# Age and growth of two sharpnose shark species (*Rhizoprionodon lalandii* and *R. porosus*) in subtropical waters of the south-western Atlantic

*Jéssica T. Corsso* [iD] [A], *Otto B. F. Gadig*[B], *Fabio P. Caltabellotta* [iD] [C,D],
*Rodrigo Barreto*[E] *and Fabio S. Motta* [iD] [A,F]

[A]Laboratório de Ecologia e Conservação Marinha, Instituto do Mar, Universidade Federal de São Paulo, Rua Dr Carvalho de Mendonça 144, Encruzilhada, Santos, SP 11070-100, Brazil.

[B]Laboratório de Pesquisa de Elasmobrânquios, Instituto de Biociências, Universidade Estadual Paulista, Campus do Litoral Paulista, Praça Infante Dom Henrique, Parque Bitaru, São Vicente, SP 11330-900, Brazil.

[C]Coastal Oregon Marine Experiment Station, Oregon State University, 2030 SE Marine Science Drive, Newport, OR 97365, USA.

[D]Fisheries and Aquatic Sciences Program, School of Forest Resources and Conservation, University of Florida, 118 Newins-Ziegler Hall, PO Box 110410, Gainesville, FL 32611-0410, USA.

[E]Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul do Brasil, Instituto Chico Mendes de Conservação da Biodiversidade, Avenida Carlos Ely Castro, 195 Centro, Itajaí SC, 88301-445, Brazil.

[F]Corresponding author. Email: fmotta@unifesp.br

**Abstract.** The age and growth of subtropical populations of the Brazilian and Caribbean sharpnose sharks (*Rhizoprionodon lalandii* and *R. porosus* respectively) were determined by combining direct and indirect ageing methods, maximising the use of available information. Using vertebrae ageing for *R. lalandii*, the theoretical maximum length $L_\infty$ and growth coefficient $k$ were 661.9 mm and 1.14 year$^{-1}$ for males and 751.7 mm and 0.59 year$^{-1}$ for females. Vertebrae were not sampled for *R. porosus*. Values of $L_\infty$ and $k$ from electronic length–frequency analyses (ELEFAN) were 762 mm and 0.71 year$^{-1}$ for male *R. lalandii*, 791 mm and 0.67 year$^{-1}$ for female *R. lalandii*, 1040 mm and 0.41 year$^{-1}$ for male *R. porosus* and 1165 mm and 0.31 year$^{-1}$ for female *R. porosus*. Growth during the first year of life in relation to birth size was 80.3% for *R. lalandii* and 55% for *R. porosus*. Both species exhibit rapid growth, primarily in the first year of life. The growth estimates for *R. lalandii* and *R. porosus* are even faster than those reported in previous studies from tropical populations.

**Keywords:** elasmobranch, fishery management, length–frequency ageing, life history, vertebrae ageing.

## Introduction

Improved understanding of age and growth patterns is essential for assessing population vulnerability and evaluating demographic changes over time (Cailliet 2015). In addition, age and growth estimates are crucial for constructing age-structured population dynamic models (Cailliet *et al.* 2006). Thus, life history information is relevant for elasmobranchs considering that 44.7% of species are classified as 'Data Deficient' by the International Union for Conservation of Nature (IUCN; Dulvy *et al.* 2014).

The genus *Rhizoprionodon* Whitley, 1929 comprises seven small- to medium-sized shark species (maximum total length (TL) ~1780 mm), distributed worldwide in inshore waters of tropical and subtropical seas (Ebert *et al.* 2013). Because of their coastal distribution, the genus is one of the most frequently caught in the world's fisheries, especially small-scale fisheries (Castillo-Géniz *et al.* 1998; Motta *et al.* 2005). Like other small coastal shark species, rapid growth is a common characteristic of *Rhizoprionodon* species (Carlson and Baremore 2003; Loefer and Sedberry 2003; Harry *et al.* 2010), with the highest growth rate reported in the literature for the Australian sharpnose shark *R. taylori* (Ogilby, 1915) from Australia and Papua New Guinea (Simpfendorfer 1993; Baje *et al.* 2018).

The Brazilian sharpnose shark *R. lalandii* (Valenciennes, 1839) occurs from western Panama to southern Brazil (Compagno 1984), and the Caribbean sharpnose shark *R.*

*porosus* (Poey, 1861) occurs from the Caribbean Sea to Uruguay. Two populations were identified for *R. lalandii*: the first in the Caribbean and the second in Brazil (Mendonça *et al.* 2013). However, this geographical segregation possibly occurs along the Brazilian coast due to observed differences in size at maturity between the north and south-east regions (Motta *et al.* 2007). Similarly, molecular and morphometric data suggest two management units for *R. porosus* along their distribution area: the first between the Caribbean and the northern coast of Rio Grande do Norte State and the second between the east coast of Rio Grande do Norte State and the extreme south of Brazil (Mendonça *et al.* 2011; Lucena and Lessa 2019). In Brazil, where these two species co-occur, *R. lalandii* is more abundant in the south-eastern region and *R. porosus* is more abundant along the northern and north-eastern coasts (Motta *et al.* 2005).

Both species exhibit placental viviparity as the main embryo nutrition mode, with an annual reproductive cycle and concurrent ovarian and gestation cycles (Parsons 1983; Compagno 1984; Ferreira 1988). Although age and growth parameters have been estimated within tropical waters in northern Brazil (Lessa *et al.* 2009), parameters for populations belonging to the south-eastern region remain unknown. In this area, *R. lalandii* is the most frequent small coastal shark species caught by small-scale artisanal fisheries, followed by *R. porosus*, comprising ∼60 and 15% of shark landings respectively (Motta *et al.* 2005).

In Brazil, fisheries management is nearly non-existent. Fishery statistics data have not been collected since 2007. In addition, in regions where fishing monitoring is still conducted, there is low taxonomic resolution of elasmobranch data, making it difficult to assess the vulnerability of species (Barreto *et al.* 2017). The threat status of *R. lalandii* is 'Data Deficient' globally and 'Near Threatened' in Brazilian waters (Rosa *et al.* 2004; Instituto Chico Mendes de Conservação da Biodiversidade, 2018),whereas *R. porosus* is listed as 'Least Concern' in global assessment and 'Data Deficient' in Brazil (Lessa *et al.* 2006; Instituto Chico Mendes de Conservação da Biodiversidade, 2018).

Considering the increase in the consumption of shark meat, the lack of effective fishery management of sharks and increases in the number of elasmobranchs threatened with extinction in Brazil (Barreto *et al.* 2017), the present study is the first to describe patterns of age and growth for *R. lalandii* and *R. porosus* in subtropical waters of the south-western Atlantic, making an important contribution to the science-based management of these populations.

