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Age, growth, maturity and extinction risk of an exploited and endangered skate, *Atlantoraja castelnaui*, from off Uruguay and northern Argentina

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ABSTRACT

The spotback skate *Atlantoraja castelnaui* (Arhynchobatidae) is a large and threatened skate species subjected to fishing pressure, endemic to the Southwest Atlantic that occurs from Rio de Janeiro, Brazil, to San Jorge Gulf, Argentina. The age, growth, age at maturity and the maximum intrinsic rate of population increase r_{max} of *A. castelnaui* were studied using 152 specimens collected from off Uruguay and north Argentina (35°–42° S), between June 2013 and February 2020. Vertebrae from 143 individuals were used for ageing (females: $n = 83$, size range 404–1300 mm total length, *TL*; males: $n = 60$, size range 400–1270 mm *TL*). Maximum ages determined for females and males were 30 and 28 years, respectively. To fit growth models, non-linear and Bayesian estimation approaches were considered. For the first approach, a set of four candidate growth (size-at-age) models were fitted: three-parameter von Bertalanffy, two-parameter von Bertalanffy with fixed L_0, Gompertz and Logistic. In the second approach, von Bertalanffy, Gompertz and Logistic were fitted. For non-linear estimation, model selection indicated that the entire set of candidate growth models were supported by the data. The von Bertalanffy was selected as the best model for Bayesian estimation. There were no differences in growth between sexes. For the sexes combined, the von Bertalanffy growth model by Bayesian method was considered the most adequate to describe the growth of *A. castelnaui* (growth mean parameters ± S.D.: $L_\infty = 1210.29 \pm 40.68$ mm; $k = 0.12 \pm 0.01$ years^{-1}; $L_0 = 179.20 \pm 11.62$ mm). The age at maturity was estimated at 16.21 and 14.04 years for females and males, respectively. The maximum intrinsic rate of population increase r_{max} was estimated as 0.252 years^{-1}. Life-history traits and r_{max} provided in the present study suggest that this species has a relatively low productivity and may be vulnerable to an intense fishing pressure.

KEYWORDS
age at maturity, elasmobranchs, growth modelling, maximum intrinsic rate of population increase (r_{max}), Rajiformes

1 | INTRODUCTION

Chondrichthyan fishes (sharks, skates, rays and chimaeras) are commercially valuable, but an intense fishing exploitation has profoundly altered the abundance of their populations at a global level, given that they have a very low population productivity, as compared to teleost fishes (Dulvy *et al*., 2017; Ferretti *et al*., 2010). For commercially valuable species, their management is uncertain when stock assessments are lacking (Bradshaw *et al*., 2018). To determine efficient management strategies for the exploitation of chondrichthyans and identify priority species for conservation, it is essential to know their life-history parameters. For example, in Argentinian waters, species-specific life-history data of skates are not considered in the management of these species. In consequence, many skate species have been negatively impacted by the fishing (Massa *et al*., 2004). Among life-history traits, age and growth studies, and estimates of age at maturity are the first step to define fundamental biological processes of a population exposed to fishing pressure. In the same way, the use of these life-history traits allows one to quantify demographic parameters that are useful to determine sensitivity and vulnerability to non-natural mortality.

In this context, a demographic parameter of direct practical importance in conservation and fisheries fields is the maximum intrinsic rate of population increase (r_{max}), that allows the quantification of the potential susceptibility to over-exploitation (Cortés, 2016). The estimation of r_{max} is a simple method using point estimates of life-history traits that has simplified the assessment of the extinction risk and sustainability of the fisheries of data-poor species (Bradshaw *et al*., 2018; Pardo *et al*., 2018).

In Argentinian waters, the fishing effort of the industrial trawl fleet increased by 108% between 1990 and 1995 (Campagna *et al*., 2006), and this region has become one of the areas with the highest fishing effort in the world (Guiet *et al*., 2019; Tyedmers *et al*., 2005; Watson *et al*., 2013). Also, Argentina is among the first five countries with the largest landings of chondrichthyan fishes in the world (Dulvy *et al*., 2017).

Skates, in particular, are subjected to an intense fishing pressure. Skates are the group of chondrichthyan fishes with the largest declared landings in Argentinian harbours (Massa *et al*., 2004), with an annual average of 17,798 tons between 2010 and 2019 (Ministerio de Agricultura, Ganadería y Pesca, Argentina). Along the coastal waters from north Argentina and Uruguay (34°–41° S), five skate species are subjected to heavy fishing pressure in a multi-species fishery for coastal demersal species (Tamini *et al*., 2006). Skates, as a group, present a high variability in life-history parameters, and therefore the response to exploitation may differ among species (Dulvy & Reynolds, 2002). In general, skate species with large body sizes (Dulvy *et al*., 2000; Dulvy & Reynolds, 2002), late age at sexual maturity (Hutchings *et al*., 2012) and a narrow niche breadth (Barbini *et al*., 2020) present biological characteristics that make them more sensitive to anthropogenic stressors.

The spotback skate, *Atlantoraja castelnaui* (Miranda Ribeiro 1907) (Arhynchobatidae), is one of the largest species of skates endemic to the Southwest Atlantic, attaining 1400 mm in total length. It is distributed from Rio de Janeiro, Brazil (22° S), to the San Jorge Gulf, Argentina (46° 39′S) (Bovcon *et al*., 2011; Menni & Stehmann, 2000). In Argentinian and Uruguayan waters, this species occurs from shallow coastal waters to approximately 100 m depth (Cousseau *et al*., 2007). *A. castelnaui* is a predator with a narrow trophic niche breadth, feeding almost exclusively on teleost fishes (Barbini *et al*., 2020; Barbini & Lucifora, 2012). Females mature between 1050 and 1089 mm, and males mature between 910 and 980 mm total length (Colonello *et al*., 2012; Oddone *et al*., 2008). *A. castelnaui* has been categorized as critically endangered by the IUCN (Pollom *et al*., 2020). Nonetheless, this species is one of the skates landed by the fleet that operates in Argentinian waters. Despite the fact that it is a species considered highly vulnerable, growth parameters and age at maturity are two aspects of its biology essential for understanding its population dynamics that are poorly known. As antecedents, only an internal technical report in Argentina (Hozbor and Massa, 2013) and a Master of Science Thesis in Brazil (Casarini, 2006) have dealt with age and growth of *A. castelnaui*. Differences in the maximum ages were reported between these previous studies. This incongruence undermines the design of efficient management strategies.

