

# Size structure, age, and growth of the blue shark, *Prionace glauca* (Linnaeus, 1758) in southern Brazil

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## Abstract

The blue shark is a highly migratory species with a worldwide distribution, making it susceptible to multiple fishing fleets across the globe. In southern Brazil, it is an important target, comprising up to 40% of the total biomass landed by the commercial surface longline fleet. This study aims to contribute to a better understanding of how the species uses the region and to update its life-history information available for future assessments. Over five consecutive years (2018–2022) of landings and onboard monitoring, we gathered size data and vertebral samples to describe the species size composition in the region, as well as its seasonal and interannual variability and to update estimated life-history parameters. The results showed that southern Brazil is mainly inhabited by large juvenile males that arrive during winter (July–September) and stay until spring (October–December), when their frequency decreases. Small adult males are present throughout the year but in higher frequencies during summer. A small number of adult females are present with higher frequencies during spring and summer, which decreases during the austral autumn and winter. Some variability in the presence of each life stage was observed among years. The estimated life-history parameters were as follows:  $L_{\infty}$ : 255.02 cm fork length (FL),  $k$ : 0.20,  $L_0$ : 35.68 cm FL for males;  $L_{\infty}$ : 246.47 cm FL,  $k$ : 0.23,  $L_0$ : 36.77 cm FL for females; and  $L_{\infty}$ : 269.58 cm FL,  $k$ : 0.18,  $L_0$ : 36.19 cm FL for pooled sexes. However, the estimated values must be cautiously interpreted, as the obtained samples cannot be construed as representative of the entire harvested stock due to the lack of consistent presence of some life stages in the study region.

## KEYWORDS

elasmobranch, fisheries, landings, life history, migratory, vertebral ageing

## 1 | INTRODUCTION

Chondrichthyan species are among the most vulnerable taxa in the ocean due to their life-history strategies, which result in slow population growth. This makes them particularly sensitive to intense biomass removal by fishing (Dulvy et al., 2014; Musick et al., 2000; Stevens et al., 2000; Talwar et al., 2022). However, there is a spectrum of sensitivity to exploitation among the species due to the high variation in life-history traits (Jorgensen et al., 2022; Stevens et al., 2000). One of

the less vulnerable species is the blue shark, *Prionace glauca*, which has the highest population growth rates among pelagic sharks due to its relatively fast growth, early sexual maturity, and the production of large litters (Rigby et al., 2019). The blue shark is the most commonly caught elasmobranch species by longline fishing fleets across the globe due to its worldwide distribution and highly migratory behavior (Coelho et al., 2017; Druon et al., 2022; Dulvy et al., 2008; Mucientes et al., 2022). In southern Brazil, blue shark catches represent up to 40% of the total biomass landed by the commercial surface longline

fleet (Barreto et al., 2016; FURG/SEMA, 2020; Gilman et al., 2008; Hazin et al., 2008). In 2014, the species was locally assessed as vulnerable (VU) according to the IUCN criteria (Decree 51797, RS, 2014).

Coelho et al. (2017) and Mas et al. (2023) have shown that juveniles are the main blue shark catches in the southern portion of the southwestern Atlantic (south of 32°S). However, both analyses considered large-scale spatial resolutions, which may result in the loss of finer-scale processes. Montealegre-Quijano and Vooren (2010) measured a considerable number of individuals from longline catches in southern Brazil and pointed out the area as being dominated by large juveniles and fewer small adults. These samplings ranged from 2004 to 2006 but had weak seasonal representation. Since 2018, the blue shark project (Projeto Tubarão Azul) has been sampling a large number of individuals with high seasonal and interannual representativeness to better understand the species' use of the southern Brazilian waters given its local status as vulnerable to extinction. Therefore, the first aim of this paper was to describe the temporal and spatial dynamics of different life stages observed off the coast of Rio Grande do Sul, Brazil, using a finer seasonal and spatial scale.

Changes in biomass and fluctuations in fishing-related abundance can result in altered life histories due to density-dependent effects, such as earlier maturation and changes in individual growth. These changes can impact a species' susceptibility to exploitation (Audzijonyte et al., 2016; Jennings & Kaiser, 1998). Additionally, life-history traits are influenced by environmental conditions, so temporal changes in growth and sexual maturity are expected for any species (Hoenig & Gruber, 1990). The most common method for studying growth in elasmobranchs is by interpreting band pairs (one obscure and one opaque) in vertebral centra to estimate growth parameters such as asymptotic length ( $L_{\infty}$ ) and growth coefficient ( $k$ ) using available growth models (Goldman et al., 2012). Accurate information about growth-related life history is crucial for the sustainable management of an exploited species and for monitoring how these parameters may change over time (Fujinami et al., 2019).

Montealegre-Quijano (2007) estimated the growth parameters for blue sharks in the southwestern Atlantic region during the 2004–2006 period (Table 1). The study also presented the age structure of the catches for that period, which mainly consisted of subadult males and females in the early stages of sexual maturity. The maximum ages recorded were 13 years for males and 12 years for females. Given the vulnerable status of the blue shark and the potential changes in their life history due to abundance changes, the second aim of this study was to update the growth parameters 15 years after the initial estimation for the region.

## 2 | METHODOLOGY

We monitored the landings of the commercial pelagic longline fleet at the port of Rio Grande, Rio Grande do Sul, Brazil. This fleet targets swordfish (*Xiphias gladius*), tunas (*Thunnus obesus*, *Thunnus albacares*, and *Thunnus alalunga*), blue shark (*P. glauca*), and escolar (*Lepidocybium flavobrunneum*). Between 2018 and 2022, the fleet's fishing effort was

characterized by remaining in the proximity of the continental slope within the Brazilian Exclusive Economic Zone (BEEZ). However, there were also rare trips up to the Rio Grande Rise and the Central Atlantic (0°W). Therefore, we gathered information on the fraction of the blue shark stock that occurred within the co-ordinates 27°S–39°S, 53°W–0°W (Figure 1).

During the landings, sharks had already been eviscerated and had their heads removed, so we recorded the interdorsal length (IL) to the nearest centimeter. In this study, IL was measured between the posterior insertions of the first and second dorsal fins, referred to as ILPP. This measurement was then converted to FL (in centimeters) for males ( $n = 908$ ) and females ( $n = 88$ ) separately, due to significant differences between the regression lines for each sex (ANCOVA;  $p = 2.02$ ,  $F = 5.12$ ), using the following equations (FURG/SEMA, 2020):

$$\text{Males: FL (cm)} = 3.1346 \times \text{ILPP (cm)} + 20.749 \quad (R^2 = 0.851),$$

$$\text{Females: FL (cm)} = 2.7846 \times \text{ILPP (cm)} + 34.147 \quad (R^2 = 0.849).$$

The size classes were categorized into four life stages: small juveniles (70–129 cm FL), large juveniles (130–179 cm FL), small adults (180–219 cm FL), and large adults (>220 cm FL), following the classification proposed by Montealegre-Quijano and Vooren (2010).