## Materials and methods

### Study area and sampling

Specimens were collected weekly from small-scale fisheries operating in south-eastern Brazil (Fig. 1) through the monitoring program Projeto Cação, which has been ongoing since 1996 (Gadig *et al.* 2002). Fishing operations were conducted from small, motorised boats (4–10 m long) using monofilament gill nets (1500 m long, stretched mesh sizes 7, 12 and 14 cm on average). The nets were set at distances of 5–20 km from the shore, in waters between 5 and 35 m deep, and checked once a day after 12–24 h (Namora *et al.* 2009). Although the target

fishing species (primarily sciaenids) were king weakfish (*Macrodon atricauda*), weakfishes (*Cynoscion* spp.) and white mouth croaker (*Micropogonias furnieri*), sharks had commercial value (Namora *et al.* 2009; Motta *et al.* 2014).

Individuals from both sharpnose shark species landed were sexed and measured (TL; mm). For *R. lalandii*, a subset of livers was weighed (liver mass (MH); g) after landed individuals had been eviscerated by fishermen. Vertebrae were collected whenever possible for *R. lalandii* and growth parameters were estimated using both direct (vertebrae ageing) and indirect (length–frequency analysis) methods. Because of the small sample size of *R. porosus* vertebrae, growth parameters were estimated using indirect methods only.

### Age determination

Vertebrae were sampled in two periods for *R. lalandii*: 1996–2003 and 2012–13. A segment of 5–10 cervical vertebrae was removed from the anterior to the origin of the first dorsal fin, fixed in 4% formaldehyde for 24 h, stored in 70% ethyl alcohol and manually cleaned following standard protocols (Cailliet and Goldman 2004). One vertebral centrum from each specimen was air dried, mounted on a microscope slide using thermoplastic resin (Crystalbond 509; Electron Microscopy Sciences, Hatfield, PA, USA) and sectioned using a low-speed Isomet saw with two Buehler 102-mm (4-inch) diamond blades (Buehler, Lake Bluff, IL, USA) separated by a spacer (∼0.35 mm thick). Each vertebral centrum was cut along the mid-sagittal axis through the focus, resulting in one 'bowtie' section that was 0.30–0.35 mm thick (Fig. 2).

Each vertebral section was immersed in mineral oil to enhance the banding patterns, then observed and photographed with a digital camera attached to a stereomicroscope under transmitted and reflected light. All images were analysed using Motic Image Plus 2.0 imaging software (Motic China Group; www.motic.com, accessed 5 December 2019). Band pairs, composed of one wide band (opaque) and one narrow band (translucent), were identified according to the pattern described by Cailliet *et al.* (2006). A subsample of all images taken comprising all size ranges of both sexes was randomly selected and read by two independent readers (J. T. Corsso and F. S. Motta) to ensure consensus regarding the interpretation of the band patterns. After establishing ageing criteria, each section was read by primary reader (J. T. Corsso) twice with a minimum interval of 30 days between readings. Measures of vertebrae were taken from the focus to the beginning of each translucent ring, and the birthmark (BM) was identified as the first distinct translucent band after the focus and was generally associated with a change in the angle of the corpus calcareum (Fig. 2).

Differences in growth between 1996–2003 and 2012–13 periods were examined for *R. lalandii* using analysis of covariance (ANCOVA). Linear regressions were adjusted for growth rate (mean length at age $x$ – mean length at age ($x-1$)) *v*. the mean length between years (Barreto *et al.* 2011).

### Precision and error analysis

The precision of ageing between reads (Reads 1 and 2) was calculated using the Index of Average Percentage Error (IAPE;
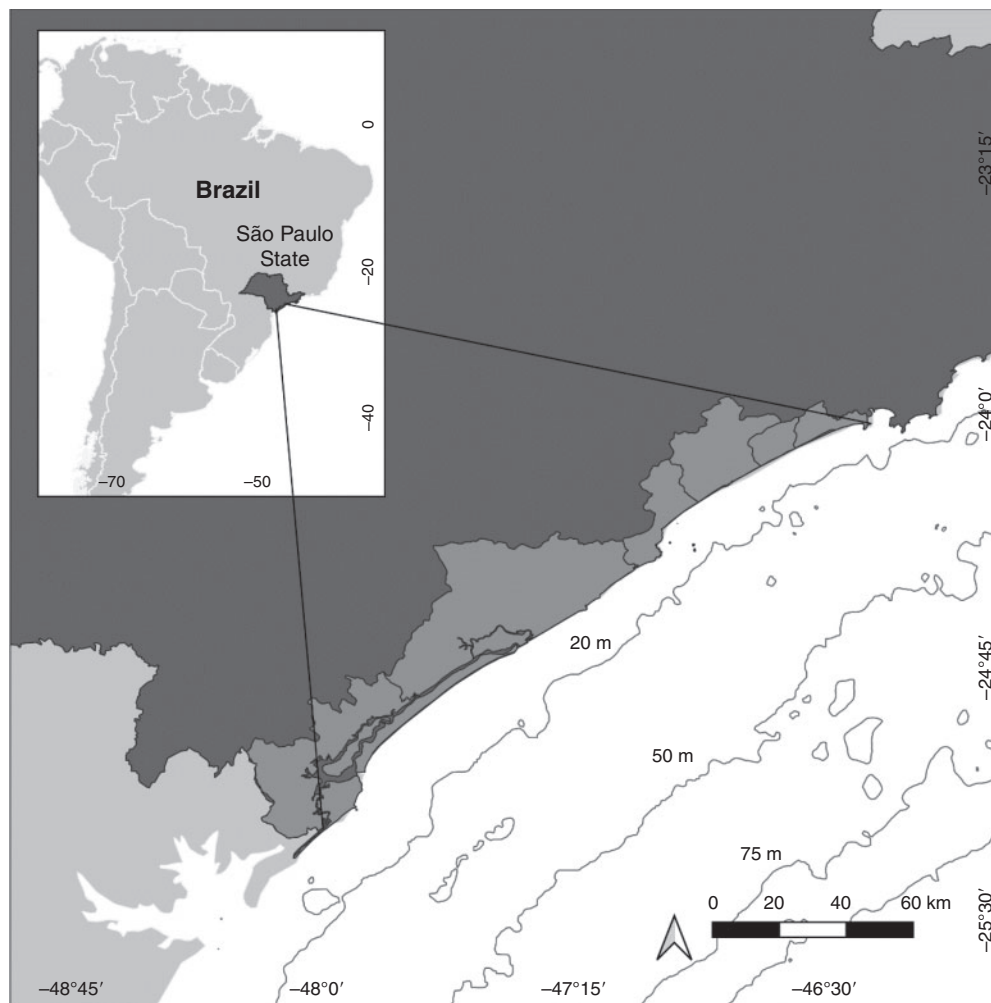
**Fig. 1.** The fishing area (depth 5–35 m) and landing beaches of the artisanal fishery fleet from Praia Grande municipality to Cananéia municipality, São Paulo State, southern Brazil, where samples of *Rhizoprionodon lalandii* and *Rhizoprionodon porosus* were collected.