Limited life-history information for skates has made it difficult to determine the response of skate populations to fishing and has complicated adequate management actions. Therefore, given the increasing fishing pressure on skates in Argentinian waters, it is important to know and identify all biological and demographic parameters that are essential for conservation and management, in particular in those species with potentially elevated risk, such as *A. castelnaui*. The aims of the present study were to determine the age of *A. castelnaui* through growth bands in vertebrae, obtain growth models and estimate both age at sexual maturity and the maximum intrinsic rate of population increase (r_{max}).

2 | MATERIALS AND METHODS

2.1 | Sample collection

Specimens used in this study were caught by commercial bottom-trawl vessels operating on the continental shelf off Uruguay and northern Argentina, in the Southwest Atlantic (Figure 1). A total of 152 individuals landed in Mar del Plata harbour, Argentina (38°00′S, 57°33′W) were collected between June 2013 and February 2020.

For each individual, the total length (*TL*, mm) was measured, and sex was determined. *TL* was measured as the distance from tip of the snout to the tip of the tail (Last *et al*., 2008). A relationship (linear regression) between *TL* and disc width (*DW*; the distance between the wing tips) was estimated ($DW = -3.85 + 0.69\ LT$; $P < 0.05$; $r^2 = 0.99$). Also, maturity stage (immature or mature) was determined by a macroscopic observation of the reproductive organs (Colonello *et al*., 2011; Stehmann, 2002). Females were categorized as immature when they had undeveloped thread-like uteri, and ovaries contained only non-vitellogenic ovarian follicles and undeveloped oviducal glands. Mature females had wide uteri, ovaries with yellow ovarian follicles and oviducal glands that were distinctly differentiated. Males were categorized as immatures when testes were thin, the efferent ducts were straight and the claspers were uncalcified and shorter than

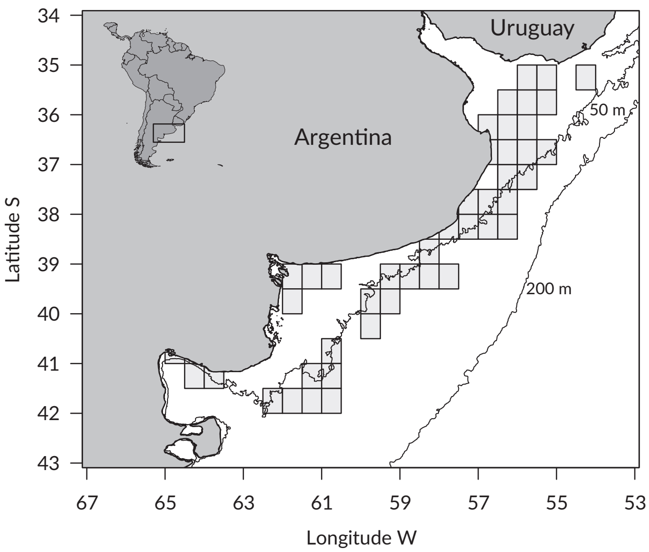

FIGURE 1 Map of the area off Uruguay and northern Argentina showing the location of cells of the fishing grid (black rectangles) where specimens of *Atlantoraja castelnaui* were collected

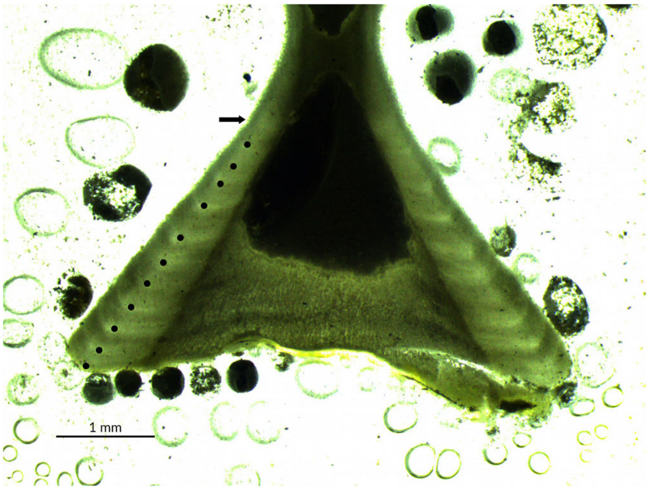

FIGURE 2 A vertebral centra section from a 1180 mm *TL* female *Atlantoraja castelnaui*. The black dots indicate translucent bands; the black arrow indicates the birthmark

the pelvic fins. Mature males had enlarged testes, highly coiled efferent ducts and large and calcified claspers. Vertebrae were extracted from the region above the abdominal cavity and stored at -20°C.

2.2 | Age determination

To prepare vertebrae, they were first defrosted and manually cleaned removing excess tissue using scalpels and tweezers. Each vertebral centra was separated and soaked in 5% sodium hypochlorite, with immersion times between 5 and 15 min depending on the size of the vertebrae. Following immersion in sodium hypochlorite, vertebrae were thoroughly washed and dried in an oven at 50°C by 24 h. Dry vertebrae were polished along the central longitudinal axis using 300–1000 grit dry abrasive papers to just above the centrum. Then, the flat surface was mounted on a glass microscope slide with silicone, and the other side was polished to produce a thin horizontal section. A digital photograph of each vertebral section was taken using a Leica MC 170 Full High Definition 1080 P camera under a stereoscopic microscope (Leica M165C), with transmitted light. The images were processed, increasing their contrast and clarity to enhance visibility of the vertebral growth bands.

Vertebral radius (*Rv*) measurements and bands counts were taken from digital photographs using the RfishBC package (Ogle, 2019), under the R statistical environment, version 3.6.3 (R Core Team, 2020). *Rv* was measured from the focus of the vertebrae to the outer edge of the *corpus calcareum*. To determine age, we assumed a band pair to be representative of 1 year of growth, where each band pair consisted of one opaque band and one translucent band (Figure 2). Each subsequent translucent band deposited on the *corpus calcareum* was counted. The birthmark was identified as the first translucent band after the focus of the vertebra and sometimes associated with a slight change in the angle, that was determined to be age 0 (Smith *et al*., 2007). The age of each vertebral section was read by two independent readers without any prior knowledge of the sex or size of the individuals, to prevent bias while counting bands. Age readings were compared, and when the age differed by at least three band counts between the two readers, the reading process was repeated by both readers until an agreement was reached. If agreement was not achieved between both readers, then those vertebral sections ($n = 9$) were excluded from subsequent analyses.

