



Age and growth of the blacknose shark, *Carcharhinus acronotus* (Poey, 1860) off the northeastern Brazilian Coast

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ABSTRACT

From August 1994 to January 1999 and July 2004 to December 2007, 369 blacknose sharks, *Carcharhinus acronotus* (Poey, 1860), (43.5–146 cm in total length, TL) were collected from gillnets and surveys (long-line) carried out on the continental shelf off the state of Pernambuco, Brazil (07°15'45"S and 09°28'18"S). Vertebral sections from 131 males (43.5–124 cm TL) and 146 females (46–146 cm TL) were analyzed. The index of average percentage of error (IAPE) estimated from two readings ranged from 1.61 to 4.83 (mean: 6.66%) in the vertebrae of specimens between 0 and 15 years of age. The monthly marginal increment (MIR) ratio revealed a tendency toward band pair deposition between autumn and winter, whereas the monthly distribution of growth band pair classes revealed that the first band pair appears on the vertebrae of newborns (ages 0+) about 6 months after birth (by June). This deposition pattern was found in specimens with one, two and three band pairs on the vertebrae (1+ and 2+, respectively), thereby confirming annual band pair completion in winter. Growth parameters were derived using the von Bertalanffy model (VBGM), VBGM_b (modified by length at birth: L_0), the Richards, Gompertz and Schnute models. No significant differences in growth rates were detected between the two sampling periods (1994–1999 and 2004–2008). Models with multiple inflection points, particularly the Richards model, best represented growth for the species, which was evidenced by the lowest Akaike information criterion value. There were no differences in growth between sexes. Growth parameters estimated for both sexes were $L_\infty = 129.34$ cm (SE = 1.35), $k = 0.24$ (SE = 0.009) and $m = 1.34$ with the Richards model. The "average" model was determined by averaging L_∞ between the models with substantial statistical support that were considered the most plausible (Richards and Gompertz). Thus, a consensual $L_\infty = 130.69$ cm, estimated by multi-model inference, was employed to minimize the effects of sample size and selectivity. Males and females mature at 6 years of age and the largest specimen in the catches was 15 years of age (132 cm TL). Local fishing exploitation using gillnets caught only juveniles, whereas the longlines used for the surveys caught subadult and adult specimens. *C. acronotus* is a relatively fast-growing species inhabiting shallow coastal waters throughout its lifespan, which is a pattern to be taken into account in the years to come for the management of coastal exploitation targeting valuable teleosts.

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1. Introduction

The blacknose shark, *Carcharhinus acronotus*, is a relatively small carcharhinid found in coastal waters of the Atlantic Ocean from North Carolina (USA) to Santa Catarina (Brazil), including the Gulf of Mexico, Caribbean and Bahamas (Castro, 1983; Compagno, 1984). Size at birth of approximately 50 cm in total length (TL) and maximal size of 140 cm TL have been effectively recorded (Castro,

1983; Hazin et al., 2002). The abundance of this species in near-shore areas throughout its distribution range renders it accessible to commercial and recreational fishing, which occurs mainly in inshore areas using hook-and-line and gillnets (Trent et al., 1997). Although this species makes up a significant portion of gillnet catches, it is a minor component in other fisheries (Branstetter and Burgess, 1997; Trent et al., 1997; Carlson and Cortés, 2003; Lessa et al., 2009). On the coast of Pernambuco (northeastern Brazil), neonates and juveniles are caught only by gillnets in the shallow areas in which they remain until reaching maturity, moving thereafter to deeper waters. A number of authors have reported the existence of segregation by size and sex, with smaller specimens

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(juveniles) generally found at depths reaching 10 m, while adults are caught at greater depths (>10 m) (Compagno, 1984; Schwartz, 1984).

