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

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ABSTRACT

The blue shark, Prionace glauca, is frequently caught in pelagic fisheries, being the most captured shark by the Portuguese pelagic longline fishery in the Indian Ocean. The biology of blue sharks has been extensively studied in the Atlantic and Pacific oceans. However, high levels of uncertainty still persist regarding many of its biologic aspects in the Indian Ocean region, specifically in terms of age estimation and growth modelling. A total of 818 vertebral samples were collected from blue sharks between March 2013 and September 2016, with sizes ranging from 82 to 301 cm fork length (FL). The age of individuals was estimated through counting growth band pairs in sectioned vertebrae. Two growth models were fitted to the age data, a three-parameter von Bertalanffy growth function (VBGF) re-parameterized to calculate L_0 *(size at birth) and a two-parameter VBGF with a fixed* L_0*. The latter was the most adequate to describe the growth of the species, with the estimated parameters being* L_{inf} *= 272.2 cm FL, k = 0.15 year*$^{-1}$ *for males and* L_{inf} *= 283.2 cm FL, k = 0.13 year*$^{-1}$ *for females. The maximum age estimated was 25 years, this being the highest attributed age to this species so far. Further work is needed regarding blue sharks in the Indian Ocean, but this study adds important life-history information that can contribute for the management and conservation of the species.*

Keywords: blue shark, bycatch, growth modelling, fisheries, pelagic longline

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Introduction

The blue shark, *Prionace glauca,* is a shark species belonging to the Carcharhinidae Family (Nakano & Seki, 2003). Blue sharks have a worldwide distribution, both over temperate and tropical waters, and are considered by many authors as the most abundant of pelagic sharks (Compagno, 1984; McKenzie & Tibbo, 1964; Nakano & Seki, 2003; Nakano & Stevens, 2008). Therefore, these apex predators are a highly important component of pelagic ecosystems globally (IOTC, 2007).

P. glauca is one of the pelagic shark species most frequently caught as bycatch of fisheries all over the world (Campana *et al.*, 2009; Pratt, 1979), especially by pelagic longline fisheries targeting tuna and swordfish (Anderson, 1980; Bailey *et al*., 1996; Campana et al., 2009; Carruthers *et al.*, 2011; Francis *et al.*, 2001; IOTC, 2016; Pratt, 1979; Stevens, 1992). In the Indian Ocean, blue shark is the most caught shark by Portuguese pelagic longlines, and it is the second most caught species following swordfish, which is the main target (Muñoz-Lechuga *et al.,* 2016).

When it comes to stock assessment, age and growth of organisms are very important parameters to estimate growth rates, mortality rates, longevity, and other relevant aspects to evaluate the condition of stocks (Campana, 2014; Campana, 2001; Goldman *et al.,* 2012). In that context, the biology of blue sharks has been extensively studied, that including age and growth studies. However, despite being highly studied in the Atlantic and Pacific Oceans, when it comes to the Indian Ocean there are still a considerable lack of information regarding this species. Only two studies of age and growth were accomplished for blue sharks in the Indian Ocean so far, namely the studies of Jolly *et al.* (2013) and Rabehagasoa *et al.* (2014).

The aims of the present study are to: 1) estimate the age of blue shark specimens through reading of growth bands in vertebrae and 2) model growth on both sexes. The results presented extended and complement the age and growth information for blue shark in the data poor region of the Indian Ocean.

Materials and methods

Sample collection

All vertebral samples used in this study were collected by scientific fishery observers from *Instituto Português do Mar e da Atmosfera* (IPMA), on board of Portuguese commercial longline vessels that target swordfish (*Xiphias gladius*) in the Indian Ocean. A total of 818 samples were collected from March 2013 to September 2016 in the South Indian Ocean, between 23.75°S and 34.85°S (latitude) and from 40.70°E to 92.97°E (longitude) (**Figure 1**).