To obtain a more detailed understanding of changes in size distribution within and between years, we divided each year of study into quarters representing the austral seasons: summer (January, February, and March), autumn (April, May, and June), winter (July, August, and September), and spring (October, November, and December). We conducted significance tests using the ggstatsplot (Patil, 2021) R package in the R programme environment (R Core, 2022).

In addition, we analysed the data collected by onboard observers during 20 monitored commercial fishing trips on seven longline vessels. These data provided us with co-ordinates recorded at haulback, which is the end of fishing gear retrieval. We used this information to create spatial distribution maps of a subsample using the “ggOcean-Maps” (Vihtakari, 2022) and “marmap” (Pante & Simon-Bouhet, 2013) R packages in the R programme environment (R Core, 2022).

### 2.1 | Vertebral sample preparation

The vertebrae were extracted from the area above the branchial chamber, cleaned of any remaining flesh, bleached, and embedded in crystal polyester resin (Goldman et al., 2012). The resin blocks were then sliced into 0.5–0.7-mm-thick sections on a sagittal plane through the centrum using a low-speed metallographic saw with a diamond powder disc (Isomet Buehler Ltd.). The resulting bowtie sections were stained with alizarin red at a concentration of 0.38% (Montealegre-Quijano, 2007) for 15 min, rinsed in tap water, and fixed using Entellan<sup>®</sup> novo on microscope slides. Each section was photographed using transmitted light with an OLYMPUS U-TV0.63XC video camera attached to an OLYMPUS SZX10 microscope.

**TABLE 1** von Bertalanffy growth parameters for *Prionace glauca* estimated in several studies from different areas.

Area	Sex	$L_{\infty}$ (cm)	$k$ (year <sup>-1</sup> )	$L_0$	$t^0$	Size measurement	Reference
North Pacific	Pooled	265.5	0.223	43.5	-0.802	TL	Cailliet et al., 1983
	Male	295.3	0.175		-1.113		
	Female	241.9	0.251		-0.795		
	Male	369	0.10		-1.38	TL	Tanaka, 1990
	Female	304	0.16		-1.01		
	Pooled	303.4	0.10		-2.68	TL	Blanco-Parra et al., 2008
	Male	299.85	0.10		-2.44		
	Female	237.5	0.15		-2.15		
	Male	284.9	0.117		-1.35	PLC	Fujinami et al., 2019
	Female	257.2	0.146		-0.97		
South Pacific	Male	297.18	0.165			FL	Manning & Francis, 2005
	Female	235.05	0.229				
	Male	418	0.08			TL	Briones-Mendoza & Armijos-Bravo, 2012
	Female	454	0.07				
	Male	376.6	0.128		-1.48	TL	Joung et al., 2018
	Female	330.4	0.164		-1.29		
	Male	283.8	0.13	39.5		FL	Andrade et al., 2019
	Female	290.6	0.12	39.5			
	Pooled	350.8	0.07	45.8		TL	Mukherji et al., 2021
	Male	379	0.07	45.8			
Female	329.2	0.08	45.8				
North Atlantic	Pooled	423	0.110		-1035	TL	Stevens, 1975
	Pooled	302	0.58		-0.24	TL	MacNeil & Campana, 2002
	Males	282	0.18		-1.35	FL	Skomal & Natanson, 2003
	Females	310	0.13		-1.77		
South Atlantic	Pooled	352.1	0.157		-1.01	TL	Lessa et al., 2004
	Male	256.8	0.149		-1561	FL	Montealegre-Quijano, 2007
	Female	245.6	0.160		-1549		
	Pooled	311.6	0.12		-1.66	TL	Jolly et al., 2013
	Male	291	0.102	34.7		FL	Mas, 2015
	Female	283	0.106	34.8			
	Pooled	352.1	0.13		-1.31	TL	Joung et al., 2017
	Pooled	269.58	0.18	36.19		FL	This study
	Males	255.02	0.20	35.68			
	Females	246.47	0.23	36.77			

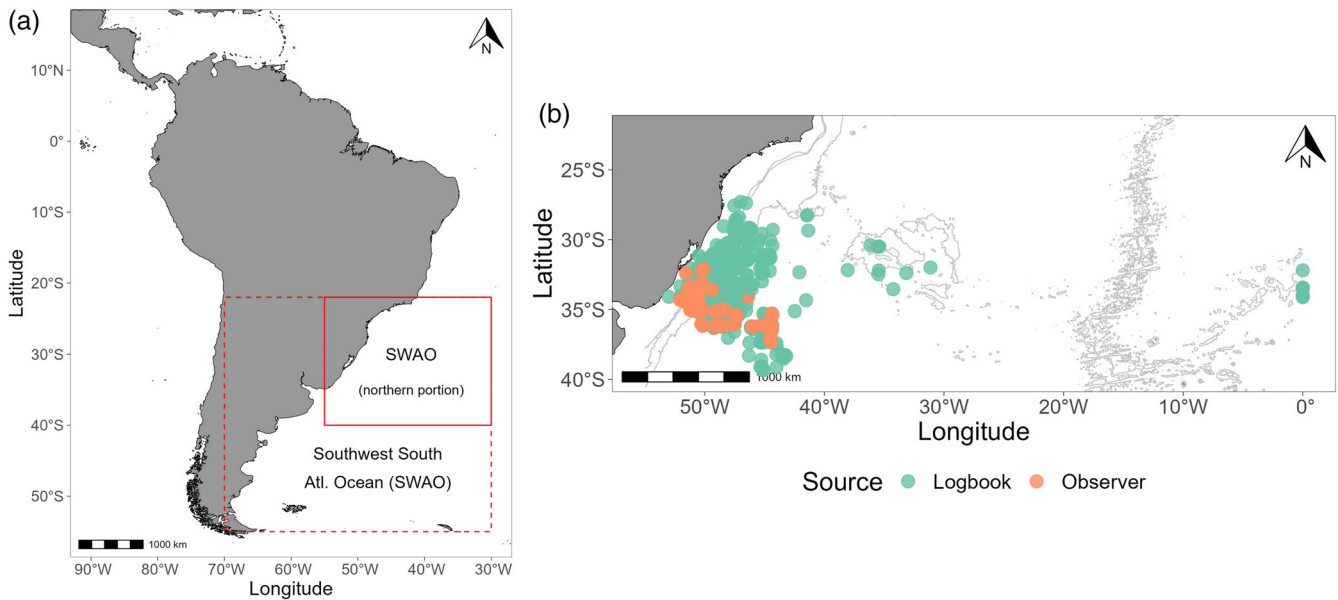
Abbreviations: FL, fork length; PCL, precaudal length; TL, total length.

