Age and growth of the blue shark *Prionace glauca* (Linnaeus, 1758) off northeastern Brazil

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Abstract

Between 1992 and 2000, 681 blue sharks, *Prionace glauca* (173.8–310 cm total length, TL) were collected off northeastern Brazil (Brazilian EEZ). Vertebral sections of 156 males (173.8–310 cm TL) and 80 females (185.5–283 cm TL) were analysed. The index of average percentage error (IAPE) ranged from 0 to 3.1% for 3–12 growth rings (GRs). Mean marginal increment (MI) decreased from November to January without, however, conclusively confirm the annual pattern of deposition. Growth parameters were derived using the von Bertalanffy growth function (VBGF), the Richards function and the Schnute function. VBGF was that which best fit the data. Parameters derived from back-calculated lengths, $K = 0.157$, $L_\infty = 352.1$ cm and $t_0 = -1.01$ year, were considered to best describe growth. First maturity sizes of 225 cm for males and 228 cm for females corresponded to 5-GRs individuals. A 310-cm male had 12 GRs which was the highest number in the entire sample. Growth rates of 33.9 cm per GR were estimated from birth to the first band corresponding to 60.2% of size at birth, which is 56.4 cm. Adult males were 90.5% of the entire male sample and, adult females corresponded to 79.6% of the sample of females. The male sample was composed of individuals from 3 to >11 GRs and females were 3 to 10 GRs. Males were larger (with higher number of GRs) and outnumbered females in the overall sample, as commonly occurs in catches worldwide. Despite the hypothesis of differential growth by sex, postulated by several authors, the present study demonstrated that growth curves did not differ significantly, even considering significant vertebral radius (VR)–TL regressions for males and females. Higher growth rates were found in the southern Hemisphere, leading to significant differences in VBGF when compared to other areas. Discards and unreported catches are of great concern for conservation of this important apex predator.
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1. Introduction

The blue shark, *Prionace glauca*, is oceanic and circumglobal in temperate and tropical waters from 40°N to 40°S from the surface to at least 152 m in depth. This species exhibits the widest geographic distribution among all large sharks, occasionally occurring inshore in areas with narrow continental shelves or around islands (Bigelow and Schroeder, 1948; Castro and Mejuto, 1995).

Due to its abundance in gill net and longline fisheries, the species has been studied intensively in

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both the northern and southern hemispheres. In the southwestern Atlantic, where it is chiefly caught as a by-catch in longline fisheries directed at tuna and swordfish, studies have focused on morphometrics, reproduction, relative abundance, segregation, stomach contents (Hazin, 1991; Amorim, 1992; Hazin et al., 1994; Amorim et al., 1998) and aspects of population dynamics (Amorim, 1992), both in equatorial and sub-tropical areas. Stevens (1975) first studied age and growth of the species in the northeast Atlantic, however, no similar information from the southern Atlantic has been published.

Data from swordfish fisheries, monitored by observers operating in international waters off Brazil, indicate that the blue shark is the most abundant species accounting for 52.6% of catches in certain areas (Marín et al., 1998). In a survey of pelagic fishes conducted from 1992 to 1997, using a research vessel equipped with traditional Japanese tuna longline within the Brazilian Exclusive Economic Zone (EEZ) (1°N to 9°S/30 to 40°W), sharks made up 26.4% of total catches and 57.4% of the elasmobranchs were blue sharks. CPUE, in southern Atlantic ranges from 3 individuals per 1000 hooks in equatorial areas to 37.5 individuals per 1000 hooks in southern Brazil (33°S) (Hazin, 1991; Vooren et al., unpublished).

For national fleets targeting sharks based in Santos (23°58′S/046°20′W) and Natal, total landings of the species have exhibited an increasing trend in recent decades, reaching 30% in catches obtained from 17 to 33°S and ∼43% in equatorial oceanic areas (0–10°S) (Hazin, 1991; Amorim et al., 1998).

Although the status identity of blue shark stocks in the Atlantic has not yet been ascertained, there are suggestions of two independent stocks in the southern and northern Hemispheres, based on biological traits, movements and migrations (Pratt, 1979; Castro and Mejuto, 1995; Hazin, 1991).

Since the blue shark is considered a keystone predator in the ecosystem, the annual removal of large numbers of specimens, estimated to be 10–20 millions per year, is of great concern. Monitoring data are inadequate, making it impossible to assess population decline (Hilton-Taylor, 2000). Such concerns are reflected in a decision by FAO to develop an international plan of action for conservation and management of sharks and in the increasing number of scientific papers on the subject (Walker, 1998).

In such a context, age and growth information are required for age-based methods that can be used for the management of the species in the Atlantic. The aim of the present study is to supply the first growth curve using a vertebral analysis of *P. glauca* caught in the southern Atlantic. Growth parameters were estimated by a statistical fit to different growth functions.