Beamish and Fournier 1981) and the mean CV (Chang 1982), using the equations below:

$$IAPE = \frac{1}{N} \sum_{j=1}^{N} \left( \frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} X_j|}{X_J} \right) \times 100$$

$$CV = \frac{1}{N} \sum_{j=1}^{N} \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} X_j)^2}{R-1}}}{X_j} \times 100$$

where $N$ is the number of individuals aged, $R$ is the number of readings, $X_{ij}$ is the $i$th age determination for the $j$th fish and $X_j$ is the mean age calculation for individual $j$. Low IAPE and CV values indicate high ageing precision.

Differences between readings were also evaluated using an age–bias plot (Campana *et al.* 1995) and Bowker's test of symmetry (Bowker 1948; Hoenig *et al.* 1995).

*Edge and marginal increment analysis*

Periodicity of band pair formation was verified using marginal increment ratio (MIR) and centrum edge analysis (Cailliet *et al.* 2006; Smith *et al.* 2007). The annual periodicity of band formation was quantified using the MIR according to Conrath *et al.* (2002), namely:

$$MIR = MW \div PBW$$

where *MW* is the margin width and *PBW* is the previous band pair width. Mean ± s.e.m. MIR was plotted against months and the Kruskal–Wallis test with Dunn's post hoc test was used to detect significant differences between months for *R. lalandii* (Sokal and Rohlf 1995).

Centrum edge analysis was used to classify the edge type of the vertebral centra into one of four categories: (1) narrow translucent (NT); (2) broad translucent (BT); (3) narrow opaque (NO); (4) broad opaque (BO). Narrow bands were classified as
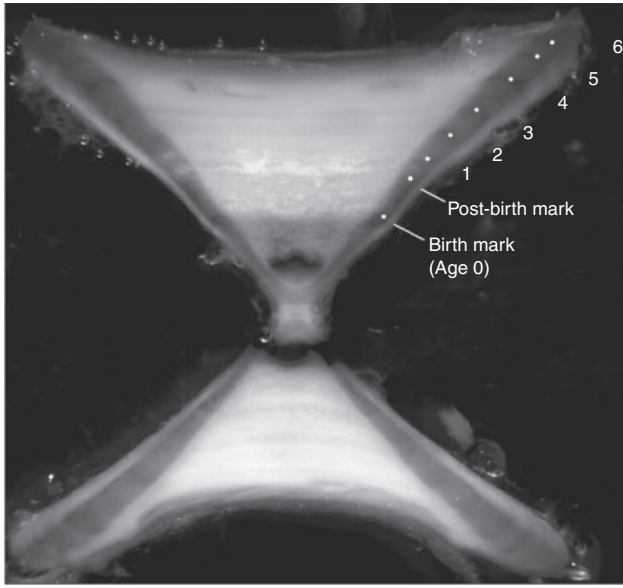
$$L_t = L_\infty \left( 1 - e^{-k_2(t-t_2)} \right)^{-1} \qquad (4)$$

where $L_t$ is length at age $t$, $L_\infty$ is the theoretical asymptotic length, $k_1$ (year$^{-1}$) is Brody's growth coefficient, which determines how quickly $L_\infty$ is attained, $t_0$ is the theoretical age at zero length, $k_2$ (year$^{-1}$) is the instantaneous growth coefficient when $t = t_1$, $t_1$ is the time at which the absolute growth rate starts to decrease (i.e. the inflection point in the curve), $k_3$ (year$^{-1}$) is the relative growth coefficient, $t_2$ is the inflection point of the curve. $L_0$, the length at birth, was fixed at 350 mm based on the average of the smallest free-swimming individuals observed in the sample. In all models, growth parameters were estimated through the non-linear least-squares method using R software (ver. 4.0.0, R Foundation for Statistical Computing, Vienna, Austria, see http://www.R-project.org/, accessed 5 December 2019). Starting values for all parameters in the models were estimated using the 'vbStarts' function of the Fish Stock Assessment (FSA) package (D. H. Ogle, R package, ver. 0.8.25;  https://cran.r-project.org/web/packages/FSA/index.html, accessed 30 August 2019).

### Model selection

The performance of the growth models was evaluated using Akaike's information criterion (AIC; Akaike 1973), resulting in the best-fit growth model with the lowest AIC value. Differences in AIC ($\Delta_i$) were calculated for all growth models as follows:

$$\Delta_i = AIC_i - AIC_{min}$$

where $AIC_i$ is the AIC from the model analysed and $AIC_{min}$ is the lowest AIC value between all models.

Models with $\Delta_i < 2$ have substantial support, models with $\Delta_i > 10$ have essentially no support and models with $4 < \Delta_i < 7$ have considerably less support (Burnham and Anderson 2002). The Akaike weight ($w_i$) of each growth model was calculated to support the best model among the candidate models (Burnham and Anderson 2002). Ultimately, the likelihood ratio test was used to determine the significance of differences in growth parameters between sexes (Kimura 1980).

### Length–frequency analysis

Length–frequency (LFQ) data used in growth parameter estimation were collected between January 1997 and December 2002. The VBGF growth parameters were estimated using the TropFishR package (ver. 1.1.2, see https://github.com/tokami/TropFishR/releases/tag/v1.1.2, accessed 5 December 2019; Mildenberger *et al.* 2017) and electronic length–frequency analysis (ELEFAN) through response surface analysis, allowing the estimation of $L_\infty$ and $k$ simultaneously. Data were grouped by biennium to optimise sample size: 1997–98 was linked as a 12-month interval, as were 1999–2000 and 2001–02. Parameters were estimated for each growth cycle, as well as the sequence of growth cycles.

### Age–length key

An age–length key was used to estimate the age structure of the *R. lalandii* population collected between January 1997 and December 2002 (Ogle 2016). For *R. porosus*, the inverse von



**Fig. 2.** Section of a sagittal vertebra under reflected light from a 6-year-old female *Rhizoprionodon lalandii*. Band pairs are marked with white dots and a number sequence.

having a bandwidth <50% of the previously fully formed band, whereas broad bands had a bandwidth ≥50% of the previously fully formed band. The proportion of each edge type was then plotted against month of sampling to evaluate the seasonality of band pair formation (Smith *et al.* 2007).

### Hepatosomatic index

The hepatosomatic index (HSI) was calculated for pooled sexes of *R. lalandii* using the equation:

$$HSI = 100 \times MH \div MT$$

where $MT$ is the total body mass. This equation was used to examine the relationship between HSI trends and the mark observed after the BM in young-of-the-year of this species during the summer.