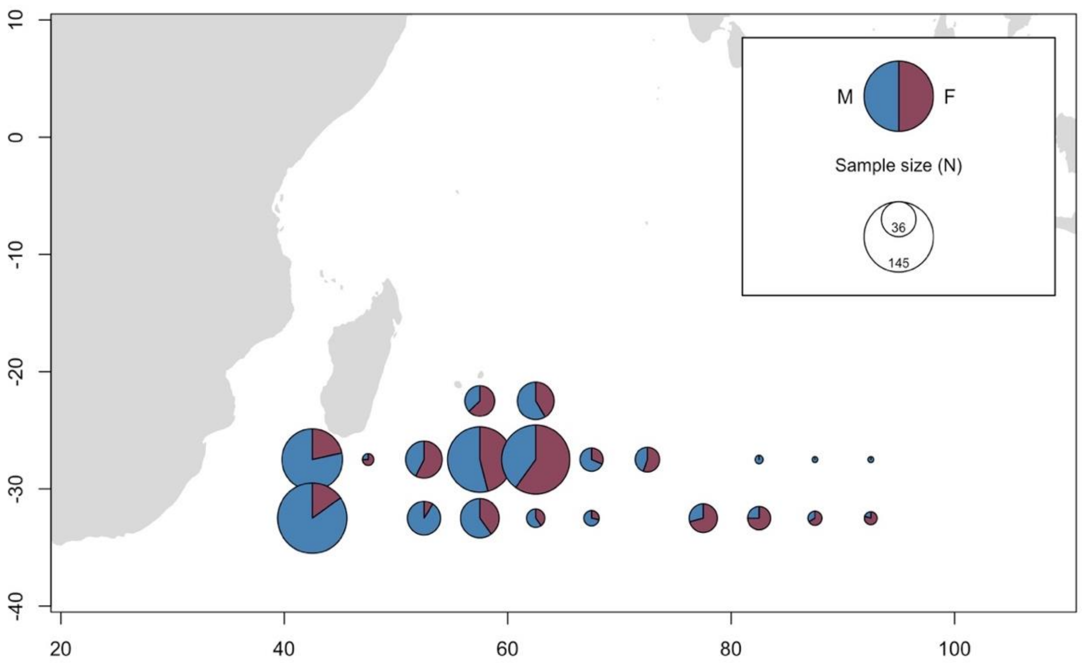

Figure 1. Map of the area of collection of *Prionace glauca* samples (females and males represented) in the South Indian Ocean. The plots are represented in 5x5 degree grids, with the sizes of the plots proportional to sample size (N).

Still on board of the fishing vessels, the sex of all specimens was recorded and the fork length (FL) measured to the nearest lower cm. Vertebral samples were kept frozen after removal, and stored frozen during their transportation to IPMA and until processing in the laboratory.

Sample processing

All the collected vertebrae were first cleaned and then sectioned. For the cleaning process, the organic tissues around each vertebra were removed with scalpels and tweezers. To remove any remaining tissue, samples were then immersed in 4–6% sodium hypochlorite (commercial bleach) during approximately 5 or 10 minutes, depending on their size. Once cleaned, samples were stored in 70% ethanol until further use. Before starting the sectioning process, vertebrae are first left air-drying to remove the storing ethanol, and then mounted to microscope slides using polymer glue when they are fully dried. After 24h, when the polymer glue has dried, each vertebra was placed in a sectioning cutter (Buehler Isomet 1000 precision low-speed saw), with two diamond waffering blades, producing 0.5 mm sagittal sections.

In order to enhance the band pattern in the sagittal sections obtained, these were stained with Crystal Violet solution (Sigma-Aldrich Co., St. Louis, MO). Only one of the two sections obtained for each vertebra was stained, to later compare the visibility of the stained versus the non stained bow-ties of the vertebrae. After staining, both sections of each sample were left tightly wrapped between two microscope slides to maintain their original shape as they dried for about 24h.

The sections of each sample were mounted onto microscope slides using Neo-Mount, and left to dry completely. Once dried, these were observed under a Nikon dissecting microscope with a mounted high resolution digital camera, using transmitted white light, in which each section was photographed. Photographs were then digitally enhanced using the Image J software (Schindelin *et al.,* 2015) by adjusting the contrast and brightness. Growth bands, the focus and the outer edge of the *corpus calcareum* of each vertebral sample were marked in the photos using the same software.

Age estimation and precision analysis

Age estimation was accomplished by counting the number of wide/narrow band pairs in each sample (wide corresponding to the opaque bands and narrow to the translucid bands), through the respective recorded photographs (**Figure 2**). Annual deposition of the band pair was assumed. The first distinct band, where a slight angle change was noted, was considered to be the birthmark (Blanco-Parra *et al.*, 2008; Francis & Maolagáin, 2016; Hsu *et al.,* 2015; Jolly *et al*., 2013; Lessa *et al.,* 2004; Megalofonou *et al.,* 2009; Rabehagasoa *et al*., 2014; Skomal & Natanson, 2003; Wells *et al.,* 2016).

