

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

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the [Version of Record](https://doi.org/10.1111/jfb.14839). Please cite this article as doi: [10.1111/jfb.14839](https://doi.org/10.1111/jfb.14839)

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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 ($35^{\circ} - 42^{\circ}$ S), between June 2013 and February 2020. Vertebrae from 143 individuals were used for ageing (females: $n = 83$, size range 404 to 1300 mm total length, TL ; males: $n = 60$, size range 400 to 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 \pm SD: $L_{\infty} = 1210.29 \pm 40.68$ mm; $k = 0.12 \pm 0.01$ years $^{-1}$; $L_0 = 179.20 \pm 11.62$ years). The age at maturity was estimated in 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 have a relatively low productivity and may be vulnerable to an intense fishing pressure.

Keywords: Elasmobranchs, Rajiformes, growth modelling, age at maturity, maximum intrinsic rate of population increase (r_{max})

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 (Ferretti *et al.*, 2010; Dulvy *et al.*, 2017). 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 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 to quantify 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 (Tyedmers *et al.*, 2005; Watson *et al.*, 2013; Guiet *et al.*, 2019). 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 harbors (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, therefore the response to exploitation may differ among species (Dulvy and Reynolds, 2002). In general, skate species with large body sizes (Dulvy *et al.*, 2000; Dulvy and 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) (Menni and Stehmann, 2000; Bovcon *et al.*, 2011). In Argentinian and Uruguayan waters, this species occurs from shallow coastal waters to approximately 100 m depth (Cousseau *et al.*, 2007). *Atlantoraja castelnaui* is a predator with a narrow trophic niche breadth, feeding almost exclusively on teleost fishes (Barbini and Lucifora, 2012; Barbini *et al.*, 2020). Females mature between 1050 and 1089 mm and males mature between 910 and 980 mm total length (Oddone *et al.*, 2008; Colonello *et al.*, 2012). *Atlantoraja castelnaui* has been categorized as critically endangered by the International Union for the Conservation of Nature (IUCN) (Pollom *et al.*, 2020). However, 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 harbor, 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.*, 2018). A

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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 macroscopic observation of the reproductive organs (Stehmann, 2002; Colonello *et al.*, 2011). 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 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 mins 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 hours. 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 in order to enhance visibility of the vertebral growth bands.

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Vertebral radius (R_v) 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). R_v 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* were 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, in order 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 and Fournier, 1981) in order 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 we 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 were 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 R_v and TL for both sexes. Differences between sexes were evaluated using analysis of covariance (ANCOVA) (Zar, 1999).

To verify the periodicity of band pair formation we used the semi-direct method of edge analysis (Cailliet and 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 and 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 and Maravelias, 2008; Smart *et al.*, 2016). The multi-model approach is considered to provide better growth estimates as to avoid mis-specification 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 follow:

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

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 form:

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

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

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

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

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 (Imura, 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 Akaike information criterion (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 and Anderson, 2002). The model with the lowest AICc value was chosen as the model with the highest support (Johnson and 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 and Anderson, 2002). To obtain the likelihood of each model fitted, the Akaike's weight

(w) was calculated (Johnson and 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 and 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 and Maravelias, 2008; Symonds and 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 and 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 standard deviation (SD) of observed data ($L_\infty = 1301 \pm 55$ mm; Colonello *et al.*, 2012; our study) ($L_0 = 174 \pm 12$ 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 values (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, standard deviation and 95% credible interval of a normally distributed posterior distribution of each growth model (Smart and 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), that it is 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 and 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 and 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. In order 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 *et al.*, 2016a). The simplified Euler-Lotka equation has the following form:

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

where l_{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 our analysis, and M is the instantaneous natural mortality. The estimate of l_{mat} was calculated with the following equation:

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

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 our study. M was used to calculate survival to maturity l_{mat} (Pardo *et al.*, 2016a). 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).

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 \pm SD = 875.93 ± 235.07 mm *TL*) and 400 to 1270 mm *TL* for males ($n = 60$; mean \pm SD = 877.30 ± 212.59 mm *TL*) (Figure 3). Age readings included individuals from age 0 to age 30 in females and from age 2 to age 28 in males.