### Growth modelling

Different growth models were fitted to observed size-at-age data for male and female *R. lalandii* following the recommendations of Cailliet *et al.* (2006). Four models were used: (1) the traditional von Bertalanffy growth function (VBGF; Beverton and Holt 1957; see Eqn 1); (2) the VBGF with length at birth $L_0$ (von Bertalanffy 1934; see Eqn 2); (3) the Gompertz growth model (Gompertz 1825; see Eqn 3); and (4) the logistic growth model (Ricker 1979; see Eqn 4). The equations used for the four growth models were:

$$L_t = L_\infty \left( 1 - e^{-k_1(t_1-t_0)} \right) \qquad (1)$$

$$L_t = L_\infty - (L_\infty - L_0)e^{-k_1 t} \qquad (2)$$

$$L_t = L_\infty e\left( -e^{-k_2(t-t_1)} \right) \qquad (3)$$

Bertalanffy growth equation was used to estimate the age structure of the population between January 1997 and December 2002 (Sparre *et al.* 1989). The VBGF growth parameters ($L_\infty$ and $k$) were estimated using the LFQ analysis to calculate $t_0$ according to Natanson *et al.* (1995) as follows:

$$t_0 = t + (1 \div k)(\ln(L_\infty - TL) \div L_\infty)$$

### Age at maturity

Age at maturity was estimated for males and females using the inverse von Bertalanffy growth equation (Sparre *et al.* 1989) based on size-at-maturity estimates reported for *R. lalandii* (Motta *et al.* 2007) and *R. porosus* (Ferreira 1988).

### Growth in the first year of life

Growth rates during the first months of life were estimated using a linear regression between the mean TL for the month of capture and the month of capture, between 1996 and 2004. Outliers were considered to represent individuals older than 1 year, based on the LFQ analysis, and were removed previously (Rountree and Able 1996). The sampling periods for each analysis performed are listed in Table S1, available as Supplementary material to this paper.

## Results

### Sampling

The sample of *R. lalandii* for vertebral analysis consisted of 237 specimens (118 males, 119 females). ANCOVA did not detect significant differences in growth rates between the two sampling periods considered ($F = 0.2954$; $P = 0.5973$; Fig. S1). The size of males ranged from 310 to 700 mm TL, whereas females ranged in size from 315 to 790 mm TL. For LFQ analyses, 7560 *R. lalandii* individuals (4046 males, 3514 females) and 1977 *R. porosus* individuals (1072 males, 905 females) were sampled. Male and female specimens of *R. lalandii* were in the size range 310–700 and 315–790 mm TL respectively; the size range of male and female specimens of *R. porosus* was 360–1130 and 360–895 mm TL respectively (Fig. 3; Table S1).

### Age determination

The BM was measured in ~94.1% of *R. lalandii* individuals at a mean (±s.e.m.) distance of 1.710 ± 0.004 mm from the focus. The oldest *R. lalandii* specimen was a 775-mm TL female aged at 8 years; the oldest male *R. lalandii* specimen was 700 mm TL and aged at 4 years.

#### Precision and error analysis

Precision agreement between readings was high (Fig. 4). For *R. lalandii*, IAPE was 7.23% and the mean CV was 10.22%. The Bowker symmetry test did not detect significant differences between readings (*R. lalandii*: $\chi^2 = 12.8$, d.f. = 7, $P = 0.076$).

#### Edge and marginal-increment analysis

Monthly analysis of MIR for *R. lalandii* revealed significant differences between April and June ($H = 26,389$; $P = 0.0018$; Dunn's test, $P < 0.05$). This analysis suggests band pair
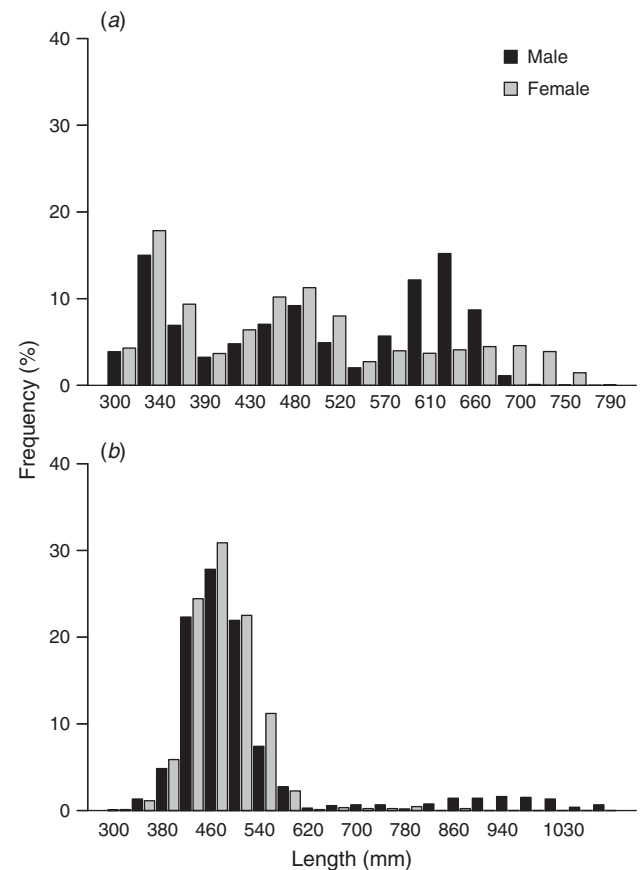


**Fig. 3.** Size frequency distribution per size class for male and female (*a*) *Rhizoprionodon lalandii* (30-mm size classes) and (*b*) *Rhizoprionodon porosus* (40-mm size classes) caught between January 1997 and December 2002.
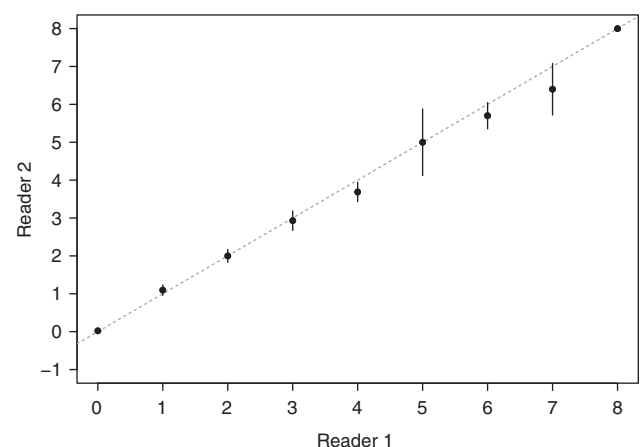


**Fig. 4.** Age bias plot showing agreement between the two readers for *Rhizoprionodon lalandii*.

deposition for *R. lalandii* in mid-winter, with the lowest mean values occurring from June to September (Fig. 5).