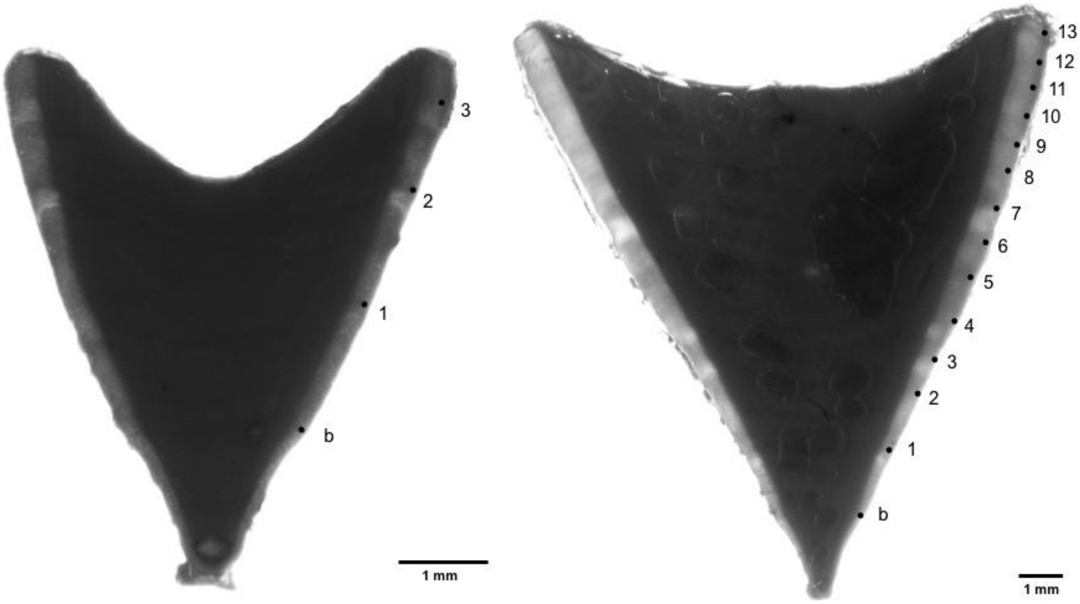

Figure 2. Microphotograph of two vertebral samples of *Prionace glauca* specimens with identification of the birthmark (b) and the growth bands (indicated by numbers). The individual on the left has an estimated age of 3 years and the one on the right has an estimated age of 13 years.

From the total sample size (n=818), 793 samples were used for age readings and 25 were initially discarded since no obvious/consistent band pattern was visible. Those 793 samples were read three times without previous knowledge of either the length or sex of each specimen. Each reading of all the samples was finished before starting the following reading, in order to prevent bias (i.e., familiarity with any particular vertebra) when counting the growth bands in each vertebra. For the samples whose three readings produced three different estimated ages, but with two of the three differing only by one year, a fourth reading was carried out. After all readings, only those samples whose band pair counts obtained three or two out of three identical readings were considered for the age and growth analysis.

The precision between the three initial readings was compared using the coefficient of variation (CV) (Chang, 1982) and the percentage of agreement

(PA) (Beamish & Fournier, 1981), as well as percentage of agreement within one growth band, and two growth bands (PA ± 1 year, PA ± 2 years). To graphically compare the accuracy of these readings, age bias plots were plotted between each reading against the agreed age (i.e., identical age between the three readings or between two out of the three). The R statistical language version 3.2.3 (R Core Team, 2015) was used for the precision analysis.

Growth modelling

The vertebral radius (VR) of each vertebra was obtained by measuring the distance between the *focus* and the outer edge of the *corpus calcareum* using the Image J software. All distances were measured to the nearest 0.001 mm as according to the scale present in the dissecting microscope magnification initially used to take the photos of all samples. Only 727 samples out of the 818 were used to measure VR since the remaining ones had a missing focus or an incomplete *corpus calcareum*. The relationship between the vertebral radius and fork length (FL) of each specimen was then obtained using a linear model following the equation:

$FL = a + b VR$

where, b is the slope and a is the intercept.

Growth curves were obtained for each sex separately and for sexes combined using two growth models. The first model used was a three-parameter von Bertalanffy growth function (VBGF) re-parameterized to estimate L_0 (size at birth) instead of t_0 (theoretical age at which the expected length is zero) (Cailliet *et al*., 2006):

$$L_t = L_{inf} - (L_{inf} - L_0) \times \exp(-kt),$$

where L_t = mean size (FL, cm) at age t (years);

L_{inf} = maximum asymptotic size (FL);

L_0 = size (FL, cm) at birth;

K = growth coefficient and t = age (years).

The second model used was a two-parameter VBGF where L_0 was fixed to the maximum size at birth described for this species by Pratt (1979), and by IOTC (2007) in the Indian Ocean, which is 44 cm (FL). The two models were fitted to the age data using nonlinear least squares (nls function in R) and all plots were obtained with the package “ggplot2” (Wickham, 2009) in R (R Core Team, 2015). Growth parameters were estimated, along with standard error (SE) and 95% confidence intervals (CIs).