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 other hand, 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 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 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 was 1154.51 mm and for both sexes combined was 1163.06 mm. Coefficient of determination for non linear models are given in Supporting Information (Table S1).

For Bayesian approach the posterior mean, standard deviation 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 present a high overlapping between sexes for L_∞ (78.92%) and L_0 (95.07%), and moderate for k (44.19%) (Supporting Information, Figure S1).

3.3 Age at maturity

The oldest immature female and male were 21 and 17 years old, respectively, while 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. Hence, assuming a 1:1 sex ratio, 30.65 female offsprings per year was considered as b to estimate r_{max} . The calculated natural mortality (M) was 0.043 years^{-1} . Using the values of b , t_{mat} (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 our reading method represents a non-biased and precise approach to age assessment. For Bayesian estimation, the von Bertalanffy growth model provided the best fit. Our 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-pairs periodicity in elasmobranch vertebrae (Cailliet and 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 *et al.*, 2011; *Rioraja agassizii* (Müller and Henle 1841), Caltabellotta *et al.*, 2018). In this study, a slightly

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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. However, 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. Secondly, 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 other hand, 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 our results, 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 are very similar, the maximum age reported by Hozbor and Massa (2013) was much younger. These differences in maximum ages between Hozbor and Massa (2013) with our 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 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, since 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 (Caillet *et al.*, 2006). The multi-modelling selection allow to assess 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 other hand, 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 on 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 describes the growth. On the other hand, 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 *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 under-represented 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 and 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 under-represented. Our 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) seems 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 (Oddone *et al.*, 2008; Barbini and Lucifora, 2012; Colonello *et al.*, 2012).

Our results determined that growth parameters of *A. castelnaui* were very 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 very variable among skate species, ranging from a high dimorphism (Frisk and Miller, 2006; Sulikowski *et al.*, 2007; Caltabellotta *et al.*, 2018) to no dimorphism (Frisk and 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 (Braccini *et al.*, 2007; Dale and Holland, 2012; Baje *et al.*, 2018; Caltabellotta *et al.*, 2019). These differences in the intensity of sexual 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 other hand, 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.

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 *et al.*, 2016a). The r_{max} values estimated among 96 chondrichthyan species varied between 0.03 and 1.4 years⁻¹ (Pardo *et al.*, 2016b), indicating a wide range of both different population dynamics and resiliency to fisheries pressure. While 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 and 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 (Simpfendorfer and Dulvy, 2017; Bradshaw *et al.*, 2018). 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 (Walker and Hyslop, 1998; Dulvy and Reynolds, 2002). 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 (Reynolds *et al.*, 2005; Cortés, 2016). 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. However, population trends in the abundance for *A. castelnaui* are unknown in the Southwest Atlantic. Our 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 over-exploitation and subsequent population depletion (Walker and Hislop, 1998; Dulvy *et al.*, 2000; Dulvy and Reynolds, 2002). In summary, 1) due to the antecedents of population declines of similar skate species, 2) given the slow growth, late sexual maturity and relative high extinction risk of *A. castelnaui*, and 3) 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.

Authors contributions

S.A.B, D. E. S and J. M. R. sampled *A. castelnaui* individuals. S. A. B. and L. O. L. idea conceptualization. S. A. B. made the statistical data analysis, wrote the original manuscript and funding acquisition. 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.

Acknowledgments

We wish to thank M. Fitipaldi, A. Altamiranda, D. Altamiranda, R. Sánchez and all processing plant personnel of the F.V. El Corsario for allowing us access to samples. We also thank M. Irigoitia and D. Cantatore for their assistance in the sampling, and the Ictioparasitología research group (IIMyC) by the assistance with the camera and stereoscopic microscope. We thank J. Smart for assistance to plot posterior distribution and F. Cortés for suggestions on the Bayesian method. We are grateful to two anonymous reviewers for their constructive comments and suggestions. This study was supported by Fondo para la Investigación Científica y Tecnológica (FONCyT) PICT 2017-0946.

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Figure captions

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.