2. Materials and methods

Research and commercial vessels operating from 1992 to 2000 in the area 1°N to 8°S/29 to 34°W (Fig. 1), collected 681 individuals (173.8–310 cm TL). Five to six vertebrae were removed from 236 individuals and, sex, total length (TL, cm), fork length (FL, cm) and interdorsal space (IDS, cm) were recorded during research operations. Sex and IDS were recorded from carcasses in commercial landings.

To estimate TL for carcasses and TL for FL, relationships were established from subsamples of IDS vs. TL and FL vs. TL. Linear regressions derived for each sex were tested for homogeneity and analysed for co-variances (ANCOVA). As significant differences were not detected, the resulted equations for sexes combined were: $TL = 3.845IDS + 44.575$ ($r^2 = 0.8068$, $n = 121$, $P = 0.093$) and $TL = 1.211FL + 0.08044$ ($r^2 = 0.9222$, $n = 122$, $P = 0.161$). Whenever length is mentioned hereafter, we refer to TL.

Cleaned vertebrae were fixed in 4% formaldehyde (24–48 h) and preserved in 70% alcohol. Vertebrae were embedded in polyester resin and sectioned approximately 1 mm thick containing the nucleus using a low-speed BUEHLER® saw. Longitudinal sections were made up of translucent (dark-narrow) and opaque (bright-broad) bands. Growth rings (GRs), defined as a band pair, were counted in each section and distances from the focus to the margin of each narrow zone were recorded in accordance to procedures described by Cailliet et al. (1983).

Vertebral radius (VR) was measured using a binocular dissecting microscope equipped with an ocular micrometer. Measurements were made at 8× magnification (1 μm unit = 0.8 mm) with both reflected and transmitted light. Sections were read twice at different times, without knowledge of the individual size or previous count. Whenever counts differed between the two readings, a third reading was done and
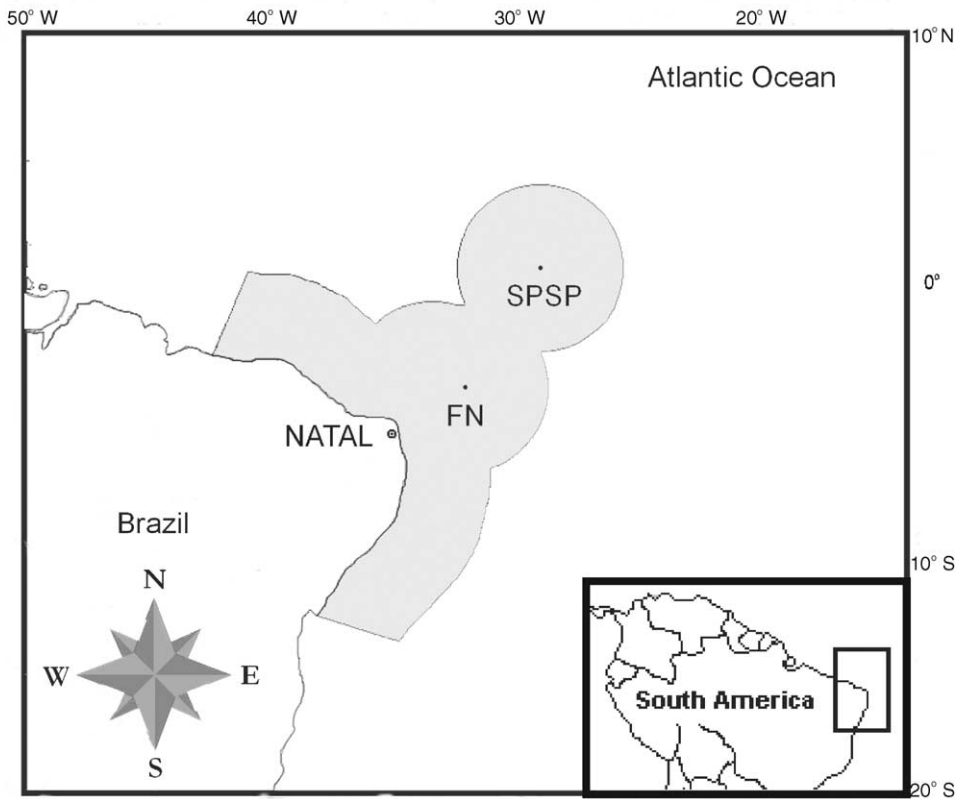
Fig. 1. Location of the study area in the southwestern equatorial Atlantic where 681 specimens of *P. glauca* were caught from 1992 to 2000. FN: Fernando de noronha Archipelago and SPSP: São Pedro/São Paulo Archipelago.

measurements were used for back-calculation of size per GR class.

The index of average percentage error (IAPE) (Beamish and Fournier, 1981) was calculated to compare reproducibility of age determination between readings:

$$[IAPE] = \frac{1}{N} \sum \left(\frac{1}{R} \sum \left(\frac{|X_{ij} - X_j|}{X_j} \right) \right) \times 100 \tag{1}$$

where N is the number of fish, R the number of readings, X_{ij} the number of GR of the jth fish at the ith reading, and X_j the mean number of GRs calculated for the jth fish.