The vertebral edge was characterised in 231 specimens (pooled sexes) of *R. lalandii*. Translucent edges (NT and BT)
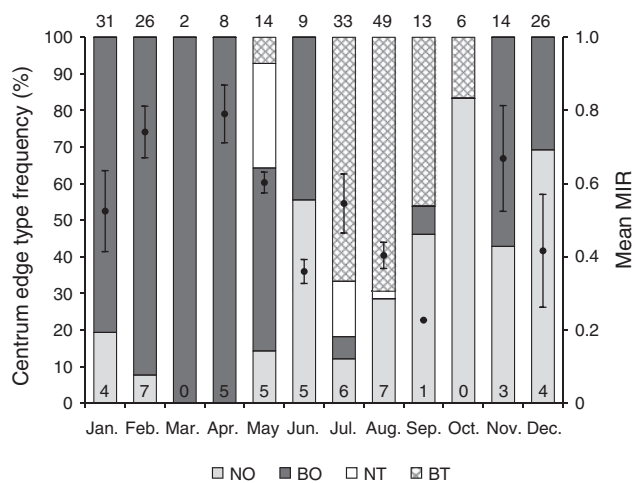
**Fig. 5.** Monthly variation in edge type frequency and monthly mean (±s.e.m.) marginal increment ratios (MIR) determined from pooled sexes for *Rhizoprionodon lalandii*. Edge types was coded as follows: BT, broad translucent; NT, narrow translucent; BO, broad opaque; NO, narrow opaque. Numbers above and at the bottom of the columns are sample sizes for edge type and MIR analyses respectively.



**Fig. 6.** Mean (±s.e.m.) hepatosomatic index for length classes of pooled sexes of *Rhizoprionodon lalandii* (*n* = 2071). Numbers above the *x*-axis are sample sizes for individual length classes.

were recorded from May to October, although they were not recorded in June. Translucent edges, especially BT, were predominant in July, August and September (Fig. 5).

An additional band pair after the BM and before the first year was found for *R. lalandii*. The formation of this band pair occurred during the summer in young-of-the-year individuals belonging to the 400- to 450-mm size class. This mark was visible in 108 specimens, measured at a mean (±s.e.m.) distance of 2.290 ± 0.0017 mm from the vertebral centrum (Fig. 2). There was a coincident relationship between this mark and low health condition in these young-of-the year individuals, which had depleted their liver reserves at this life stage, indicating potential physiological stress (Fig. 6).

The age composition of the *R. lalandii* sample showed that recruitment to the fishery occurs shortly after birth, with specimens of age-0 (Fig. 7; Tables S2, S3).

### Age at maturity

Age at maturity for males (590 mm TL) and females (620 mm TL) of *R. lalandii* was estimated at 1.08 and 1.59 years respectively. Most *R. lalandii* specimens were immature individuals, with ~65% of males and 80% of females in the age classes between 0 and 1 year. The age composition of *R. porosus* revealed that recruitment to the fishery also occurred in the first months of life (Fig. 7; Tables S4, S5). Age at maturity was 2.27 and 2.73 years for male (800 mm TL) and female (850 mm TL) *R. porosus* respectively, and the percentage of immature individuals captured in the sample was 90.5% for males and 99.3% for females.

### Growth analysis and model selection

Growth parameters derived from vertebrae analysis of *R. lalandii* are given in Table 1 and Fig. 8. The likelihood ratio test indicated that the growth parameters of males and females were significantly different ($\chi^2 = 22.11$, d.f. = 3, $P < 0.001$). The VBGF was selected as the best fit for both sexes.
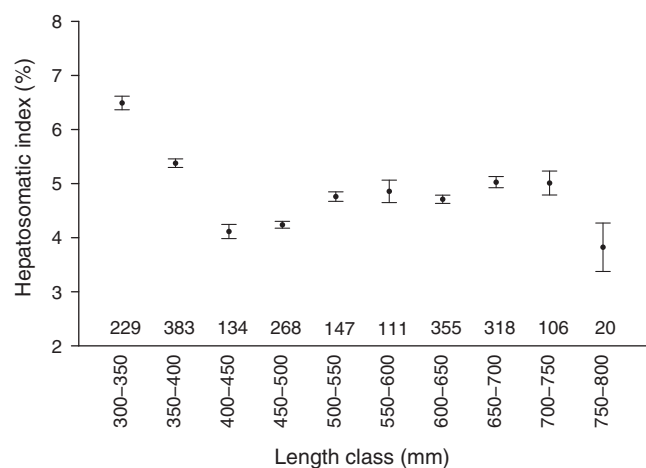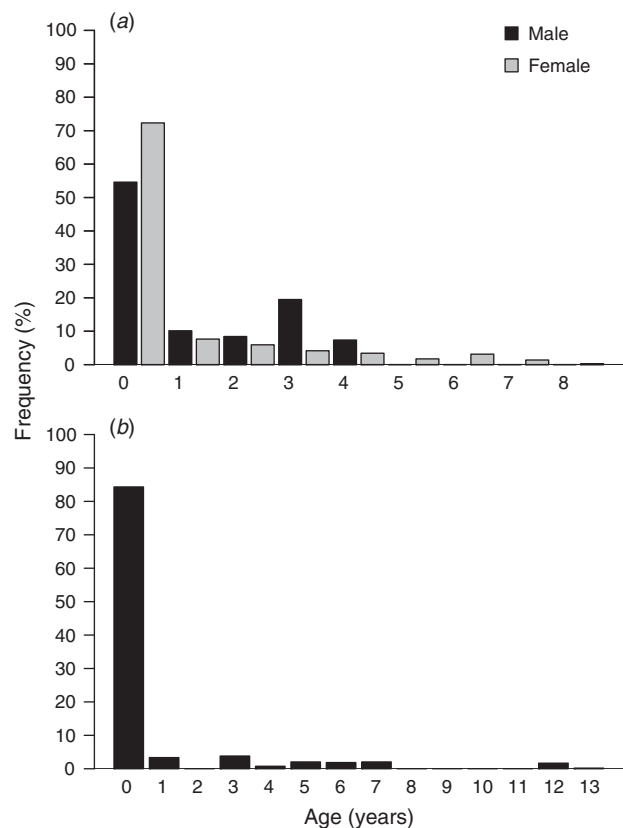


**Fig. 7.** Age frequency distribution for (*a*) male (*n* = 4075) and female (*n* = 3541) *Rhizoprionodon lalandii* and (*b*) male (*n* = 1050) and female (*n* = 905) *R. porosus*, caught between January 1997 and December 2002.