## 2.2 | Vertebrae analysis

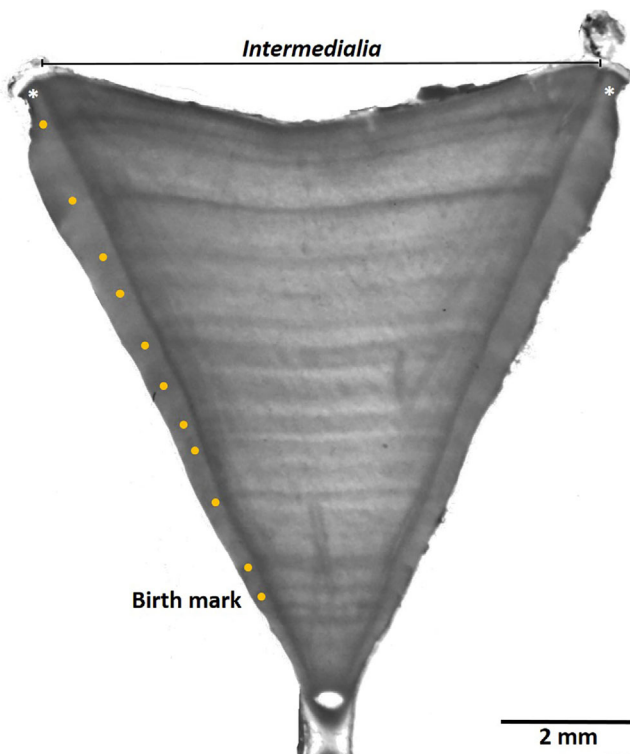
The images of sectioned vertebrae were digitally enhanced with Photoshop (Adobe Inc., 2019) to improve the contrast of the growth bands. The examination of sectioned vertebrae images allowed us to count adjacent opaque and translucent bands, known as band pairs, in the *corpus calcareum* (Figure 2). The birthmark was identified by a change in the angle of the inner margin of the *corpus calcareum*, exhibiting the transition from pre- to postnatal growth, thus, established as age zero (Goldman et al., 2012) (Figure 2). The vertebral radius

(VR) was measured from the focus to the edge of the centrum of the vertebrae perpendicular to the direction of the cutting plane (Fujinami et al., 2019) using the measuring programme ImageJ (Schneider et al., 2012). The VR to FL relationship was estimated by using a linear regression and was compared by sex using the ANCOVA.

Band pairs were counted independently by two readers without prior knowledge of the size or sex of the individuals to reduce bias in age estimation (Cailliet et al., 1983; Goldman et al., 2012). Samples were re-examined collaboratively until a consensus age was agreed upon; if no consensus on ageing was reached, the sample was



**FIGURE 1** Detail of the South Atlantic area (a) and study area and spatial distribution of the set of each fishing trip that landed at the port of Rio Grande (b). Green dots represent the sets gathered from logbook data, and orange dots represent the sets gathered by onboard observers.



**FIGURE 2** Sagittal section of a vertebral centrum of a *Prionace glauca* individual (sex: female; fork length: 199.4 cm) caught by the surface longline fleets that land at the port of Rio Grande. White asterisks indicate the *corpus calcareum* of the vertebra.

discarded as recommended by Cailliet et al. (2006). To verify the consistency of age interpretation, we carried out a CV test and an average percentage error (APE) test using the “FSA” package (Ogle et al., 2022) in R. Growth modeling.

Bayesian approaches are an effective tool when frequentist approaches cannot determine appropriate estimates from the data alone. These methods incorporate prior knowledge into an analysis and produce a combined output using priors along with the available data (Smart & Grammer, 2021). The underrepresentation of the younger and older age classes in the samples led us to apply a Bayesian approach through the “BayesGrowth” R package (Smart, 2020). When estimating the species growth, prior information was incorporated into length-at-age modeling by creating informative priors for  $L_0$  and  $L_\infty$  based on known length-at-birth. For males,  $L_0$  was 35.55 cm FL, SE = 0.82; for females,  $L_0$  was 36.75 cm FL, SE = 0.65; and for both sexes combined,  $L_0$  was 36.09 cm FL, SE = 0.54. The species' maximum observed length ( $L_\infty$ ) was 251.3 cm FL, SE = 37.85 for males; 271.5 cm FL, SE = 27.91 for females; and 271.5 cm FL, SE = 2.73 for both sexes combined.

The package “BayesGrowth” (Smart, 2020) uses tree growth functions to fit the observed length-at-age data:

von Bertalanffy

$$L_t = L_0 + (L_\infty - L_0)(1 - e^{-kt}),$$

Gompertz

$$L_t = L_0 e^{\left(\left(\log\left(\frac{L_\infty}{L_0}\right)\right)(1 - e^{-kt})\right)},$$

and Logistic

$$L_t = \frac{L_\infty L_0 e^{kt}}{L_\infty + L_0(e^{kt} - 1)}$$

where  $L_t$  is the length as a function of time,  $L_0$  is the length at birth,  $L_\infty$  is the asymptotic length, and  $k$  is the growth completion coefficient. Model selection was performed using leave-one-out

cross-validation (LOOCV), which estimates pointwise out-of-sample prediction accuracy by evaluating the log-likelihood at the posterior parameter distributions (Smart & Grammer, 2021). The “Bayes-Growth” R package (Smart, 2020) calculates the leave-one-out information criterion (LOOIC) using LOOCV, which has the same interpretation as AIC for model selection.

### 3 | RESULTS

#### 3.1 | Sex and size distribution in southern Brazil

A total of 26,865 blue sharks were measured during commercial landings at the port of Rio Grande between 2018 and 2022. Of these, 24,376 were males, with sizes ranging from 92.6 to 287.5 cm FL, and 2489 were females, with sizes ranging from 86.5 to 276.4 cm FL. The subsample gathered by onboard observers consisted of 2035 individuals and presented a sex ratio of 11 males for each female. The sizes ranged from 87 to 288 cm FL for males and from 107 to 255 cm FL for females. Figure 3 shows that both sexes were present in the entire area. However, females were more abundant over the continental slope, whereas males were evenly distributed in both inshore and offshore areas. This spatial overlap was also observed for the different size classes.