We calculated the coefficient of variation (CV) (Chang, 1982) and the average percent error (APE) (Beamish & Fournier, 1981) to compare precision between the two readers. We also used the age bias plot to graphically compare the accuracy between two sets of ages (Campana *et al*., 1995) and calculated the Bowker's test of symmetry to determine whether there was systematic bias between readers (Hoenig *et al*., 1995). For the age bias plot, the readings made by the senior reader served as the reference set (Ogle, 2016). The precision analysis was performed using the Fisheries Stock Assessment (FSA) package (Ogle *et al*., 2020) within the R statistical environment (R Core Team, 2020).

To determine if vertebral growth remained proportional to body growth, we fitted linear regressions between *Rv* and *TL* for both sexes. Differences between sexes were evaluated using ANCOVA (Zar, 1999).

To verify the periodicity of band pair formation we used the semi-direct method of edge analysis (Cailliet & Goldman, 2004). The optical quality, as translucency or opacity, in the outermost band of the *corpus calcareum* was examined for each individual. Edge analysis compares the translucency and opacity of the edge over time in different individuals to discern seasonal changes in growth (Cailliet & Goldman, 2004). Thus, we evaluated the seasonality of the formation of the band-pairs plotting proportion of each edge type against month and season of collection.

2.3 | Growth modelling

To determine the growth parameters of *A. castelnaui* we adopted a multi-modelling approach, which is recommended as a better and more robust alternative to study fish growth (Katsanevakis & Maravelias, 2008; Smart *et al*., 2016). The multi-model approach is considered to provide better growth estimates as to avoid misspecification and biases compared to the use of only one model (Cailliet *et al*., 2006; Smart *et al*., 2016). To fit growth models we used two approaches of estimation: one based on non-linear estimation and another based on Bayesian estimation. For non-linear estimation, a set of four candidate length-at-age models were fitted, as recommended by Cailliet *et al*. (2006): three-parameter von Bertalanffy, two-parameter von Bertalanffy, Gompertz and Logistic growth functions. The equation for the three-parameter von Bertalanffy (1) growth model is as follows:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \tag{1}$$

where L_t is total length-at-age t, L_∞ is asymptotic length, k is the growth coefficient which determines how quickly L_∞ is attained and t_0 is the theoretical age at zero length. The two-parameter von Bertalanffy model (2) includes a known size at birth (L_0) as one of its parameters, and it has the following form:

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt} \tag{2}$$

L_0 was fixed at 174 mm based on the mean smallest free-swimming individuals observed in previous studies (Colonello *et al*., 2012; Oddone *et al*., 2008). The Gompertz (3) and Logistic (4) growth functions have the following forms:

$$L_t = L_\infty e^{\left(-e^{-g(t-t_i)}\right)} \tag{3}$$

$$L_t = L_\infty \left(1 - e^{-g(t-t_i)}\right)^{-1} \tag{4}$$

where g is the instantaneous growth coefficient at the inflection point and t_i is the age at the inflection point in the curve. Growth models were fitted with the arithmetic average between readers for females and males separately and for sexes combined. To determine if there were significant differences in growth parameters between sexes, we used the likelihood ratio test (Kimura, 1980). Growth models were fitted using the FSA package (Ogle *et al*., 2020) with the R statistical language (R Core Team, 2020).

To determine performance of each alternative growth model, the small-sample bias adjusted form of the AICc was calculated. We used AICc because sample size (n) was small in comparison to the number of estimated parameters (p) (*i.e*., $n/p < 40$) (Burnham & Anderson, 2002). The model with the lowest AICc value was chosen as the model with the highest support (Johnson & Omland, 2004). AICc differences (Δ_i) were computed for all growth models. Sets of models with $\Delta_i < 2$ are considered to be essentially as good as the best model (Burnham & Anderson, 2002). To obtain the likelihood of each model fitted, the Akaike's weight (w) was calculated (Johnson & Omland, 2004). w can be interpreted as the probability of the model being the best one describing the data, given the set of candidate models (Johnson & Omland, 2004). When the data support more than one model, parameter estimation can be made from all candidate models (Katsanevakis, 2006). Then, if the best model was not clearly superior to some of the others in the set, we used multi-model inference by model averaging (Katsanevakis & Maravelias, 2008; Symonds & Moussalli, 2011).

In the Bayesian framework, we fitted a set of three candidate length-at-age models: von Bertalanffy, Gompertz and Logistic growth functions (Smart & Grammer, 2021). A Bayesian approach requires specifying prior information of the growth parameters L_∞ and L_0, k for von Bertalanffy, g for Gompertz and Logistic, and the residual standard error (σ). The priors L_∞ and L_0 are informative and normally distributed, based on the mean and S.D. of observed data ($L_\infty = 1301$ ± 55 mm; Colonello *et al*., 2012; this study) ($L_0 = 174$ ± 12 mm; Oddone *et al*., 2008; Colonello *et al*., 2012). The remaining priors are uninformative and have a uniform distribution bounded from zero to a maximum probable value (k and g: range $= 0$–0.5 years^{-1}; σ: range $= 0$–200). Bayesian growth models were fitted for females, males and two sexes combined. The Markov Chain Monte Carlo algorithm was used to apply Bayes theorem to growth estimation and determine parameter uncertainty from the posterior distribution. Parameters estimated are summarized by using mean, S.D. and 95% credible interval of a normally distributed posterior distribution of each growth model (Smart & Grammer, 2021). We estimated the degree of overlap of posterior distributions of each parameter between sexes using the overlapping package (Pastore, 2018) in R (R Core Team, 2020). We expect 0% to indicate the absence of overlapping, and 100% to indicate the perfect overlap between the two posterior distributions (*i.e*., sexes have identical distributions).

A model selection approach to test the level of support for alternative Bayesian growth models was performed using leave-one-out information criterion (LOOIC). The LOOIC is calculated using leave-one cross validation (LOOCV), a robust method for estimating pointwise out-of-sample prediction accuracy from a fitted Bayesian model using the log-likelihood evaluated at the posterior parameter values (Smart & Grammer, 2021). Besides, LOOIC weights (LOOIC*w*) for each candidate model were calculated. LOOIC and LOOIC*w* have the same interpretation as AIC and *w*, respectively (Smart & Grammer, 2021). Bayesian growth models were fitted using the BayesGrowth package (Smart, 2020) with the R statistical language (R Core Team, 2020).

2.4 | Age at maturity

Reproductive stage (*i.e*., immature or mature) was used to estimate age at maturity. To estimate age at which 50% of individuals were sexually mature, a logistical ogive was fitted to binomial maturity data using a generalized linear model (GLM) fitted by maximum-likelihood. Females and males were analysed separately. Then, we estimated the age at which 50% individuals were mature from the ogive. These analyses were conducted using MASS and FSA packages with the R statistical language (R Core Team, 2020).