Marginal increment analysis (MI) (Liu et al., 1999) was carried out either for GR groups or for the overall sample using vertebrae collected from 1996 to 2000, when samples were more regularly collected every month:

$$MI = VR - R_n \tag{2}$$

where VR is the vertebral radius and R_n the last complete band.

Mean $MI \pm S.D.$ was calculated monthly, tested for normality and for significant differences using analysis of variance (ANOVA) to locate periodic trends in band formation.

Proportionality between the structure and individual size was verified through linear and curvilinear regressions using ANOVA. Differences between regressions by sex were tested using ANCOVA. As regressions did not pass through the origin, the Fraser–Lee method

was employed for back-calculation (Ricker, 1969):

$$[TL]_n = \left(\frac{R_n}{VR}\right)([TL]) - a) + a \tag{3}$$

where $[TL]_n$ is the back-calculated length-at-GR n, R_n the vertebral radius at the time of the ring n, VR the vertebral radius-at-capture, TL the length-at-capture and a the intercept on the length axis. Back-calculated lengths were analysed to detect the Lee's phenomenon.

Growth parameters were estimated using different functions, fitted to the same length-at-GR data:

von Bertalanffy (1938) function (VBGF, 1938):

$$Lt = L_\infty[1 - e^{-k(t-t_0)}] \tag{4}$$

Richards function (1959, in Schnute, 1981):

$$L_t = \frac{L_\infty}{(1 + e^{(-Kt+b)})^m} \tag{5}$$

Schnute function (1981):

$$L_t = \left\{ L_1^b + [L_2^b - L_1^b]\left[\frac{1 - e_1^{-a(t-\tau)}}{1 - e_1^{-a(t-\tau)}}\right]\right\}^{(1/b)} \tag{6}$$

where L_t is predicted length-at-GR t; L_∞ the mean asymptotic total length; K the coefficient of growth; t_0 the age when length is theoretically zero; a, b (both $\neq$ 0) and m the constants. L_1 and L_2 are estimated lengths at selected reference GRs τ_1 and τ_2.

VBGF parameters derived from back-calculated lengths-at-GR were tested for comparing male and female growth using both the Kappenman method (1981) method and the Hotelling T^2 test (Cerrato, 1990).

The simplex and quasi-Newton algorithms of the Statistica package were employed to obtain the parameters of functions (4), (5) and (6). For Eq. (6), the L_∞ and t_0 were estimated as per Schnute (1981). Also, the choice of the function that best fit the data was done using an analysis of variance in accordance with procedures described by the mentioned author.

Using a number of GR-length key, based on ring counted from vertebrae, the GR structure of the overall sample (681 specimens) was estimated (Bartoo and Parker, 1983). All statistical inferences were made to a significance level of 0.05.

The growth pattern obtained in the present study was compared to others available in literature, generated through hard structure analysis (Stevens, 1975; Cailliet et al., 1983), for sexes combined, using the bivariate Hotellings' T^2 (Cerrato, 1990).

3. Results

The total sample was made up of 410 males (173.8–310 cm), 225 females (185.5–283 cm) and 46 specimens of undetermined sex (179.4–298.8 cm) (Fig. 2). Vertebral sections were analysed from 236 individuals, of which 156 were males and 80 females.

Differences for VR to TL regressions for males and females were significant (ANCOVA, $P < 0.05$). Therefore, samples were treated separately by sex and the average percentage error, calculated between two readings, provided results ranging from 0 to 3.1%. This included 3–12 GRs for males and 3–10 for females.

VR to TL relationships were estimated using linear and multiplicative models. Once tested through ANOVA, statistics of linear ($r^2 = 0.765$; $F = 725.23$) and multiplicative ($r^2 = 0.769$; $F = 739.61$) models were of the same magnitude. The observed dispersion of residuals indicated that either of these models is appropriate for describing such a relationship, as no tendency in distribution was detected. For the sake of simplicity, the linear model was chosen for back-calculations (Fig. 3).

The mean MI ± S.D. for GR groups 3–5 and for the overall sample reaches a minimum in December/January (Fig. 4). Some band formation seems to occur throughout the entire period as demonstrated by low and high MI values the year round. Differences in mean MI are significant throughout the year for these age groups. However, for GRs 6–8, although a decreasing tendency is observed in the same period as for the last mentioned groups, no significant difference was detected (Fig. 4). In view of inconsistent statistical results for all GRs, due, certainly, to the absence of a clear trend of low and high periods in MI throughout the year, we consider that the analysis does not conclusively supports the annual periodicity of GR deposition.