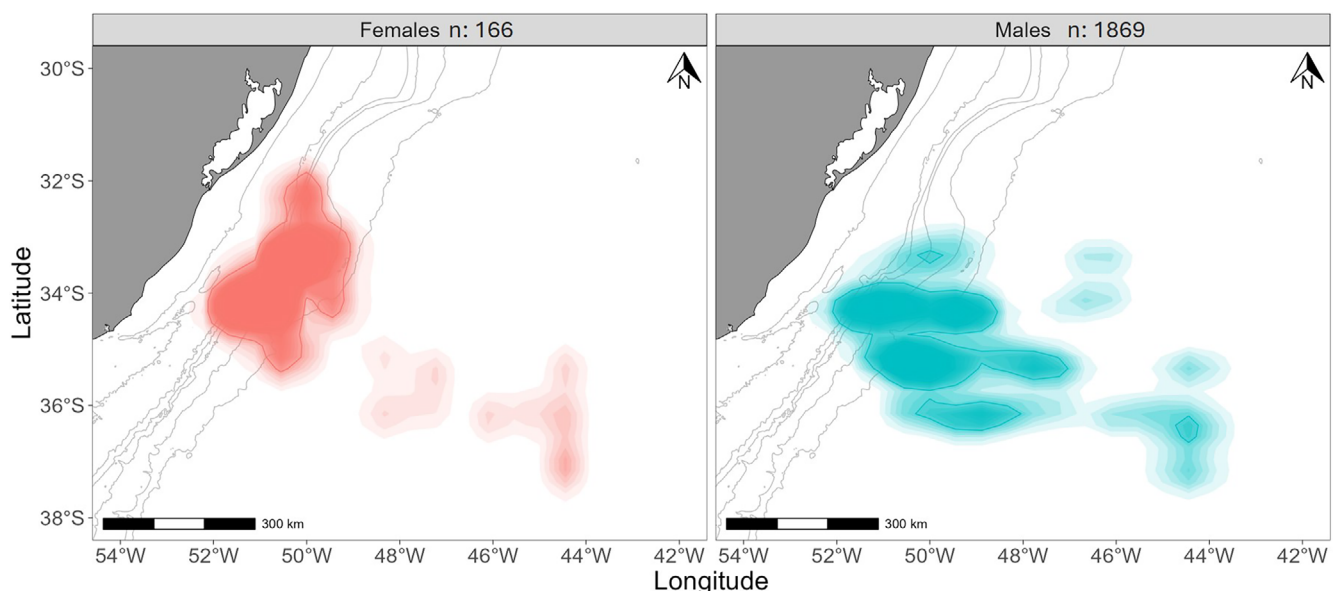
The ANOVA revealed significant differences ( $p < 0.05$ ) in the average size among seasons for both males and females. Figure 4 shows that the average size is at its lowest during the winter and at its highest during the summer for both sexes. The pair-wise test reveals significant differences in average size among all seasons (Figure 4) except for females during summer and spring (Figure 4b).

To account for historical changes, we included data from Montealegre-Quijano (2007) on the seasonal size distribution patterns for male and female for each period in Figure 5. During the 2018–2022 period, we observed that female sizes were evenly distributed during autumn and winter, but skewed toward small adult sizes during spring and summer. Male sizes showed a season-related cyclical pattern, with distributions skewed toward small adults during summer and large juveniles in winter, whereas autumn and spring appeared as transition periods with even amounts of both size classes (Figure 5).

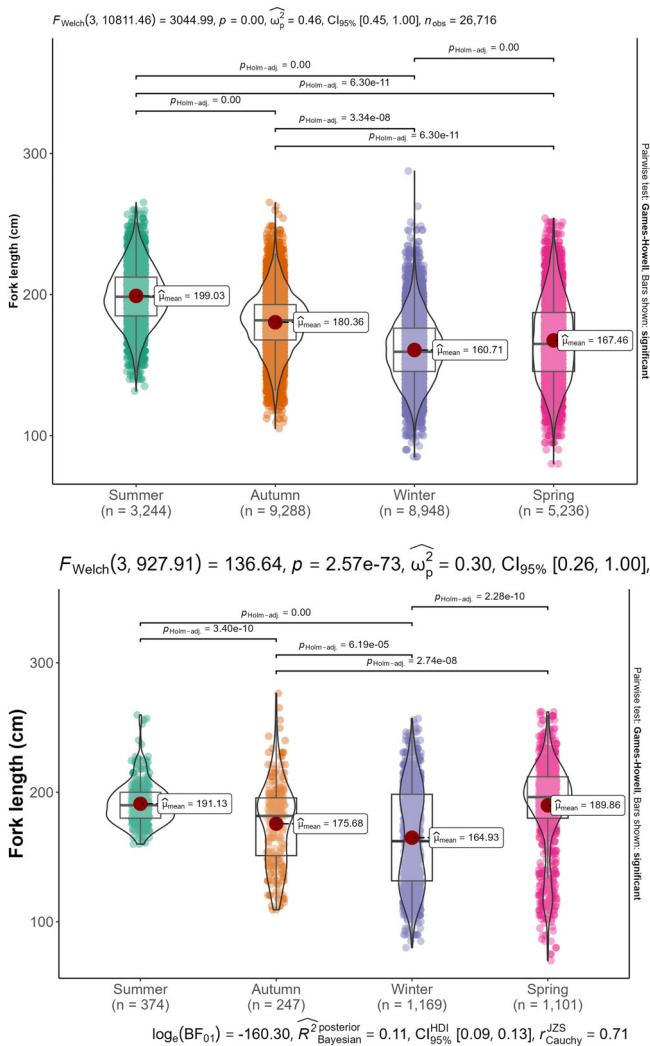
The size distribution patterns for the 2004–2006 period slightly diverged from the ones observed in this study. Female sizes were evenly distributed during all seasons, with a significant number of small juveniles during winter and spring. Male sizes were evenly distributed between the small adult and large juvenile size classes during summer and autumn and skewed toward large juveniles during the winter and spring, with a significant number of small juveniles during the spring. These variations between periods were caused by differences in the temporal coverage of sampling methods for each period (Figure 6). The only season sampled throughout the 3 years of the 2004–2006 period was winter, with 1- or 2-year sample gaps during the remaining seasons. In contrast, the 2018–2022 period had every season of every monitored year (Figure 6).

Figure 6 also shows that although small juveniles were present during all years of both periods (2004–2006; 2018–2022), mainly during winter and spring, individuals  $<100$  cm FL were scarce, and a negligible number of  $<75$  cm FL individuals (YOY) only appeared during spring 2005. Additionally, Figure 6 shows that although there was a clear general size distribution pattern for each sex (Figure 4) during the 2018–2022 period, each year showed variations from it.

CPUE (catch per unit of effort) data (Figure 7) showed a large numerical difference between male and female catches, with males



**FIGURE 3** Spatial distribution of the *Prionace glauca* catches by sex (males and females) observed in the subsample gathered by onboard observers.