The life history of the blacknose shark in the northern hemisphere has been extensively investigated, focusing on age and growth estimates, estimation of size at maturity and the length of reproductive cycles (Springer, 1938, 1960; Clark and von Schmidt, 1965; Branstetter, 1981; Schwartz, 1984; Carlson et al., 1999, 2007; Driggers et al., 2004a,b; Sulikowski et al., 2007). With exception of reproductive aspects (Hazin et al., 2002), information on the species in the southwestern Atlantic is scarce. Regional differences in growth aspects between populations have been suggested among areas along the US coast (Schwartz, 1984; Carlson et al., 1999, 2007; Driggers et al., 2004a, 2008). Due to the variability in growth parameters, accurate information is needed on each population for species-specific management. Although populations of blacknose shark have not yet shown any signs of overfishing anywhere (Carlson et al., 1999), their participation as bycatch in coastal fisheries throughout the Brazilian coast raises concerns due to the increasing levels of fishing effort targeting the Brazilian-Spanish mackerel (*Scomberomorus brasiliensis*), king mackerel (*Scomberomorus cavalla*) and red reef fish of the Lutjanidae family, particularly in the study area, where the blacknose shark ranks second among landings of coastal sharks. The aim of the present study was to provide the first growth estimates for *C. acronotus* in the southern hemisphere employing vertebral analysis.

2. Materials and methods

From August 1994 to January 1999 and July 2004 to December 2007, artisanal landings were sampled from fishing boats deploying gillnets in different areas (07°15'45"S and 09°28'18"S). Samples were also collected from a longline vessel operating on the continental shelf, fishing between depths of 10 and 30 m in an area near the city of Recife, Pernambuco, Brazil (07°30'S to 09°30'S).

Total length [snout to a perpendicular line from the tip of the upper caudal fin (TL, cm) in natural position (Garrick, 1982)] and sex were recorded for each individual and a block of five vertebrae was removed from each specimen. The vertebrae were cleaned and fixed in 4% formaldehyde for 24 h and stored in 70% alcohol until use. The samples were then embedded in polyester resin and each vertebra was sectioned to a thickness of approximately 0.3 mm using a low-speed metallographic saw (Cailliet and Goldman, 2004; Cailliet et al., 2006). Length mentioned hereafter refers to total length (TL).

Each growth band pair (GB) – consisting of one wide band (opaque) and one narrow band (translucent) – was examined and measured using a stereomicroscope at a magnification of 10× (Cailliet and Goldman, 2004; Cailliet et al., 2006). Only transmitted light was used so that the narrow bands would appear light and wide bands would appear dark. The distances from the focus of the vertebra to the outer margin of each band pair and to the edge of the section (vertebral radius) across the corpus calcareum were recorded (Cailliet and Goldman, 2004; Cailliet et al., 2006).

Due to the long sampling period, differences in growth between 1994–1999 and 2004–2009 were investigated. To this end, mean lengths at age were back-calculated and growth rates were derived. To identify differences between linear regressions, growth rates (Y) versus the average length between years (X) were related (Sparre et al., 1989) in each sampling period. Differences between regressions were tested using analysis of covariance (ANCOVA).

The average percentage of error (APE) (Beamish and Fournier, 1981) was calculated to compare the reliability of the readings:

$$APE = 100\% \times \frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j}$$

in which N is the number of vertebrae; R is the number of readings of individual j ; X_{ij} is age i determined for individual j ; and X_j is the mean age calculated for individual j .

Two independent readings were performed by two separate readers with no prior knowledge on the length of the specimen. When counts differed between readers, a third reading was performed for consensus. All age groups with APE values greater than 10% were read again. The age-bias plot (Campana et al., 1995; Campana, 2001) was used to detect count differences between readers. The percent agreement ($PA = [No. (agreed/No.) \cdot read] \times 100$) and percent agreement plus or minus 1 year ($PA = [\pm 1 \text{ yr}]$) were calculated for the entire sample. The relationship between vertebral radius and TL was calculated for the sexes separately and compared using ANCOVA.

Excluding newborns with only the birth mark on vertebrae, the periodicity of band pair deposition was analyzed through the monthly marginal increment ratio (MIR) in order to locate the period in which the narrow band is formed and a new band pair begins to form (Natanson et al., 1995), using the following equation:

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

in which VR is the vertebral radius; R_n is the distance from the core to the last band pair; and R_{n-1} is the distance to the penultimate band pair. Monthly median values were analyzed using the Kruskal–Wallis test with Dunn's post hoc test (Sokal and Rohlf, 1995).

