140	20.4
	CI \pm		0.02			

and female growth past age 11 was markedly different and the sexes required different growth functions to best describe them. The female data

do not appear to reach an asymptote while the male curve did. For the female, the VBGF produced an unrealistically high estimate of size

Table 4 Growth function parameters for shortfin makos from seven studies

Study		Size range cm FL	L_{∞} cm FL	K	t_0	n	Location	Age at maturity	Oldest aged	Bands/ year	Longevity years
Pratt and Casey (1983)**	Male	69–328*	302	0.266–1	49	Western North Atlantic	3	4.5	2	10	
	Female		345	0.203–1	54	Western North Atlantic	7	11.5	2	14	
Cailliet and Bedford (1983)		80.6–293	292.8	0.072–3.75	44	Pacific, California	7–8	17	1	38	
Ribot-Carballal et al. (2005)		68.6–264	375.4	0.05	–4.7	109 Pacific, Baja, CA	7 m; 15 f	18	1	55	
Bishop et al. (2006)	Male	100–347*	302.2	0.052–9.04	145	Pacific, New Zealand	7–9	29	1	48	
	Female		820.1	0.013–11.3	111	Pacific, New Zealand	19–21	28	1	219	
Hsu (2003)	Male	72.6–250.9	321.8	0.049–6.07	133	China	13–14	23.6	1		
	Female	72.6–314.9	403.62	0.040–5.27	174	China	18–19	30.6	1		
Chan (2001)**	Male	66–274	267.0	0.312–0.95	24	Pacific, Australia	Not reported	7	2	9	
	Female	74–314	349.0	0.155–1.97	52	Pacific, Australia	Not reported	10	2	17	
Natanson et al. (this volume)***	Male	72–260	253.3	0.125	71.6	118 Western North Atlantic	8	29	1	21	
Gompertz	Female	64–340	365.6	0.087	88.4	140 Western North Atlantic	18	32	1	38	

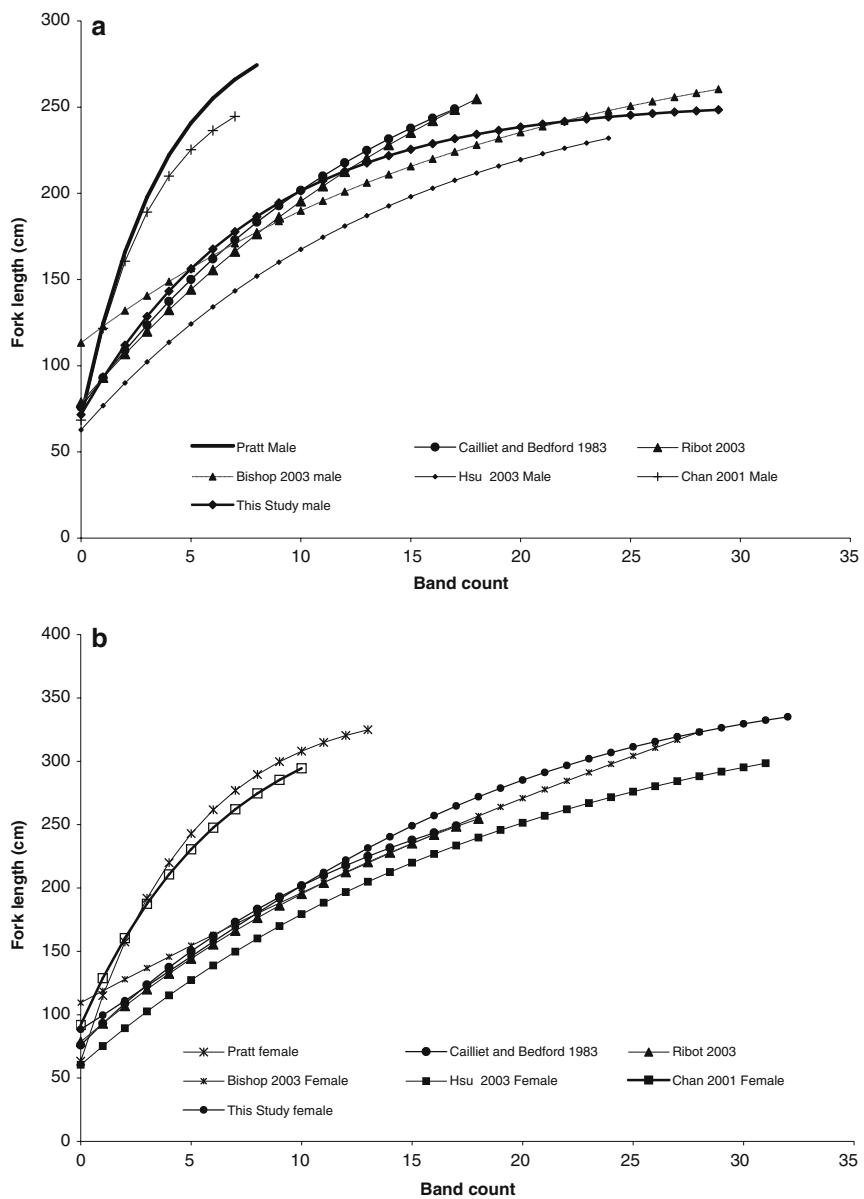
All lengths are fork length, those originally presented in total length were converted using equations published in the study or conversions from Bishop (2004) for the Pacific and Kohler et al. (1996) for the Atlantic. 95% Longevity is calculated