A likelihood ratio test (LRT) (Kimura, 1980) was calculated using the “fishmethods” package (Nelson, 2017) in R, in order to test if there were differences in growth between females and males. The Akaike Information Criteria (AIC) and the Bayesian information criterion values (BIC) were used to assess the model goodness-of-fit.

Results

Sample characteristics

A total of 818 vertebral samples were collected for the present study, from which 491 belonged to male sharks and 327 to females. The size distribution for males ranged from 93 to 301 cm FL (mean ± SD: 203 ± 50.2 cm) and females ranged from 82 to 284 cm FL (mean ± SD: 204 ± 40.9 cm) (**Figure 3**). From the 818 samples, 793 were used for age readings, with 133 of these having three different readings but at least two of them differing only by 1 year, thus a fourth reading was carried out for these 133 samples. After all readings completed, 679 vertebrae (421 males and 267 females) were considered to have a valid estimated age (at least two identical readings) and were thus considered for the age and growth analysis.

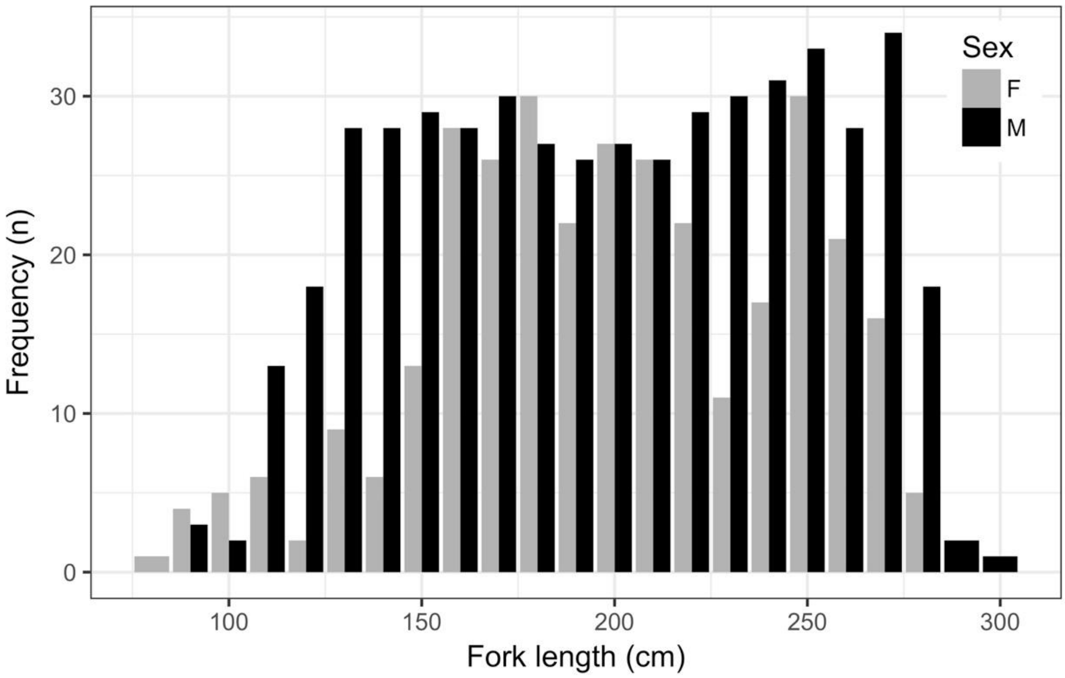

Figure 3. Size (FL, cm) frequency distribution of males (n=491) and females (n=327) vertebrae samples of *Prionace glauca* individuals collected in the South Indian Ocean between March 2013 and September 2016.

Age estimation and precision analysis

The PA between the three readings, first and second, first and third and the second and third was 29%, 37%, 44% and 54%, respectively. PA ± 1 year between the first and second, first and third, and second and third readings was 67%, 71% and 78%, respectively and PA ± 2 years between the first and second, first and third, and second and third readings was 83%, 85% and 89%, respectively. The CV between the three readings, the first and second, first and third, and second and third was 8.95%, 9.15%, 8.05% and 5.65%, respectively, and APE between the three readings, the first and second, first and third, and second and third is 6.72%, 6.42%, 5.69% and 3.99%. The age bias plots (**Figure 4**) between each reading and the agreed age between the three reveal a high agreement with no systematic bias.