Figure 3. Length-frequency distributions of *Atlantoraja castelnaui* off Uruguay and northern Argentina. [Size at birth is shown as a vertical dotted line.](#)

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

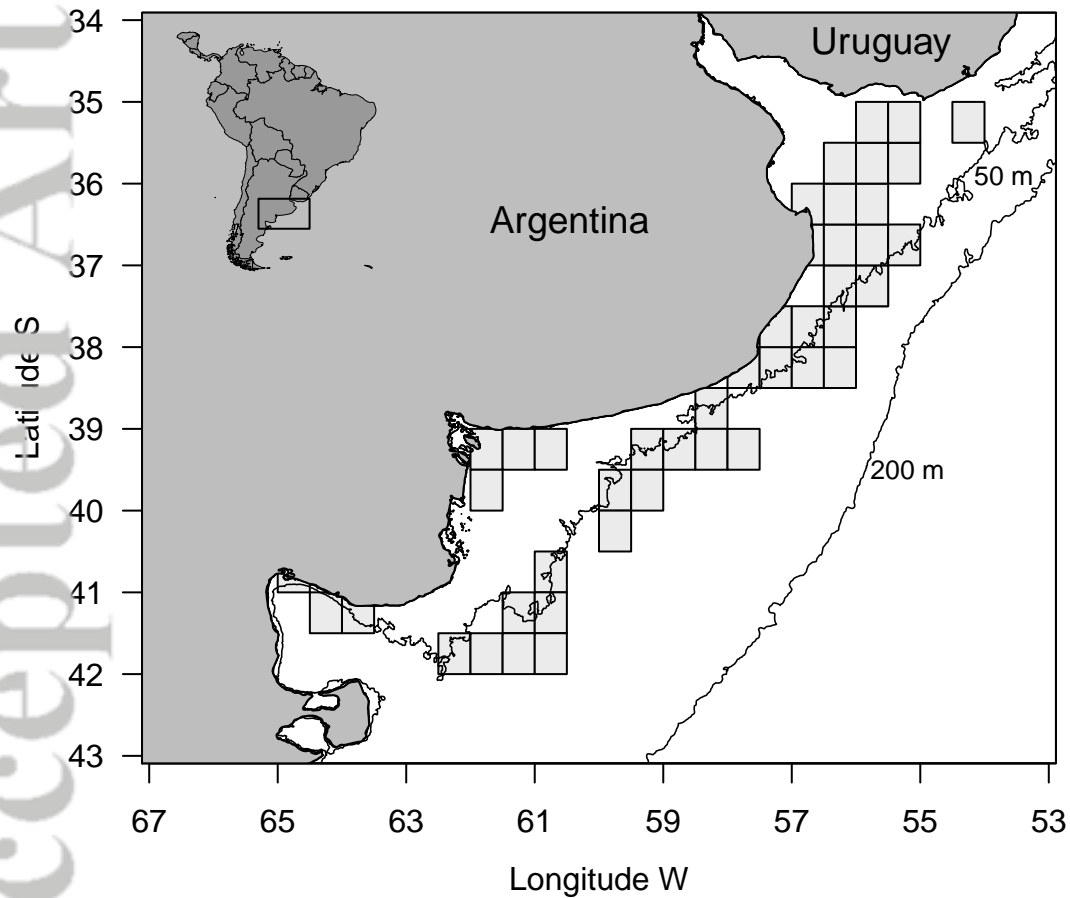
Figure 5. Relationship between vertebral radius and total length of *Atlantoraja castelnaui*. Female: dashed line and open circles; male: solid line and black circles.