Lee's phenomenon was not evident and, in all instances, the back-calculated length-at-GR was smaller than observed length-at-GR for both sexes. Values of standard deviations for observed length per GR class were higher than those for back-calculated length per
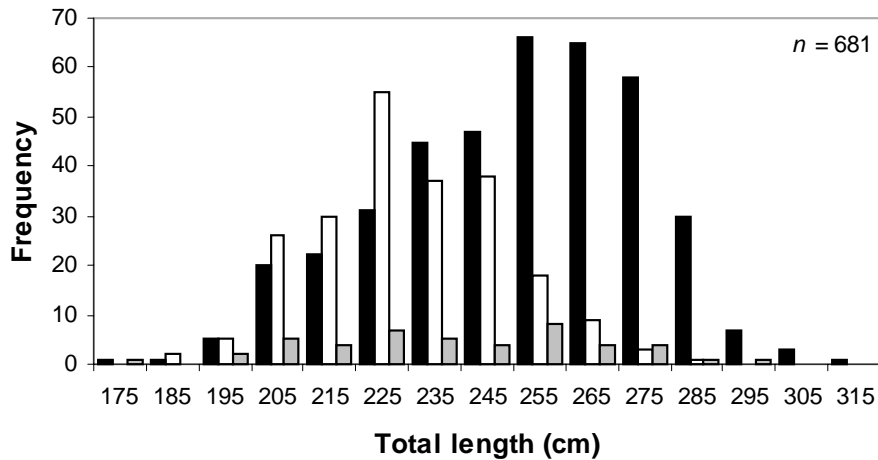
Fig. 2. Length–frequency distribution of *P. glauca* caught off northeastern Brazil (black bar: males; white bar: females; grey bar: undetermined sex).

GR class, indicating a strong variation in size for each GR class. Due to missing observed lengths for GRs 0, 1, 2 and 11, back-calculated and observed lengths were combined for these GRs classes (Table 1).

Tests for growth comparisons between sexes ($P > 0.05$) did not indicate significant differences for growth curves derived from back-calculation and back-calculated lengths combined to observed lengths. Growth curves estimated from observed length per GR class could not be tested by sex due to missing values in different GR classes by sex. Since there were no differences between sexes in growth, data were treated together.

Between all growth functions, the VBGF was the most appropriate, according to the *F* distribution, indicated for deciding the model that best represents growth for large sample sizes (Schnute, 1981) (Table 2). Furthermore, among the VBGF parameters generated, observed lengths provided higher K and lower L_∞, in comparison with back-calculated

