

# Bayesian age and growth analysis of the shortfin mako shark *Isurus oxyrinchus* in the Western South Atlantic Ocean using a flexible model

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**Abstract** Age and growth estimates of shortfin mako sharks *Isurus oxyrinchus* from the western South Atlantic Ocean were obtained through the analysis of vertebral sections of 245 specimens (126 females, 116 males and 3 with undetermined sex), ranging in size from 78 to 330 cm fork length (FL), using a flexible growth model (Schnute model) and a Bayesian approach. A significant linear relationship was found between FL and vertebral radius for sexes combined. Marginal increment analyses were inconclusive about periodicity of growth band deposition and an annual periodicity was assumed to make age estimations. Specimens were estimated to be between 0 and 28 years of age. The Schnute model provided a good description of the individual growth for both sexes up to 15 years of age. Shortfin mako growth during the first year of life was 33.9 cm ( $IC_{95\%}=19.9\text{--}40.8$ ) for females and

30.5 cm ( $IC_{95\%}=25.6\text{--}35.4$ ) for males. Until approximately 15 years of age, both sexes showed similar growth and reached ~217 cm FL. Sigmoid shaped growth curves obtained for both sexes indicated a change in the growth pattern close to 7 years of age. Inconclusive results about periodicity of growth band deposition in the study area make necessary the application of more robust validation techniques in the future. Meanwhile, a precautionary approach that assumes an annual deposition pattern in the western South Atlantic can be used for the assessment and management of stocks of this species, characterized by low fecundity and late maturity.

**Keywords** *Isurus oxyrinchus* · Age and growth · Schnute growth model · Bayesian approach

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## Introduction

The shortfin mako shark *Isurus oxyrinchus* is a large lamnid found in tropical and temperate waters worldwide (Compagno 2001). Mainly caught as bycatch in pelagic longline fisheries targeting tuna (*Thunnus* spp.), swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*), shortfin makos are retained for their valuable meat and fins (Compagno 2001; Clarke et al. 2006). In the South Atlantic, *I. oxyrinchus* is highly susceptible to these fisheries (Cortés et al. 2010), being the second-most common shark species in the catches (Domingo et al. 2002; Montealegre-Quijano et al. 2007). A stable trend of the standardized catch per unit of effort was reported for this species in the Atlantic (Carvalho et al. 2009; Mejuto et al. 2009; Pons and Domingo 2009). However, there are still difficulties to assess the current status of the stocks in this ocean due to the high uncertainty in past catch estimates and deficiency of important biological data (ICCAT 2012).

Assessment of the stock status of living resources and estimating a level of sustainable exploitation requires knowledge of the age structure of the population, including individual growth characteristics, mortality and longevity estimates (Ricker 1975). Age estimation studies provide the basis data to generate this knowledge (Campana 2001). Age estimations associated with observed individual sizes (age-at-length data) could be fit to growth models to describe the mean growth of individual fish in a population.

Several models have been proposed to estimate growth in fishes. However, in most of age and growth studies of chondrichthyans, including studies for *I. oxyrinchus*, only the von Bertalanffy growth model (VBGM) (von Bertalanffy 1938) was applied (Ribot-Carballal et al. 2005; Cerna and Licandeo 2009; Semba et al. 2009). A few studies in mako sharks used the VBGM and tested other models such as the logistic (Cailliet et al. 1983), Gompertz (Natanson et al. 2006) and Schnute (Bishop et al. 2006). When more than one model was used, the VBGM did not provide the best fit in different elasmobranch species (Araya and Cubillos 2006; Katsanevakis and Maravelias 2008) and in *I. oxyrinchus* also (Cailliet et al. 1983; Bishop et al. 2006; Natanson et al. 2006). Given this scenario, the use of a flexible model as the Schnute growth model (SGM) (Schnute 1981) appears as an interesting alternative, since its formulation includes several classical growth models -such as von Bertalanffy, Gompertz,

Richards and logistic- as special cases. The SGM considers not only asymptotic growth, but also linear, quadratic, power or exponential growth and allows the data to be used directly in deciding which type of model is most appropriate (Schnute 1981).

The first studies on age and growth of shortfin mako sharks (Cailliet et al. 1983; Pratt and Casey 1983) obtained contrasting growth parameters estimates, due to different assumptions on the periodicity of growth band deposition. Pratt and Casey (1983) assumed a biennial (2 growth bands per year) periodicity, whereas Cailliet et al. (1983) assumed an annual periodicity (1 growth band per year). More recently, age and growth studies of shortfin mako sharks have been conducted in the North Pacific (Ribot-Carballal et al. 2005; Semba et al. 2009), South Pacific (Bishop et al. 2006; Cerna and Licandeo 2009) and North Atlantic (Campana et al. 2002; Ardizzone et al. 2006; Natanson et al. 2006). All these studies reported an annual pattern in growth band formation, but only the studies in the North Atlantic validated the annual periodicity with bomb radiocarbon techniques (Campana et al. 2002; Ardizzone et al. 2006) and one individual chemically-tagged with oxytetracycline (OTC) (Natanson et al. 2006). Recently, Wells et al. (2013) using OTC in specimens <200 cm FL from North Pacific, concluded that at least for the first 5 years, young shortfin makos deposit 2 growth bands per year.

*I. oxyrinchus* is a species of low fecundity (Stevens 1983; Costa et al. 2002; Semba et al. 2011), late maturity (Mollet et al. 2000; Francis and Duffy 2005) and a reproductive cycle of 3 years (Mollet et al. 2000; Joung and Hsu 2005). These life history traits added to the fact that is a common by-catch species in the western South Atlantic, make *I. oxyrinchus* a species susceptible to be overexploited. Despite this, there are still no studies on the age and growth for this species in the South Atlantic. In this study we used a flexible growth model and a Bayesian approach to provide the first age estimation and growth analysis for shortfin mako sharks in the western South Atlantic.

## Materials and methods

### Data and sample collection

Shortfin mako sharks were obtained from research cruises and commercial fishing vessels within the EEZ of southern Brazil and the EEZ of Uruguay, as well as in

the international waters adjacent to both countries, between 24°29'S and 45°50'S and between 30°02'W and 54°50'W (Fig. 1). Research cruises took place between 1996 and 1999 and commercial cruises between 2004 and 2012. Sampling covered all months of the year. The fishing gear used in all cruises was surface pelagic longline, which in commercial fishery targeted swordfish, tuna and sharks. One neonate caught in coastal waters of southern Brazil was also included.