The monthly frequency distribution of specimens displaying a birth mark (0+), (1+) and (2+) GBs were analyzed in order to determine the period of the year in which narrow band deposition is accomplished as well as the length of the period from birth (Hazin et al., 2002) to the first band pair deposition. Different growth models were fitted to the observed age and length data: the von Bertalanffy growth model (VBGM; von Bertalanffy, 1938); a modified form of the von Bertalanffy growth equation (VBGM_b) (Cailliet et al., 2006); the Gompertz growth model (Campana and Jones, 1992); the Richards growth model (Schnute, 1981); and the Schnute growth model (Schnute, 1981). These models are delineated as follows:

$$\begin{aligned} VBGM - L_t &= L_\infty [1 - e^{-K(t-t_0)}] \\ VBGM_b - L_t &= L_0 + (L_\infty - L_0) [1 - e^{(-k)t}] \\ Gompertz - L_t &= L_\infty e^{[-ae^{(-kt)}]} \\ Richards - L_t &= L_\infty / [1 + e^{(-kt+b)}]^m \\ Schnute - L_t &= \{L_1^{b^*} + [L_2^{b^*} - L_1^{b^*}] [1 - e_1^{-a(t-\tau_1)} / 1 - e_1^{-a(\tau_2-\tau_1)}]^{(1/b^*)}\} \end{aligned}$$

in which L_t = length at age t ; L_∞ = maximal asymptotic length; L_0 = length at birth; k = growth coefficient; t_0 = theoretical age at which fish has zero length; L_1 and L_2 = estimated lengths at age τ ; τ_1 = first specified age, τ_2 = last specified age; a and b = regression parameters; m = constant; a^* = constant relative rate of relative growth rate; b^* = incremental relative rate of relative growth rate. For the Schnute model, L_∞ and t_0 were estimated based on Schnute (1981).

The VBGM_b fixes the beginning of the curve at pre-defined birth sizes (L_0 , in cm, estimated based on a) the mean between the size of the smallest free-swimming individual and largest embryo and the mean of the back-calculated lengths for age 0 of individuals with an evident birth mark. The lowest value of the residual sum of squares (RSS) was the criterion used to define which L_0 provided the best fit to the VBGM_b for use in subsequent analyses.

Table 1Average observed lengths for age class data for combined sexes of blacknose shark, *Carcharhinus acronotus*, off northeastern Brazil; SE = standard error.

Age class (year)																
n = 277	BM	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+
Mean	52.93	59.08	66.13	77.57	89.80	95.48	103.02	106.12	108.75	111.95	114.74	119.46	119.73	123.91	124.92	130.00
SE	3.63	3.73	6.68	13.69	6.58	7.34	7.01	6.46	3.30	4.10	5.16	3.52	5.44	2.51	5.54	2.10

The parameters for all models were derived using the Solver function on the Excel program. The likelihood tools and bootstrap iteration functions of the PopTools program (Hood, 2006) were used to generate confidence intervals for each parameter based on minimum likelihood. The results for the definition of the best fit among the models was evaluated based on (1) the Akaike information criterion (AIC) and (2) corrected Akaike information criterion (AIC_c) (Katsanevakis, 2006):

$$(1) AIC = -2 \log(\theta) + 2k$$

$$(2) AIC_c = n \ln \left(\frac{RSS}{n} \right) + 2k + \frac{k+1}{n-(k+1)}$$

in which θ is the minimum likelihood; k is the number of model parameters; and RSS is the residual sum of squares.

Differences in AIC_c values ($\Delta_i = AIC_{C,i} - AIC_{C,min}$) were estimated between all models used in the study (Table 1). The criteria established for assessing the statistical support of each model were based on the premises proposed by Burnham and Anderson (2002), in which $\Delta_i > 10$ evidences essentially no support from data, $4 < \Delta_i < 7$ evidences very little support; and $\Delta_i < 2$ evidences substantial support. The Akaike weight (w_i) was also used to demonstrate which model best fit the data, using the following formula:

$$w_i = \frac{e^{(-0.5 \times \Delta_i)}}{\sum_{k=1}^5 e^{(-0.5 \times \Delta_i)}}$$