2.5 | Maximum intrinsic rate of population increase

To estimate the maximum intrinsic rate of population increase r_{max}, we used the simplified version of the Euler-Lotka equation, which is an updated method that uses a simple mortality estimator that also accounts for juvenile mortality (Pardo, Kindsvater, Reynolds, & Dulvy, 2016). The simplified Euler-Lotka equation has the following form:

$$l_{t_{mat}} b = e^{r_{max} t_{mat}} - e^{-M}\left(e^{r_{max}}\right)^{t_{mat}-1}$$

where lt_{mat} is survival to maturity in the absence of fishing, b is the annual reproductive output of female offspring, t_{mat} is age at maturity in years based on the results of this analysis and M is the instantaneous natural mortality. The estimate of lt_{mat} was calculated using the following equation:

$$l_{t_{mat}} = \left(e^{-M}\right)^{t_{mat}}$$

M was calculated as:

$$M = \left(\frac{t_{max} + t_{mat}}{2}\right)^{-1}$$

where t_{max} is the longevity based on the female maximum age recorded in this study. M was used to calculate survival to maturity lt_{mat} (Pardo, Kindsvater, Reynolds, & Dulvy, 2016). The annual reproductive output of *A. castelnaui* is not known; therefore, we provided a value of b (in number of female offspring) calculated from the fecundity of other skate species. For this, we obtained the mean number of egg cases produced annually by skates documented by Last *et al.* (2016). The simplified Euler-Lotka equation was calculated to solve r_{max} using the uniroot function with the R statistical language (R Core Team, 2020).

2.6 | Ethical statement

Fishes were collected as part of commercial fleet cruises, with agreement of the Argentinean government. Specimens were killed during capture from the sea with the fishing net. No experimental work was undertaken. No ethical permission was necessary.

3 | RESULTS

3.1 | Sample characteristics, precision and verification analyses

In total, 143 samples were used for ageing. The size range of individuals varied from 404 to 1300 mm *TL* for females ($n = 83$; mean ± S.D. $= 875.93 \pm 235.07$ mm *TL*) and 400 to 1270 mm *TL* for males ($n = 60$; mean ± S.D. $= 877.30 \pm 212.59$ mm *TL*) (Figure 3). Age readings included individuals from ages 0 to 30 in females and from ages 2 to 28 in males.

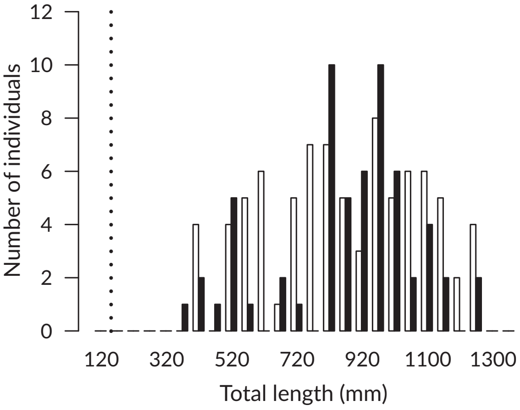

FIGURE 3 Length–frequency distributions of *Atlantoraja castelnaui* off Uruguay and northern Argentina. Size at birth is shown as a vertical dotted line. (□) Female; (■) Male

The CV and APE between the two readers were 9.74% and 6.89%, respectively. The age bias plot showed a low disagreement (Figure 4), and Bowker's test indicated no systematic bias ($\chi^2 = 53.20$, $df = 44$, $P = 0.16$) between both readers.

A positive linear relationship between *Rv* and *TL* was found (Figure 5). The interaction term between *Rv* and sex was significant (ANCOVA: $P < 0.05$). Therefore, the relationships between *Rv* and *TL* were estimated for females ($LT = 182.40 + 184.94\ Rv$; $r^2 = 0.81$) and males ($LT = 88.38 + 218.20\ Rv$; $r^2 = 0.91$) separately.

Edge analysis was conducted on 85 individuals sampled. A monthly and seasonal trend in edge type was not clearly detected (Figure 6). A slight variation in proportions of edge types is found among seasons. Translucent edges were observed with a higher proportion during summer and autumn seasons. On the contrary, opaque edges had a higher proportion during spring.

3.2 | Growth models

For each candidate non-linear growth model, the estimated parameters, AICc, Δ_i and w are given in Table 1. Growth curves were fitted to total length-at-age data for each sex and sexes combined (Figure 7). For both sexes, all growth models were supported by the data, with the two-parameter von Bertalanffy model having the lowest AICc and the highest w values. The likelihood ratio test indicated that growth parameters were not significantly different between sexes for all models (three-parameter von Bertalanffy: $\chi^2 = 1.13$, $P = 0.77$; two-parameter von Bertalanffy: $\chi^2 = 1.45$, $P = 0.56$; Gompertz: $\chi^2 = 1.18$, $P = 0.75$; Logistic: $\chi^2 = 1.25$, $P = 0.74$). For the sexes combined, the three-parameter von Bertalanffy model had a smaller AIC value, but all other growth models had some support. As all models had very similar support by the data, model averaging was computed. L_∞ is the

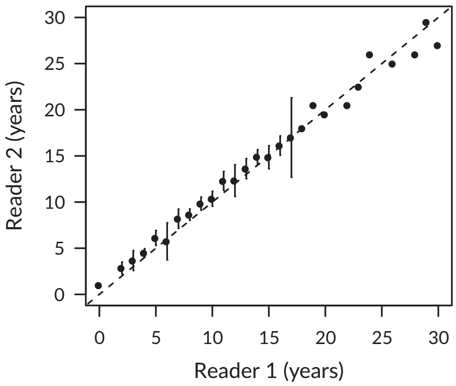

FIGURE 4 Age bias plot of pair-wise comparison between reader 1 and reader 2, for vertebral samples of *Atlantoraja castelnaui*. Each error bar represents the 95% C.I. of the mean counts of reader 2 relative to reader 1. The 1:1 equivalence (dashed line) is also indicated

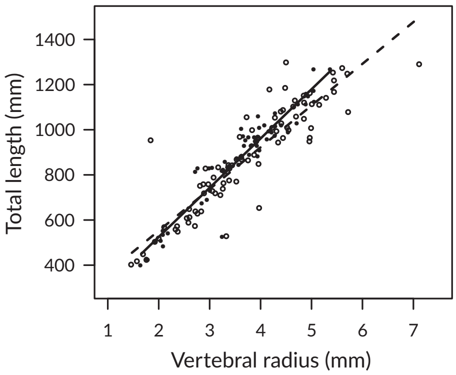

FIGURE 5 Relationship between vertebral radius and total length of *Atlant oraja castelnaui*. Female: dashed line and open circles; male: solid line and black circles