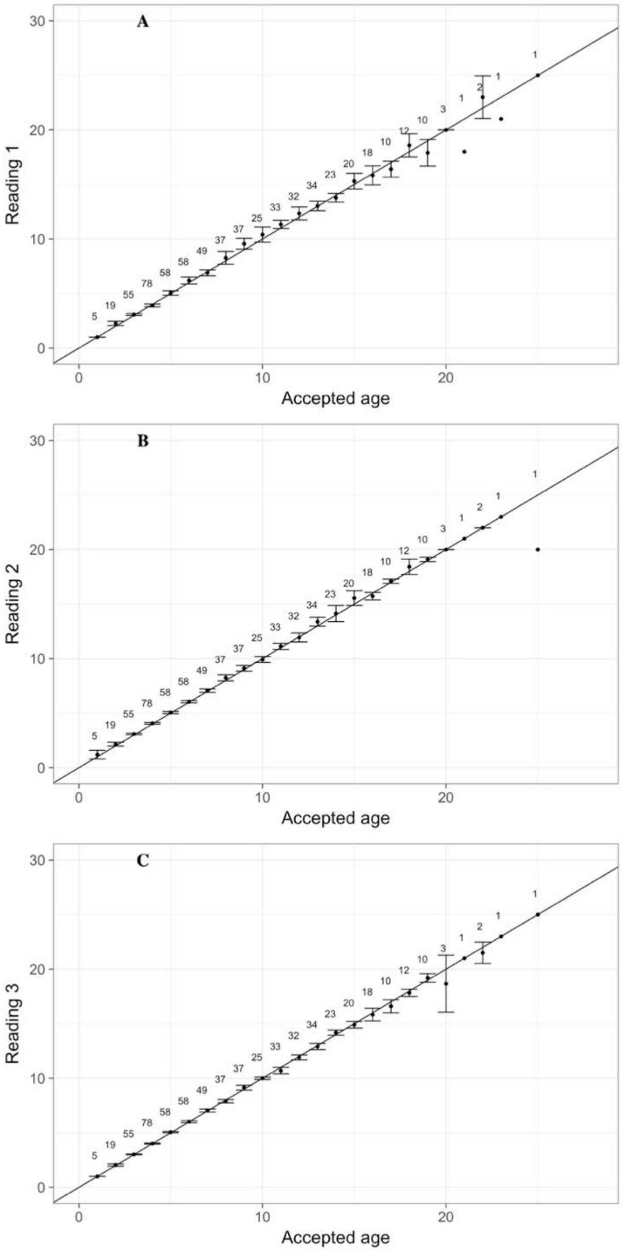

Figure 4. Age-bias plots of pairwise age comparisons between reading 1 (A), reading 2 (B), reading 3 (C) and the accepted band pair count, for vertebral samples from *Prionace glauca* from the South Indian Ocean.

Growth modelling

Regarding the relationship between vertebral radius (mm) of each vertebra and the fork length (cm) of the respective specimen, significant differences were found between sexes ($P < 0.05$). Therefore, the regression equations between VR and FL were calculated for females (FL = 17.45 VR +

13.26; r^2 = 0.91) and males (FL = 15.82 VR + 29.82; r^2 = 0.95) separately (**Figure 5**).

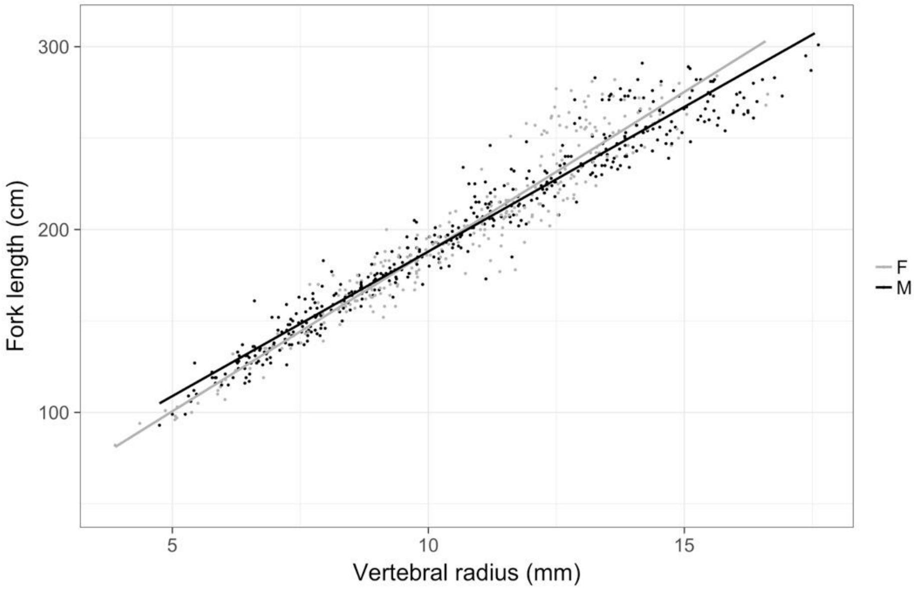

Figure 5. Relationship between fork length (cm) and vertebral centrum radius (mm) for *Prionace glauca* males (M) and females (F) from the South Indian Ocean. Dots represent individual observations and the solid lines represents the linear regressions where FL = 15.82 VR + 29.82 for males and FL = 17.45 VR + 13.26 for females. FL = fork length and VR = vertebral radius.