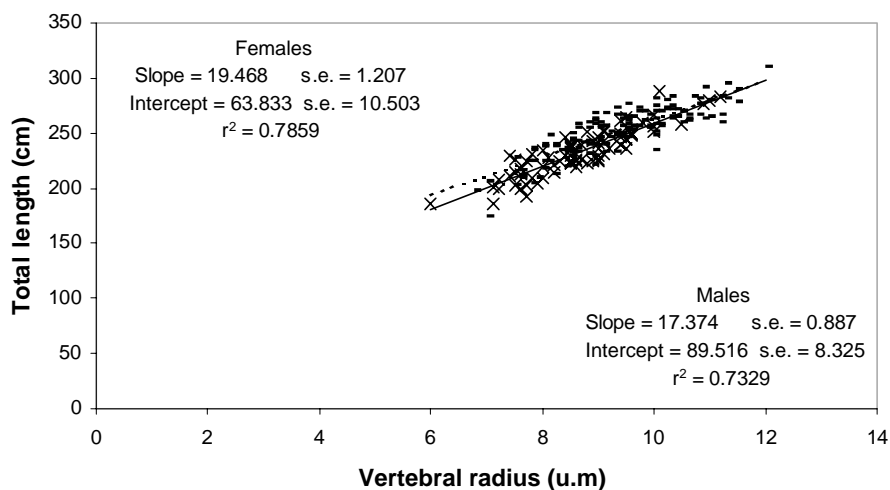

Fig. 3. Relationship between vertebral radius and total length (parameters of the equation and standard errors, S.E.) for the blue shark, *P. glauca*, off northeastern Brazil (×, females; –, males).
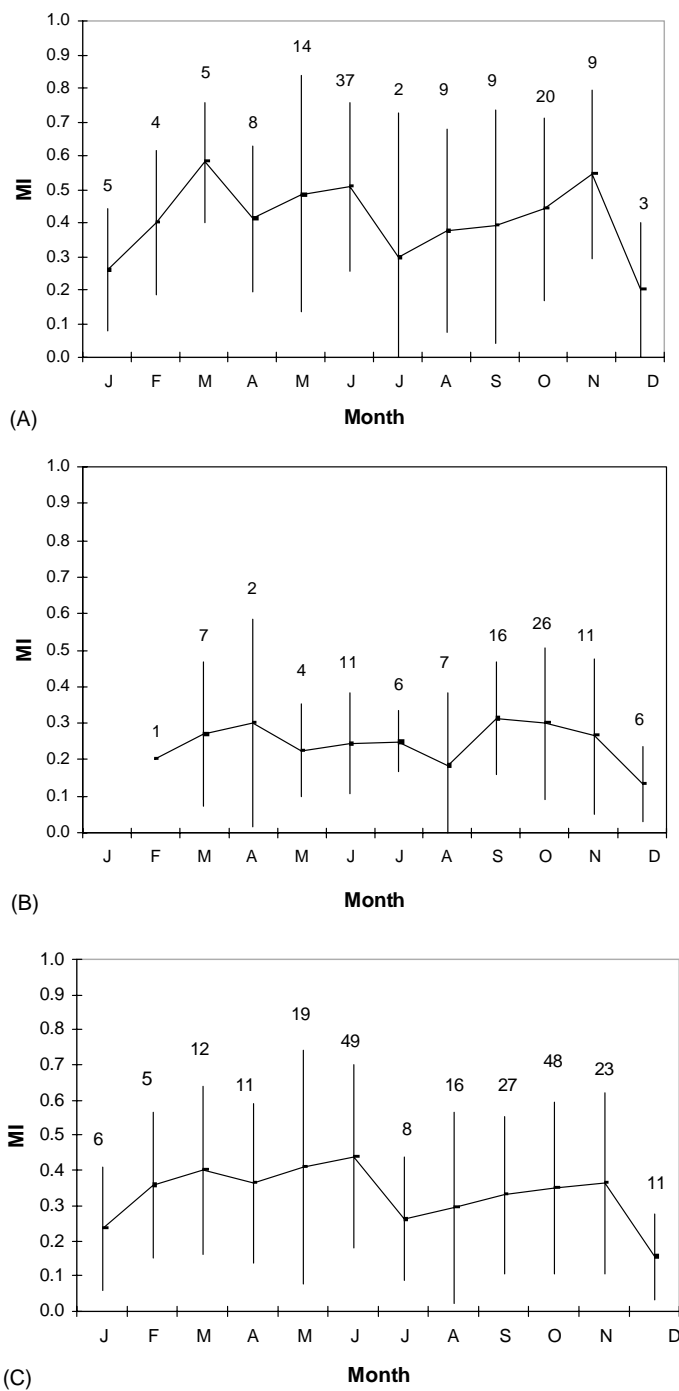
Fig. 4. Mean vertebral marginal increment (MI) by month for the blue shark, *P. glauca*. Vertical bars are standard deviation of means: (A) 3–5 GRs; (B) 6–8 GRs and C: overall sample (ages 3–12).

Table 1
Back-calculated (a) and observed length-at-GR class data (b) (cm) for combined sexes of the blue shark *P. glauca* off northeastern Brazil

t	n	GR												
		0 (236)	1 (236)	2 (236)	3 (236)	4 (230)	5 (189)	6 (110)	7 (52)	8 (22)	9 (13)	10 (4)	11 (1)	12 (1)
(a) Back-calculated														
3	6	56.79	92.06	138.02	174.95									
4	41	57.67	94.04	135.35	172.78	204.35								
5	79	57.18	92.89	133.81	170.91	202.59	228.89							
6	58	56.45	91.74	131.29	167.07	198.35	225.65	247.59						
7	30	54.98	93.03	130.27	164.48	164.05	220.09	242.62	261.02					
8	9	55.09	86.03	123.64	157.77	187.61	211.9	233.89	252.11	266.3				
9	9	55.39	87.56	124.29	158.39	187.8	213.68	236.65	254	267.84	279			
10	3	54.3	87.31	120.32	155.68	188.69	212.27	231.13	247.63	261.78	273.57	280.64		
12	1	60.17	89.28	125.66	162.04	191.15	215.4	234.81	254.21	271.19	283.32	293.02	300.3	305.15
Mean TL		56.45	90.44	129.18	164.90	190.57	218.27	237.78	253.79	266.78	278.63	286.83	300.3	305.15
S.D.		1.79	2.93	6.01	6.99	12.64	6.79	6.15	4.83	3.91	4.89	8.75	0	0
(b) Observed														
Mean TL		–	–	–	195.3	218.54	238.77	254.41	267.62	271.14	282.87	283	–	310
S.D.		–	–	–	13.20	14.37	13.48	12.02	9.96	8.65	9.51	0	–	0

Table 2
Estimated parameters of the growth models for blue shark, *P. glauca*, off northeastern Brazil (TL in cm, t_0 in years)

Parameters[a]	VBGF	Richards	Schnute
L_∞	352.1	313.4	360.3
K	0.157	0.312	–
t_0	−1.01	–	−0.145
a	–	–	0.094
b	–	−1.608	2.322
m	–	8.943	–
r^2	0.999	0.998	0.85
F	30089.88	9650.71	27803.49

[a] *F*: Fisher distribution; r^2: correlation coefficient.

observed length-at-GR and back-calculated lengths combined with observed length-at-GR, in comparison to back-calculated lengths alone. Back-calculated VBGF provided lowest K and the largest L_∞; lowest S.E. and coefficients of variation were also obtained for back-calculated VBGF.