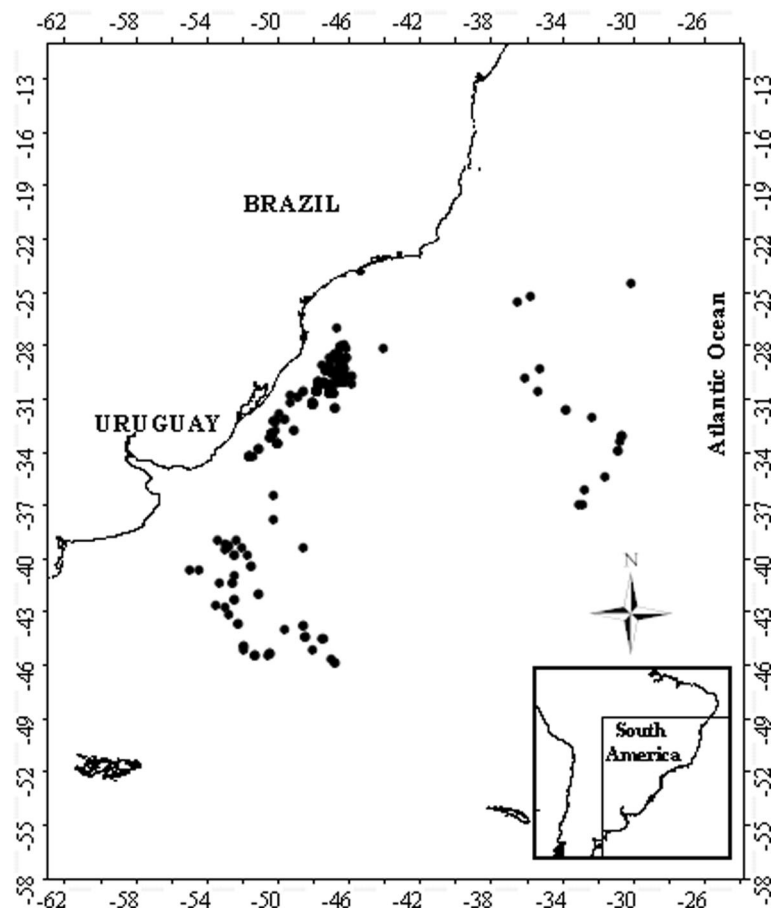
All shortfin mako sharks were measured and their sex identified. The fork length (FL) was recorded to the nearest centimeter, as a straight-line distance from the tip of the snout to the fork of caudal fin (Compagno 2001). For age determination, a section of 3 to 5 vertebrae was removed from the vertebral column. Samples from research cruises were collected below the first dorsal fin (11 % of vertebrae) and samples from commercial vessels were collected over the branchial region (89 % of vertebrae) to avoid damaging the carcasses, which would later be sold. Since no difference in age

estimates was found between vertebrae from the branchial and dorsal regions for this species (Bishop et al. 2006; Natanson et al. 2006), samples were pooled. Vertebrae were stored until analysis either frozen or fixed in 10 % formalin for 24 h and then preserved in 70 % ethanol.

#### Vertebral processing and age estimation

Excess tissue was cut off from the column sections, and one vertebra was chosen for processing. Neural arch, lateral processes and intervertebral cartilages were removed with use of a blade, to expose the surface of the centrum. Each vertebral centrum was sectioned in a sagittal plane through the focus (notochordal remnant, Casey et al. 1985) with an Isomet low-speed saw (Buehler®) provided with a diamond blade. “Bow tie” shaped sections of 0.5–0.7 mm thick were obtained and stored in 70 % ethanol to avoid shrinkage and deformation.

**Fig. 1** Sampling area showing the start-of-set positions (*black points*) in which shortfin mako sharks were caught in research and commercial cruises using surface pelagic longline in the western South Atlantic Ocean



Vertebral sections were read *in natura*, while submerged in 70 % ethanol, using a stereo microscope provided with one ocular with micrometric scale, and under reflected light against a black background. Under reflected light, the more calcified band (opaque) does not transmit light but reflects it, so this zone appears white (Casselman 1983). The number of opaque bands that traverse the *intermedialia* was counted and referred to as “growth band” or simply “band”. Measurements of the radius of each band and of the vertebrae were performed from the focus to the outer edge of each band and to the outer edge of the vertebral section, respectively with the micrometric scale positioned along the transverse axis of the *intermedialia*. Magnification was held constant at 10x.

To assess if vertebra grows proportionally with shark body in this species, the relationship between vertebral radius (VR) and fork length (FL) was assessed with a regression analysis for sexes combined. Two readings of each vertebral section were performed by the same reader. A third reading was made independently by a second reader. Band counts were made without knowledge of the fish length, sex, date of capture or number of bands in previous counts.

The second count of the first reader was compared with the single count of the second reader. When the difference was two or fewer bands, the second count of the first reader was used to estimate age. Otherwise, counts were reevaluated by both readers to reach a consensus. If no consensus was reached, the vertebra was classified as “unreadable” and discarded.

Bias was analyzed using the age bias plot (Campana et al. 1995). Reproducibility between readings of the same reader and between readers was tested for the entire sample with the index of average percent error (IAPE) (Beamish and Fournier 1981).

To identify the periodicity in growth band formation, two variations of marginal increment analysis were performed: edge analysis and mean marginal increment ratio (MIR) analysis (Campana 2001). Vertebrae collected between 1996 and 1999 were excluded for both analyses. In the first, the edge of the vertebral section was classified as opaque or translucent and relative frequencies of each category were compared monthly; whereas in the second, the mean MIR by month and by quarter was calculated and analysis of variance (ANOVA) was performed to test for differences at 5 %

significance. MIR for each vertebral section was calculated according to Natanson et al. (1995):

$$MIR = \frac{(VR - R_n)}{(R_n - R_{n-1})}$$

where  $R_n$  is the radius of the last opaque band and  $R_{n-1}$  is the radius of the next to last opaque band. Months and quarters with mean MIR values close to one, were interpreted as the time of year in which a growth band formation is closest to be completed, and therefore a growth cycle is being closed (Campana 2001; Lessa et al. 2006). The MIR analysis was conducted both for the overall sample (per month and per quarter of year) and for three age groups: 0–5 years of age, 6–10 years of age and 11–26 years of age (per quarter of year). From the individual age and length data, length-age keys (Sparre and Venema 1995) were constructed for females and for males. These ‘keys’ can be used in studies aimed to determine the age structure of the shortfin mako catches in western South Atlantic fisheries.

### Growth modeling

The Schnute growth model (SGM) (Schnute 1981) was fitted to each sex separately. The general equation of the model (case with  $a \neq 0$  and  $b \neq 0$ ), used in this study, is described by the following function:

$$Y_{(t)} = \left[ y_1^b + (y_2^b - y_1^b) \times \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{1/b}$$

where  $Y_{(t)}$  is the size of a fish at age  $t$  and  $a$ ,  $b$ ,  $y_1$  and  $y_2$  are the four parameters which SGM is based. The parameters  $a$  and  $b$  define the shape of the curve, where  $a$  is the relative rate of relative growth (e.g., growth acceleration) and  $b$  is the increase or decrease (variation) in growth acceleration. The parameters  $y_1$  and  $y_2$  are expected mean sizes that a fish takes at two particular ages  $\tau_1$  and  $\tau_2$ . These ages are arbitrary choices within the age range of the observed data, restricted to the condition  $\tau_1 < \tau_2$ . In this study  $\tau_1$  was fixed as the minimum estimated age in the sample and  $\tau_2$  as 15 years of age.

Depending on the values of parameters  $a$  and  $b$ , a set of eight regions is defined, in which the growth curve has specific shapes (e.g., region 1 and 2 are associated with the generalized VBGM) (Schnute 1981, Table 1, Figs. 1 and 2). These convenient parametric properties

**Table 1** Mean marginal increment ratio (MIR) and standard deviations (s.d.) per quarter of year for the age classes: 0–5 years, 6–10 years and 11–26 years and for all ages combined (n is sample size by quarter)

Quarter	0–5 years			6–10 years			11–26 years			All ages combined		
	MIR			MIR			MIR			MIR		
	n	mean	s.d	n	mean	s.d	n	mean	s.d	n	mean	s.d
1	2	0.49	0.23	2	0.46	0.29	35	0.5	0.23	39	0.5	0.23
2	8	0.43	0.29	29	0.52	0.27	14	0.55	0.27	52	0.52	0.27
3	30	0.47	0.21	53	0.6	0.29	8	0.69	0.23	92	0.57	0.27
4	6	0.58	0.33	10	0.55	0.23	4	0.5	0.33	20	0.55	0.27

allow direct use of the data in selecting an appropriate growth curve.