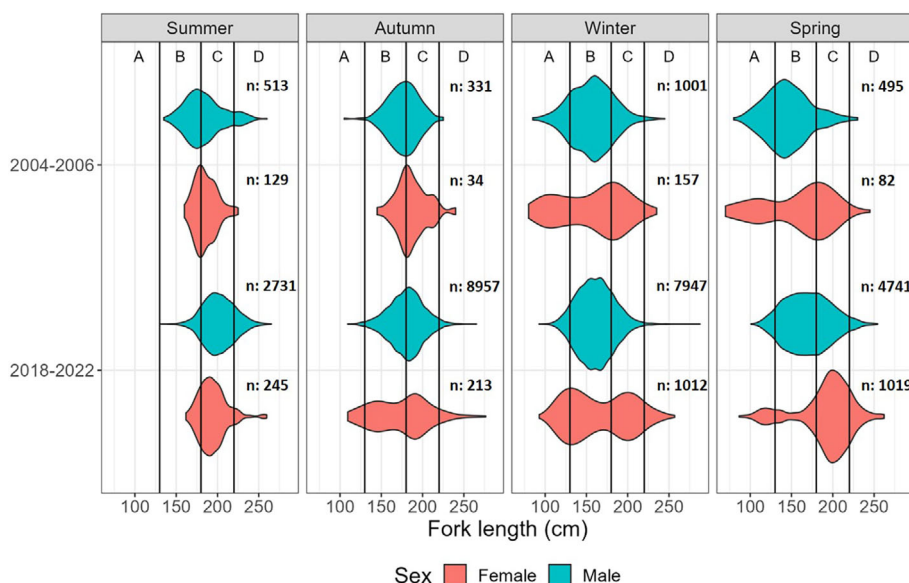


**FIGURE 4** The ANOVA of the average size of *Prionace glauca* among seasons (summer, autumn, winter, spring) for (a) males and (b) females.

being ever larger than females. There was a cyclical seasonal capture pattern for each sex, with female catches being more abundant during winter and spring and less so during summer and autumn, and with male catches peaking during autumn and decreasing across the seasons until they reached their lowest abundance during summer (Figure 7). Although there were dim variations between years, particularly during winter 2022 for males and spring 2021 for females, where catches were higher than usual for each season, the general catch pattern remained.

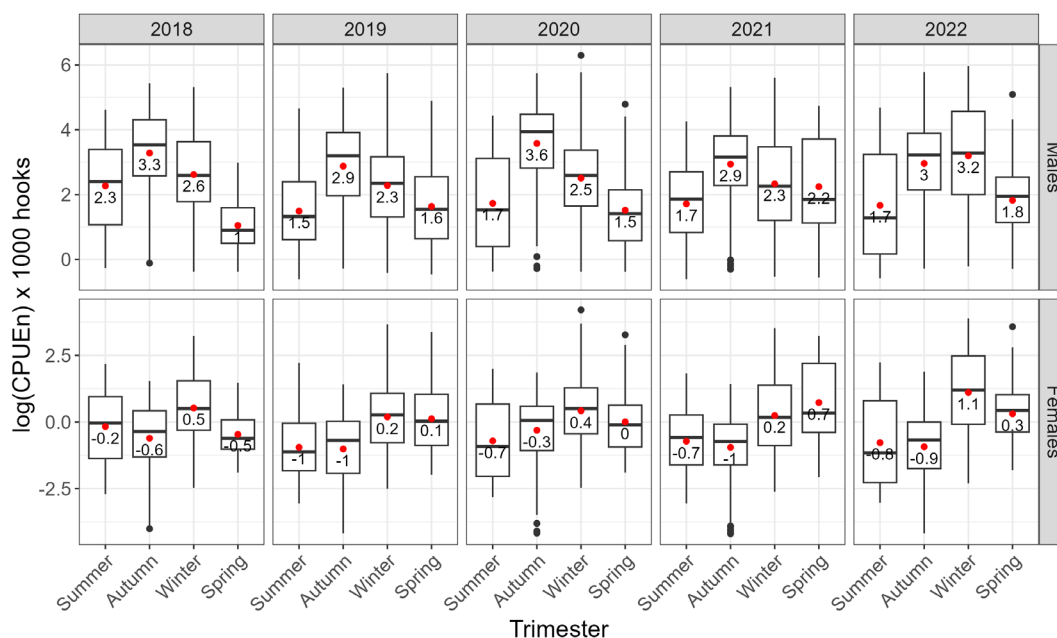
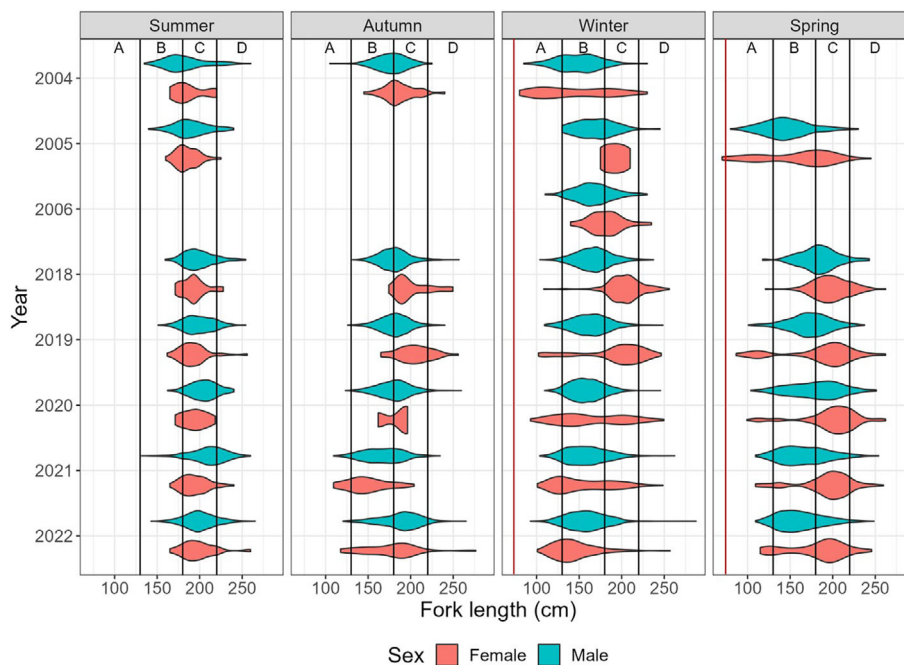
### 3.2 | Age and growth

A total of 200 vertebrae were initially selected for the study, with 59 being the largest available and 141 being randomly chosen from the remaining samples. After 49 unreadable samples were discarded, a total of 151 vertebrae were left for analysis. Among these, 22 samples were discarded due to the inability to reach a consensus in band pair reading. The remaining 129 vertebrae, 71 from males and 58 from females, were used for growth modeling. The sizes ranged from 103.76 to 251.35 cm FL for males and from 171.21 to 271.52 cm FL for females. The relationship between FL and VR was found to be linear for both males and females. We observed differences between the regression lines for males and females (ANCOVA,  $p < 0.05$ ) (Figure 8). This suggests that male and female growth patterns may differ, with females reaching a larger FL with respect to VR than males. The independent band pair readings showed a 72.82% agreement between the two readers, resulting in a 4.96% CV and 3.51% APE, with higher variation between readers at larger sizes (Figure 9). The age range was 2–13 years for males and 4–12 years for females (Figure 10). The LOIC test revealed that of the three growth models tested, the von Bertalanffy better fitted the data for males ( $L_{\infty}$ : 255.02 cm FL,  $k$ : 0.20,  $L_0$ : 35.68 cm FL), females ( $L_{\infty}$ : 246.47 cm FL,  $k$ : 0.23,  $L_0$ : 36.77 cm FL), and pooled sexes ( $L_{\infty}$ : 269.58 cm FL,  $k$ : 0.18,  $L_0$ : 36.19 cm FL) (Table 2).