The size-at-maturity was 225 cm for male and 228 cm for females (Hazin, 1991), corresponding to 5 GRs individuals in both cases; the oldest specimen whose vertebrae were analysed was a 310-cm 12 GRs male.

Growth rate of about 33.9 cm per GR was estimated from birth to the first band corresponding to 60.2% of the birth size, considering the length-at-birth as being 56.4 cm.

The overall sample ($n = 681$) was composed of 86.4% of the specimens showing more than 5 GRs, which is the number of GRs at first maturity (>225 cm). Adult males and females were 90.5 and

length-at-GR, whereas the VBGF estimated from the combination of observed and back-calculated lengths yielded the highest value of K parameter and the lowest L_∞ (Table 3; Fig. 5). Higher values of standard errors (S.E.) were obtained for L_∞ and K derived from

Table 3
von Bertalanffy growth parameters (standard errors, S.E.; coefficient of variation, CV) generated by back-calculated (BC) and observed length-at-GR data (OB) and observed length combined with back-calculated lengths (OB + BC) for both sexes of the blue shark *P. glauca* off northeastern Brazil

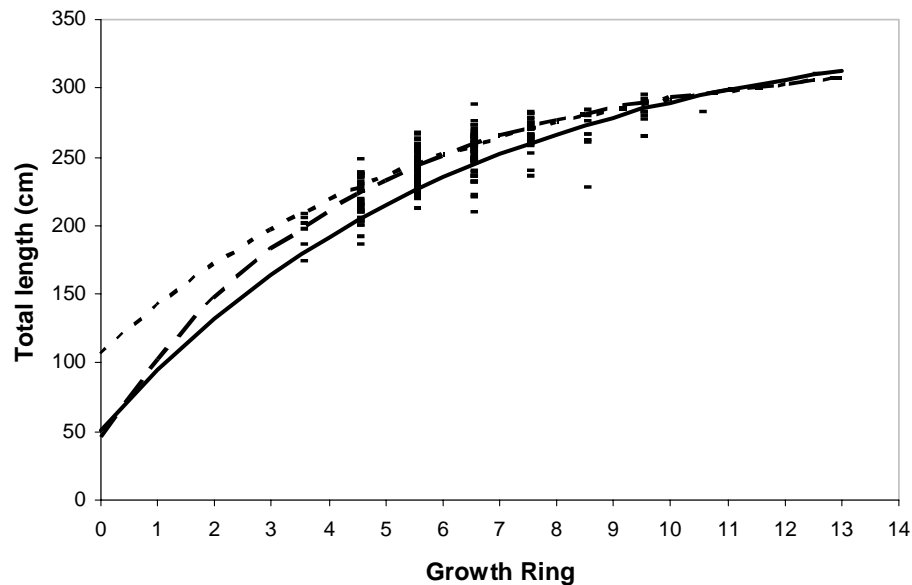| Methods	L_∞	S.E.	CV	K	S.E.	CV	t_0	S.E.	CV	r^2
BC	352.1	6.14	0.017	0.157	0.007	0.046	−1.01	0.075	−0.075	0.999
OB	331.9	17.92	0.054	0.172	0.043	0.252	−2.246	1.022	−0.454	0.984
OB + BC	321.1	10.8	0.034	0.229	0.026	0.114	−0.678	0.178	−0.263	0.987

Fig. 5. von Bertalanffy growth curves generated from: (1) mean back-calculated lengths (full line), (2) observed length per GR class (dotted line) and (3) observed lengths combined with back-calculated lengths per GR class (narrow full line) for both sexes of blue shark, *P. glauca,* off northeastern Brazil.

79.6% of the entire sample, respectively. In general, the sample was composed of individuals ranging from 3 to >11 GRs (Table 4; Fig. 6). Of these, males ranged from 3 to >11 GRs and females from 3 to 10 GRs.

Graphical comparison of the growth curve estimated in the present study with others from literature suggests that it differs from that estimated by Stevens (1975) and Cailliet et al. (1983), both derived for sexes

Table 4
Number of GR-length key (percentage) for the blue shark *P. glauca* caught off northeastern Brazil