Based on multi-model inference (MMI) (Burnham and Anderson, 2002), when a model had $w_i \leq 90\%$, average L_∞ (\bar{L}_∞) values were estimated across models with substantial support from the data:

$$\bar{L}_\infty = \sum_{i=1}^2 w_i \times \hat{L}_{\infty,i}$$

Unconditional standard errors were estimated as:

$$SE(\bar{L}_\infty) = \sum_{i=1}^5 w_i \times (\text{var}(\hat{L}_{\infty,i} | m_i) + (\hat{L}_{\infty,i} - \bar{L}_\infty)^2)^{1/2}$$

Age composition was estimated using an age-length key (Bartoo and Parker, 1983) for the entire sample. Using this same method, age at maturity was calculated for sizes at maturity of 104 and 103 cm for males and females, respectively (Hazin et al., 2002). Longevity (ω) – considered to be the age at which 99% of the theoretical maximal size is reached – was estimated using the Fabens algorithm: $7.21 \ln 2/k$ (Cailliet et al., 2006). All statistical tests were considered significant at an α level of 0.05.

3. Results

Among the overall sample (205 females and 164 males), size ranged from 44 to 132 cm for females and 43.5 to 128 cm for males (Fig. 1). Length frequency distribution for sexes separately exhibited two modes – one made up of juveniles caught with gillnets (43.5–80 cm) and another made up of adults and subadults near maturity caught with a bottom longline (80–132 cm). The composition of the samples in separate periods were as follows: 1994–1999: 51 males (49–119.5 cm) and 69 females (46–131 cm); 2004–2008: 80 males (43.5–122.5 cm) and 77 females (51.3–132 cm). Based on

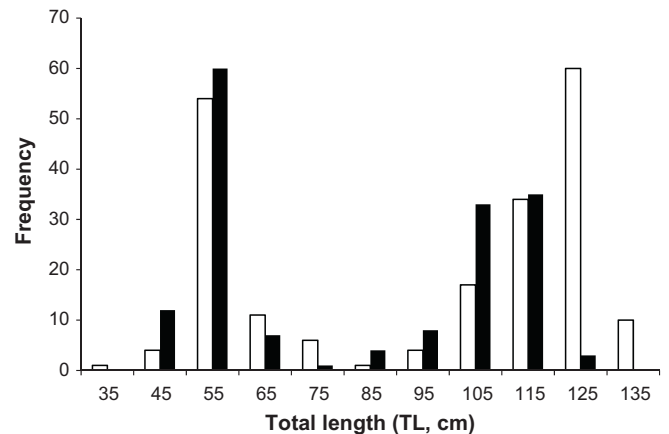


Fig. 1. Length frequency distribution (absolute numbers) for blacknose sharks, *Carcharhinus acronotus*, caught off northeastern Brazil; white bars represent females and black bars represent males ($n = 369$).

the ANCOVA results ($F = 20,595$, $p = 0.65$), no significant differences in growth rates were found between the two periods considered (1994–1999, $n = 120$; 2004–2009, $n = 157$) (Fig. 2).

For the determination of growth parameters, 277 vertebrae were analyzed from 146 females (44–132 cm) and 131 males (43.5–128 cm). Vertebrae were also examined from full-term male (43.5 and 46.8 cm) and female (44.3 and 48.5 cm) embryos on which no pre-birth or birth marks were observed. The first distal narrow band to the focus was interpreted as the birth mark (BM), equivalent to age 0+. The location of the BM coincided with a slight angle change in the corpus calcareum. In two independent readings, one birth mark and 15 complete bands pairs were recorded. The former group was composed of individuals with only a BM (age 0+) and the latter group was made up of individuals at age 15+ (Table 1).

The average percentage error (APE) calculated between readings was 6.66% for the entire sample and the variation among the classes was 1.61% at age 0 (1 band pair) and 4.83% at age 15 (16 band pairs). The third reading was a consensus for classes for which the read-

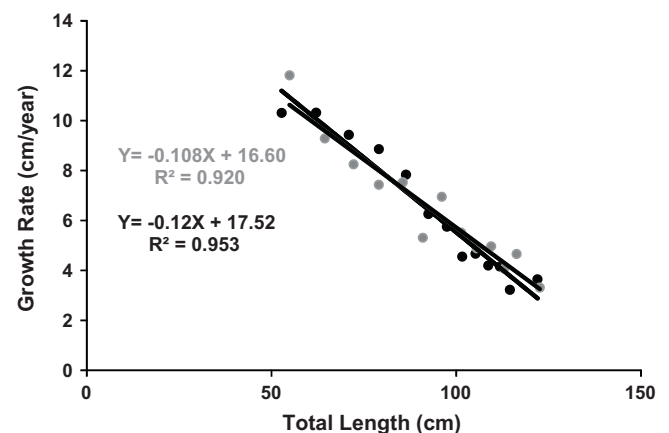


Fig. 2. Relationship between growth rate (cm/year) and total length (cm) of blacknose sharks in 1994–1999 (grey dots, $n = 120$) and 2004–2008 (black dots, $n = 157$).