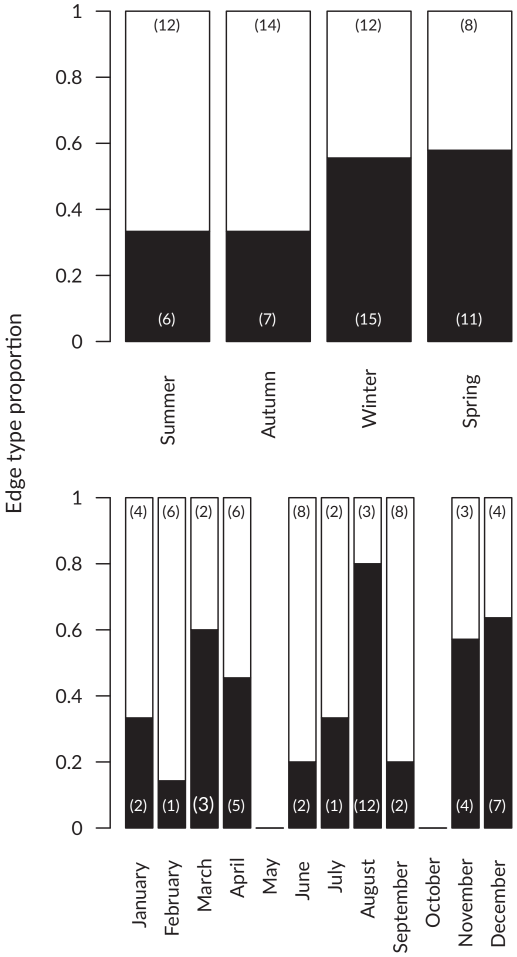

FIGURE 6 Edge type proportion by month and season for *Atlantoraja castelnaui*. (□) translucent edge; (■) opaque edge. Sample size in brackets

only comparable parameter because it has the same meaning in all growth functions; therefore, this parameter was model-averaged using the four growth models. Parameters *k* and *g* do not have the same meaning in all models and cannot be model-averaged. The averaged L_∞ for females was 1172.19 mm, for males it was 1154.51 mm and for both sexes combined it was 1163.06 mm. Coefficient of determination for non-linear models is given in Table S1 (Supporting Information).

For Bayesian approach the posterior mean, S.D. and 95% credible interval of each parameter in each model are presented in Table 2. The resulting Bayesian growth curves of posterior distributions were fitted to total length-at-age data for females, males and sexes combined (Figure 8). For the set of candidate Bayesian models, the result of model selection using LOOIC indicated that von Bertalanffy was best to explain the growth of *A. castelnaui*. Posterior mean values of growth parameters of the von Bertalanffy were more realistic than those mean values for Gompertz and Logistic models (Table 2). Posterior probability distribution of each parameter in von Bertalanffy model presents a high overlapping between sexes for L_∞ (78.92%) and L_0 (95.07%), and moderate for *k* (44.19%) [Figure S1 (Supporting Information)].

3.3 | Age at maturity

The oldest immature female and male were 21 and 17 years old, respectively, whereas the youngest mature female and male were 10 and 8 years, respectively. The age at which 50% of individuals were sexually mature was estimated as 16.21 years for females and 14.04 years for males (Figure 9).

3.4 | Maximum intrinsic rate of population increase

The mean number of egg cases produced annually by 13 skate species was 61.30. Therefore, assuming a 1:1 sex ratio, 30.65 female offspring per year were considered as *b* to estimate r_{max}. The calculated natural mortality (*M*) was 0.043 years^{-1}. Using the values of *b*, t_{mat}

TABLE 1 Results from the non-linear growth models fitted to length-at-age for *Atlantoraja castelnaui*

	Growth model	Parameters	Estimate	S.E.	AICc	Δ_i	*w*
Female	von Bertalanffy	L_∞	1219.25	99.61	1077.02	0.10	0.31
		k	0.10	0.03			
		t_0	−2.98	1.57			
	von Bertalanffy with $L_0 = 174$ mm	L_∞	1139.66	53.12	1076.91	0	0.33
		k	0.14	0.02			
	Gompertz	L_∞	1171.81	78.83	1077.74	0.82	0.22
		g	0.14	0.03			
		t_i	0.84	0.81			
	Logistic	L_∞	1145.26	64.41	1078.65	1.73	0.14
		g	0.19	0.04			
		t_i	3.02	0.77			
Male	von Bertalanffy	L_∞	1197.98	111.74	756.72	1.6	0.22
		k	0.11	0.03			
		t_0	−2.35	1.54			
	von Bertalanffy with $L_0 = 174$ mm	L_∞	1141.37	62.49	755.13	0	0.48
		k	0.13	0.02			
	Gompertz	L_∞	1154.99	84.85	757.16	2	0.17
		g	0.15	0.04			
		t_i	1.35	0.78			
	Logistic	L_∞	1128.81	71.14	757.71	2.6	0.13
		g	0.19	0.04			
		t_i	3.53	0.81			
Combined	von Bertalanffy	L_∞	1212.29	75.21	1828.73	0	0.41
		k	0.10	0.02			
		t_0	−2.81	1.13			
	von Bertalanffy with $L_0 = 174$ mm	L_∞	1136.66	39.95	1829.63	0.90	0.26
		k	0.14	0.01			
	Gompertz	L_∞	1165.97	57.23	1829.97	1.23	0.22
		g	0.14	0.02			
		t_i	0.99	0.58			
	Logistic	L_∞	1139.78	48.50	1831.53	2.80	0.10
		g	0.19	0.03			
		t_i	3.19	0.57			

Note. L_∞ = mean asyntotic length (mm); k = growth coefficient (years^{-1}); t_0 = theoretical age at zero length (years); g = the instantaneous growth coefficient (years^{-1}); t_i = the age at the inflection point (years); S.E. = standard error; AICc = the small-sample bias adjusted from the Akaike's Information Criteria; Δ_i = difference in AICc; w = AICc weights.

(16.21 years), t_{max} (30 years) and M, we estimated the maximum intrinsic rate of population increase r_{max} for *A. castelnaui* to be 0.252 years^{-1}.

4 | DISCUSSION

This study increases the knowledge of the life-history traits of *A. castelnaui*, providing essential information on the main growth parameters, age at maturity and extinction risk. Precision between the two readers indicated that this reading method represents a non-biased and precise approach to age assessment. For Bayesian estimation, the von Bertalanffy growth model provided the best fit. The results indicated that *A. castelnaui* is not sexually dimorphic in its growth parameters. This species is late maturing and has a relatively high extinction risk.