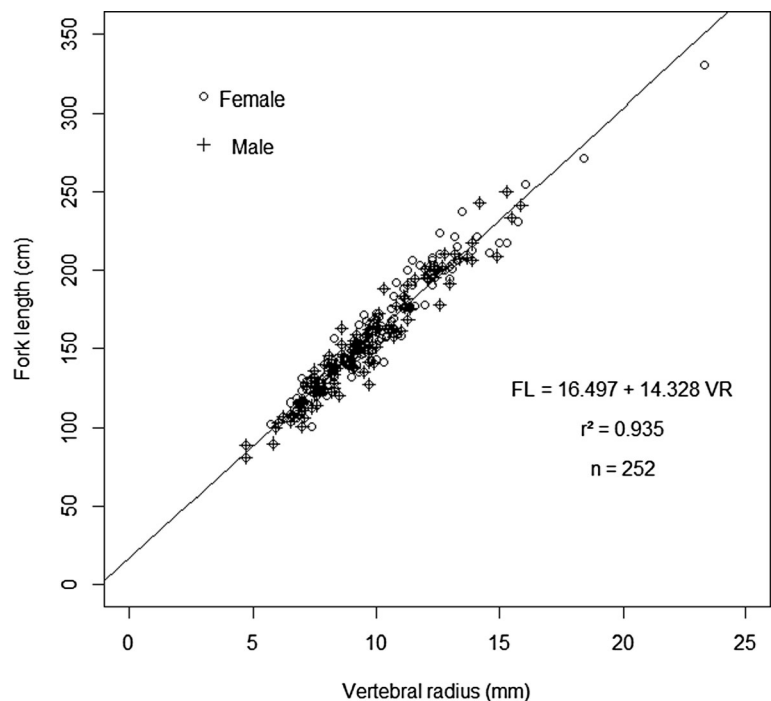
Depending on the region selected based on the estimates of  $a$  and  $b$ , four additional parameters, defined as tau zero ( $\tau_0$ ), tau star ( $\tau^*$ ), y star ( $y^*$ ) and asymptotic size ( $y^\infty$ ) can exist.  $\tau_0$  is an age corresponding to a projected size zero,  $\tau^*$  and  $y^*$  are the age and the size, respectively, where the growth curve has an inflection point and  $y^\infty$  is the asymptotic size.

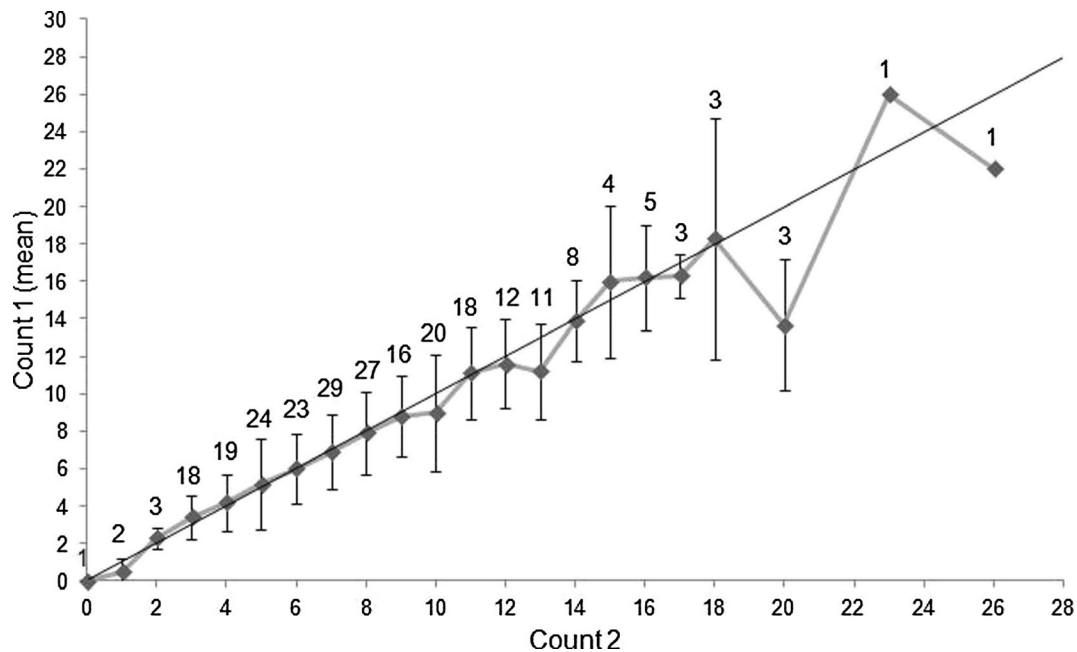
The VBGM was also fitted to each sex separately to facilitate comparisons with the literature. A multiplicative error was assumed which implied that, for

individual  $[i]$  the length $[i]$ , given age $[i]$ , follow a log-Normal distribution with mean  $\mu[i]$  and a precision  $\tau$ , where  $\mu[i]$  were fitted in the von Bertalanffy equation that follows:

$$\mu[i] = \log(L_\infty) + \log(1 - \exp(-k(\text{age}[i] - t_0)))$$

where  $L_\infty$  is the theoretical maximum length reached;  $k$  is the growth coefficient expressed in  $\text{years}^{-1}$  and  $t_0$  is the theoretical age that a fish would have at length zero.

**Fig. 2** Relationship between vertebral radius and fork length for shortfin mako sharks (sex combined) in the western South Atlantic Ocean



**Fig. 3** Age bias plot for within reader band counts. Error bars represent the 95 % confidence intervals about the mean of band counts assigned in the 1st reading (Count 1) for all individuals

assigned a given count in the 2nd reading (Count 2). The 1:1 equivalence (*solid line*) is also indicated. The number above each error bar is the sample size for each number of bands in the count 2

### Bayesian fit

A Bayesian approach was used to fit the SGM and VBGM to the data. In the Bayesian approach the estimates of the growth parameters are given as a probability distribution. This probability distribution denoted “*posterior distribution*”, is the most complete expression of the plausibility of different parameter values and the central element to make inference (Kinas and Andrade 2010). In cases like ours, where the posterior distribution cannot be derived analytically, stochastic simulation methods are used instead.

The stochastic method Sampling Importance Resampling (SIR) (Rubin 1988) was used. It uses another probability density (importance function) from which samples can be generated easily. A non-central multivariate Student distribution for the SGM parameters vector  $(a, b, y_1, y_2)$  with 8 degrees of freedom, centered at the maximum likelihood estimate “*m*” and with covariance proportional to the inverse Hessian matrix “*E*” was used as the importance function. Weakly informative priors were chosen. The algorithm described in Kinas and Andrade (2010) was used to implement the SIR method. Firstly, a sample of 50,000 observations from the importance function

was drawn. Secondly, the posterior density of the sampled points and the importance densities were calculated. The ratios for each draw of both densities (standardized to add one) were defined “importance weight”.

In the importance resampling (2nd stage of SIR) a redrawn sample of 4,000 from the first stage sample was obtained, using the importance weights as probabilities. This final sample (a matrix of 4,000 rows and 4 columns) is an approximate random sample of the posterior distribution of interest for  $(a, b, y_1 \text{ and } y_2)$ . To assess closeness between the target posterior distribution and the distribution that provided the importance sample, two diagnostics were used: the one proposed by Mc Allister et al. (2004) and the entropy relative to uniformity (ERU) proposed by West (1993).