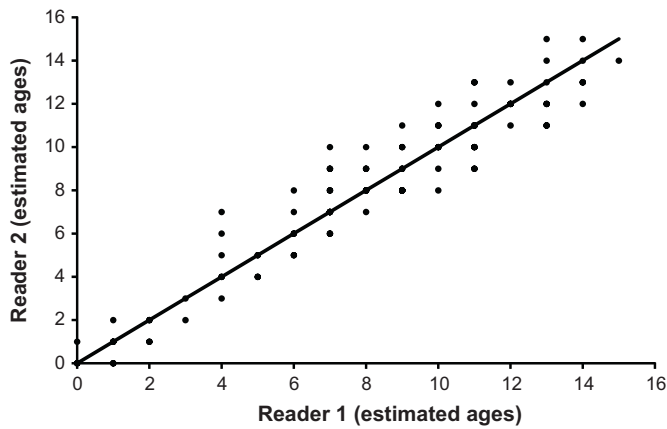


Fig. 3. Age bias plot (observed ages) for blacknose sharks, *Carcharhinus acronotus*, caught off northeastern Brazil.

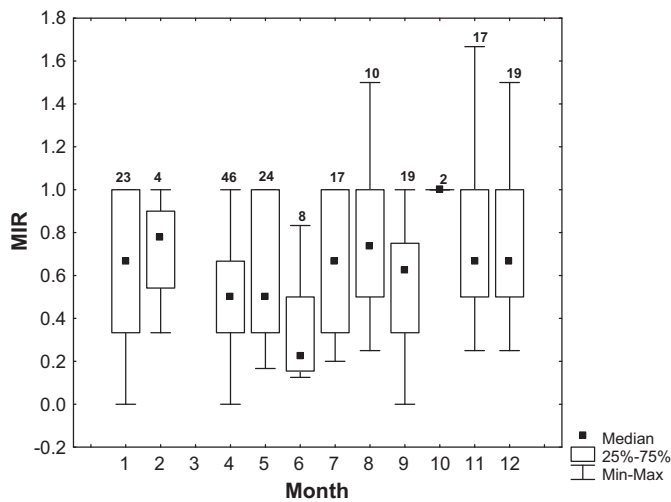


Fig. 4. Median vertebral marginal increment ratio (MIR) ($n=189$) by month for blacknose sharks, *Carcharhinus acronotus*, on coast of northeastern Brazil.

ing error was greater than 10% (Fig. 3), i.e. Classes 1 and 3 (10.47% and 10.60%, respectively), which resulted in relative errors of 1.66% ($n=14$) and 3.57% ($n=2$). The overall final APE was 4.31%, with a percent agreement (PA) of 80.38% and percent agreement ± 1 ($PA \pm 1$) of 93.21%.

The monthly analysis of the marginal increment ratio (MIR) (carried out on 189 individuals) revealed significant differences ($H=17.17$, $gl=9$, $p<0.05$), clearly showing decreasing median values from January to June, when the MIR was lowest, and increasing thereafter (Fig. 4). Furthermore, the monthly frequency distribution of growth band pairs (GB) for newborns (0 GB) as well as specimens with one and two GBs revealed that the former (displaying only the

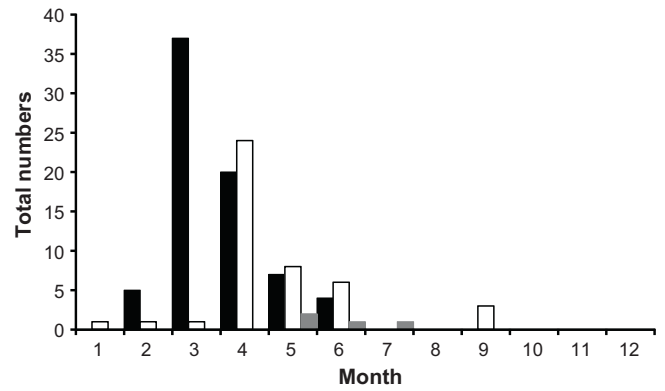


Fig. 5. Monthly frequency distribution (absolute numbers) for blacknose sharks, *Carcharhinus acronotus*, caught off northeastern Brazil; black bars = newborns (0+); white bars = age 1+; grey bars = age 2+.