Edge analysis is commonly used to investigate band-pair periodicity in elasmobranch vertebrae (Cailliet & Goldman, 2004), and annual deposition has been verified in several other studies of skates in the Southwest Atlantic [*i.e.*, *Zearaja brevicaudata* (Marini 1933), Aversa

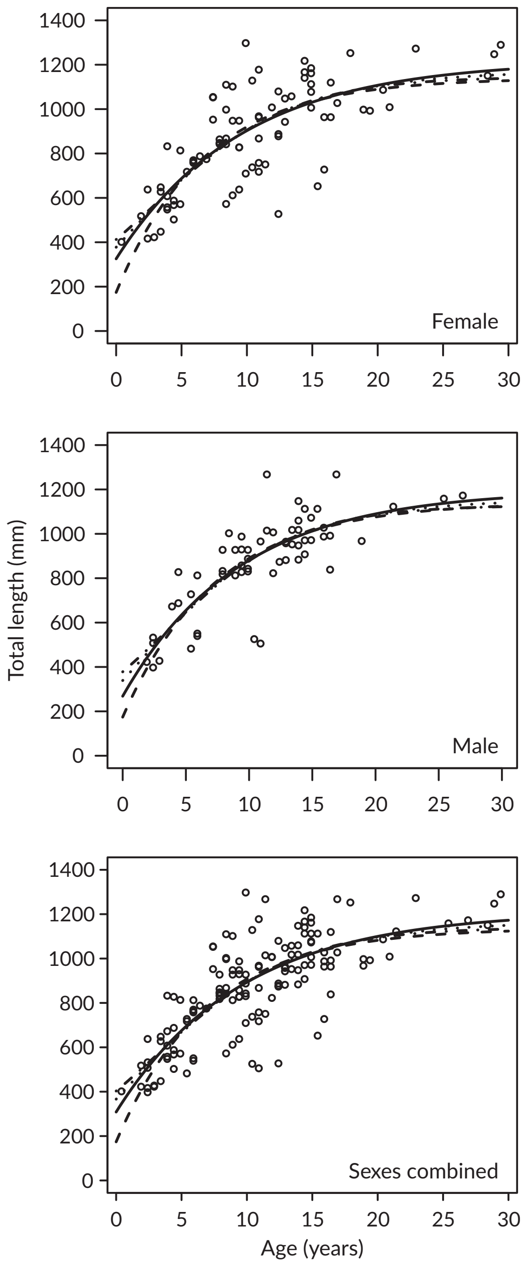

FIGURE 7 Growth curves fitted for non-linear models of observed length-at-age for *Atlantoraja castelnaui*. Three-parameter von Bertalanffy: solid lines; two-parameter von Bertalanffy: dashed lines; Gompertz: dotted lines; Logistic: dotdash lines. Circles represent observed data

et al., 2011; *Rioraja agassizii* (Müller and Henle 1841), Caltabellota *et al*., 2018]. In this study, a slightly higher proportion of opaque edges in spring and a higher proportion of translucent edges in autumn were found, suggesting a possible annual band-pair deposition. Nonetheless, this result does not show a clear trend of monthly band-pair formation in vertebrae of *A. castelnaui* for two possible reasons. First, this is probably due to the small sample size for edge analysis. Second, many months have a very low representation of individuals. For this reason, further studies are needed to test variability of band-pair deposition patterns in this species.

For the same region, the technical report by Hozbor and Massa (2013) reported maximum ages for *A. castelnaui* of 16 years for females (size range = 243–1368 mm *TL*) and 15 years for males (size range = 185–1250 mm *TL*). On the contrary, the maximum age observed in this study was much higher with values of 30 and 28 years for females and males, respectively. In agreement with the results of this study, off the south coast of Brazil (between 23° S and 29° S), the maximum age reported in *A. castelnaui* was 29 years for females and 31 years for males (Casarini, 2006). Although the range of body size among studies is similar, the maximum age reported by Hozbor and Massa (2013) was much younger. These differences in maximum ages between Hozbor and Massa (2013) with this study's results and Casarini (2006) may potentially be related to the difference in methodologies and criteria to read ages between the studies. In addition, the maximum age observed in the current study is consistent with many skate species with a similar maximum body size. For example, *Bathyraja griseocauda* (Norman 1937) in Patagonian waters attain 1570 mm *TL* and a maximum age of 28 years (Arkhipkin *et al*., 2008), *Beringraja rhina* (Jordan and Gilbert 1880) from the Gulf of Alaska attain 1400 mm *TL* and a maximum age of 25 years (Gburski *et al*., 2007) and *Dipturus oxyrinchus* (L. 1758) from the Gulf of Gabés in the Mediterranean attain 1500 mm *TL* and a maximum age of 25 years (Kadri *et al*., 2014a). Comparing age and growth parameters of the same species on a regional scale may help to monitor populations and identify potential long-term effects of fishing pressure (Coutré *et al*., 2013). For this reason, it is important to have a common criterion for age readings and growth parameter estimations, because the differences will not allow to adequately identify temporal changes in life-history traits within the same population.

All elasmobranch species do not follow the same growth pattern, because different stages of their life history may undergo varied growth trajectories (Cailliet *et al*., 2006). The multi-modelling selection allows the assessment of several growth curve possibilities, offering an improved framework over a single-model approach, increasing growth estimate accuracy and producing more biologically reasonable growth estimates (Katsanevakis, 2006; Smart *et al*., 2016). Growth curves fitted with both von Bertalanffy and two-parameter von Bertalanffy models (*i.e*., reverse exponential shape) have the underlying principle that the growth rate of fish decline linearly with age. On the contrary, sigmoid-shaped models (*i.e*., Gompertz and Logistic functions) suggest acceleration and deceleration in the growth rate with age (Katsanevakis, 2006; Smart *et al*., 2016). It was demonstrated that both types of functions are independent of taxa (*i.e*., sharks or batoids) and reproductive mode (*i.e*., live-bearing or egg-laying) (Smart *et al*., 2016). In this study, for the non-linear estimation approach none of the four candidate models was the best model strongly supported by the data with a $w > 0.90$. But we interpreted the lowest AICc values, and both von Bertalanffy models best describe the growth. On the contrary, for the Bayesian estimation approach the von Bertalanffy growth model was doubtless selected. Among the candidate models, the model with a reverse exponential shape was better supported by the data and appeared more appropriate for describing growth in

TABLE 2 Results from the Bayesian growth models fitted to length at age for *Atlantoraja castelnaui*. Posterior mean values and 95% credible intervals (lower quartile: 2.5%; upper quartile: 97.5%) are provided