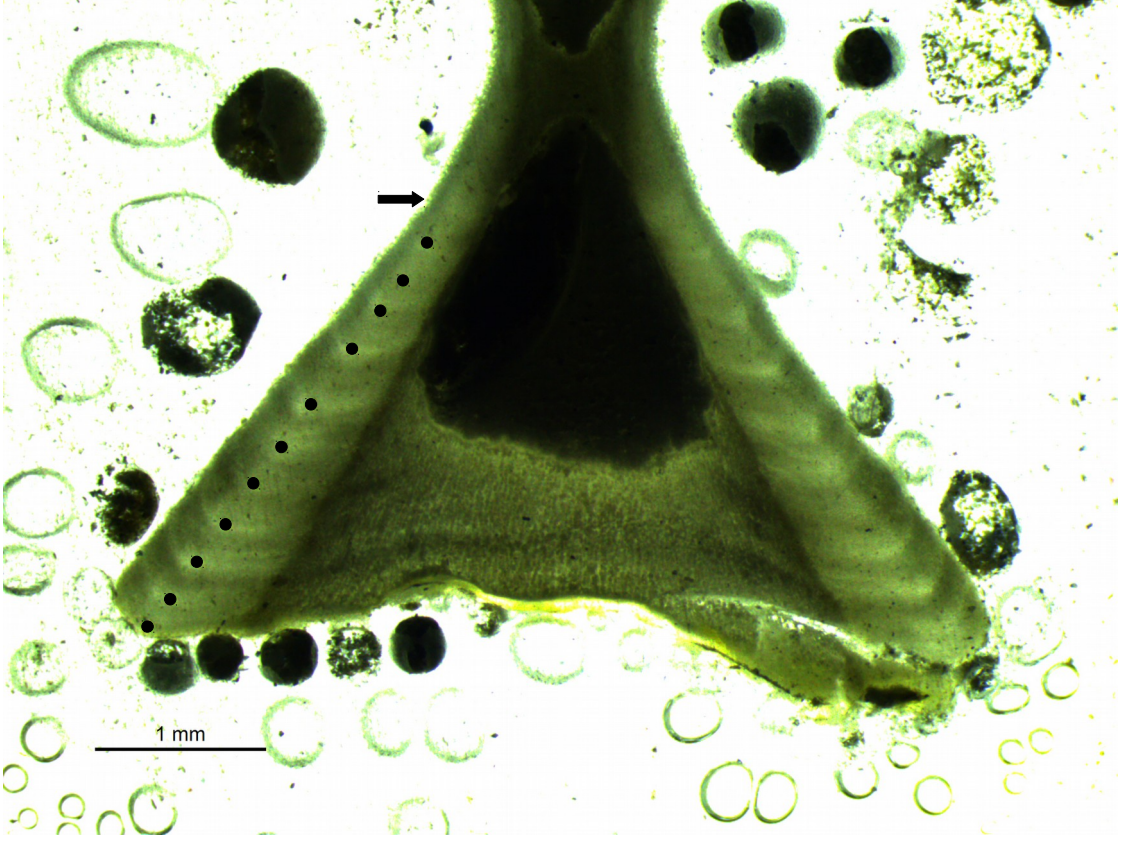
Figure 6. Edge type proportion by month and season for *Atlantoraja castelnaui*. (□) translucent edge; (■) opaque edge. Sample size in brackets.

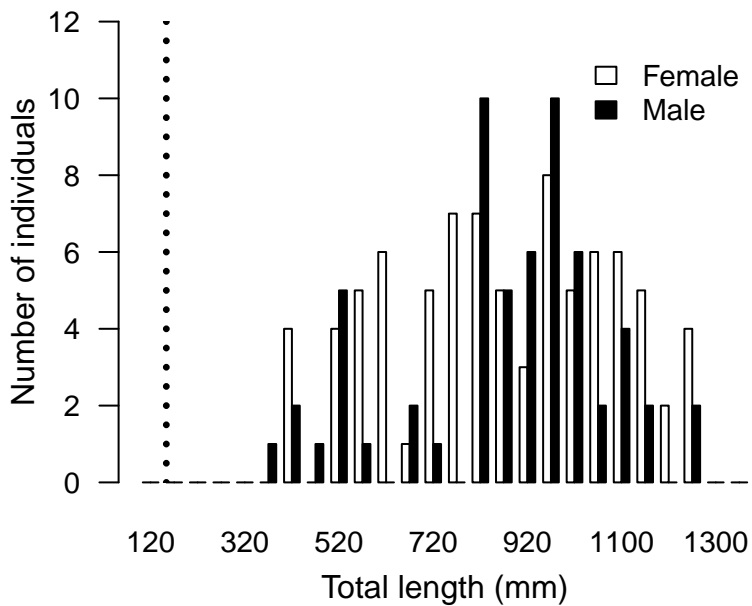
Figure 7. Growth curves fitted for non-linear models of observed length-at-age for *Atlantoraja castelnaui*. Three-parameter von Bertalanffy: solid lines; two-parameter von Bertalanffy: dashed lines; Gompertz: dotted lines; Logistic: dotdash lines. Circles represent observed data.