**FIGURE 5** General size distribution pattern of *Prionace glauca* individuals caught by the surface longline fleet in the southwestern South Atlantic during 2004–2006 (Montealegre-Quijano, 2007) and 2018–2022 (this study). A, small juveniles; B, large juveniles; C, small adults; D, large adults.

**FIGURE 6** Size distribution of *Prionace glauca* individuals caught by the surface longline fleet in the southwestern South Atlantic by trimester for each year of this study (2018–2022) and between 2004 and 2006 (Montealegre-Quijano, 2007). Red lines signal the 75-cm-fork length size class during winter and spring to highlight how very few individuals fall under this size class. A, small juveniles; B, large juveniles; C, small adults; D, large adults.

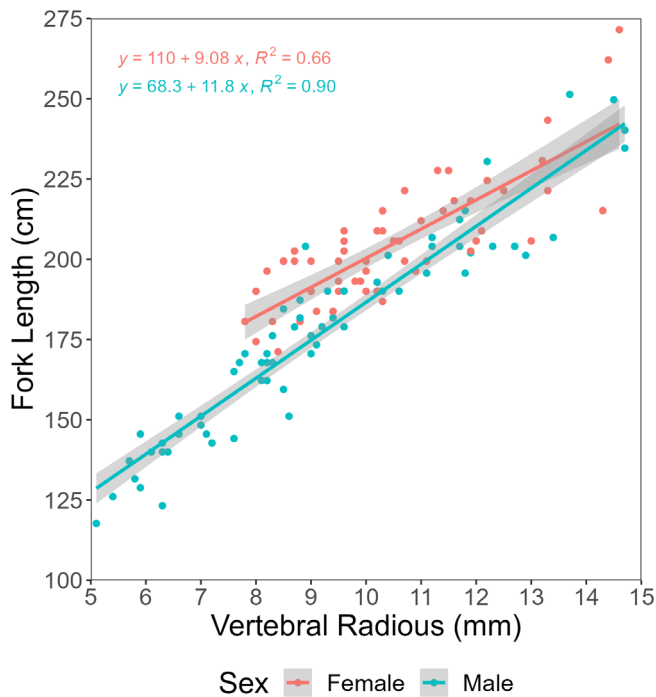


**FIGURE 7** Nominal CPUE (catch per unit of effort,  $n/1000$  hooks) for *Prionace glauca* catches for each season of each year of study (2018–2022) caught by the surface longline fleet in the southwestern South Atlantic.

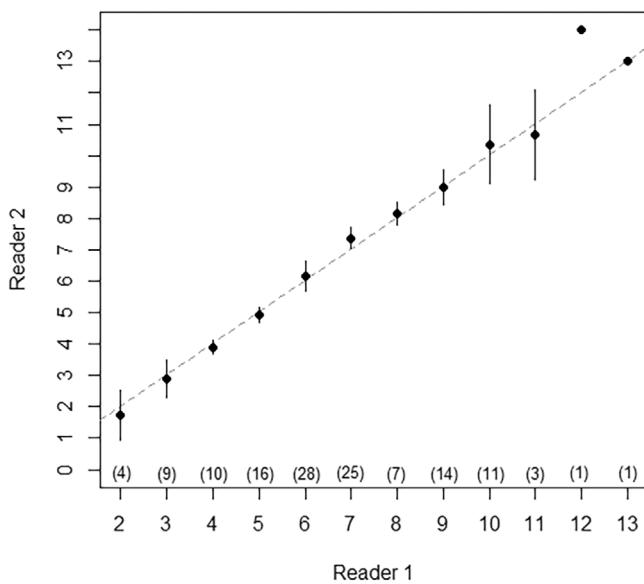
## 4 | DISCUSSION

The size composition of blue sharks observed off the coast of southern Brazil shows that the study area is mainly inhabited by large juvenile males and a few small adult females. The higher proportion of males in the catches (9.86:1) indicates a pattern of sexual segregation, with males dominating the area throughout the year, especially in autumn. This is consistent with the findings of Mas et al. (2023) for the southwestern Atlantic Ocean, where males also dominated the

catches. Additionally, there are signs of size-related segregation for males during summer, with adults making up the majority of the catches and very few juveniles in the area, whereas the opposite pattern is observed during winter. Sexual and growth-related segregation patterns have been widely observed for the blue shark (Bigelow et al., 1999; Coelho et al., 2017; Fujinami et al., 2022; Hiraoka et al., 2016; Kohler et al., 2002; Maxwell et al., 2019; Nakano & Nagasawa, 1996; Tavares et al., 2012). In this study, these patterns were consistent each year, with a slight increase in juveniles present