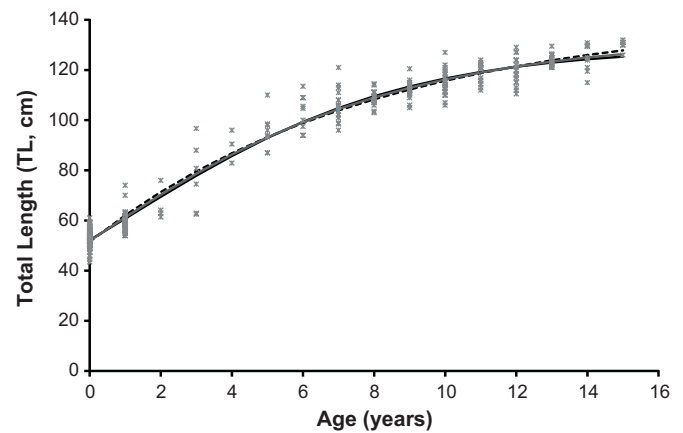


Fig. 6. Estimated growth curves for blacknose sharks, *Carcharhinus acronotus*, off northeastern Brazil; black line = Richards; grey line = Gompertz; dashed black line = von Bertalanffy; asterisks = observed length-at-age; $n=277$.

birth mark) and the majority of the latter were found in samples in the first half of the year (Fig. 5), indicating that these age groups complete band pair formation in this period. Considering the consistent trend for the overall sample (Fig. 4) as well as for young specimens (0–2 GBs) (Fig. 5), the analyses support the annual periodicity of one growth band pair per year for *C. acronotus* in the study area.

The lowest AIC value was estimated using the Richards model, which was considered the best model for describing the growth of the blacknose shark (Fig. 6). This was followed by the Gompertz model, which achieved a very similar AIC value ($\Delta i < 1$) (Fig. 6). The VBGM (Fig. 6), $VBGM_b$ ($L_0 = 43.5$, cm TL) and Schnute models ranked third, fourth and fifth, respectively (Table 2).

The “average” model was determined by averaging the predicted L_∞ response as a consensus parameter between the models

Table 2

Growth models and parameters estimated for *Carcharhinus acronotus* using von Bertalanffy (VBGM), modified von Bertalanffy ($VBGM_b$), Richards, Gompertz and Schnute models; L_∞ = maximal asymptotic length (cm); k = growth constant; t_0 = theoretical age at which fish has zero length (years).

Model	L_∞	SE	CI (–/+)	k	SE	CI (–/+)	t_0	SE	CI (–/+)
VBGM	142.06	2.84	132.11/148.37	0.12	0.007	0.10/0.13	3.65	0.17	–3.39/–3.32
$VBGM_b$	137.19	2.25	129.24/135.92	0.14	0.007	0.12/0.15	–	–	–
Richards ^a	129.34	1.35	126.69/131.99	0.24	0.009	0.23/0.26	–	–	–
Gompertz ^b	132.98	1.67	129.70/136.25	0.19	0.008	0.17/0.21	–	–	–
Schnute ^c	212.21	4.24	73.53/262.21	–	–	–	0.11	0.005	0.20/–0.02

^a Other parameter: $b = -0.03$; $m = 1.34$.

^b Other parameter: $a = 0.94$.

^c Other parameter: $a = -0.5$; $b = 8.39$.

Table 4

Growth parameters estimated for *Carcharhinus acronotus* in Atlantic Ocean (modified from Driggers et al., 2008) using von Bertalanffy growth model (VBGM); L_{∞} = maximal asymptotic length; k = growth constant for each model; t_0 = theoretical age at which length is 0.