	Growth model	Parameters	Mean	S.E.	2.5%	97.5%	LOOIC	LOOICw
Female	von Bertalanffy	L_∞	1235	47.4	1146	1332	1078	0.98
		k	0.12	0.01	0.1	0.15		
		L_0	177.2	11.99	153.8	201.4		
	Gompertz	L_∞	1162	41.41	1085	1248	1086	0.02
		g	0.22	0.02	0.18	0.27		
		L_0	182.5	11.68	159.2	205.3		
	Logistic	L_∞	1107	36.89	1039	1185	1093	0
		g	0.37	0.04	0.3	0.45		
		L_0	185.3	11.9	162.1	208.5		
Male	von Bertalanffy	L_∞	1249	50.29	1154	1352	756.5	0.99
		k	0.11	0.01	0.09	0.14		
		L_0	176.5	12.09	153.3	200		
	Gompertz	L_∞	1183	48.36	1093	1282	765.3	0.01
		g	0.19	0.02	0.16	0.23		
		L_0	182.5	11.78	159.8	205.6		
	Logistic	L_∞	1130	47.28	1048	1226	773.8	0
		g	0.31	0.03	0.25	0.38		
		L_0	186.8	11.78	163.8	209.7		
Combined	von Bertalanffy	L_∞	1210	40.68	1295	1295	1831	1
		k	0.12	0.01	0.1	0.15		
		L_0	179.20	11.62	155.8	202		
	Gompertz	L_∞	1121	32.56	1060	1189	1842	0
		g	0.23	0.02	0.19	0.27		
		L_o	186.9	11.54	164.2	209.7		
	Logistic	L_∞	1065	26.42	1017	1120	1852	0
		g	0.37	0.03	0.31	0.44		
		L_0	191.6	11.64	168.7	214.7		

Note. L_∞ = mean asyntotic length (mm); L_o = the length at birth (mm); k = growth coefficient (years^{-1}); g = the instantaneous growth coefficient (years^{-1}); S.E. = standard error; LOOIC = leave-one-out information criteria; LOOICw = LOOIC weights.

A. castelnaui, indicating that growth in this species could be constant throughout life.

Small sample sizes often can cause poor growth parameter estimates when not all length or age classes have a good representation in the sample (Gwinn *et al*., 2010). Small and/or large fish can be underrepresented because fishing gear is size selective and often cannot catch the smallest- or largest-size classes (Binion *et al*., 2009). When biased samples compromise a robust estimation, Bayesian growth models are an effective tool (Smart & Grammer, 2021). The greatest improvement of Bayesian growth models is the capability to account for missing younger or older individuals incorporating priors on known minimum and maximum lengths. The data set of *A. castelnaui* used in this study is limited, because smaller and older individuals are underrepresented. The results demonstrated that the inclusion of L_∞ and L_0 priors allowed Bayesian models to better fit than non-linear models, providing more precise results. Also, parameters estimated by the best Bayesian growth model (*i.e*., von Bertalanffy) seem to be quite realistic because the values of L_∞ and L_0 are close to the maximum and minimum sizes observed in previous studies on this species, respectively (Barbini & Lucifora, 2012; Colonello *et al*., 2012; Oddone *et al*., 2008).

The results determined that growth parameters of *A. castelnaui* were similar between sexes. Female and male growth functions converged to similar parameters fitted with these length-at-age data, and thus this species requires the same combined growth parameters to characterize them. Sexual dimorphism in growth is variable among skate species, ranging from a high dimorphism (Caltabellota *et al*., 2018; Frisk & Miller, 2006; Sulikowski *et al*., 2007) to no dimorphism (Frisk & Miller, 2006; Kadri *et al*., 2013, 2014b). On the contrary, sexual dimorphism in growth is greater in many viviparous elasmobranch species, with females having slower growth rates and attaining much larger sizes and older ages than males (Baje *et al*., 2018; Braccini *et al*., 2007; Caltabellotta *et al*., 2019; Dale & Holland, 2012). These differences in the intensity of sexual

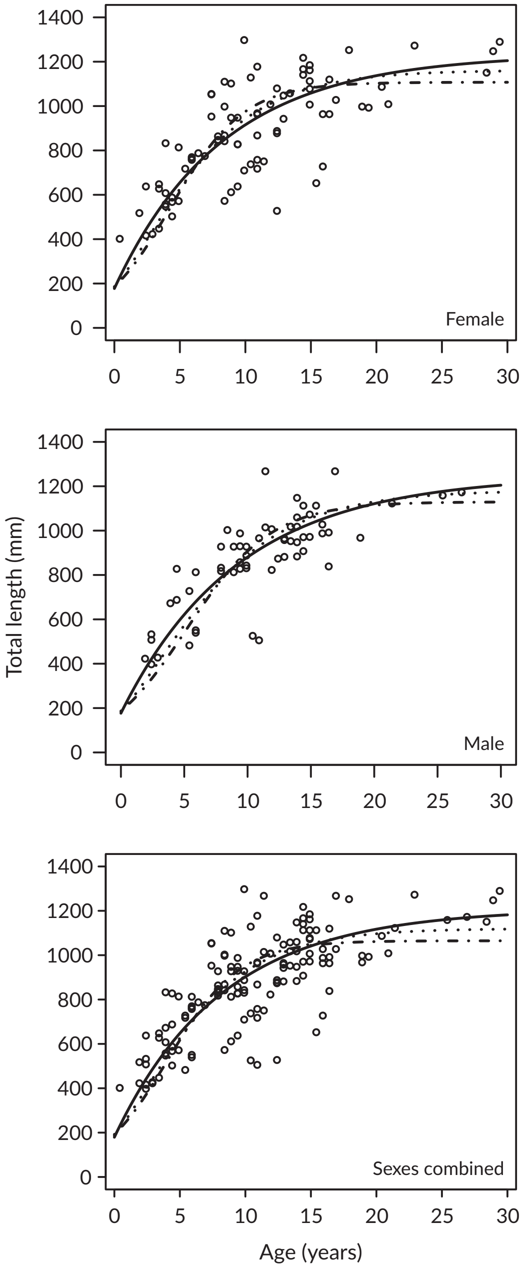

FIGURE 8 Growth curves fitted for Bayesian models of observed length-at-age for *Atlantoraja castelnaui*. Von Bertalanffy: solid lines; Gompertz: dotted lines; Logistic: dotdash lines. Circles represent observed data

dimorphism between skates and viviparous species could be related to their reproductive mode (Ebert *et al*., 2008). The reproductive mode of skates is oviparity, characterized by the production of fertilized egg capsules and oviposition on the seabed. On the contrary, viviparous females need to attain a large body size, which will allow for larger litters and embryos. Although this explanation needs empirical testing, it is possible to hypothesize that the selective pressure on the female's body size of skates is more relaxed in oviparous than in viviparous elasmobranchs, because there are no advantages to attain a larger size to produce larger litters or embryos, which could partially explain the variable degree of sexual dimorphism in growth observed among skates.