Posterior means were used as parameter estimates and posterior medians as length-at-age estimates, due to asymmetric shaped distribution. Uncertainty about these estimates were expressed in 95 % posterior credibility intervals ( $ICr_{95\%}$ ) with lower and upper limits equal to the quartiles 2.5 and 97.5 % of the posterior sample, respectively.

From the matrix containing the posterior distributions of the parameters  $a, b, y_1$  and  $y_2$ , a new matrix of length



predictions was constructed separately for females and males for different ages (1, 5, 10, 15 and 20 years) and shown in length frequency histograms.

The posterior distribution indicating the plausibility for each of the eight regions was also obtained from the joint posterior distribution as the relative frequency of posterior draws contained in each region.

The VBGM was also fitted with a Bayesian approach. Posterior distributions of each parameter, with its median and  $ICr_{95\%}$ , were obtained using the simulation method of Monte Carlo Markov chains (MCMC). Weakly informative *priors* were used. To assess convergence of the posterior distribution, three Markov chains were simulated with a total of 600,000 iterations, burn in of 440,000 and a thinning of 40.

To compare SGM with VBGM the Deviance Information Criterion (DIC) was calculated. The DIC is a method to compare Bayesian models as the Akaike's Information Criterion (AIC) is in a frequentist context. Lower values of DIC represent better fit. Differences between models above 10 points allow discarding the worst model, whereas differences below 5 suggest similar fit.

The software R (R Core Team 2012) was used to do all statistical analyses, simulations and graphical displays. The software OpenBUGS (Thomas et al. 2006) and the libraries R2WinBUGS (Sturtz et al. 2005) and BRugs (Thomas et al. 2006) were used to fit the VBGM.

## Results

### Age estimation

Vertebrae from 252 mako sharks were processed for age and growth analysis. Females ranged from 101 to 330 cm FL and males from 81 to 250 cm FL. Seven vertebral samples were classified as unreadable and discarded. The age estimation was based on 126 females, 116 males and 3 individuals with undetermined sex.

A significant linear relationship was found between FL and VR for sexes combined ( $r^2=0.935$ ,  $P<0.001$ ) (Fig. 2), evidencing proportionality in growth between vertebrae and body. Thus, the vertebrae are suitable structures for describing individual growth in this species.

Age estimation bias was observed for counts by the same reader only above 18 bands (Fig. 3), indicating a higher difficulty to interpret distal bands in larger

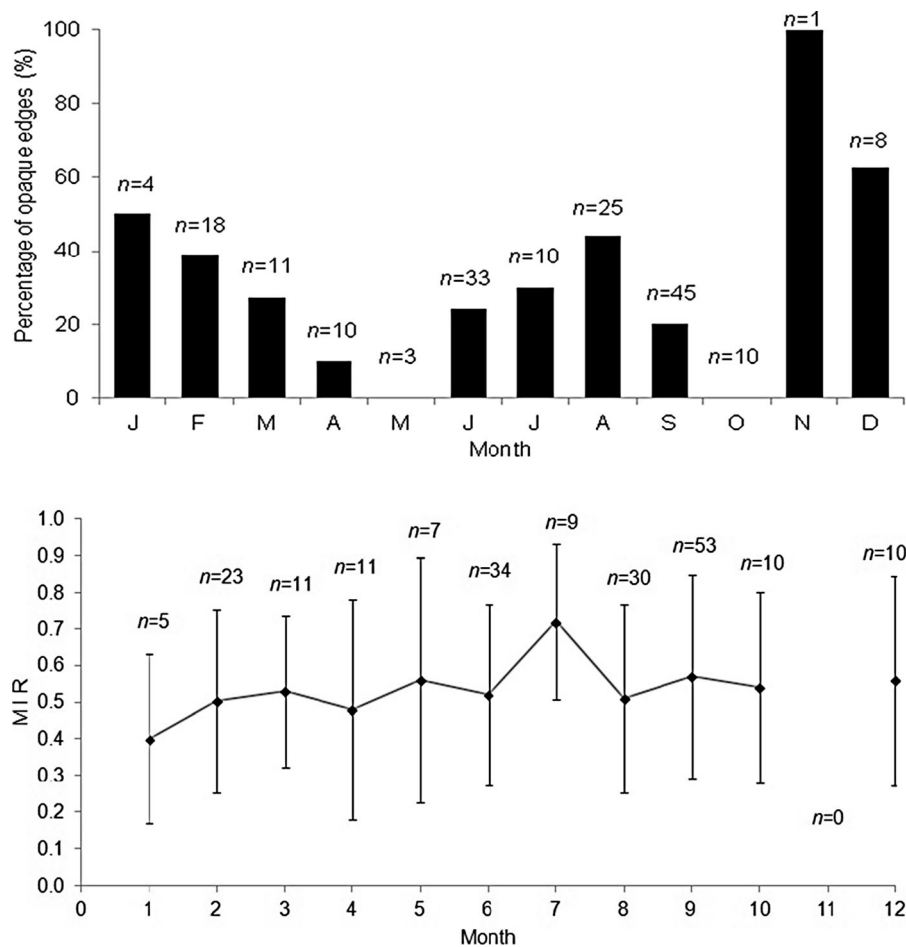
(presumably older) individuals. IAPE was 11.9 % between counts of the same reader and 14.3 % between readers. These values expose some difficulties to reproduce readings in vertebrae of shortfin makos. Precision was improved with the reassessment between readers and consensus.

Vertebral sections with edges difficult to assess were discarded in marginal increment analyses, reducing the sample size to 178 in edge analysis and 203 in MIR analysis. The edge analysis for all ages combined showed no clear trend with respect to time of year with highest frequency of opaque edges to indicate time of deposition of growth bands. A progressive decrease in the proportion of the opaque edges from December to April was evidenced by the analysis without showing any trend in the rest of the year (Fig. 4). The edge analysis per quarter of year was also inconclusive, with a proportion of opaque bands of 34 % in the first quarter, 20 % in the second quarter, 29 % in third quarter and 32 % in the fourth quarter.

The MIR analysis for the overall sample (all ages combined) per month suggested that growth band deposition appears to be close to being completed in July, when the highest mean MIR value was reached (Fig. 4). However, no significant differences were found in mean MIR between months over the year (ANOVA:  $F=0.815$ ,  $P=0.6145$ ) and the analysis was inconclusive about the periodicity pattern in band deposition. The MIR analysis per quarter for age groups was also inconclusive as well as the analysis per quarter for all ages combined (ANOVA:  $F=0.7876$ ,  $P=0.5021$ ) (Table 1).

Since marginal increment analyses were inconclusive about the periodicity pattern in growth band deposition for shortfin makos in the South Atlantic, age was assigned by assuming an annual pattern, on the basis of the validation tests conducted in the North Atlantic (Campana et al. 2002; Ardizzone et al. 2006; Natanson et al. 2006). Under this assumption, one growth band represented 1 year of age.

The first distinctive growth band was defined as the birth band (BB), since it was the only one present in two individuals with size close to the reported size at birth. The mean radius of the BB was 3.8 mm (s.d. =0.32 mm,  $n=252$ ). In some vertebral sections, a pre-birth band was identified close to the focus, at a radius of ~1.7 mm. The pre-birth band was narrower than the growth bands and was seen as a translucent line in the *corpus calcareum*. The pre-birth band was not considered for age assignment whereas the BB was regarded as age 0.