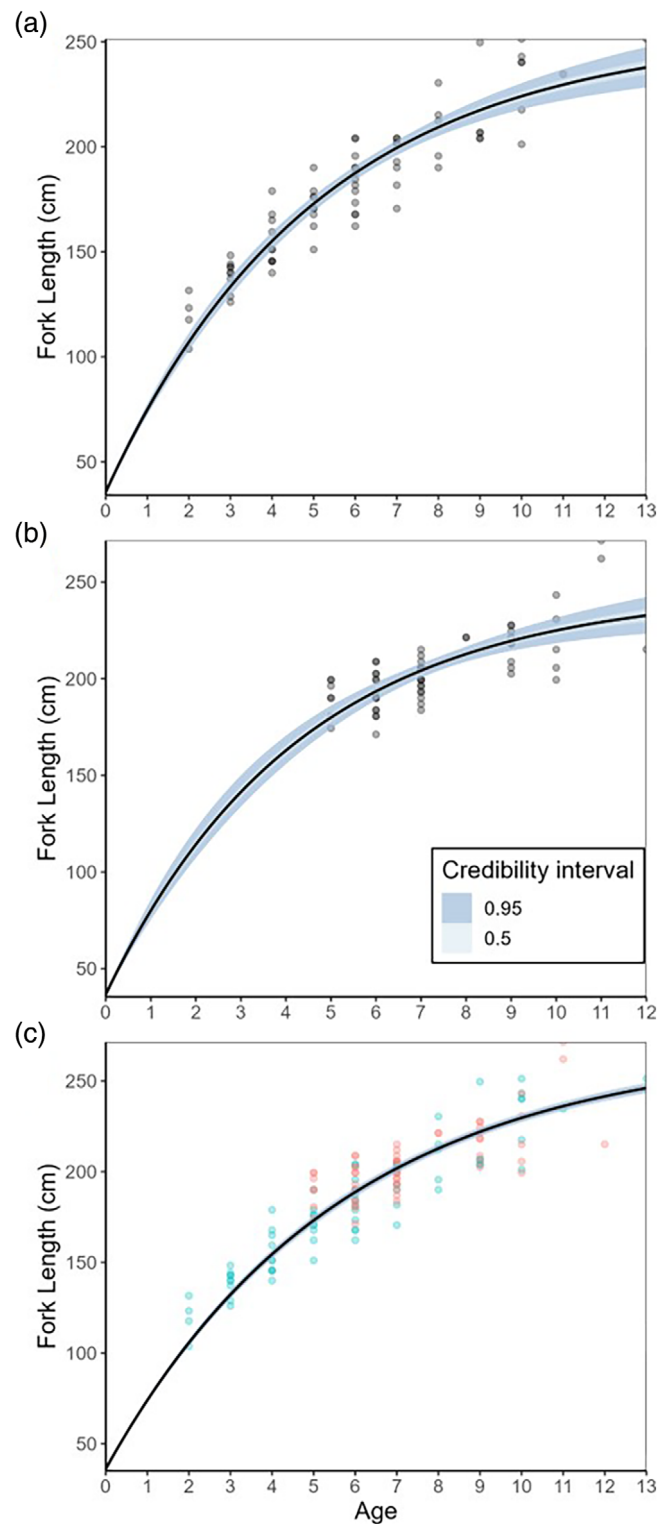


**FIGURE 8** Relationship between the vertebral radius (in millimeters) and the fork length (in centimeters) of *Prionace glauca* for males and females.



**FIGURE 9** Age-bias plot for 129 *Prionace glauca* with age-specific agreements between two independent readers. Numbers between parentheses represent the number of individuals in each age class.

during the summer of 2021 and 2022. The description of yearly size composition patterns for females is imprecise due to their small occurrence within the area. However, we can assume a dynamic distribution pattern over time based on the presence of different female life stages throughout the year.



**FIGURE 10** von Bertalanffy length-at-age growth curves for *Prionace glauca* for (a) males, (b) females, and (c) pooled sexes in pink and blue for females and males, respectively.

The main factors affecting the distribution of blue sharks are latitude and temperature (Nakano & Nagasawa, 1996). The species' populations tend to move from mesotrophic to oligotrophic environments throughout their life span, which are generally higher and lower

**TABLE 2** Life-history parameters estimated through von Bertalanffy, Gompertz, and logistic models for males, females, and pooled sexes.

	Model	Parameter				
		$L_{\infty}$	$k$	$L_0$	LOOIC	LOOICw
Males	<b>von Bertalanffy</b>	<b>255.02</b>	<b>0.20</b>	<b>35.68</b>	<b>576.44</b>	<b>1</b>
	Gompertz	227.46	0.39	35.85	596.10	0
	Logistic	214.81	0.65	35.99	617.72	0
Females	<b>von Bertalanffy</b>	<b>246.47</b>	<b>0.23</b>	<b>36.77</b>	<b>472.28</b>	<b>0.89</b>
	Gompertz	232.65	0.39	36.78	476.51	0.11
	Logistic	224.63	0.59	36.81	482.00	0.01
Pooled sexes	<b>von Bertalanffy</b>	<b>269.58</b>	<b>0.18</b>	<b>36.19</b>	<b>1047.74</b>	<b>1</b>
	Gompertz	264.91	0.29	36.47	1108.67	0
	Logistic	263.2	0.46	36.65	1180.6	0

Note: Signaled in bold are the models that best described the data.

Abbreviations: LOOIC, leave-one-out information criterion; LOOICw, leave-one-out information criterion weight-for-model selection.

latitudes, respectively (Adams et al., 2016). The species also undergoes seasonal latitudinal migrations observed on both sides of the Atlantic and the Pacific oceans (Adams et al., 2016; Coelho et al., 2017). In the southwestern Atlantic Ocean, several studies (Carvalho et al., 2011; Hazin et al., 2000; Joung et al., 2017 and Mas et al., 2023) propose a size segregation pattern of male blue sharks in which the mean sizes increase as latitude decreases. Therefore, based on the results of this study, we hypothesize that a new batch of large juvenile male blue sharks arrives in the region (27–39°S) during autumn and remains through the winter to feed and grow. Then, during spring, these individuals reach the small adult size and start to leave the area, yet a few of these new adults remain through the summer.

Our study area is located within the Subtropical Shelf Front (STSF) oceanographic region (20°S–40°S). This area comprises two water masses: the cold and fresh sub-Antarctic shelf waters that dominate south of 33°S, and the warm and salty subtropical shelf waters that extend primarily north of that latitude (Piola et al., 2008). However, there are seasonal changes in the range extension of the water masses. During the winter, along with the freshwater outflow of the La Plata River and the Patos-Mirin lagoon, sub-Antarctic shelf waters brought by the Malvinas Current are able to reach further north of the STSF. Additionally, due to the action of the wind in the region, the mean flow of the Brazil Current, which carries subtropical shelf waters, reverses seasonally, flowing toward the southwest during the summer and toward the northeast during the winter (Piola et al., 2008). These oceanographic changes could be the source of the seasonal size variation in male blue sharks in the area. Due to the presence of these two water masses, the STSF appears as an extension of the Brazil-Malvinas Confluence on the South American continental shelf (Piola et al., 2008). During autumn and winter, its productivity intensifies, which could be the reason for the increase in abundance (Figure 6) of large juveniles (Figure 4) that could be feeding in the area. The Brazil Current is stronger during the summer, flowing southwestward with sea surface temperatures (SSTs) >23°C (Matano et al., 2010). Male blue sharks are more abundant in SSTs from 12 to

20°C, with larger sharks preferring warmer temperatures (Nakano & Nagasawa, 1996). In the North Pacific, a higher nominal CPUE over an SST range of 14–18°C was observed, which decreased to very low CPUE values in SSTs >23°C (Bigelow et al., 1999). Therefore, we presume that male blue sharks either leave the area during spring and summer due to the temperature or that the warmer waters of the subtropical shelf waters bring a small batch (Figure 6) of small adults (Figure 4). This general dynamic shows that southern Brazil is used by different life stages during the year, being part of a larger area of stock structuring.