LFQ analyses estimated VBGF parameters for each growth cycle and for the sequence of growth cycles of both species and sexes (Tables 2, 3). The growth rate constant *k* for *R. lalandii* males ranged from 0.44 to 0.89 year$^{-1}$, with the mean of 0.71

**Table 1.   Growth estimates and model selection criteria for male and female *Rhizoprionodon lalandii***

AIC, Akaike information criterion; AICc, Akaike's information criterion corrected for small sample size; $\Delta_i$, differences in AIC; $k$, growth coefficient; $L_\infty$, theoretical maximum length; $L_0$, length at age zero; $t_0$, theoretical age at zero length; VBGF, von Bertalanffy growth function

| Growth model | Sex | Parameter | Estimate | Standard error | AIC | AICc | $\Delta_i$ | Akaike weight (%) |
|---|---|---|---|---|---|---|---|---|
| VBGF | Male | $L_\infty$ (mm) | 661.9 | 10.6 | 1254.1 | 1254.5 | 0 | 39.94 |
| | | $k$ (year$^{-1}$) | 1.14 | 0.19 | | | | |
| | | $t_0$ | −0.82 | 0.13 | | | | |
| | Female | $L_\infty$ (mm) | 751.7 | 16 | 1305.4 | 1305.8 | 0 | 52.81 |
| | | $k$ (year$^{-1}$) | 0.59 | 0.1 | | | | |
| | | $t_0$ | −1.37 | 0.21 | | | | |
| VBGF with $L_0$ ($L_0 = 350$ mm) | Male | $L_\infty$ (mm) | 658.3 | 12 | 1313.1 | 1313.3 | 58.8 | 0.00 |
| | | $k$ (year$^{-1}$) | 1.37 | 0.25 | | | | |
| | Female | $L_\infty$ (mm) | 741.8 | 18.4 | 1385.3 | 1385.5 | 79.7 | 0.00 |
| | | $k$ (year$^{-1}$) | 0.78 | 0.15 | | | | |
| Gompertz | Male | $L_\infty$ (mm) | 659.4 | 9.7 | 1254.5 | 1254.9 | 0.39 | 32.86 |
| | | $k$ (year$^{-1}$) | 1.33 | 0.2 | | | | |
| | | $t_0$ | −0.54 | 0.07 | | | | |
| | Female | $L_\infty$ (mm) | 746.8 | 14.3 | 1306.5 | 1306.9 | 1.1 | 30.46 |
| | | $k$ (year$^{-1}$) | 0.72 | 0.1 | | | | |
| | | $t_0$ | −0.77 | 0.1 | | | | |
| Logistic | Male | $L_\infty$ (mm) | 657.3 | 9.02 | 1254.9 | 1255.2 | 0.77 | 27.18 |
| | | $k$ (year$^{-1}$) | 1.54 | 0.21 | | | | |
| | | $t_0$ | −0.3 | 0.04 | | | | |
| | Female | $L_\infty$ (mm) | 743 | 13.3 | 1307.7 | 1308.1 | 2.3 | 16.72 |
| | | $k$ (year$^{-1}$) | 0.85 | 0.11 | | | | |
| | | $t_0$ | −0.31 | 0.06 | | | | |

year$^{-1}$, whereas for females $k$ ranged from 0.64 to 0.67 year$^{-1}$, with the mean of 0.67 year$^{-1}$. For *R. porosus* males, $k$ ranged from 0.41 to 0.61 year$^{-1}$, with the mean of 0.41 year$^{-1}$, whereas in female *R. porosus* $k$ ranged from 0.21 to 1.01 year$^{-1}$, with the mean of 0.31 year$^{-1}$.

### Growth in the first year of life

The growth rate of *R. lalandii* during the first months of life ranged from 20.12 to 26.25 mm per month (Table 4), with a mean ± s.e.m. of 23.43 ± 0.75 mm per month. Extrapolating the results for the first year of life, the total growth in the period was 281.16 mm on average, corresponding to 80.3% growth in length in relation to birth size (~350 mm TL).

The growth rate of *R. porosus* from August to March ranged from 12.27 to 25.86 mm per month (Table 5), indicating that the species grows ~98.16 to 206.88 mm in this period. The mean ± s.e.m. growth per month was 19.75 ± 1.55 mm. Total growth in the first year of life was 237 mm on average, corresponding to 55% growth in length in relation to birth size (~430 mm TL).

## Discussion

This study is the first to estimate the age and growth parameters of *R. lalandii* and *R. porosus* in the subtropical waters of the Atlantic, where these species represent the sharks most captured by artisanal fisheries (Motta *et al.* 2005). The reliability of age readings of *R. lalandii* (IAPE and CV) were within the usual range observed in shark studies (Campana 2001). Marginal increment and edge analyses suggested that band pair deposition

occurs annually in mid-winter for *R. lalandii*. The annual deposition of growth bands has already been recorded for *Rhizoprionodon* species (Branstetter 1987; Simpfendorfer 1993; Carlson and Baremore 2003; Loefer and Sedberry 2003).

The mark recorded after the BM in *R. lalandii* young-of-the year could be associated with the physiological stress in the 400- to 450-mm-TL size class due to depletion of the maternally provided liver reserves for the initial postnatal life of neonates (Corsso *et al.* 2018). In this context, Simpfendorfer (1993) associated the formation of vertebral bands in *R. taylori* with probable stress caused in individuals during the mating season, reflected by low HSI and condition factor. In addition, vertebral growth would be linked to food absorption, and low food intake for short periods of time can cause subtle marks to appear in the vertebrae centrum of some species, as suggested by Goldman (2004). Therefore, future studies are needed to elucidate the possible relationships between condition metrics and band formation in shark vertebrae.

The use of multiple growth models is encouraged to evaluate the growth characteristics of species (Cailliet *et al.* 2006; Smart *et al.* 2016), although the choice of which growth curve to use is often subjective (Wang *et al.* 1995). The selection of the best model is context dependent (Araya and Cubillos 2006) and the decision is often made based on previous studies and experience rather than goodness of fit (Wang *et al.* 1995). In the present study we selected the VBGF model for *R. lalandii* after considering AIC and Akaike weight. According to Thorson and Simpfendorfer (2009), VBGF with fixed $L_0$ is useful in studies with a small sample size and performs well when there are accurate estimates of $L_0$ available, as in the present study.