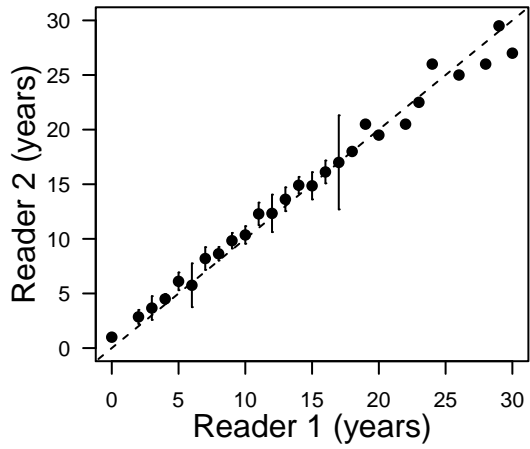
Figure 8. Growth curves fitted for Bayesian models of observed length-at-age for *Atlantoraja castelnaui*. von Bertalanffy: solid lines; Gompertz: dotted lines; Logistic: dotdash lines. Circles represent observed data.

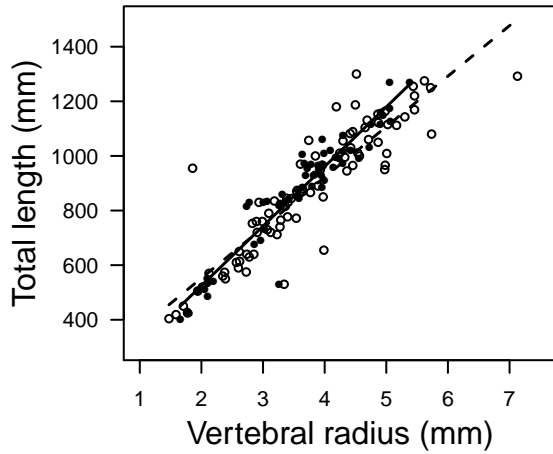
Figure 9. Relationship between the percentage of mature *Atlantoraja castelnaui* and age for females and males. Solid line is a logistical ogive fitted by maximum-likelihood and dashed line marks the age at which 50% of individuals are mature.

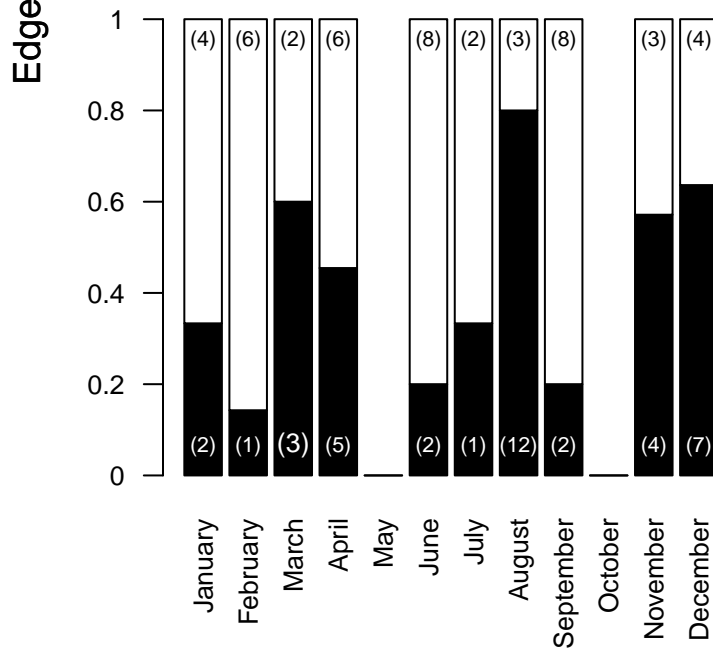
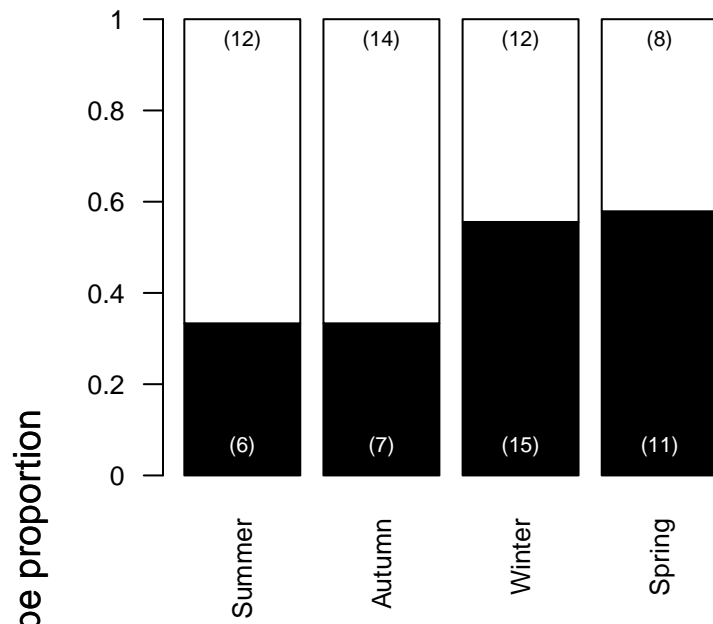