**Fig. 4** Marginal increment analyses. *Top*: Percentage of opaque edges for each month from vertebral sections of shortfin makos. *Bottom*: Marginal increment ratio (MIR) by month from vertebral

sections of shortfin makos. Monthly mean (black points) and standard deviation (bars) are shown (*n* is sample size by month)

Based on vertebral band counts, the age range estimated for shortfin mako sharks of the western South Atlantic was from 0 to 28 years. Young-of-the-year sharks (aged 0) were between 78 and 81 cm. The oldest and largest shark was a female of 330 cm FL aged in 28 years. The oldest male was 18 years old and measured 241 cm FL. The largest male (250 cm) was aged 17 years. The oldest female was excluded for the model fitting, since its data point was far removed from the overall data set and was very influential in the fit. Length-age keys, obtained for females and males, are shown in Table 2.

#### Growth analysis

The SGM provided a good description of the overall pattern of the data for both sexes, with a well fit

up to ~15 years. At older ages data were sparse and the posterior probability intervals started to be wider, indicating less reliable estimates (Fig. 5). An accurate estimates of the parameters  $a$ ,  $b$ ,  $y_1$  and  $y_2$  with narrow probability intervals was given by the Bayesian fit for both sexes (Table 3).

Lengths at age zero predicted by the SGM were 88.7 cm ( $ICr_{95\%}=65.1-97.1$ ) for females and 81.2 cm ( $ICr_{95\%}=71.1-89.5$ ) for males, which were close to the size at birth of the species (63 cm FL, Mollet et al. 2000). Lengths at age 1 were 96.9 cm ( $ICr_{95\%}=82.9-103.8$ ) for females and 93.5 cm ( $ICr_{95\%}=88.6-98.4$ ) for males. Shortfin mako growth during the first year of life, estimated from the difference between the median length predicted by the model for age 1 and the known length at birth of the species (63 cm FL), was 33.9 cm ( $ICr_{95\%}=19.9-40.8$ ) for females and 30.5 cm ( $ICr_{95\%}=25.6-35.4$ )



**Table 2** Length-age keys for female (top) and male (bottom) shortfin mako sharks for the western South Atlantic Ocean. Numbers in the centre of the table corresponds to the percentage ofindividuals within each length class of fork length (FL) in the different age classes. *n* is the total number of individuals in each length class

Length classes FL (cm)	Age classes (years)																							Mean (years)	S.d.
	n	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	28				
71–80	0																						–	–	
81–90	0																						–	–	
91–100	0																						–	–	
101–110	6	33	50	17																			2.8	0.75	
111–120	5		60	20	20																		3.6	0.89	
121–130	14		7	50	29	14																	4.5	0.85	
131–140	13		8	0	31	23	31	8															5.9	1.32	
141–150	20				25	30	30	15															6.4	1.04	
151–160	12					58	0	17	17	0	0	8											7.3	1.92	
161–170	12					17	33	8	25	8	8												8	1.6	
171–180	10						10	30	10	20	20	10											9.4	1.65	
181–190	4							25	25	0	0	25	0	25									10.8	2.75	
191–200	8									25	25	13	25	0	0	13							12	2	
201–210	9									11	44	11	11	11	11								12	1.66	
211–220	5											20	0	60	0	0	0	0	0	20			14.8	3.03	
221–230	3										33	33	0	0	33								12.7	2.08	
231–240	2														50	0	0	0	0	50			17.5	3.54	
241–250	0																						–	–	
251–260	1																100						–	–	
261–270	0																						–	–	
271–280	1																	100					–	–	
281–290	0																						–	–	
291–300	0																						–	–	
301–310	0																						–	–	
311–320	0																						–	–	
321–330	1																				100		–	–	

for males. The narrower probability intervals for males showed more accurate estimates for this sex, possibly due to the better representation of younger makos in males sample.

Posterior predictive length distributions indicated that females and males grow at similar rates until approximately 15 years (217 cm) (Fig. 6, Table 3). From this age on, males seemed to outgrow females. However, estimates after 15 years were inaccurate and not reliable.

The Bayesian fit of the SGM for females showed that 79 % of the combinations of the *a*, *b* parameters lied in the region 8 of the *a*, *b*-plane. The curve associated with this region presents asymptotic growth and is sigmoid-

shaped with an inflection point ( $\tau^*$ ,  $y^*$ ) (Schnute 1981; Fig. 2), which indicates a change in the growth pattern. The inflection point was at 7 years of age and 153 cm FL (Table 4). Asymptotic size (244 cm FL) seemed to be underestimated if related with the greatest observed maximum length for shortfin mako females (362 cm FL, Bigelow and Schroeder 1948).

For males, 57 % of the (*a*, *b*) combinations favored the region 3, followed by the regions 1, 2 and 8 which were less probable. The curves associated with the more probable regions show an inflection point, which indicates a change in growth pattern (Schnute 1981; Fig. 2). This change occurred at 6.7 years of age and 148 cm FL

**Table 2** (continued)

Length classes FL (cm)	Age classes (years)																		Mean (years)	S.d.		
	n	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
71–80	0																				–	–
81–90	3	33	67																		0.67	0.58
91–100	1				100																–	–
101–110	8		13	25	50	13															2.6	0.92
111–120	9				44	44	11														3.7	0.71
121–130	12				17	42	25	0	17												4.6	1.31
131–140	15					33	27	20	13	7											5.3	1.29
141–150	13					8	23	38	23	8											6	1.08
151–160	11						9	18	18	27	9	18									7.6	1.63
161–170	11							9	18	9	36	27									8.5	1.37
171–180	5								20	40	20	0	0	20							8.8	1.92
181–190	4							25	0	0	0	0	50	25							10	2.71
191–200	8										13	25	38	13	0	0	0	13			11.3	2.12
201–210	11												18	0	45	9	9	18			13.5	1.69
211–220	1															100					–	–
221–230	0																				–	–
231–240	1																100				–	–
241–250	3															33	0	0	33	33	16.3	2.08
251–260	0																				–	–
261–270	0																				–	–

(Table 4). Adding the probabilities for the regions 1, 2 and 8, there was a probability of 43 % that males growth curve reach an asymptote at 261 cm FL (Table 4), which was close to the maximum length reported for this sex (270 cm FL; Bishop et al. 2006). Although the growth curves defined by the SGM for females and males had an inflection point, the parameters  $\tau^*$  and  $y^*$  were poorly estimated by the model (Table 4).

A low probability for the region associated with a von Bertalanffy growth curve type (region 2) for both sexes (5 % for females and 12 % for males) was shown by the SGM Bayesian fit. The low probability suggested that VBGM did not fit the data well. This fact was confirmed when VBGM was fit to the data and the parameters were poorly estimated for both sexes (Table 3). The estimates of  $L_\infty$  were more realistic for females than for males (416 cm and 580 cm, respectively); though they were considerably higher to the maximum lengths reported for the species and seemed to be overestimated.