However, this growth model recorded the worst fit of the models used (Akaike weight <0.5%), reinforcing the potential of this model to produce poor parameter estimates (Pardo *et al.* 2013; Smart *et al.* 2016).
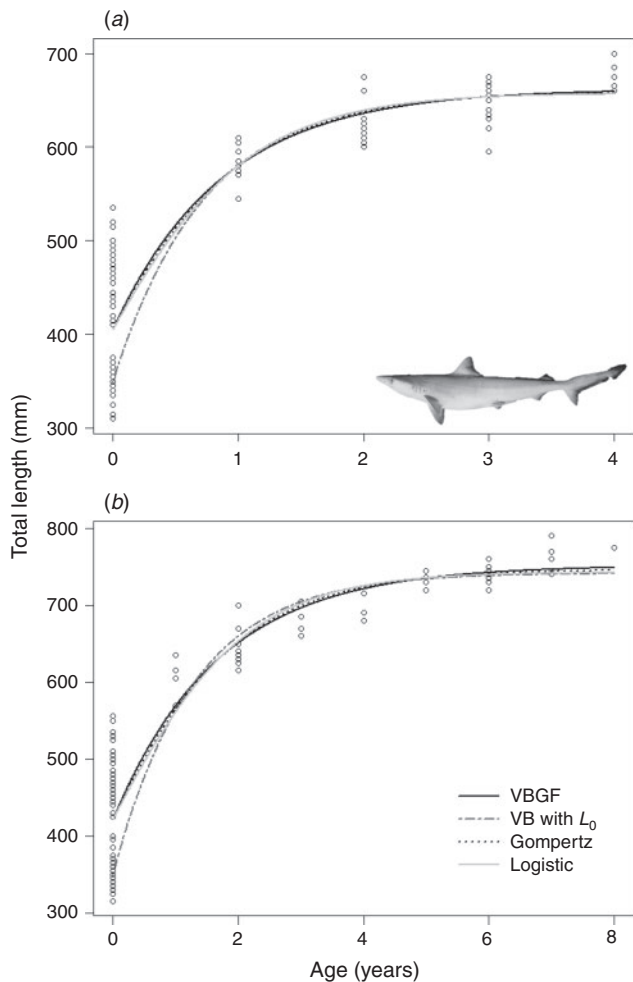


**Fig. 8.** Growth curves fitted to length-at-age data for (*a*) male and (*b*) female *Rhizoprionodon lalandii*. Fitted candidate models were the von Bertalanffy growth function (VBGF), VBGF with length at age zero $L_0$ fixed (at 350 mm), Gompertz and logistic.

The $L_\infty$ obtained for male *R. lalandii* was underestimated due to the difference between the mean TL of adults in the sample (mean ± s.e.m. 643.70 ± 0.41 mm TL) and the largest individual recorded in the study area (775 mm TL). Similarly, the $L_\infty$ for female *R. lalandii* was slightly underestimated. Previous studies have highlighted that the lack of large individuals can affect growth parameter estimates (Goldman *et al.* 2012; Natanson *et al.* 2014). The $k$ values produced by vertebrae and LFQ analysis for *R. lalandii* and LFQ analysis for *R. porosus* indicate fast growth for both species. Considering the inverse relationship between $k$ and $L_\infty$ (Cailliet *et al.* 2006), the value of $k$ may have been overestimated in vertebrae analysis, primarily for *R. lalandii* males. Therefore, the $k$ resulting from LFQ analysis (0.71 year$^{-1}$) may be more realistic than that resulting from vertebrae ageing (1.14 year$^{-1}$). The differences in $k$ estimates for *R. lalandii* females among ageing approaches were lower, possibly indicating a more robust estimate. *R. porosus* had the most reliable $k$ values: 0.41 year$^{-1}$ for males and 0.31 year$^{-1}$ for females.

The fast growth of *R. lalandii* and *R. porosus* demonstrated in the present study was expected based on congeneric species, which are known to have the highest growth rates among elasmobranchs (Table 6). The parameters obtained for *R. lalandii* resemble those reported for *R. terraenovae* from subtropical waters of the north-west Atlantic (Carlson and Baremore 2003) and *R. acutus* from the tropical and subtropical Indian ocean (Harry *et al.* 2010), whereas parameters for *R. porosus* only resemble those for *R. terraenovae* from subtropical waters of the north-west Atlantic (Parsons 1985; Branstetter 1987). In the Atlantic Ocean, all *Rhizoprionodon* species from subtropical waters (Parsons 1985; Branstetter 1987; Carlson and Baremore 2003; Loefer and Sedberry 2003), including the species in the present study, grow at faster rates than species from tropical waters (Lessa *et al.* 2009; Ba *et al.* 2015).

Comparing the results obtained in the present study (VBGF) with those reported by Lessa *et al.* (2009), *R. lalandii* grows more rapidly in subtropical waters (1.14 year$^{-1}$ for males, 0.59 year$^{-1}$ for females) than in tropical regions (0.30 year$^{-1}$ for pooled sexes). These differences may be explained by differences in the length structure of samples, usually due to gear selectivity (Thorson and Simpfendorfer 2009; Harry *et al.* 2013; Geraghty *et al.* 2014). For example, *R. lalandii* specimens ranged in size from 310 to 790 mm TL in the present study, compared with 480–765 mm TL in the study of Lessa *et al.*

**Table 2.  Growth parameters estimated from length–frequency analyses (TropFishR package) of *Rhizoprionodon lalandii***

$k$, growth coefficient; $L_\infty$, theoretical maximum length

| Sex | Growth cycle | $L_\infty$ (mm) | $k$ (year$^{-1}$) | Number of individuals |
|---|---|---|---|---|
| Male | Sequence of growth cycles | 762 | 0.7 | 4046 |
| | 1997–98 | 766 | 0.6 | 1452 |
| | 1999–2000 | 709 | 0.9 | 1627 |
| | 2001–02 | 731 | 0.4 | 967 |
| Female | Sequence of growth cycles | 791 | 0.7 | 3514 |
| | 1997–98 | 760 | 0.6 | 936 |
| | 1999–2000 | 790 | 0.6 | 1765 |
| | 2001–02 | 793 | 0.7 | 813 |

(2009). The lack of the smaller specimens in the study of Lessa *et al.* (2009) may have reflected a slower growth rate, given the rapid growth of the species in the first months of life (Table 4). Another possibility is the difference in clinal nature intrinsic to population differences, considering that there are two identified populations for this species, as supported by molecular data and reproductive parameters (Mendonça *et al.* 2013; Motta *et al.* 2007).

The growth rates determined for *R. porosus* in north-east Brazil using LFQ analysis (0.42 year$^{-1}$ for males, 0.30 year$^{-1}$ for females; Mattos and Pereira 2002) are consistent with those found in the present study (0.41 year$^{-1}$ for males, 0.31 year$^{-1}$ for females). This similarity was expected due to molecular results indicating that both studies were dealing with the same population of this species (Mendonça *et al.* 2011).

Males and females of the subtropical population of *R. lalandii* reached maturity at an earlier age (1.08 and 1.59 years

for males and females respectively) than tropical specimens (2.6 years; Lessa *et al.* 2009). The same was observed for *R. porosus*, with males and females reaching maturity at 2.27 and 2.73 years respectively in the subtropical region compared with 3.3 years in tropical waters (Lessa *et al.* 2009). These findings reflect latitudinal variation, suggesting that maturity is achieved at younger ages at higher latitudes for these species. Age at first maturity revealed that males matured earlier than females and had faster rates growth rates, as commonly observed for elasmobranchs (Cortés 2000; Natanson *et al.* 2006).