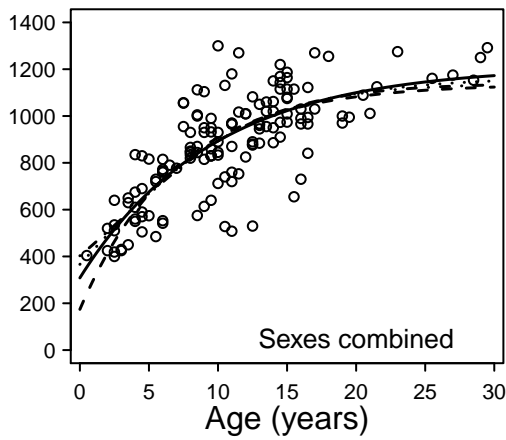
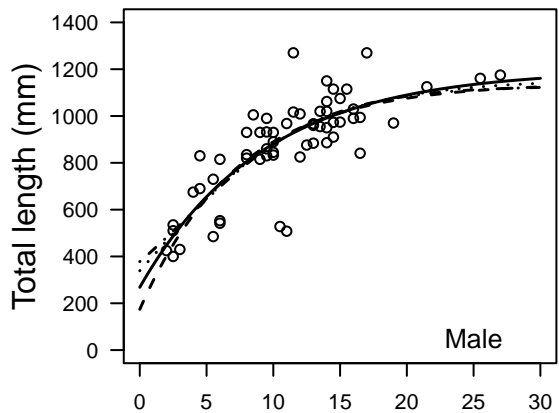
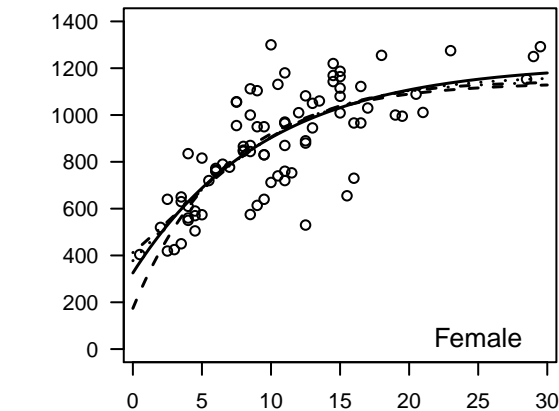