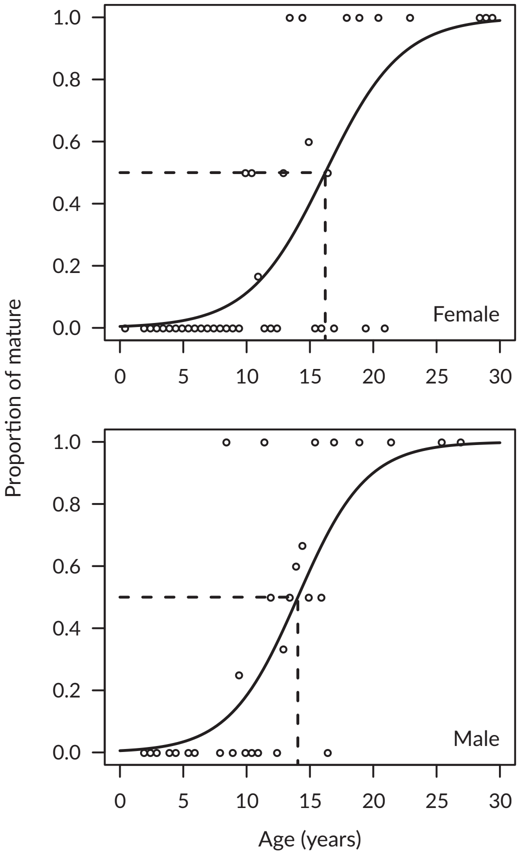

FIGURE 9 Relationship between the percentage of mature *Atlantoraja castelnaui* and age for females and males. Solid line is a logistical ogive fitted by maximum-likelihood, and dashed line marks the age at which 50% of individuals are mature

Ages at first maturity for *A. castelnaui* are consistent with those found for skates of large body size [*e.g*., *Zearaja chilensis* (Guichenot 1848), Licandeo *et al*., 2006; *B. griseocauda*, Arkhipkin *et al*., 2008; *Rostroraja alba* (Lacepède 1803), Kadri *et al*., 2014b; *D. oxyrinchus*, Bellodi *et al*., 2017]. On average, elasmobranchs attain sexual maturity at 38% of their maximum age and 73% of their maximum size (Frisk *et al*., 2001). In the present study, female and male reached maturity at 54.03% and 50.14% of their maximum observed age, respectively. In the same region, Colonello *et al*. (2012) found that sexual maturity occurred at 80% and 78.4% of maximum size for female and male, respectively. These values represent the proportion of time and growth that occurs before maturation (Frisk *et al*., 2001), and *A. castelnaui* is above the mean values of elasmobranchs in general. The present study provides information that can have important effects on stock assessments and fishery models, because age at maturity is a critical variable for demographic modelling of elasmobranch populations, and therefore for fisheries management.

When time series of population abundance of exploited species are lacking, and stock assessment methods cannot be applied, a useful tool for evaluating a species' relative risk of overexploitation is to calculate r_{max}, because it is an indicator of relative population productivity (Cortés, 2016; Pardo, Kindsvater, Reynolds, & Dulvy, 2016). The r_{max} values estimated among 96 chondrichthyan species varied between 0.03 and 1.4 years^{-1} (Pardo, Kindsvater, Cuevas-Zimbrón, *et al*., 2016), indicating a wide range of both different population dynamics and resiliency to fisheries pressure. Although species with very low productivity (r_{max} < 0.1) are not capable of supporting sustainable fisheries, fisheries identified as sustainable are more commonly based on species with an r_{max} > 0.3 (Simpfendorfer & Dulvy, 2017). We found that *A. castelnaui* have a r_{max} value of 0.252 years^{-1}, which indicates a relatively low productivity, that we would associate mainly to its late age at maturity and high longevity. Chondrichthyans with similar r_{max} values as *A. castelnaui* would support sustainable fisheries but in a frame of a strong science-based management and strict controls of the fishery (Bradshaw *et al*., 2018; Simpfendorfer & Dulvy, 2017). Current management measures for skates in Argentinian and Uruguayan fisheries are maximum landing limits for skates as a percentage of the total species caught per fishing trip (Resolución CFP N° 4/2013, Argentina, https://cfp.gob.ar/) and the annual maximum permitted catch (Resolución CTM N° 17/19, Uruguay-Argentina, http://ctmfm.org/). Skates species have a high variability in their life-history traits and demographic dynamics that make populations to have different resilience to exploitation (Dulvy & Reynolds, 2002; Walker & Hislop, 1998). For long-term sustainability of exploited populations for this region, management measures based on the biology of each skate species are necessary, and those measures must be controlled by the institution in charge of enforcing the law and respected by commercial fishers.

Large size, high longevity, late maturation and a low r_{max} are all indicators that a species has a low population productivity and is highly vulnerable to overexploitation (Cortés, 2016; Reynolds *et al*., 2005). In the same way, as a first step for assigning conservation status, formal estimates of abundance and identification of population trends through time are essential. Nonetheless, population trends in the abundance for *A. castelnaui* are unknown in the Southwest Atlantic. The results support the hypothesis that *A. castelnaui* is a species highly vulnerable to an intense fishing pressure, meaning that this species has a low resilience to fishing mortality. Similar large skate species have suffered overexploitation and subsequent population depletion (Dulvy *et al*., 2000; Dulvy & Reynolds, 2002; Walker & Hislop, 1998). In summary, (a) due to the antecedents of population declines of similar skate species, (b) given the slow growth, late sexual maturity and relative high extinction risk of *A. castelnaui*, and (c) applying the precautionary principle action to avert risks of serious or irreversible harm, this species requires urgent species-specific management measures for its protection, like other elasmobranch species highly susceptible in the region.

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AUTHOR CONTRIBUTIONS

S.A.B., D.E.S. and J.M.R. sampled *A. castelnaui* individuals. S.A.B. and L.O.L. conceptualized the idea. S.A.B. made the statistical data analysis, wrote the original manuscript and acquired funding. D.E.S., J.M.R., P.A.S. and L.O.L. critically revised the drafted paper. All authors helped for the interpretation of data and approved the manuscript.

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