*R. lalandii* neonates grow by 80.3% of their birth length in the first year of life, and *R. porosus* neonates grow 55% of their birth length, which classifies both species as fast-growing, small coastal sharks ($k > 0.1$ year$^{-1}$ and >40% of growth in the first year; Branstetter 1990; Cortés 2000). These results are comparable with those reported for other coastal species, such as *R. terraenovae* (69%), *Carcharhinus brevipinna* (67%),

**Table 3.    Growth parameters estimated from the length–frequency analyses (TropFishR package) of *Rhizoprionodon porosus***
$k$, growth coefficient; $L_\infty$, theoretical maximum length

| Sex | Growth cycle | $L_\infty$ (mm) | $k$ (year$^{-1}$) | Number of individuals |
|---|---|---|---|---|
| Male | Sequence of growth cycles | 1040 | 0.4 | 1053 |
| | 1997–98 | 1190 | 0.4 | 404 |
| | 1999–2000 | 1045 | 0.5 | 448 |
| | 2001–02 | 1110 | 0.6 | 201 |
| Female | Sequence of growth cycles | 1165 | 0.3 | 884 |
| | 1997–98 | 860 | 1 | 370 |
| | 1999–2000 | 1170 | 0.3 | 335 |
| | 2001–02 | 1050 | 0.2 | 179 |

**Table 4.    Growth rates of *Rhizoprionodon lalandii* by sampling period during the first months of life (from June to March)**

| Year | Slope (s.e.) | $r^2$ | Number of individuals |
|---|---|---|---|
| 1996–97 | 22.47 (2.86) | 0.883 | 376 |
| 1997–98 | 26.25 (3.26) | 0.914 | 538 |
| 1998–99 | 20.12 (1.01) | 0.980 | 1540 |
| 1999–2000 | 23.91 (1.28) | 0.977 | 779 |
| 2000–01 | 25.88 (3.21) | 0.888 | 528 |
| 2001–02 | 24.67 (2.06) | 0.953 | 592 |
| 2002–03 | 21.82 (1.63) | 0.951 | 371 |
| 2003–04 | 22.35 (1.54) | 0.967 | 414 |

**Table 5.    Growth rates of *Rhizoprionodon porosus* by sampling period during the first months of life (from August to March)**

| Year | Slope (s.e.) | $r^2$ | Number of individuals |
|---|---|---|---|
| 1996–97 | 22.16 (7.38) | 0.643 | 103 |
| 1997–98 | 17.22 (8.45) | 0.453 | 346 |
| 1998–99 | 12.27 (2.64) | 0.782 | 466 |
| 1999–2000 | 17.90 (2.12) | 0.922 | 414 |
| 2000–01 | 23.75 (3.83) | 0.864 | 287 |
| 2001–02 | 17.08 (3.19) | 0.904 | 97 |
| 2002–03 | 25.86 (3.78) | 0.886 | 143 |
| 2003–04 | 21.78 (5.15) | 0.817 | 68 |

**Table 6.    Comparison of selected life history parameters of *Rhizoprionodon* species reported by different authors**

F, female; *k*, growth coefficient; $L_\infty$, theoretical maximum length; $L_0$, length at age zero; M, male; $t_0$, theoretical age at zero length; VBGF, von Bertalanffy growth function

| Species | $L_\infty$ (mm) | $k$ (year$^{-1}$) | $t_0$ | Number of individuals | Maximum age (years) | Length range (mm) | Reference |
|---|---|---|---|---|---|---|---|
| R. lalandii | 781 | 0.3 | −1.46 | 84 | 6 | 480–765 | Lessa *et al.* (2009) |
| R. porosus | 1129 | 0.17 | −1.75 | 134 | 5 | 379–855 | Lessa *et al.* (2009) |
| R. terraenovae | 925 | 0.45 | −2.01 | 215 | – | 300–1070 | Parsons (1985) |
| R. terraenovae | 1080 | 0.36 | 0.98 | 20 | 5.75 | 400–1000 | Branstetter (1987) |
| R. terraenovae | 919 (M); 956 (F) | 0.85 (M); 0.63 (F) | −0.73 (M); −1.03 (F) | 304 | 6.5 (M); 9.5 (F) | – | Carlson and Baremore (2003) |
| R. terraenovae | 745 (M); 749 (F) | 0.50 (M); 0.49 (F) | −0.90 (M); −0.94 (F) | 376 (M); 430 (F) | 11 | 197–828 | Loefer and Sedberry (2003) |
| R. taylori | 652 (M); 732 (F) | 1.34 (M); 1.01 (F) | 0.41 (M); 0.45 (F) | 52 (M); 85 (F) | 6 (M); 7 (F) | 230–780 | Simpfendorfer (1993) |
| R. acutus | 821 (M); 861 (F) | 0.94 (M); 0.63 (F) | – | 153 (M); 59 (F) | 5 (M); 8 (F) | 385–940 | Harry *et al.* (2010) |
| R. acutus | 1265 (M); 1395 (F) | 0.18 (M); 0.17 (F) | – | 156 (M); 267 (F) | 8 (M); 9 (F) | 370–1120 | Ba *et al.* (2015) |
| R. taylori | 460 (M); 580 (F) | 3.69 (M); 1.98 (F) | – | 55 (M); 131 (F) | 3.6 (M); 4.6 (F) | 310–660 | Baje *et al.* (2018) |

*Sphyrna tiburo* (67%), *Carcharhinus limbatus* (65%) and *Carcharhinus isodon* (50%; Branstetter 1990). Despite the rapid growth in the first year observed for *R. lalandii*, the highest percentage of growth observed for elasmobranchs was found in another species of *Rhizoprionodon*, namely *R. taylori* (140%; Simpfendorfer 1993).

The present study combined different approaches and used the maximum data available to assess the age and growth of the two coastal shark species most caught by artisanal fisheries in south-eastern Brazil. The results indicate that *R. lalandii* and *R. porosus* are fast-growing and short-lived species that mature between 1 and 2.73 years and exhibit latitudinal population differences in their growth rates. Because of their life history characteristics, *Rhizoprionodon* species are commonly acknowledged as more resilient to overexploitation (Smith *et al.* 1998; Musick 1999; Simpfendorfer 1999), although, in practice, studies have reported both cases of fishery sustainability (Krishnamoorthi and Jagadis 1986) or resilience to regional fishing efforts (Simpfendorfer 1999; Harry *et al.* 2010; Baje *et al.* 2018), as well as cases indicating high vulnerability and population declines (Cortés 1995; Márquez-Farias and Castillo-Geniz 1998; Carlson and Baremore 2003; Ba *et al.* 2015). Immature individuals (from 0 to 2 years) of *R. lalandii* and *R. porosus* predominated in the artisanal catches studied here. Given that these populations are also caught by other types of fisheries and that they exhibit latitudinal variation in life history traits, it is critical that the parameters estimated in the present study are incorporated in further stock assessments in subtropical areas.

## Conflicts of interest

The authors declare that they have no conflicts of interest.

## Declaration of funding

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