A total of 679 of blue shark specimens were given a final agreed estimated age. Ages ranged between 1 and 20 years for females, and between 1 and 25 years for males.

The LRT test did not reveal significant differences between sexes for each growth parameter individually (L_{inf} LRT: X^2 = 0.07, $P > 0.05$; k LRT: X^2 =0.29, $P > 0.05$; t_0 LRT: X^2 = 2.73, $P > 0.05$), but for all parameters together there were significant differences (LRT: X^2 = 10.25, $P < 0.05$). Therefore, both VBGF models used were fitted to males and females separately and also for the sexes combined (**Figure 6**).

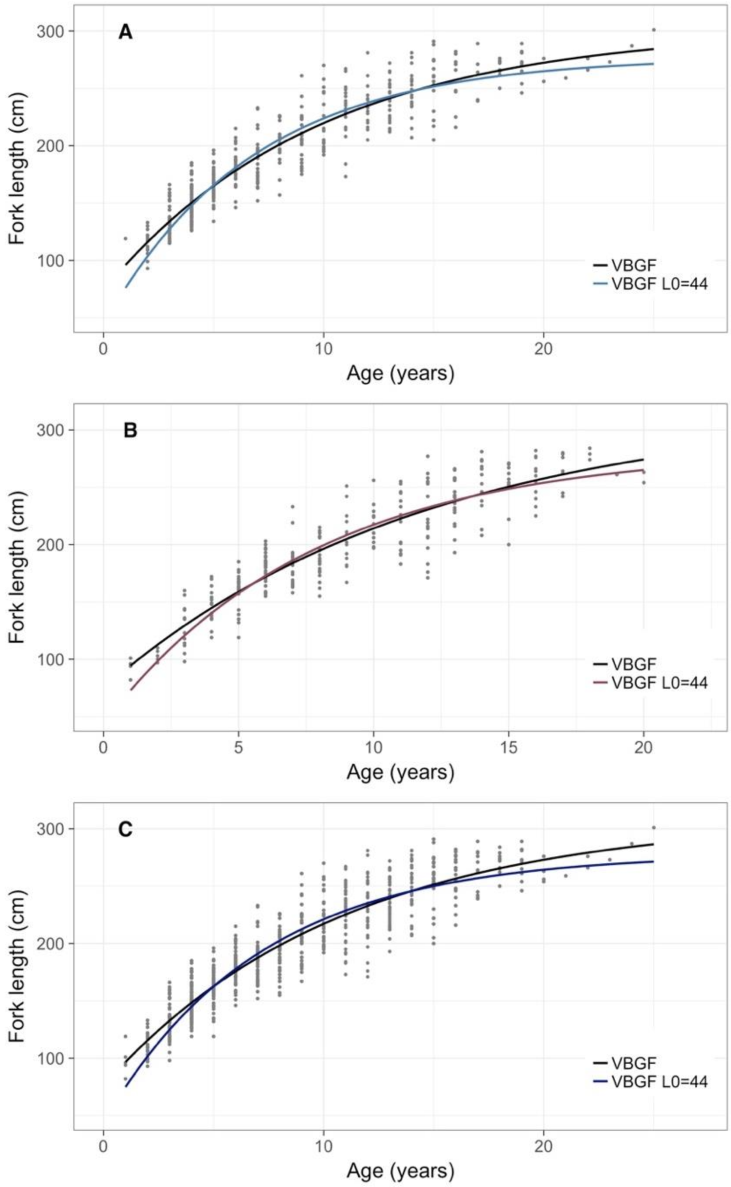

Figure 6. The von Bertalanffy growth function (VBGF) for *Prionace glauca* based on age estimations through vertebrae growth bands counting. Circles represent observed data and the lines represent the VBGF (three-parameters VBGF and VBGF with fixed L_0) for males (A), females (B) and combined sexes (C).

The growth parameters estimates are displayed in **table 1**. The estimated values of L_{inf} were higher for both sexes when using the three-parameter VBGF instead of VBGF with fixed L_0, and were also higher for females than males, using both models. The values for K were slightly higher when using VBGF with a fixed L_0. AIC and BIC were lower for the three-parameter VBGF, suggesting this model represents a better fit to the data than the VBGF with fixed L_0 (**table**

1). The results obtained with the recommended model *(see discussion section for details)* suggest females reach a higher asymptotic length (L_{inf}) than males, and males have a higher growth coefficient (K), indicating a slower growth for females (males: L_{inf} = 272.2 cm FL, K = 0.15 year^{-1}; females: L_{inf} = 283.2 cm FL, K = 0.13 year^{-1}).