SGM fitted better than VBGM under the DIC criteria for males. The difference of 22 points allowed

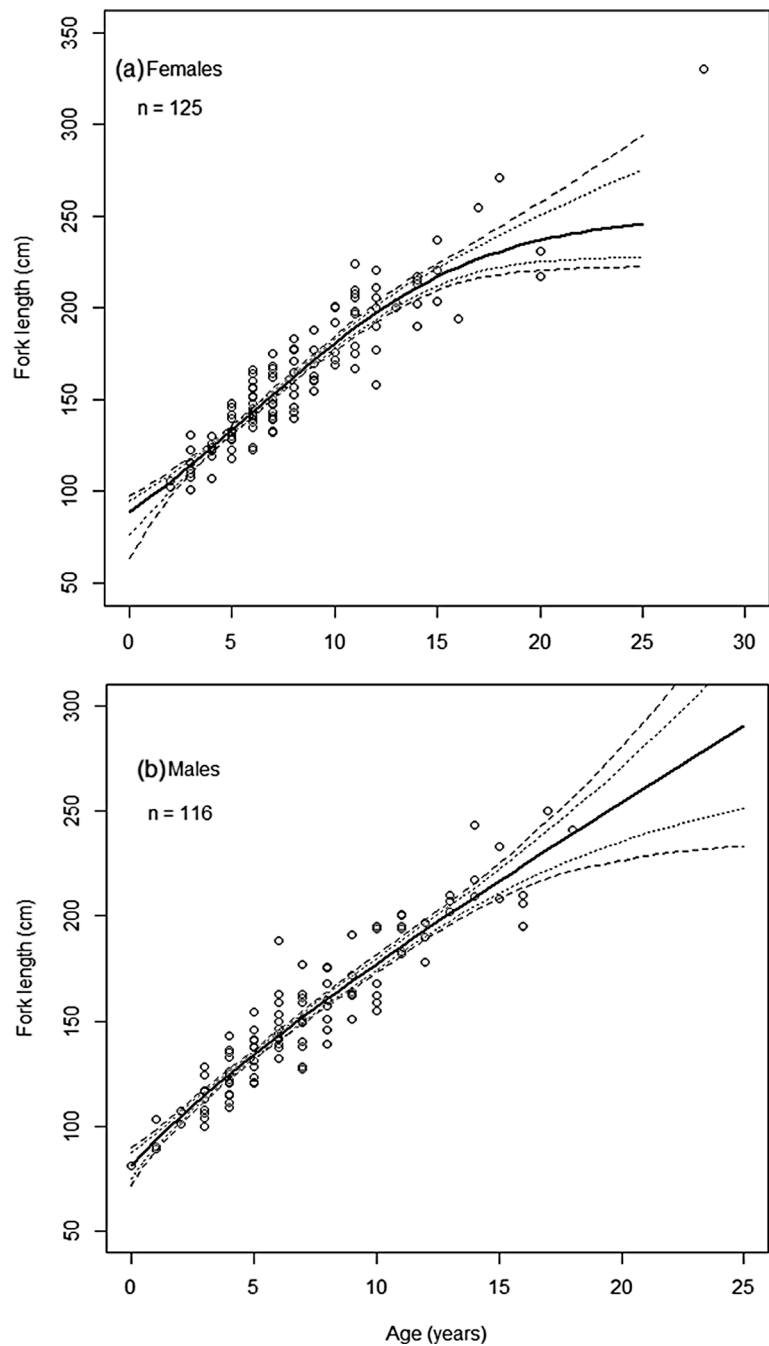
discarding VBGM for this sex. Similar values of DIC for females supported that both SGM and VBGM fit the data well (Table 3).

## Discussion

A representative sample of the shortfin makos caught by the longline fishery in the western South Atlantic was used with females and males close to the maximum length reported for the species. The largest shortfin mako female caught during 15 years of monitoring by the Uruguayan National Observers Program on Board the Tuna Fleet (PNOFA) was included. Males length classes were better represented than females length classes, since largest females are rarely caught by longline fishery.

Based on the age at sexual maturity estimated for makos of the western North Atlantic (18 years for females and 8 years for males, Natanson et al. 2006), all the females sampled in commercial fishing cruises in the EEZ of southern Brazil and international adjacent

**Fig. 5** Posterior Schnute growth curves fitted to average length-at-age data for (a) female and (b) male shortfin mako sharks. Posterior median (*solid line*) and posterior probability intervals of 80 % (*dotted lines*) and 95 % (*dashed lines*) are shown

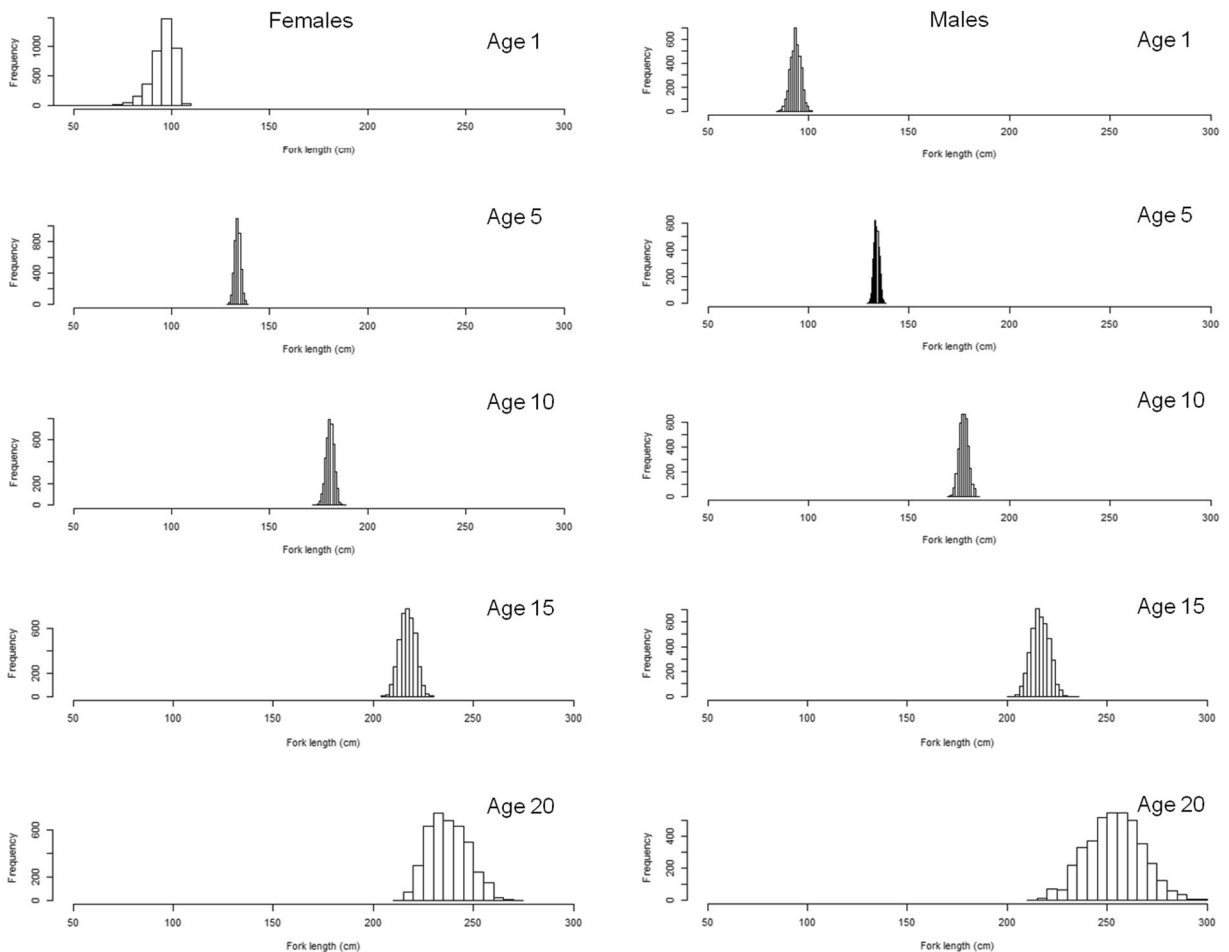


waters, were juveniles (aged 2 to 12), whereas males were juveniles and adults (aged 1 to 18) (Fig. 7). The low frequency of mature and large females in the catches of pelagic longline fisheries was observed for the South Pacific (Cerna and Licandeo 2009), North Atlantic (Campana et al. 2005) and western South Atlantic (Pons and Domingo *in press*)

representing less than 2 % of the females caught. Rare occurrences in the study area, preference for deeper waters, gear selectivity or low survival rate to maturity are factors that can explain the low catches. Wood et al. (2007) suggested for the North Atlantic that only 9 % of the female mako population would reach reproductive capability.