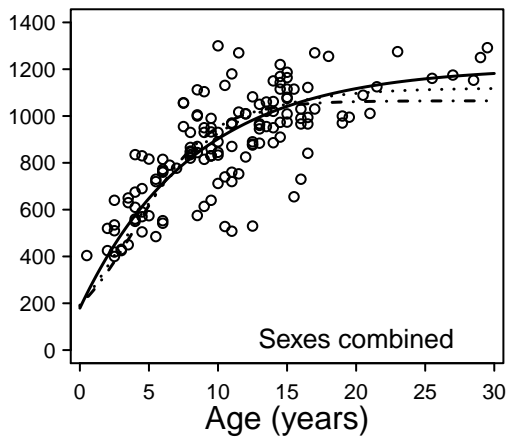
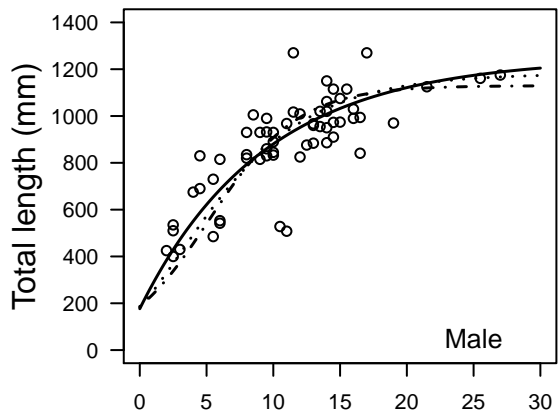
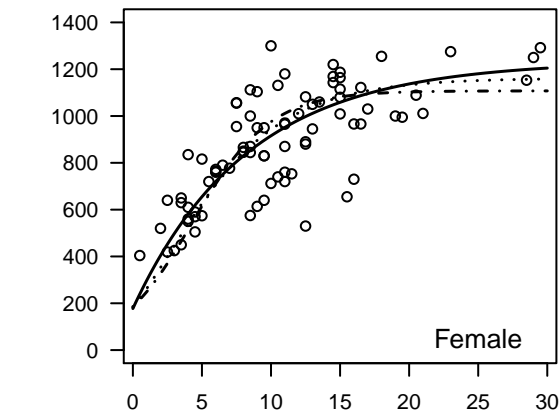


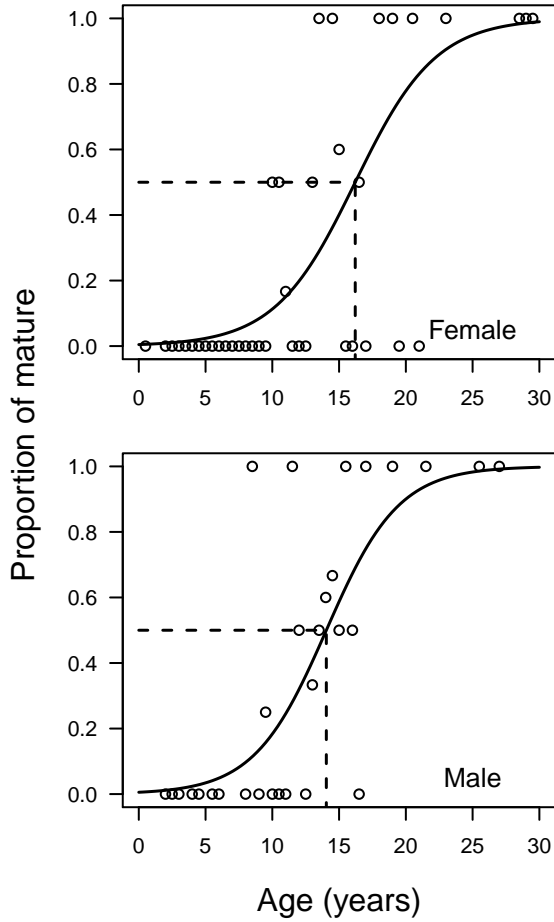












Significance Statement

Gathering new information on life-history traits of spotback skate *Atlantoraja castelnaui* in the Argentinian coastal waters is imperative, since studies on this exploited species are very scarce.

This skate is captured by a multi-species fishery for coastal demersal species and its abundance has decreased, being categorized as critically endangered. Our results provide new information to determine the response of the spotback skate to fishing and to generate adequate management actions and conservation.

Table 1. Results from the non-linear growth models fitted to length at age for *Atlantoraja castelnaui*. L_{∞} = mean asymptotic 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), SE = standard error, AICc = the small-sample bias adjusted from the Akaike's Information Criteria, Δ_i = difference in AICc, w = AICc weights.

	Growth model	Parameters	Estimate	SE	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			

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. L_∞ = mean asymptotic length (mm), L_0 = the length at birth (mm), k = growth coefficient (years⁻¹), g = the instantaneous growth coefficient (years⁻¹), SE = standard error, LOOIC = leave-one-out information criteria, LOOIC_w = LOOIC weights.

	Growth model	Parameters	Mean	SE	2.5%	97.5%	LOOIC	LOOIC_w
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		