Table 1. Growth parameters estimated for *Prionace glauca* (males, females and combined sexes) in the South Indian Ocean with the three-parameter von Bertalanffy growth function (VBGF) and VBGF with fixed L_0 at 44 cm fork length (FL). All estimates for both models are presented with standard error (SE) and 95% confidence levels (95% CI). L_{inf}: maximum asymptotic length, K = growth coefficient (year^{-1}), L0= size at birth (cm FL). Final parameters recommended to be used are represented in bold (*see discussion section for details*).

Sex	Model	AIC	BIC	Parameter	Estimate	SE	95% CI	
							Lower	Upper
Males	VBGF	3543	3559	L_{inf}	302.0	8.3	287.6	321.2
				K	0.102	0.009	0.084	0.121
				L_0	73.8	5.1	63.3	83.6
	VBGF L0=44	3567	3579	$\mathbf{L_{inf}}$	**277.2**	**3.4**	**270.6**	**284.2**
				K	**0.147**	**0.005**	**0.138**	**0.157**
Females	VBGF	2350	2364	L_{inf}	319.7	18.4	291.1	371.8
				K	0.084	0.013	0.058	0.111
				L_0	74.7	7.4	59.3	88.9
	VBGF L0=44	2362	2373	$\mathbf{L_{inf}}$	**283.2**	**6.2**	**271.6**	**284.8**
				K	**0.129**	**0.007**	**0.115**	**0.143**
Combined	VBGF	5900	5918	L_{inf}	309.5	8.4	295.0	328.6
				K	0.093	0.007	0.078	0.108
				L_0	75.9	4.2	67.6	83.9
	VBGF L0=44	5944	5958	L_{inf}	278.3	3.0	272.3	284.6
				K	0.141	0.004	0.133	0.149

Discussion

In the present study, two growth models were tested, namely a three-parameter VBGF re-parameterized to estimate L_0 and a two-parameter VBGF with a fixed L_0. Using the von Bertalanffy growth function over other growth models was an obvious choice since this is the most commonly used in fisheries biology for stock assessment (Cailliet *et al*., 2006; Haddon, 2011). When comparing the two approaches used, the three-parameter VBGF seems to be a better fit to the data considering the AIC and BIC results. However, it is important to highlight this is a better mathematical fit, but in biological terms it might be more adequate to use the VBGF with a fixed L_0, since the size of birth for the studied species is already known (IOTC, 2007; Pratt, 1979). Thus, this is the recommended model by the present study, more specifically with a growth curve for each sex separately since significant differences were found between sexes.

When comparing the results obtained of the present study with the ones obtained by others in the Indian Ocean, namely Jolly *et al.* (2013) and Rabehagasoa *et al.* (2014) (**table 2**), the maximum asymptotic length estimates are slightly higher in the present study than in the other two. In terms of K, the values here obtained are around the ones estimated by the previous authors. The maximum size reported for blue sharks by Compagno (1984) is of 380 cm TL (317.3 cm FL*[12]) which is higher than both L_{inf} values estimated in this study. However, when considering the previous age and growth studies of *P. glauca* made all over the world that are summarized in **table 2**, the estimates for L_{inf} here obtained are within the range of values of those studies, which ranged between 198.8 cm FL* to 353 cm FL* (Blanco-Parra et al., 2008; J. D. Stevens, 1975). The same happens for the K estimates of the present study which are between the range of 0.10 $year^{-1}$ and 0.68 $year^{-1}$ observed in the other studies. Nevertheless, it is relevant to point that the 0.68 $year^{-1}$ value for K obtained by MacNeil and Campana (2002) is much higher than all other studies here presented, where values vary mostly between 0.10 and 0.18 $year^{-1}$.

Regardless of the VBGF with a fixed L_0 being the model recommended to use, it is still interesting to look at the values estimated for L_0 using the three-parameter VBGF, and compare those with the known size at birth. The estimated L_0 for males was 73.8 cm FL, 74.65 cm FL for females and 76 cm FL for combined sexes. All three values are higher than the size at birth range of 35-44 cm FL described by Pratt (1979) for blue sharks, as well as by IOTC (2007) in the Indian Ocean. The L_0 obtained by Cailliet *et al.* (1983) of 37.6 cm FL* and 47.1 cm FL obtained by Henderson *et al.* (2001) fall in the previously described size range. Megalofonou *et al.* (2009) and Rabehagasoa (2014) estimated slightly lower values of 26.8 cm FL* and 30.2 cm FL*, respectively,

[12] **Note:** All FL* measures were obtained by converting original TL measures using the equation by Kohler *et al.* (1995) for blue sharks: FL = 0.8313 x TL + 1.39.

with the latter one corresponding to a study in the Indian Ocean. In the present study, the higher results for size at birth can be explained by the lack of samples of younger ages when comparing with the remaining ages within the total sample size.