Locality		L_{∞} (FL, cm)	L_{∞} (TL, cm)	k	t_0 (years)
Northern Gulf of Mexico (Carlson et al., 2007)	♀	136.32	156.49	0.10	−3.23
	♂	105.36	123.16	0.22	−2.04
	♀♂	117.48	136.21	0.15	−2.59
South Atlantic Bight (Driggers et al., 2004a)	♀	113.55	131.98	0.18	−4.07
	♂	105.86	123.70	0.21	−3.90
	♀♂	110.69	128.90	0.19	−4.17
Areas combined (Driggers et al., 2008)	♀	104.26	121.98	0.30	−1.71
	♂	97.93	115.16	0.36	−1.62
	♀♂	101.23	118.72	0.32	−1.70
Present study	♀	–	137.91	0.14	−3.21
	♂	–	137.77	0.12	−3.70
	♀♂	–	142.02	0.12	−3.66

accepted for not estimating a t_0 parameter, which is considered artificial and meaningless (Cailliet et al., 2006; Simpfendorfer et al., 2002).

Regarding the Akaike weight (w_i), which represents the probability of choosing the correct model from a set of models, when no growth model has $w_i \geq 90\%$, multi-model inference (MMI) should be performed (Katsanevakis, 2006) for consensus parameters among plausible models. As the Richards and Gompertz models both achieved $\Delta i \leq 1$, their weights (w_i) were similar, indicating the applicability of the consensus estimate (MMI) between them. Thus, when there is no “clear winner”, the choice of the second best model is highly dependent on the first (Katsanevakis and Maravelias, 2008). Therefore, the results of the present study are in agreement with the authors cited, as the Richards model yielded the best fit, followed by the Gompertz model in second place and the VBGM in third.

Furthermore, the Richards and Gompertz models generated similar parameters to those estimated for *C. acronotus* in the North Atlantic. Re-estimating parameters from a previous study, Carlson et al. (2007) suggest that the Gompertz model is the most appropriate, lending support to the tendency toward models with inflection points for describing the growth of this species.

A number of studies address aspects of the life history of *C. acronotus* in the northwestern Atlantic, with regional differences regarding age and growth (Schwartz, 1984; Carlson et al., 1999, 2007; Driggers et al., 2004a, 2008). Considering two main areas for the species in the South Atlantic Bight, Northern Gulf of Mexico and both areas combined, Driggers et al. (2008) found significant differences between sexes when adjusting the VBGM, with females having higher L_{∞} values and lower k and t_0 values.

In the present study, the length range of the specimens was similar to that reported for the USA (43.67–128.26 cm TL) (Driggers et al., 2008). However, while similar L_{∞} values were estimated for males and females, the growth rate (k) for females was higher than for males, which contrasts the results reported for America. Schwartz (1984) describes a similar result to that of the present study in North Carolina (USA). When parameters obtained in combined areas in the United States (Driggers et al., 2008) are compared to those in the present study, the growth rates estimated for America are substantially higher (Table 4).

The comparison of the growth pattern between the two periods considered in the current study is mandatory, since the species is exploited and may have developed compensatory mechanisms for the mortality brought about from fisheries, as has been suggested but not yet ascertained for other shark species, such as *Carcharhinus plumbeus* (Sminkey and Musick, 1995). The results of this comparison, which reflect the moderate level of exploitation to which the species is submitted, as no differences in growth rates were detected, are in agreement with findings described by Carlson et al.

(1999), who concluded that populations of blacknose shark have not yet shown any signs of overfishing anywhere.

In summary, the blacknose shark is a relatively fast-growing shark (Branstetter, 1990) inhabiting relatively shallow coastal waters for the duration of its lifespan, with juveniles and adults of both sexes sharing the same areas. This pattern makes the species highly vulnerable to fisheries. Increased mortality in early life stages due to the lack of nurseries (Knip et al., 2010) is thought to be compensated by the benefits of abundant resources, which promote fast growth. The fact that fisheries reach the juvenile part of the stock raises concerns, as fishing efforts in coastal areas off north-eastern Brazil are increasing. Thus, a better understanding of the life history and demographic aspects of the blacknose shark is required in order for sustainable exploitation to be ensured throughout the study area.

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