**Table 3** Schnute and von Bertalanffy growth parameter estimates by Bayesian fit for female and male shortfin mako sharks. SGM parameter estimates are the posterior means; values within brackets are the 95 % credibility intervals (ICr95%). Reference

Growth model		Females ( $\tau_1=2$ , $\tau_2=15$ )		DIC	Males ( $\tau_1=0$ , $\tau_2=15$ )		DIC
	Parameter	Posterior mean	ICr95%		Posterior mean	ICr95%	
Schnute	$a$	0.216	[−0.06; 0.56]		−0.016	[−0.24; 0.21]	
	$b$	−2.2	[−8.36; 2.73]		1.76	[−1.78; 5.22]	
	$y_1$	105.1	[97.9; 111.0]		80.89	[71.1; 89.5]	
	$y_2$	217.2	[209.8; 225.1]		216.47	[208.5; 224.7]	
	$\sigma$	0.083	[0.072; 0.094]		0.081	[0.071; 0.092]	
Von Bertalanffy		Posterior median	ICr95%	−493.56	Posterior median	ICr95%	−462.14
	$L_\infty$	416	[293; 1199]		580	[329; 1381]	
	$k$	0.035	[0.0084; 0.068]		0.021	[0.0072; 0.050]	
	$t_0$	−6.18	[−9.23; −3.99]	−494.32	−7.52	[−9.41; −5.36]	−440.54



**Fig. 6** Histograms of the lengths predicted by the SGM for the ages of 1, 5, 10, 15 and 20 years for female and male shortfin mako sharks

**Table 4** Set of parameters defined by the Schnute growth model according to the type of growth curve the model assumed for female and male shortfin mako sharks. Parameter estimates are the posterior medians; values within brackets are the 95 % probability intervals (ICr95%).  $\tau_0$  is an age corresponding to a projected size zero,  $\tau^*$  and  $y^*$  are the age and the size, respectively, where the growth curve has an inflection point and  $y^\infty$  is the asymptotic size.  $\tau_0$  and  $\tau^*$  are in years and  $y^*$  and  $y^\infty$  are in centimeters

Parameter	Females		Males	
	Posterior median	ICr95%	Posterior median	ICr95%
$\tau_0$	0.029	[−16.3; 1.36]	−1.12	[−2.7; −0.26]
$\tau^*$	7.0	[2.8; 9.8]	6.7	[2.6; 10.1]
$y^*$	153	[112; 179]	148	[109; 177]
$y^\infty$	244	[220; 302]	261	[216; 357]

### Age estimation

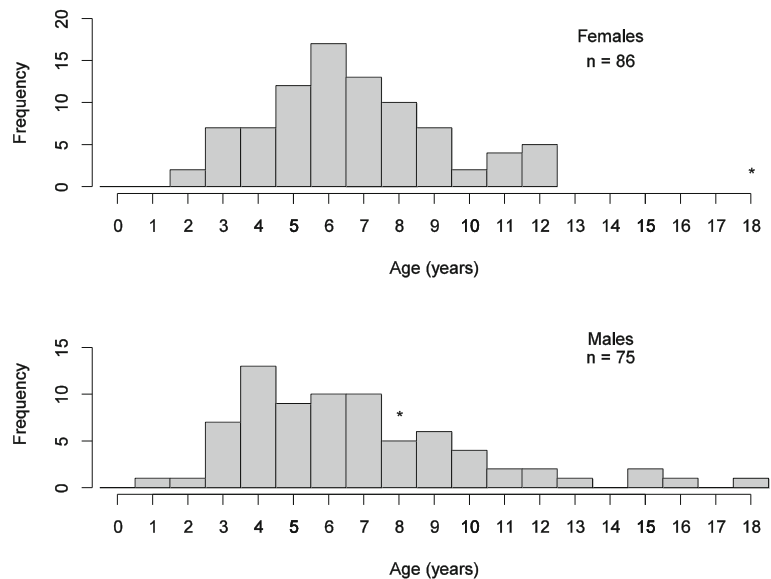
The maximum observed age in our study (28 years) was close to the maximum reported age for shortfin makos worldwide (32 years, Natanson et al. 2006) and similar to that reported by other studies based on vertebral band counts (Bishop et al. 2006; Cerna and Licandeo 2009). Bomb radiocarbon analyses obtained almost the same results than that reported using vertebral band counts (31 years, Ardizzone et al. 2006). Bomb radiocarbon results supported vertebral age estimates up to ~20 years in other lamnid (*Lamna nasus*), but in older sharks

vertebral band counts under-estimates age of up to 50 % in this species (Francis et al. 2007). This under-estimation was related to the difficulty in identifying the increasingly narrow growth bands as the individual growth slows at a point of being unresolvable (Francis et al. 2007). Similar life history traits between shortfin makos and porbeagles suggests that longevity exceeding vertebral band counts estimates can occur also in shortfin makos, noting the need to use a combination of methods for age estimation.

All the studies mentioned above (including the present study) assumed an annual periodicity pattern in band deposition for shortfin makos. However, the interpretation of growth band per year influences the estimated maximum age. If a 2 growth bands per year hypothesis had been assumed, the maximum age would decrease to 14 years; and if a 2 bands per year for the first 5 years followed by 1 band per year hypothesis had been assumed, the maximum age would be 23 years. Long term tagging studies for shortfin makos showed a maximum time at liberty of 13 years for this species (Kohler and Turner 2001). As the absolute age of this individual was unknown, these results do not support any of the three hypotheses.

Our attempts to determine the periodicity in band growth deposition through different resolutions of marginal increment analyses (overall sample, age groups, per month, per quarter) were inconclusive. Technical difficulties related to measuring and categorizing the distal bands at the margin of vertebrae where they

**Fig. 7** Age frequency histograms of *Isurus oxyrinchus* caught by commercial fishery during 2004–2009 at the EEZ of southern Brazil and at international adjacent waters. The star indicates the age at sexual maturity for each sex



become increasingly narrow (Campana 2001) may have influenced our results. Months with the smallest sample sizes ( $n < 10$ ) were also the months with the highest or lowest values of mean MIR or percentage of opaque vertebral edges, suggesting bias due to small sample size (Brothers 1983; Santana and Lessa 2004; Lessa et al. 2006). Bias due to an extended sampling period (2004–2012) may have influence the results, causing variability on account of annual bands that are not deposited at the same time every year (Brothers 1983; Santana and Lessa 2004; Lessa et al. 2006). These biases had already been reported as the causes of inconclusive results about band periodicity pattern in five species of Carcharhiniformes (Lessa et al. 2006).

Marginal increment analyses suggested an annual periodicity in growth band deposition for makos from the North Pacific (Ribot-Carballal et al. 2005; Semba et al. 2009) and South Pacific (Cerna and Licandeo 2009). However, the season of band deposition differed between studies. Ribot-Carballal et al. (2005) and Cerna and Licandeo (2009) found a high frequency of opaque bands in summer, whereas Semba et al. (2009) reported that in winter.