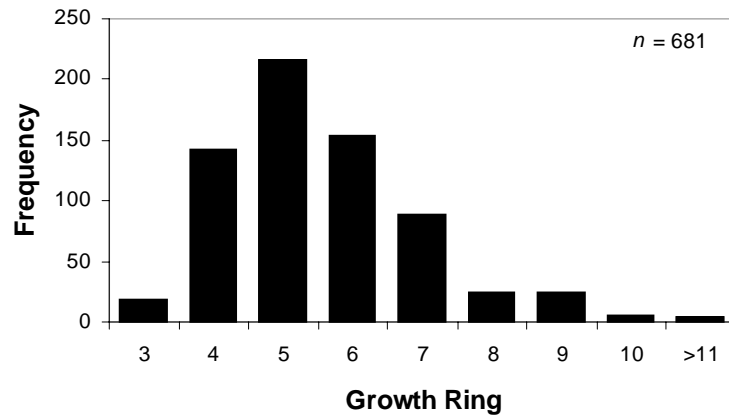| TL (cm)	*n*	GR								
		3 (19)	4 (143)	5 (217)	6 (154)	7 (89)	8 (24)	9 (25)	10 (6)	>11 (4)
170–179.9	2	100	–	–	–	–	–	–	–	–
180–189.9	3	50	50	–	–	–	–	–	–	–
190–199.9	13	33	67	–	–	–	–	–	–	–
200–209.9	52	23	69	8	–	–	–	–	–	–
210–219.9	56	–	82	18	–	–	–	–	–	–
220–229.9	93	–	27	67	3	–	3	–	–	–
230–239.9	88	–	28	44	25	3	–	–	–	–
240–249.9	90	–	3	61	36	–	–	–	–	–
250–259.9	92	–	–	42	48	9	–	–	–	–
260–269.9	82	–	–	12	41	32	12	3	–	–
270–279.9	65	–	–	–	22	56	11	11	–	–
280–289.9	34	–	–	–	11	33	11	33	11	–
290–299.9	10	–	–	–	–	50	–	50	–	–
300–309.9	0	–	–	–	–	–	–	–	–	–
310–319.9	1	–	–	–	–	–	–	–	–	100

Fig. 6. Number of growth rings composition of the blue shark sample *P. glauca* collected off northeastern Brazil.
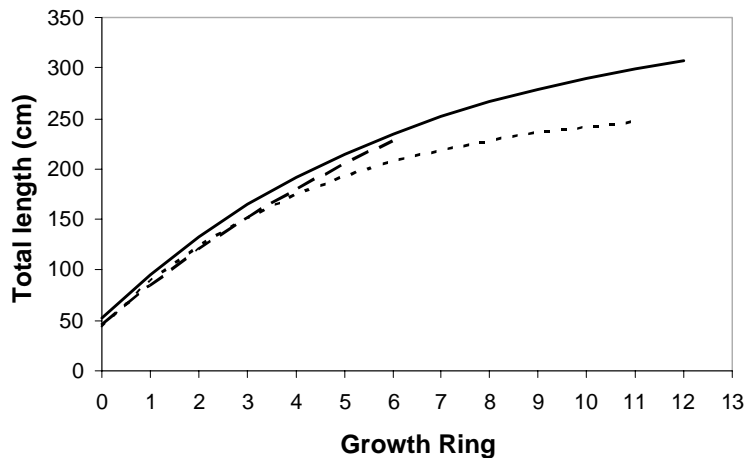

Fig. 7. Comparisons of growth curves estimated through vertebral analysis for the blue shark, *P. glauca*, from literature (Stevens, 1975, dashed line; Cailliet et al., 1983, dotted line) and present study (full line).

Table 5
von Bertalanffy growth parameters for the blue shark from the northern Atlantic (Stevens, 1975), the northern Pacific (Cailliet et al., 1983; Tanaka et al., 1990) and off northeastern Brazil (present study)

Authors	Sex[a]	L_∞	K	t_0	n
Stevens (1975)	B	423	0.11	−1.04	82
Cailliet et al. (1983)	F	242	0.25	−0.8	88
	M	295	0.18	−1.13	38
Tanaka et al. (1990)	F	304	0.16	−1.01	152
	M	369	0.1	−1.38	43
Present study	B	352	0.16	−1.01	236

[a] B: both sexes; F: females and M: males.

combined, providing higher lengths for a given GR class (Fig. 7). Also, when length per GR class, estimated by those authors, was statistically compared significant differences were found between all curves considered ($P < 0.05$) (Table 5).

4. Discussion

Dissimilarities in length–weight relationships, differences in mean sizes and in longevity and, sexual dimorphism related to external body features, suggested for the blue shark (Pratt, 1979; Amorim, 1992;

Hazin, 1991; Castro and Mejuto, 1995), led to speculations on differential growth between sexes for explaining sex-ratios that were favourable to males in catches (Castro and Mejuto, 1995).

Although distinct growth by sex has not yet been clearly ascertained, the estimation of separate equations is a common practice for the species (Cailliet et al., 1983). This is perhaps due to the assumption that biological differences determine dissimilar growth by sex (Natanson and Kohler, 1996). However, these assumed biological differences (such as dissimilar first maturity sizes) have not yet been demonstrated in the southern Atlantic.