Table 2. Summary of previous age and growth studies for *Prionace glauca* in various regions of the world. C = combined sexes, F = female, M = male, TL = total length, PCL = precaudal length, FL = Fork length, VBGF = von Bertalanffy growth function, L_{inf} = maximum asymptotic size (in cm) and k = growth coefficient. Spaces filled with "-" refer to information that is not available. The symbols "w" and "s" indicate results obtained using whole vertebrae and sectioned vertebrae, respectively.

Study	Ocean	n	Measure	Sample size (cm)	Sex	VBGF parameters L_{inf}	VBGF parameters k	Max attributed age
Aasen (1966)	N Atlantic	268	TL	-	C	394	0.133	8
Stevens (1975)	N Atlantic	82	TL	42 – 272.5	C	423	0.110	7
Cailliet *et al.* (1983)	N Pacific	130	TL	28-252.1	C M F	265.5 295.3 241.9	0.223 0.175 0.251	9
Tanaka *et al.* (1990)	N Pacific	195	TL	110 - 280	M F	369 304	0.10 0.16	11
Nakano (1994)	N Pacific	271	PCL	-	M F	289.7 243.3	0.129 0.144	10
Henderson *et al.* (2001)	N Atlantic	159	TL	64 - 228	C	376.5	0.12	6
MacNeil & Campana (2002)	N Atlantic	185	FL	147 - 282	C	300 w 302 s	0.68 w 0.58 s	8
Skomal and Natanson (2003)	N Atlantic	411	FL	49 - 312	C M F	285.4 282.3 286.8	0.17 0.18 0.16	16
Lessa *et al.* (2004)	S Atlantic	236	TL	173.8 - 310	C	352.1	0.157	12
Blanco-Parra *et al*. (2008)	N Pacific	184	TL	90 - 253	C M F	303.4 299.9 237.5	0.10 0.10 0.15	16
Megalofonou *et al*. (2009)	Mediterranean	54	TL	81.7 - 315	C	401.55	0.13	12
Jolly *et al.* (2013)	S Atlantic/ S Indian	197	TL	72 - 313	C M F	311.6 294.6 334.7	0.12 0.14 0.11	16
Rabehagasoa *et al.* (2014)	S Indian	188	FL	36 - 276	C	258	0.16	15
Hsu *et al.* (2015)	S Pacific	742	TL	-	C	352.1	0.13	15
Francis and Maolagáin (2016)	S Pacific	232	FL	Readers in this study were unable to age the samples				
Present study	S Indian	679	FL	82 - 301	C M F	278.3 277.2 283.2	0.14 0.15 0.13	25

The maximum estimated ages for blue sharks in this study were 20 and 25, for females and males respectively. The oldest individual was a 25 year old male with 301 cm FL. Both of these ages are older than any of the previously estimated ages in previous studies, as summarized in table 2. However, the longevity of this species is thought to be of about 20 to 23 years (Cailliet *et al*., 1983; Manning & Francis, 2005; Romanov *et al.*, 2011; Stevens, 2009). In their age validation study for the Indian Ocean, Romanov *et al.* (2011) obtained the ages of 19 and 23 for male specimens with 273 cm FL and 270 cm FL, respectively. Therefore, the estimates of the present study are close to those of Romanov *et al.* (2011). Nevertheless, in that study both specimens were the same sex, and despite having almost the same size still presented different ages and growth rates. This supports the need for more age and growth studies of blue sharks in the Indian Ocean, and of their biology in general.

When looking at all previous studies as well as this study (**table 2**), there are not any evident trends in growth between the Atlantic, the Pacific and the Indian oceans, suggesting a similar growth for blue sharks among different world regions. The same idea was previously mentioned by Nakano and Seki (2003), and Tanaka *et al.* (1990), who pointed that variations in the estimates between different studies are most likely due to differences in techniques used to prepare the samples, different criteria for growth zones ageing and reader precision and bias, which compromises a realistic comparison of growth between different areas.

Overall, the results obtained in this study are mostly within the ranges obtained in previous studies for other oceans. However, it should be noted that we estimated a higher maximum observed age compared to what was previously described. These results presented in this study support the fact that *P. glauca* is a long-lived slow growth species, and provide important additional knowledge to the biology of blue shark in the Indian Ocean.

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