Bomb radiocarbon techniques and mark-recapture of chemically-tagged fishes are among the more robust methods of age validation (Campana 2001; Goldman et al. 2012). Until recently, the most robust evidence of growth band deposition periodicity was that of an annual periodicity provided by these methods for the North Atlantic (Campana et al. 2002; Ardizzone et al. 2006; Natanson et al. 2006) but Wells et al. (2013) raised the discussion with their evidence of biennial deposition for juveniles in North Pacific. As none of these studies validated age for the entire age range of the species, a hypothesis that considers both evidences is one that assumes ontogenetic variation in the periodicity of growth band deposition, with juveniles of at least 5 years of age showing a biennial deposition and older aged individuals an annual deposition (Natanson et al. 2006; Wells et al. 2013). The annual hypothesis was assumed in the present study based on geographical proximity with the studies already conducted in the Atlantic Ocean. However, as uncertainty remains regarding the growth band deposition periodicity in western South Atlantic, the three possible scenarios of growth were presented for discussion: 1 band per year, 2 bands per year and 2 bands per year for the first 5 years of life followed by 1 band per year (Fig. 8).

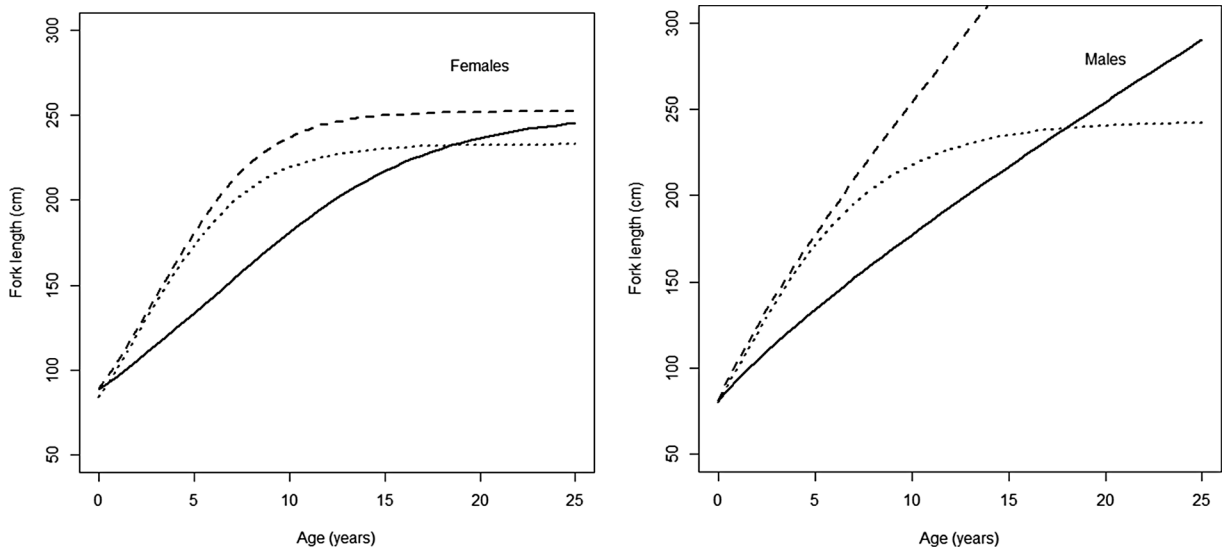
## Growth analysis

Growth during the first year of life -birth to 1 year- (34 cm for females, 31 cm for males) was slightly slower than the estimated for the North Atlantic (40 cm; Natanson et al. 2006) and for the western South Pacific (39 cm; Bishop et al. 2006) but faster than the reported for the eastern South Pacific (16–19 cm; Cerna and Licandeo 2009). Recently, Wells et al. (2013) with length frequency analyses and a tag-recapture growth model estimated a growth rate for the first year similar to the present study (27 to 36 cm/year) for the North Pacific. Length at age 1 predicted by SGM was similar to the estimated for the western South Pacific through SGM (100 cm FL for both sexes, Bishop et al. 2006) and for the eastern South Pacific through modal progression analysis and VBGM (Cerna and Licandeo 2009). Similar growth in the two first years of life was observed for shortfin makos of the western South Atlantic and makos of other regions of the world.

The use of a flexible model allowed modeling growth without forcing the data to a single type of growth curve shape. Whereas SGM detected an inflexion in growth for females and males shortfin makos, other models (von Bertalanffy, for instance) cannot showed this. An inflexion in growth had already been reported for several elasmobranch species and was associated with the age at maturity (Araya and Cubillos 2006) and with a time in life in which a change in the habitat or in the feeding habits occurred (Casey et al. 1985). In shortfin mako males, the change in growth can be associated with age at maturity (8 years; Natanson et al. 2006), whereas in females this association is not valid since reported age at maturity is 18 years (Natanson et al. 2006). However, a better estimation of  $\tau^*$  was expected for males and an underestimation for females, as older females were poorly represented.

Although the probability of an asymptotic growth curve was higher for females than for males (79 and 43 %, respectively), results about asymptotic size must be taken with caution, since after 15 years the model was forced to explain growth with the sparse data available. It is interesting to note that when the SGM was fitted with females up to age 18 (the same “window” of age available for males), excluding the three oldest females, the growth curve shape changed





**Fig. 8** Schnute growth curves for female and male shortfin mako sharks for three scenarios of growth band deposition periodicity: 1 band per year (*solid line*), 2 bands per year (*dashed line*) and 2 bands per year for the first 5 years of age followed by 1 band per year (*dotted line*)

drastically, with the shape of the region 3 becoming the most probable (61 % of probability). Similarly, when the oldest female was included, the 55 % of the  $a$ ,  $b$  combinations favored the shape of the region 3, showing that it was really very influent in the fit. The growth curve associated with region 3 is not asymptotic and has an inflection point. A no asymptotic growth curve had already been reported for female shortfin mako sharks (Bishop et al. 2006; Natanson et al. 2006) and may be result of the lack of older females in the samples and evidence that a phase of growth is being modeled. Since most of the data used in age and growth studies of shortfin makos come from longline fisheries, the lack of large (presumably older) females in the catches is a limitation to model growth for this sex and makes it difficult to determine female's asymptotic size.

Biologically, asymptotic growth is a fact. Within the phase of growth well described by the SGM an asymptote was not reached by any of the two sexes. The flexibility of the SGM allowed modeling a phase of growth in which the age window was well represented, without forcing the data to reach an asymptote that, in this study, would be unrealistic. Advantages of the use of SGM for modeling growth in shortfin mako sharks had already been reported (Bishop et al. 2006). The poor fit of the VBGM to the data suggested that when data of older individuals is sparse, VBGM probably would not be the best model to be used and uncertainty about its parameter estimates must be taken into account.

In conclusion, this study provided the first estimates of age and growth of the shortfin mako shark in the western South Atlantic Ocean. Growth phase until age 15 was well described with the use of a flexible growth model. A change in growth was observed in both sexes, which in males was close to the age at maturity. Inconclusive results about periodicity of growth band deposition in the study area, make it necessary to apply more robust validation techniques in the future, as different interpretations about periodicity results in changes in growth rate, first age at maturity and maximum age. Meanwhile, a precautionary approach assuming an annual deposition pattern can be used in management efforts for this species with low fecundity and late maturity characteristics.

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