Differences in vertebral diameter by sex gave rise to significant differences in VR–TL equations, implying that growth analysis had to be carried out separately by sex, a procedure that Schwartz (1983) and Yudin and Cailliet (1990) followed. However, in defiance of different VR–TL relationship between sexes, using the largest sample ever analysed for growth assessment of the species, VBGF turned out to be statistically similar. Therefore, in the current study, as clear differences in biological traits (size-at-maturity) between males and females were not demonstrated, we accept that growth is similar for both sexes. Statistical differences, if they do exist, may have been obscured by sources of errors (such as individual variation). Identical situations were experienced by Tanaka et al. (1990) and Natanson and Kohler (1996), who speculated on biases brought about by broad confidence intervals for each growth curve parameter. Finally, Stevens (1975) and Cailliet et al. (1983), analysing 82 and 162 vertebrae, respectively, explained the inability to demonstrate differences in VBGF by sex for the blue shark due to small sample sizes.

None of the previous studies on the blue shark tried to validate the periodicity of ring deposition and just assumed the annual pattern (Stevens, 1975; Cailliet et al., 1983), common for most Carcharhinids as *C. plumbeus* and *C. obscurus* (Natanson et al., 1995; Sminkey and Musick, 1995). In current study, high and low MI were recorded from March to October, indicating that an important number of specimens either finishes band formation or starts the development of a new band in this period. From November on, decreasing MI values for all age groups analysed were recorded, implying that a majority of individuals

with recently formed bands were present. This pattern led to significant differences in mean MI throughout the year for 3–5 GRs groups and for the overall sample. However, we considered that despite significant differences, MI analysis does not conclusively supports the annual periodicity of GRs as it does not depict a clear trend of low and high periods with low standard deviations of means during the months when the new zone is forming. Because of that we assumed that GR formation may occurs annually from November to January. Further studies on MI including larger samples are recommended as well as research involving chemical marking for age validation of the blue shark since the method was recently successful for other shark species like *Lamna nasus* (Natanson et al., 2002) and *Triakis semifasciata* (Smith et al., 2003).

The period from November to January partially coincides with that proposed by Amorim (1992) for the species in southern Brazil, where deposition is thought to occur in the first and second quarters. According to this author, several other important events in the annual cycle of the blue shark take place in the first quarter, such as mating injuries (December to February, off southern Brazil) and fertilization (starting in February, off northeast Brazil, Hazin, 1991). Also, December/January is considered birth time in the southern region with embryos measuring 2–5 cm in February/March and a new class is recruited to fisheries during this period (Amorim, 1992).

Considering the hypothesis of different populations in the northern and southern Hemispheres (Hazin, 1991; Castro and Mejuto, 1995) or, even considering one single stock in the Atlantic, differences in life history (e.g. growth rates) are expected as they may be, either genetically determined, or due to environmental factors. Thus, although the populational status for the blue shark has not yet been ascertained, the present study has suggested higher growth rates for the southern Atlantic, when compared to the northern Atlantic. Also, comparisons between the southern Atlantic and the Pacific suggested distinct growth patterns (Cailliet et al., 1983; Tanaka et al., 1990). These results point to the need for additional research for stock discrimination for the blue shark.

Samples in northeastern and southern Brazil are generally made up of males larger (modal class = 255–265 cm) than females (modal class =

225–235 cm) (Hazin, 1991; Amorim et al., 1998). Males showing 5–6 GRs in vertebrae occur together with younger females with 4–5 GRs. An identical situation was found in other areas (Pratt, 1979; Castro and Mejuto, 1995). Disparities in lengths (L_{max} females = 288.5 cm, 10 GRs; L_{max} males = 310 cm, 12 GRs), although considered a possible consequence of differential growth between sexes, do not lend conclusive support to the hypothesis proposed by the last mentioned authors. Also, differences in sizes between sexes, when similar growth rates are estimated, may be explained by the reduced growth rate after maturity (for the smaller ones) (Natanson et al., 1995). None of these hypotheses was verified in the present study.

Finally, an additional cause explaining differences can be speculated. There is a vertical segregation by sex during the fertilization period, when young females stay in shallower waters than males (Hazin, 1991), leading to catches being composed of different sizes (and ages) by sex.

Regarding the reliability of estimated growth parameters, the K value generated by back-calculation is similar to that described by Tanaka et al. (1990). However, the VBGF generated from observed lengths was considered biased, providing an unrealistic birth size of greater than 100 cm. The K value estimated from observed and back-calculated lengths combined, is of the same magnitude as that estimated by Cailliet et al. (1983), who admitted some distortion in the parameter value.

The largest specimens reliably measured were 396 (Bigelow and Schroeder, 1948) and 350 cm (Pratt, 1979), both in the north-western Atlantic. In the study area maximum size was 310 cm (present study), even with extensive collecting efforts. Therefore, L_∞ derived from back-calculations conforms to maximal lengths in the area, which is extrapolated by only 11.1%, corroborating the choice of back-calculated VBGF as best describing growth for the species in the southern Atlantic.

The scarcity in catches of individuals as large as those reported for the northern Atlantic in late 1940s and late 1970s (referred to above) may be due to heavy fishing efforts, which reduced maximum lengths in the southern Atlantic. Furthermore, the small number large specimens (with high number of GRs) in catches may be the result of their current small representation in the population.

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