* Only total size range listed

** 2 Band/year assumed

*** Validated

Fig. 9 Growth curves generated from vertebral data for male (a) and female (b) shortfin makos, included for comparison are the von Bertalanffy growth curves of other studies



at birth, maximum size and longevity, while the GGF provided reasonable estimates for these parameters. Bishop (2004) and Bishop et al. (2006) had similar findings with females such as no asymptote and high estimates of size at birth from their von Bertalanffy (1938) equation and felt that the Schnute (1981) four parameter function better described growth. The best fit for the female, in this study, was the 3-parameter GGF. The VBGF 3-parameter function was the best fit for males providing reasonable estimates for all parameters.

One other possibility we explored was one in which the band deposition rate changes with size and thus with age. If we accepted that Pratt and Casey (1983) were correct that biannual band-pair deposition occurred in the size range they used (less than or equal to 155–160 cm FL), and that the current validation of the annual periodicity in the older sharks is also correct, one can construct a growth curve that reflects this change. As expected, the values for growth rate, age at maturity and longevity fall between the current values and Pratt and Casey's (1983) values

(Table 3). Without direct OTC-validation of the youngest size classes, we could not be certain that the band-pair deposition rates do not change. We feel, however, that this scenario is unlikely and that band-pair deposition is annual throughout the life of the shortfin mako.

The change from the two-band-per-year to the one-band-per-year interpretation results in a difference in growth rate, age at maturity and longevity, which has far-reaching implications for this species. The only previous study of this species in the western North Atlantic Ocean resulted in age at maturity of approximately three and seven for males and females, and a longevity estimate for females of 11–12 years (Pratt and Casey 1983). Data from the current study show an age at 50% maturity of 8 and 18 years (185 and 275 cm) for males and females respectively, and longevity estimates of 29 and 36.

The longevity estimates derived from the growth curves for males is an underestimation, while the estimate of female longevity was reasonable when compared with that obtained from vertebral analysis. The estimates provided fit the maximum size of makos in the WNA for the past 40 years (N. Kohler unpublished data) and assume that the largest-aged female is in the range of the maximum size in the current population. In an unfished population, this maximum age and corresponding size was perhaps higher. Longevity estimates calculated from other studies of mako sharks are higher in those studies using calculations based on VBGF parameters (Cailliet and Bedford 1983; Hsu 2003; Ribot-Carballal et al. 2005; Bishop et al. 2006) and lower for those based on two band pairs per year (Pratt and Casey 1983; Chan 2001) (Table 4).

Other studies have also shown the difference in growth between male and female shortfin makos. Bishop et al. (2006) had a high L_{∞} (2.1 times higher than her largest measured sample [347 cm FL]) and low K for the females using a 3-parameter VBGF. Although their curve fit the data in the size range of their samples they chose to use the Schnute (1981) curve instead of both the Gompertz and VBGF. Neither Cailliet et al. (1983b) or Ribot-Carballal et al. (2005) had sufficient samples to analyze their data by sex and

also lacked large females. Chan (2001) had only nine females over approximately 250 cm and only two over 300 cm, thus the larger sizes were underrepresented; this may account for the lower L_{∞} and higher K in his study (Fig. 9).

The occurrence of sexual differences in growth is well documented in elasmobranchs, with females usually growing larger than males. In the shortfin mako there is ample evidence that the female attains a larger size than the male. Maximum size male and female specimens in this study, 260 and 340 cm, respectively, represent the largest reliably measured shortfin makos from the North Atlantic Ocean.

Using validated vertebral band counts it has been shown that the shortfin mako grows slower, matures later and lives a longer life than previously thought in the North Atlantic Ocean. We believe that the validated vertebral interpretations generated in this study provide robust estimates of age and growth for the shortfin mako.

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