In the North Atlantic, young are born during the spring and summer (Kohler et al., 2002) in a possible nursery area located in the sub-Antarctic boundary area (50°N–70°N) (Nakano & Nagasawa, 1996). In the present study, small juveniles of both sexes were mainly present during winter and spring. However, the number of observed individuals during 2018–2021 was minimal, representing only 4% of the total catch. Individuals under 100 cm FL represented 0.8% of this size class and were only present during 2019 and 2020, indicating that they were not consistently present in the region. Based on these observations, southern Brazil does not meet the criteria that determine a nursery area proposed by Heupel et al. (2007). YOY and small juveniles (<75 cm FL) were not more commonly encountered than in other areas. They do not remain in the area for extended periods, and the area is not used repeatedly across years (Figure 5). Therefore, it is possible that young born in a nursery area further south from our study region reach the large juvenile size and travel to lower latitudes in the South Atlantic during autumn.

Finally, we presume that the sex ratio in our research is skewed toward male blue sharks because the surface longline fleet that lands at the port of Rio Grande mainly operates within the BEEZ. In their studies, Montealegre-Quijano and Vooren (2010), Cardoso (2010), and Mas (2015) observed a more even sex ratio during the months in which the cruises they studied operated in oceanic regions outside of the BEEZ and the Uruguayan Economic Exclusive Zone, respectively. This could be an indication that longitude plays a role in sex segregation in the southwestern Atlantic. Longitudinal gradients are not

unheard of, as Bigelow et al. (1999) and Kohler et al. (2002) observed longitudinal differences in nominal CPUE values in the North Pacific and the North Atlantic.

#### 4.1 | Age and growth

Although Andrade et al. (2019) argue that discarding a considerable amount represents significant age estimation problems, Cailliet et al. (2006) recommend this measure to avoid increasing ageing bias. Therefore, during the collaborative re-examination of the growth bands, both readers decided to discard 22 vertebrae from the analysis due to the inability to reach a consensus. In the age-bias plot for this collaborative reading (Figure 9), we observed that there was no systematic bias between readers and a high percentage of agreement. Jolly et al. (2013) argue that a high percentage of reader agreement and the reasonably low APE imply a high degree of reader precision. This, along with a low CV value, implies that the band pair counting in this study was reliable. The figure shows larger error bars for the smaller and larger individuals, which is a common phenomenon in growth band reading for the species, as also observed by Jolly et al. (2013).

By assessing age validation in seven shark species, Natanson et al. (2018) concluded that the relationship between band deposition and time must be considered loosely correlated due to changes in counts between vertebrae from different positions of the vertebral column and ontogenetic changes in each individual. However, Figure 8 reveals that for blue sharks, VR and FL increase proportionally. Therefore, we acknowledge that vertebral centra can be considered a suitable structure for age and growth studies for the species. In addition, Natanson et al. (2018) suggested that blue shark vertebrae appeared to be more consistent than those analysed for other shark species. Annual band pair formation has been successfully validated for the blue shark by oxytetracycline (OTC) marked sharks from tag-recapture activities in the North Atlantic by Skomal and Natanson (2003), in the northeastern Pacific by Wells et al. (2016), and by edge and marginal increment analysis in the South Atlantic by Joung et al. (2017), in the South Pacific by Joung et al. (2018), and in the North Pacific by Fujinami et al. (2019). Due to common problems regarding elasmobranch vertebrae analysis, such as concave intermedialia due to dehydration of the vertebrae that results in the narrowing of the vertebral edge and possible aggregation of adjacent bands for older specimens, neither the marginal increment analysis nor the type of edge analysis was performed in this study. Therefore, we assumed a pattern of annual band pair formation for the blue shark following the results of the aforementioned studies that validated this periodicity for the species. However, alizarin red staining and digital enhancement of band pair contrast were very helpful measures to improve band pair reading.

The life-history parameters estimated in this study fell within the range reported for the species in previous studies from both the Pacific and Atlantic Oceans (Table 1). This observation is consistent with the findings of Jolly et al. (2013), who analysed the 95% CIs of growth parameters estimated in several age and growth studies for the blue shark and reported that they mostly overlap, suggesting that there is no significant difference between the growth of blue shark

populations from different geographic regions. Although the values of  $k$  presented in this study are the highest reported for the South Atlantic, they do not exceed the historical range of the value for the species among regions (Table 1). The observed high  $k$  values might be due to the fact that the samples used for this study mainly belong to juveniles. Ramos-Cartelle et al. (2023) performed a tag and recapture assessment with International Convention for the Conservation of Atlantic Tunas (ICCAT) data in which they concluded that growth rates are higher in smaller size classes and gradually reduce as size increases. The  $L_{\infty}$  values obtained in this study were smaller compared to the values estimated by Montealegre-Quijano (2007); see Table 1. Additionally, the  $k$  values were higher for both sexes that could indicate that smaller, faster-growing individuals have become more frequent in the area over time. However, differences in the individual growth rate ( $k$ ) observed among and within a region (Table 1) might also be due to environmental variations, which are established as a main factor for growth variability within the same species (Hoenig & Gruber, 1990), as well as to approach selection and model variations.

The lack of individuals in the 0 and 1-year age classes initially created uncertainty in the fit of the growth models because we used the von Bertalanffy model variation that estimates  $L_0$ , as recommended for elasmobranch age and growth studies (Smart & Grammer, 2021). Therefore, we estimated an average length-at-birth for the species using data available in the literature (Cardoso, 2010; ICCAT, 2015; Pratt, 1979).

## 5 | CONCLUSIONS

The continuous landings and onboard monitoring provided a snapshot of the size and sex composition of blue sharks in southern Brazil. The results revealed that blue sharks use the region dynamically throughout seasons, years, and life stages. For males, as large juveniles leave the area during summer, the frequency of small adults increases. Whether this occurs due to new arrivals or individual growth is a topic for future research. The fact that females are much less frequent in the region, and longitude being a more important factor than anticipated in sex segregation, could indicate that the blue sharks being landed at the port of Rio Grande are only a fraction of a population with a larger distribution range in the South Atlantic. These results highlight the need for long-term continuous sampling to understand the spatial distribution patterns of this highly migratory species and to have fishery indicators to better understand the fishing impacts on its stocks.

### AUTHOR CONTRIBUTIONS

Raquel Marquez designed the study, conducted laboratory work, performed data analysis, and primary writing of the paper. Rodrigo Barreto contributed by teaching vertebrae sample manipulation, revised the manuscript, and made substantial contributions to its content. Luis Gustavo Cardoso provided the samples, data, and infrastructure necessary to conduct the research. Additionally, he assisted in data analysis and contributed to writing the manuscript.

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**How to cite this article:** Marquez, R., Barreto, R., & Cardoso, L. G. (2024). Size structure, age, and growth of the blue shark, *Prionace glauca* (Linnaeus, 1758) in southern Brazil. *Journal of Fish Biology*, 1–13. <https://doi.org/10.1111/jfb.15758>